PARASITIC ARTHROPODS:

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Vorgelegt von

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Für meine Eltern

Diese Dissertation wurde angefertigt
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EIDESSTATTLICHE ERKLÄRUNG

Ich versichere hiermit an Eides statt, dass die vorgelegte Dissertation von mir selbstständig und ohne unerlaubte Hilfe angefertigt ist.

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Ort, Datum Christina Nagler

ERKLÄRUNG

Hiermit erkläre ich, dass diese Dissertation nicht einer anderen Prüfungskommission vorgelegt worden ist und dass ich mich nicht anderweitig einer Doktorprüfung ohne Erfolg unterzogen habe.

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LIST OF PUBLICATIONS INCORPORATED IN THIS DISSERTATION

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III. Serrano-Sánchez ML, **Nagler C**, Haug C, Haug JT, Centeno-García E, Vega FJ. 2016. The first fossil record of larval stages of parasitic isopods: cryptoniscus larvae preserved in Miocene amber. *Neues Jahrbuch für Geologie und Paläontologie – Abhandlungen*, 279: 97–106. DOI: 10.1127/njgpa/2016/0543.

IV. **Nagler C**, Hyžný M., Haug JT. 2017a. 168 million years old ~~–m~~arine mallophagan" and the evolution of parasitism within isopods. *BMC Evolutionary Biology*, 17: 76. DOI: 10.1186/s12862-017-0915-1.

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VIII. **Nagler C,** Wagner P, Olesen J, Kerp H, Waloszek D, Haug JT, Haug C. in prep a. The 400-million-year old eucrustacean *Ebullitiocaris oviformis* re-evaluated: a thecostracan with parasite-type morphology in the Rhynie chert. *Palaeontology*.

IX. **Nagler C,** Wagner P, Olesen J, Haug JT, Haug C. in prep b. Re-evaluation of nauplius larvae from Rhynie chert supports a phylogenetic affinity to Thecostraca. *Palaeontology.*

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STATEMENT OF AUTHOR'S CONTRIBUTION

In this thesis, I present the results from my doctoral research conducted from 2014 until 2017, carried out under the supervision of Prof. Dr. Matthias J. Starck and Dr. Joachim T. Haug at the Ludwig-Maximilians-Universität München. The author contribution is written according to the CRediT taxonomy.

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„Ingen flat vei fører på toppen!"
(Unknown author, Norway)

CONTENTS

SUMMARY

Parasites are ubiquitous and abundant among most metazoan groups. Due to their influence on food webs, co-evolution, population dynamics and economy, there is a specific research interest in the evolution of parasitism. Using fossils, this thesis address the question of the evolutionary reconstruction of parasitism towards modern parasites to elucidate this gap of knowledge on the example of arthropods. Precisely, this thesis focuses on parasitic isopods (Cymothoida) and parasitic barnacles and their relatives (Thecostraca), because these parasites are relatively large and their fossils show a high preservation potential. Numerous lineages of isopods and thecostracans have independently evolved different strategies of parasitism and a diverse morphology. Hence, representatives of these groups seem to can be integrated into an evolutionary reconstruction.

The aim of this thesis was to draw conclusions about the evolution, development and ecology by studying a variety of morphological characters within these groups, both from fossils and extant representatives, and a comparison of these results. Thus, aspects of the ground pattern of parasitic adaptations of isopods and rhizocephalans have been elaborated. This study proposes a stepwise evolution within parasitic isopods from non-parasitic representatives, such as scavenging cirolanids, to highly specialized parasitic representatives, such as epicarids. Within Thecostraca, the evolutionary history is less clear, due to the ambiguous phylogeny of the major groups. However, this study suggests an alternative evolutionary reconstruction by incorporating various fossils and debatable groups, concerning their phylogenetic affinity, such as fish lice and Tantulocarida. As seen for Cymothoida and Thecostraca, fossils can provide direct evidence for parasitism and in comparison to their extant relatives these fossils can reveal important aspects of the origins and diversification of parasitism with different grading. Finally, convergent characters caused by heterochronic events and morphological convergences are compared between these two groups, their major ingroups and to other major groups among parasitic arthropods.

In summary, this thesis combines functional morphology, ecology and systematics with several methods to achieve a multidisciplinary approach to elucidate the evolution of parasitism within Cymothoida and Thecostraca. As demonstrated by this thesis, it is worth to pursue an approach with an elaborated concept of mutual views between fossil and extant species (e.g. biogeographics, taphonomy, geochemical studies, molecular studies, phylogenetics, morphological studies), hence, finally supplying a more detailed understanding of the evolutionary processes leading to modern parasitic forms.

1 INTRODUCTION

1.1 PARASITISM

Almost 60% of modern-day metazoans are neither herbivorous nor predatory, but seem to be parasites in a broad sense (Price 1980). The term parasite is derived from the ancient Greek term „παράσιτος", where „παρά" [para] means „*at*" or *„on"* and „σιτεσθαι" [sitestai] means „*eating*". Originally, this term was used for persons tasting the food for sacrificial meals and thus can eat without any return for it (Lucius et al. 2017). Therefore the term „parasite" became pejorative (Mehlhorn 2012). However, in zoology the term 'parasites' addresses organisms with a highly specialized lifestyle, with plenty exceptional adaptations that evolved over a long time. Hence, biologists, especially zoologists and parasitologists, aim at getting an insight into the parasites' own world of special organisms with different approaches (Osche 1966).

Two organisms can live in a close relation to each other. This living together can be positive, neutral or negative to one or both interaction partners, e.g. commensalism, mutualism, neutralisms and more. Parasitism is one specific antagonistic interaction between two organisms (Odum & Barret 2005). This interaction has been traditionally characterized by a combination of systematical and conceptual features (Baer 1952, Esch & Fernandez 1993, Rhode 1993, Ebert 2005). Using an entirely conceptual „definition" for parasitism, a parasite is any small organism that lives in close association with a host organism and causes any type of cost for this host organism (Rhode 2005, Nagler & Haug 2015). Parasitic strategies can be differentiated into several categories with different approaches that are different points of view and might be applied at the same time (Osche 1966, Lucius et al. 2017). To name the most commonly applied approaches, these are:

(1) Differentiation according to the intensity of the host's cost. The maximum cost for the parasitized host would be the physical or reproductive death of the host. *Parasitoids*, such as insects (Schuler et al. 1999) or *parasitic castrators*, such as rhizocephalans (Kuris 1974, Lafferty & Kuris 2009) cause this death, respectively. A clearly detectable cost is for example that the parasite harms the host physically by feeding on it, as for example seen in parasitic isopods (Nagler & Haug 2016). Indirect energetic costs can be caused for example by transportation, in the case of *phoretic* mites on flying insects (Houck & OConnor 1991), stealing nesting material, as in *kleptoparasitic* birds (Brockmann & Barnard 1979), running for space or shelter, as seen by barnacles on corals (Santos et al. 2012), or exploiting parental care, as seen by *brood parasitic* fishes (Baba et al. 1990).

(2) Differentiation according to the position of the parasite. A parasite attaching onto the surface of the host is an *ectoparasite*, such as isopods on fishes (Rhode et al. 1995). A parasite living inside the host is an *endoparasite*, such as helminthes in eels (Moravec 1985) or representatives of tapeworms in humans (Hoberg et al. 2001). Although the usage of the term endoparasite is ambiguous, this differentiation clarifies the degree of intimacy and constancy (Martin & Schwab 2013). More specialized and clear endoparasites are *intracellular* parasites that use a highly specific mechanism concerning a change in the host cell to invade this cell, e.g. *Leishmania* (Lucius et al. 2017).

(3) Differentiation according to the duration of the contact between parasite and host. A parasite attaching to the host just for feeding, e.g. mosquitoes, is a *temporary parasite* (Martínez de la Puente et al. 2011) or a *micropredator* (Bruce 1981, Lafferty & Kuris 2002). A parasite permanently attaching to the host, such as trematodes and flatworms, is a *permanent parasite* (Castro-Pampillón et al. 2002). A third category would be a *periodic parasit*e that attach to the host for longer periods, e.g. leeches (Meyer 1946).
(4) Differentiation according to the parasite‘s life stage. *Larval parasites* infect their hosts only during one specific larval phase or the whole larval stage, e.g. praniza larvae of parasitic isopods (Marino et al. 2004). Due to the possible overlap between the duration of the contact (3) and the parasitic life stage (4), all permanent larval parasites can be considered as periodic parasites at the same time. *Adult parasites* infect their hosts only during their adult stage after metamorphosis, e.g. rhizocephalans (Kuris 1974).
(5) Differentiation according to the parasites‘ size. *Microparasites*, e.g. protozoan‘s, viruses, bacteria are small with short generation times. In contrast *macroparasites*, e.g. arthropods are larger with a long generation time (Anderson & May 1981, Lafferty & Kuris 2002). Using the parasite‘s size, the parasitic strategies form a kind of continuum ranging from pathogens (mircoparasites) to predators (macroparasites, if the parasite is as large as the host), because there may be no strict limitations of the various parasitic categories (Lafferty & Kuris 2002).

Taken together there are many forms of parasitism and much more approaches to differentiate among them. Parasites are found in all habitats and most major groups of metazoans (Poulin & Morand 2000, Zrzavý 2001). Parasitism strongly influences food webs and is an important driver of evolution due to co-evolutionary aspects of host-parasite relationships (Lafferty et al. 2008, Boucot & Poinar 2010, Al-Zubaidy & Mhaisen 2013, Boyko et al. 2013, Dunne et al. 2013, Klompmaker et al. 2014, De Baets & Littlewood 2015, Jephcott et al., 2016). Parasites can be important agents of selection and thus, influence the population dynamics of itself and of the host (Goater et al. 2007). Additionally, parasites cause economic damage, because they negatively affect agriculture, fisheries and many more due to fitness reduction in their host species causing diseases and mortality (Carnegie 2005, Dailey 2005, Heuch 2005, Jones 2005, Ogawa 2005, Overstreet 2005, Östlund-Nilsson et al. 2005, Roche et al. 2013, Elumalai et al. 2014, Yong et al. 2016). Hence, parasites are economically, ecologically and evolutionary significant and understanding of parasitism and the evolution of parasitism is crucial (Hochberg et al. 1992, Rohde 2005, Yesmin & Khanum 2011, Stentiford et al. 2012, Klompmaker et al. 2014, Klompmaker & Boxshall 2015). Consequently, there is a specific research interest in studying parasites and their evolution.

Recording how often parasitism evolved independently in all metazoan groups, the parasitic lifestyle is one of the most successful modes of life (Grimaldi & Engel 2005, Poulin 2006). Due to the close relation and the co-evolution between host and parasite, it is reasonable that also in earlier times, most of animals were parasites (Anderson & May 1978, Anderson 1979, May & Anderson 1979, Anderson 1993). In other words, shortly after the origin of metazoans, parasites originated; the parasitic life style is therefore presumably quite old. However, despite the common abundance of parasites in modern ecosystems, their abundance is not reflected in the fossil record (Feldmann 1998, Labandeira 2002, Brauckmann et al. 2007, Boucot & Poinar 2010, Neumann & Wisshak

2009, Hess 2010, De Baets et al. 2011, Ceccon & De Angeli 2013, Klompmaker et al. 2014).

Fossils are an important source of information for understanding the evolution of different lifestyles in specific groups, because they contribute unique character combinations to the character evolution towards modern representatives (Donoghue et al. 1989, Rust 2006, Edgecombe 2010a, Haug et al. 2010, 2013, Edgecombe & Legg 2013, Klompmaker et al. 2013, Bracken-Grissom et al. 2014). Additionally, fossils can be used for (1) revealing a specific character evolution, if the fossil occurs close to splitting events. If the fossil represents a kind of intermediate step that exhibits characters (e.g. morphologically, ecological) that are common to both, an ancestral group and a derived group, the proposed relationship of groups can even be changed. (2) Fossils increase the accuracy of root positions for a, e.g. phylogenetic tree by validating calibration points for the first occurrence of a specific group. This temporal information is a crucial support for estimating divergence dates of lineages or groups. Combining fossil data and molecular clocks, a comprehensive, accurate and most likely divergence data for specific groups can be obtained. Furthermore, well-preserved fossils with crucial morphological characters can be used to infer their lifestyle and thus, answer ecological and functional morphological questions. By usage of fossils, this thesis address the question of the evolutionary reconstruction of parasitism‘s towards modern parasites to elucidate this gap of knowledge on the example of arthropods.

In terms of species richness, biomass, individual richness and morphological and ecological diversity, arthropods represent an impressive group (Giribet & Edgebcombe 2013, Minelli et al. 2013, Nagler & Haug 2016). Furthermore, within arthropods, numerous groups evolved independently a parasitic lifestyle leading to an adaptive radiation (Poulin & Mourand 2000, Dreyer & Wägele 2001, Baumiller & Gahn 2002, Harvey et al. 2012). Especially in insects a variety of different parasitic strategies, e.g. haematophagy, kleptoparasitism, parasitoidism and plant parasitism, evolved (Labandeira 2002, Lukashevich and Mostovki 2003, Grimaldi & Engel 2005, Kathirithamby 2009, Peñalver & Pérez-de la Fuente 2014). However, non-insect crustaceans show the same, if not a larger diversity concerning parasitic strategies (Adamowicz et al. 2008, Minelli et al. 2013, Watling & Thiel 2015).

Although the oldest fossil evidence for arthropod parasitism in general is provided by pentastomids from the Cambrian (495 ma; and thus not much older than arthropods itself; Waloszek et al. 1994, Walossek & Müller 1994, Castellani et al. 2011), body fossils of arthropod parasites have been reported just in individual cases, e.g. copepods (Cressey & Patterson 1973, Cressey & Boxshall 1989), mites (Poinar & Brown 2003, Poinar & Buckley 2008), fleas (Dampf 1911, Beaucournu & Wunderlich 2001, Beaucournu 2003, Gao et al. 2012, Huang et al. 2012, Gao et al. 2013, Huang et al. 2013, Gao et al. 2014, Huang 2014), lice (Wappler et al. 2004) and parasitic larvae of true flies (Chen et al. 2014). Yet, arthropods are one of the most abundant and diverse group preserved from the Paleozoic (540-240 mya; Briggs et al. 1994, Edgecombe & Legg 2013, Klompmaker & Boxshall 2015) due to the arthropod cuticle with a high fossilization potential and thus often exceptional preservation (Labandeira 1997, Dietl & Schweigert 2001, 2004, Moussian 2010, Pohl et al. 2010, Edgecombe & Legg 2013). Besides their large morphological, ecological and economical diversity, Crustacea is especially interesting, because representatives are relatively well preserved in rocks and amber (De Baets &

Littlewood 2015 and references therein). Yet, it is challenging to assess the true morphological and ecological diversity and prevalence of parasitism in arthropods in general and especially in crustaceans (Poulin & Morand 2000, Giribert & Edgecombe 2013), because often they have a cryptic morphology, e.g. parasitic copepods with a sack-like body form (Boxshall 2005a) or some parasites display a low abundance in natural populations (Roche et al. 2013).

1.2 ARTHROPODS

Euarthropoda sensu Walossek (1999) can be differentiated into some major groups based on molecular, morphological and palaeontological datasets: Pycnogonida (sea spiders), Euchelicerata (e.g. spiders, scorpions, mites, ticks, harvestmen and sea scorpions), Myriapoda (millipedes, centipedes and others), Hexapoda (in the German-speaking world Insecta), Eucrustacea and their fossil relatives (Telford & Thomas 1998, Mittmann & Scholtz 2003, Regier et al. 2005a, Waloszek et al. 2005, Scholtz & Edgecombe 2006, Waloszek et al. 2006, 2007 Regier et al. 2010, Edgecombe 2010b, Giribet & Edgecombe 2012, 2013, Wheat & Wahlberg 2013, Haug & Haug 2015a, Strausfeld et al. 2016a, Strausfeld et al. 2016b). However, the relation between these groups is not yet resolved due to a ~~r~~ooting problem" (Dunn et al. 2008, Meusemann et al. 2010, Campbell et al. 2011, Giribet & Edgecombe 2012, Ma et al. 2014, Mayer et al. 2013).

Due to the focus of this thesis on crustacean parasites and the evolution of parasitism within some crustacean groups, only the relationship within Crustacea will be discussed in the following. Some authors have proposed a sistergroup relationship between (Hexapoda + Crustacea) based on studies of the nervous system and have named the groups together Tetraconata (Harzsch, 2002, Sinakevitch et al. 2003, Harzsch 2006, Richter 2002, Giribert & Edgecombe 2013, Yeates et al. 2016). Eucrustacea sensu Walossek (1999) includes the groups: Remipedia (small, quasi-marine and blind crustaceans), Cephalocarida (horseshoe shrimps), Branchiopoda (e.g. clam shrimps, fairy shrimps and water fleas), Maxillopoda (e.g. barnacle, copepods and fish lice), Malacostraca (e.g. crabs, lobsters, crayfish, shrimps, krill, woodlice and mantis shrimps) and their fossil relatives. Although Remipedia has been proposed to be the sistergroup to all other extant crustaceans (Koenemann et al. 2007), the relationships between the remaining groups and within them are still debatably (Fig. 1; Wills 1998, Walossek 1999, Edgecombe et al. 2000, Richter & Scholtz 2001, Waloszek et al. 2005, Regier et al. 2005b, Meland & Willassen 2007, Møller et al. 2008, Olesen 2009, Edgecombe 2010b, Regier et al. 2010, Reumont et al. 2012, Oakley et al. 2013, Shen et al. 2013, Eyun 2017).

In this thesis, to address the question of the evolutionary reconstruction of parasitism towards modern parasites, I focus mainly on the malacostracan group Cymothoida (isopods) and the maxillopodan group Thecostraca (barnacles and their relatives). Representatives of Cymothoida and Thecostraca are comparably large in relation to their hosts and to other parasitic organisms. Consequently, it is more likely that fossils either show the parasite or traces of it preserved. Hence, these fossils can be integrated into an evolutionary reconstruction. Numerous lineages of isopods and thecostracans have independently evolved different strategies of parasitism und thus a diversity of morphologies are presented in detail in the following.

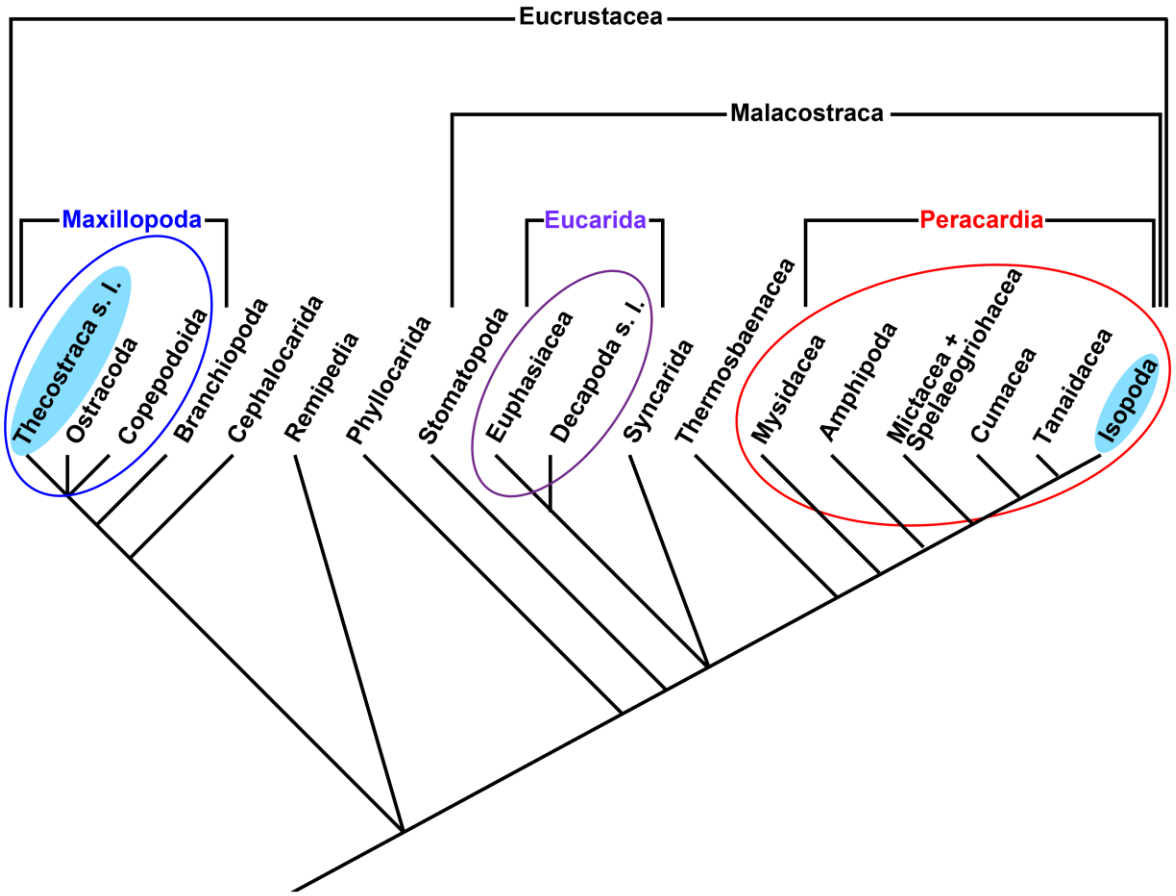

Fig. 1: Overview of major groups within Eucrustacea. Phylogenetic tree modified after some authors (Walossek 1999, Edgecombe et al. 2000, Richter & Scholtz 2001, Waloszek et al. 2005, Regier et al. 2005b, Meland & Willassen 2007, Møller et al. 2008, Olesen 2009, Edgecombe 2010b, Regier et al. 2010, Reumont et al. 2012, Oakley et al. 2013, Shen et al. 2013, Wagner et al. 2017). Groups studied in this thesis – Thecostraca *s. l.* and Isopoda – highlighted in blue.

1.2.1 CYMOTHOIDA

Isopods represent one of the most diverse groups within peraracarid malacostracans, such as mysid shrimps, side swimmers, hooded shrimps, and woodlice, concerning their lifestyle, morphology and geographical distribution (Brandt 1999). Cymothoida sensu Wägele (1989), an isopod ingroup, consists of different groups that evolved different strategies that can be used for studying the evolution of these:

- Representatives of Cirolandiae (Fig. 2A) show a scavenging lifestyle (Bruce 1986, Wong & Moore 1995, Lowry & Dempsey 2006, Wilson et al. 2011). Fossils have been reported from the Jurassic (150 mya; Polz 2004) and the Cretaceous (100mya; Wilson et al. 2011).

- Representatives of Corallanidae (Fig. 2B) are scavengers, predators and also temporary, ectoparasitic on fishes and zooplankton (Monod 1969, Bruce 1982, Bruce et al. 1982, Thatcher 1995, Brusca & Wehrtmann 2009, Gentil-Vasconcelos & Tavares-Dias 2015).
- Representatives of Aegidae (Fig. 2C) are temporary, ectoparasitic on fishes: they attach just shortly for feeding and leave their hosts afterwards (Brusca 1983, Lester 2005). One fossil representative, suggesting a similar lifestyle has been reported from the Late Miocene (20 mya; Hansen & Hansen 2010).
- Juvenile representatives of Cymothoidae (Fig. 2E) show a lifestyle similar to representatives of Aegidae, attach just shortly for feeding to their host fishes and thus can be considered as temporary ectoparasites (Brusca 1981, Fogelman & Grutter 2008); adults (Fig. 2D) are permanently ectoparasitic in their host fishes (Brusca & Iverson 1985, Bunkley-Williams & Williams 1998, Jones et al. 2008, Smit et al. 2014). The oldest fossil indicating such a lifestyle has been reported from the Jurassic (150 mya; Nagler et al. 2016, see also chapter 2.1)
- Representatives of Gnathiidae (Fig. 2F) during a specific larval phase (praniza larva) feed similar to representatives of Aegidae and juvenile Cymothoidae on host fishes and thus can be considered as temporary ectoparasites (Hispano et al. 2014). Concerning the adult representatives of Gnathiidae that are non-feeding and free-living in sponges, tunicates and tubes of sepulid worms, Gnathiidae can be also considered as larval ectoparasites (Barnard 1914, Trilles 1991, Smit et al. 1999). So far no fossils have been reported. However, likely closely related fossil representatives of *Urda* have been reported from the Jurassic (168 mya; Nagler et al. 2017a, see also chapter 2.4).
- Representatives of Epicaridea (Fig. 2G-J) show a specific lifecycle involving also a host change respectively to their ontogenetic phase. After hatching as epicaridium larva, they infest intermediate hosts, small crustaceans, such as copepods as microniscus stage. As cryptoniscus larva, they look for and infest their final hosts, such as crabs (Williams & Boyko 2010, 2012). Depending on their infection site and their adult morphology, adult epicarideans can be considered as permanent endo- or ectoparasites, while microniscus larvae can be considered as larval ectoparasites. Based on pathological changes of the host and by comparing the life habits of modern groups, a lifestyle including an ontogenetic host change must have been present since the Jurassic (150 mya; Serrano-Sánchez et al. 2016, Klompmaker et al. 2014, 2015, see also chapter 2.3).

Together with deep-time aspects based on fossils and their diversity and abundance in marine habitats, Cymothoida is an interesting group for studying the evolution of parasitism. The evolution of parasitism within Cymothoida has been proposed to have occurred stepwise by a shift from non-parasitic to parasitic lifestyles (Nagler et al. 2017a, see also chapter 2.4, 4.1).

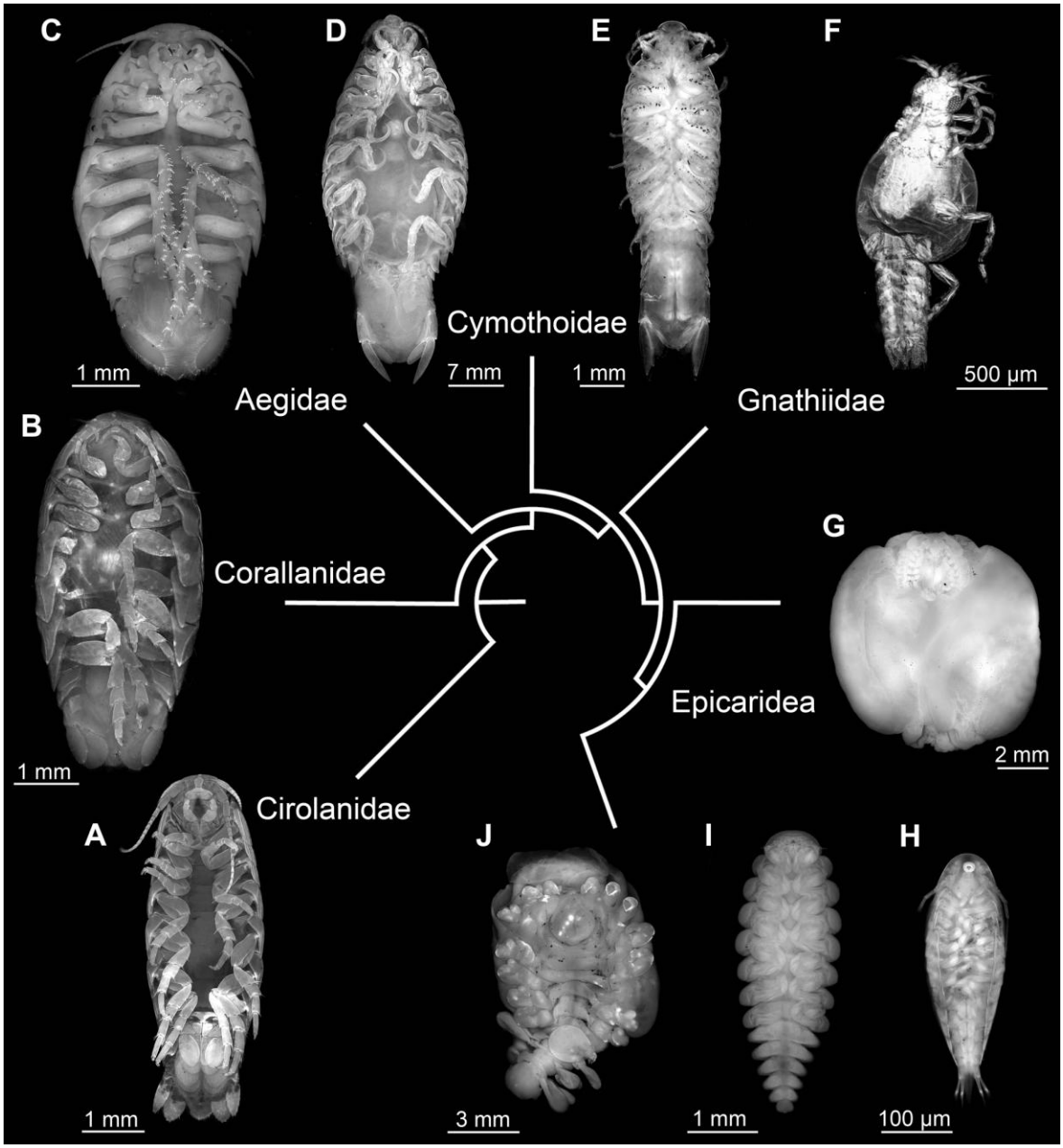

Fig. 2: Fluorescence images (A-E, G-J) and CLSM image (F) of different representatives of Cymothoida, females (A-D, G, J), male (I), and juveniles (E-F, H), ventral view. A) *Cirolana parva* (Cirolanidae). B) *Lanocira gardineri*, (Corallanidae). C) *Aega psora*, (Aegidae). D) *Anilocra physodes*, (Cymothoidae). E) *Nerolica acuminata*, (Cymothoidae). F) *Gnathia maxillaris*, praniza stage, (Gnathiidae). G) *Aspidophryxus japonicus,* (Epicaridea). H) Representative of Epicaridea, cryptoniscus stage. I) *Athleges paguri*, (Epicaridea). J) *Athleges paguri,* (Epicaridea).

1.2.2 THECOSTRACA

The group Thecostraca sensu Grygier (1987a) and Høeg et al. (2004a) includes representatives of three main groups: Facetotecta, Ascothoracida and Cirripedia. Together they provide a great diversity in morphology, lifestyle and reproduction (Høeg et al. 2009). Yet, larval thecostracans are free-living, while adults are either sessile as filter feeders or parasitic with different parasitic strategies. Furthermore, only the morphological characters of the larvae of representatives of Thecostraca combine them to a monophyletic group (Pérez-Losada et al. 2012).

- Representatives of Facetotecta (Fig. 3A-B) are known only from larval specimens, called y-larva (Grygier 1991a, b). Due to an induced metamorphosis into an infective stage (a worm-like organism, similar to the infective stage of parasitic cirripeds), they have been supposed to be endoparasitic (Grygier 1996, Glenner et al. 2008). However, the host is unknown. So far, there have been no fossils reported.
- Representatives of Ascothoracida (Fig. 3C-D) are permanently ecto- or endoparasitic in a variety of cnidarians and echinoderms (Grygier 1984, Grygier 1996). In contrast to other thecostracans groups, most representatives of Ascothoracida show not an extreme metamorphosis. In other words, the ascothoracidan parasitic adults are very similar to their cypris larvae (Grygier & Høeg 2005, Høeg et al. 2004a, 2009). Some of them can be considered as parasitic castrators (Grygier & Høeg 2005), which means they prevent or inhibit reproduction of their hosts, comparably to rhizocephalan cirripedes (Lafferty & Kuris 2009). No fossil ascothoracidans are known to date.
- The group Cirripedia can be further differentiated into Acrothoracida (Fig. 3E-F, burrowing barnacles), Rhizocephala (Fig. 3J-I, parasitic barnacles) and Thoracica (Fig. 3G-H, stalked and sessile barnacles) (Pérez-Losada et al. 2002). Beside the filter-feeding representatives of Acrothoracida and Thoracica, representatives of Rhizocephala are exclusively parasitic on other crustaceans, especially decapods (Høeg et al. 2005). Additionally, representatives of Rhizocephala castrate their hosts (Lafferty & Kuris 2009). Representatives of parasitic Thoracica are either phoretic or permanently ectoparasitic on corals, sponges, turtles, fishes and whales (Rees et al. 2014). Many fossil representatives of non-parasitic Thoracica and Acrothoracica have been reported from the Carboniferous (300 mya) until now (Newman et al. 1969, Foster & Buckeridge 1987, Glenner et al. 1995, Høeg et al. 1999). Indication for a parasitic lifestyle of representatives of Thoracica has been reported from the Jurassic (150 mya; Nagler et al. 2017b, see also chapter 3.1). So far, no fossil representatives of Rhizocephala have been reported by direct indication. However, feminized crabs have been reported from the Cretaceous (100 mya; e.g. Reinhard 1956, Rasmussen 1973, Bishop 1974, Beck 1980, Feldmann 1998). Although rhizocephalans are known to feminize male crabs, such a pathological change of the host can also induced by other parasitic organisms. Thus, these findings are ambiguous.

Taken together, representatives of Thecostraca *s str.* evolved different life styles and show a great diversity in their morphology and biology. Therefore, the ingroup Cirripedia has been used to study evolutionary adaptation (Darwin 1851, 1852, 1854, 1855, Crisp 1983, Grygier 1987a, b, c, Newman 1987, Anderson 1994, Høeg 1995a, Schram & Høeg

1995). Besides the Orsten preserved *Bredocaris admiribilis* and other debatable body fossils from chert, only fossil representatives of non-parasitic Cirripedia or equivocal cases of indirect indication of parasitism by Rhizocephala have been reported (Feldmann 1998, Müller & Walossek 1988, Haug et al. 2012, see also chapter 3.2, 3.4, 3.5). Despite the scarcity, the group Thecostraca represents an ideal model to study the evolution of different features (Charnov 1987, Pérez-Losada et al. 2009, 2012) and also of parasitism.

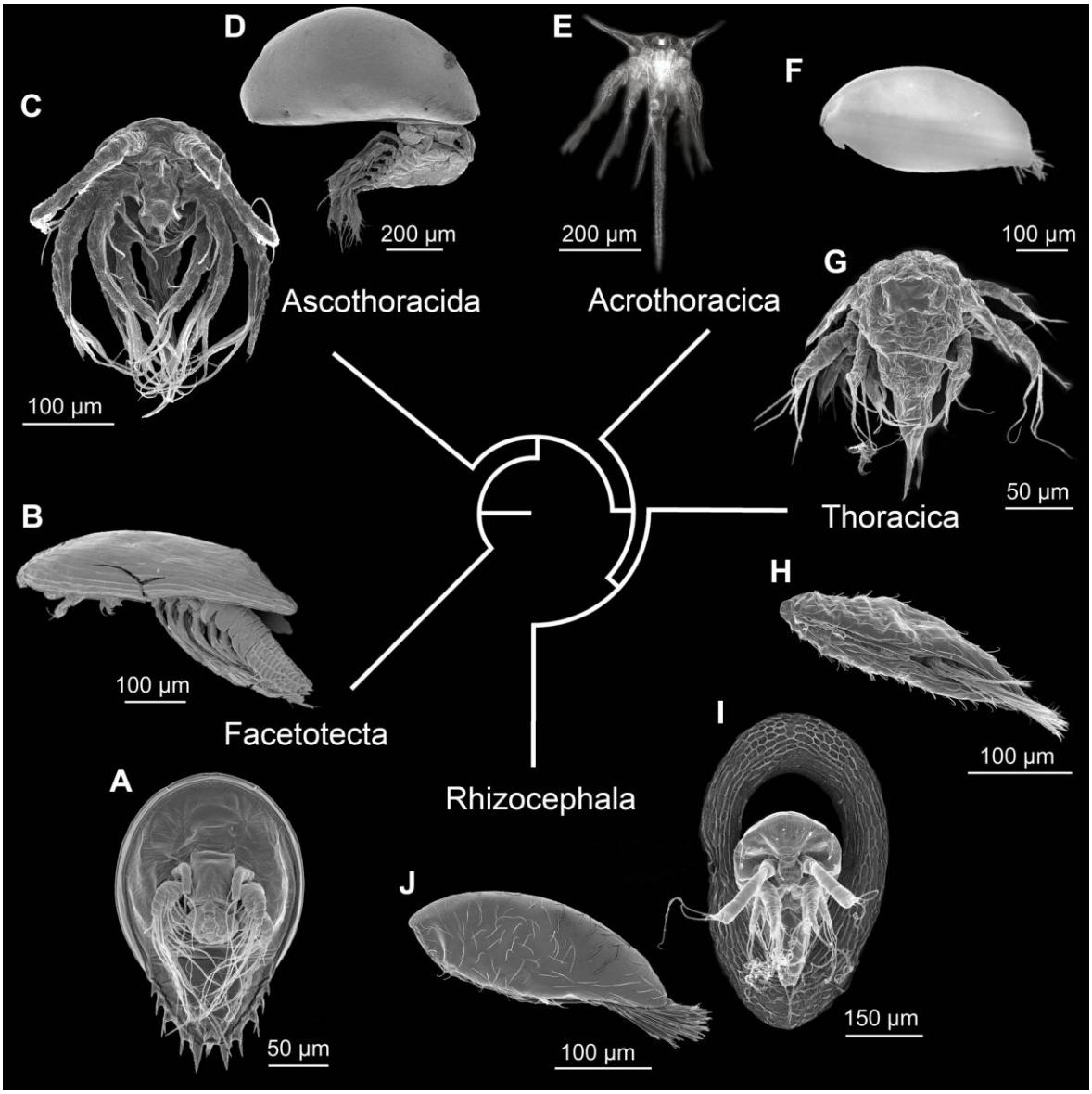

Fig 3: SEM images (A-D, F-I) of nauplius larvae in ventral view (A, C, E, G, I) and cypris larvae in lateral view (B, D, F, H, J) of representatives of Thecostraca. A–B) *Hansenocaris furcifera* (Facetotecta) C–D) *Zibrowia auriculata* (Ascothoracida). E) Lightmicroscopy of unknown naupliar representatives of Acrothoracica by courtesy of Benny Chan (National Taiwan University). F) *Trypetesa lateralis* Acrothoracica from Kolbasov & Høeg 2007. G–H) *Capitulum mitellum* (Thoracica). I–J) *Peltogaster paguri* (Rhizocephala).

1.3 FOSSIL PARASITES

Despite the common abundance of parasites in modern ecosystems, their abundance is not reported from the fossil record. The fossil sparseness of parasites in general is probably caused by the poor preservation potential of most parasites, their small size or their habitat inside the host for endoparasites (Conway Morris 1981, Cressey & Boxshall 1989, Baumiller & Gahn 2002, Labandeira 2002, Littlewood & Donovan 2003, Castellani et al. 2011, De Baets et al. 2011, Klompmaker & Boxshall 2015, Nagler & Haug 2015). Furthermore identifying parasites in the fossil record is challenging due to their cryptic nature (Minchella & Scott 1991, Kuris et al. 2008) and sometimes low abundance in natural populations and, therefore, rare preservation (De Baets & Littlewood 2015). Often fossil parasites have been removed from their hosts during the preparation process, because they were not identified as organisms (Nagler & Haug 2015). In the following, different ways of inferring a parasitic lifestyle in fossils are outlined.

1.3.1 DIRECT INDICATION

The most direct cases for fossil parasites are finding the parasite directly associated with its host. For such a case a preservation of the parasite and the host combined with the knowledge of extant relatives is needed. Especially Lagerstätten with a high preservation potential, such as Lithographic limestones or amber, are good resources for such a relationship. Inclusions in amber are perfect examples for this direct contact between parasite and host (De Baets & Littlewood 2015, Nagler & Haug 2015), e.g. mantispid neuropteran larvae on spiders (Fig. 4A, Ohl 2011), nematodes and nematomorphs emerging from their hosts in amber (Poinar et al. 1994, Poinar and Buckley 2006, Poinar et al. 2008) or twisted wing larvae emerging from plant hoppers (Poinar 2004).

Among parasitic Eucrustacea, there are only a few records of parasitism by direct indication in both, fossils from rocks and amber:

- Gall crabs associated with corals from the Eocene (ca. 40 mya; De Angeli & Ceccon 2015),
- Pentastomids associated with ostracods from the Silurian (ca. 440 mya; Siveter et al. 2015). Notably, the final hosts of modern pentastomids are exclusively vertebrates, although invertebrates are known as intermediate hosts (Walossek & Müller 1994, Christoffersen & Assis 2013). Hence, this fossil is still controversial. Additionally, the phylogenetic position of pentastomids is not finally evaluated. They have been considered to be either closely related to Branchiura or situated outside Euarthropoda as Arthropoda sensu lato branching off the lineage towards Euarthropoda (Castellani et al. 2011, Walossek & Müller 1994, Walossek et al. 1994, Waloszek et al. 2006, Wingstrand 1972, Abele et al. 1989, Peterson & Eernisse 2001. Legg et al. 2013, Edgecombe & Legg 2014).
- Copepods associated with fishes from the Early Cretaceous (ca. 140 mya; Cressey & Patterson 1973, Cressey & Boxshall 1989),
- Isopods associated with fishes from the Jurassic (ca. 150 mya; Nagler et al. 2016, see also chapter 2.1).

- Although the relationship is not clearly identified, there is another case between two organisms, barnacles and sponge, from the Jurassic (ca. 150 mya; Nagler et al. 2017b, see also chapter 3.1).

Two insects with blood in the abdomen have been reported from limestone; a mosquito (Greenwalt et al. 2013) and a flea (Wappler et al. 2004). However, this is not a direct contact, because the parasite has not been associated to the host, but parts of the host (blood) have been found inside the parasite. This example illustrates again that categories in biology are rather continuous than strict categories.

1.3.2 INDIRECT FUNCTIONAL MORPHOLOGICAL INDICATION

Most, if not all, parasitic arthropods show different morphological adaptations to their parasitic strategy. Often they show reduced locomotor appendages and sensory organs, but develop new organs and appendages to attach, anchor, cling, clasp, hook, stick, suck and pierce to and into their host (Osche 1966, Rhode 1994, 2005, Pennacchio & Strand 2006, De Baets & Littlewood 2015, Lucius et al. 2017). The reduction of locomotor appendages and sensory organs is less useful in this aspect than new organs or specific appendages, because sensory organs and locomotion appendages like setae are often reduced in deep-sea or groundwater organisms as adaptation to this specific ecological environment (Dahl 1979, Hessler & Wilson 1983, Brancelj & Dumont 2007). More important for identifying parasites with their specific morphology are at least the following two aspects: attachment to the host and specific morphology of the mouthparts. Comparing this specific morphological adaptation of fossil representatives to modern relatives, it is possible to identify any lifestyle, especially parasitism, among disarticulated fossil, because certain characters are expected.

Within Crustacea *s. l.*, there are only a few fossils that have been reported as likely parasitic by using the functional morphology to get a hint for this parasitic lifestyle of fossils. For example:

- Depending on their phylogenetic affinity, pentastomids can be considered as crustaceans. Pentastomids with a parasitic morphology independent of their phylogenetic affinity have been reported from the Cambrian (495 mya; Maas & Waloszek 2011).
- Various insects from at least the Triassic (Fig. 4B; 200 my; e.g. Grimaldi & Engel 2005, Gao et al. 2012, Nagler & Haug 2015).
- Isopods with a parasitic morphology have been reported from the Jurassic (168 mya; Nagler et al. 2017a, see also chapter 2.4). For this example, the description of the morphological parasitic adaptations of modern representatives of parasitic isopods was needed (Nagler & Haug 2016, see also chapter 2.2).
- Thecostracans with a characteristic attachment device have been reported from the Devonian (400 mya; Nagler et al. in prep a, see chapter 3.4).

1.3.3 INDIRECT TERATOLOGICAL INDICATION

As a reaction to parasites, the morphology, growth and development of hosts can be influenced (Conway Morris 1981, Wilson et al. 2011, Lucius et al. 2017). Notably, it can be difficult to identify the responsible organisms for these pathological changes. In every case, a comparison with extant relatives from both, the parasite and the host, and the pathological reaction from the host provides a better argumentation (McNaughton 1983, Klompmaker & Boxshall 2015). Consequently, such cases provide the basis to interpret the type of parasitism and the relationship between the host and the likely parasite (De Baets & Littlewood 2015). Although, some pathological changes are quite convincing due to their similarity to modern host-parasite relationships and host reactions, these pathological changes provide less evidence than finding body fossils of parasites.

The aspect of pathological changes in the morphology of the host has been often used to indirectly infer a parasitic lifestyle in fossils. Besides detected pathologies in plants caused by insects from the Carboniferous (360 mya; e.g. Brett 1978, Stephenson & Scott 1992, Knor et al. 2013, Carvalho et al. 2014), in molluscs by microparasitic infections confidently from the Eocene (50 mya; e.g. Campbell 1985, Ruiz & Lindberg 1989; Huntley 2007, De Baets et al. 2011, De Baets et al. 2015, Huntley & De Baets 2015) and in echinoderms from the Jurassic (150 mya; e.g. Radwanska & Radwanski 2005, Radwanska & Poirot 2010), there are only a few examples within Crustacea *s. l.*

- Crabs with an asymmetric swelling of the branchial chamber probably caused by parasitic isopods from the Jurassic (Fig. 4C, 150 mya; e.g. Markham 1986, Wienberg-Rasmussen et al. 2008, Klompmaker et al. 2014, Klompmaker & Boxshall 2015).
- Feminized crabs probably caused by rhizocephalans from the Cretaceous (100 mya; e.g. Reinhard 1956, Rasmussen 1973, Bishop 1974, Beck 1980, Feldmann 1998). However, the characters supporting a feminization, e.g. wider abdomen (change from v-shaped to u-shaped), and a changed segmentation of the pleon, cannot be induced by rhizocephalans exclusively (Klompmaker & Boxshall 2015). Hence, these findings are highly speculative. To provide more details for host-parasite-relationships of rhizocephalans infesting other crustaceans, modern relatives have been analyzed concerning their size in relation to the host‘s size (Nagler et al. 2017d, see also chapter 3.3).

1.3.4 INDIRECT PHYLOGENETIC INDICATION

Some species are only parasitic during a specific life stage (Combes 2001, Goater et al. 2007, Lucius et al. 2017). Finding a non-parasitic, free-living life stage of a species that has parasitic larvae, for example, makes it possible to infer its parasitic lifestyle based on phylogeny. An indirect phylogenetic indication depends on morphological characters that assign the fossil specimen to a specific monophyletic group, of which all extant representatives are parasitic:

1) Identification of a specimen as representatives from this specific monophyletic group.
2) Identification of a non-parasitic life stage of this specific monophyletic group.

Again, this case of inferring parasitism relies heavily on the comparison to modern relatives, especially if the fossil cannot be assigned to any living group (De Baets & Littlewood 2015). Inferring parasitism by indirect phylogeny, is crucial for organisms that are endoparasitic in a specific life stage, especially, because these have been rarely detected inside their hosts (Nagler & Haug 2015). Thus, many cases of haematophagous and endoparasitic insects, especially Hymenoptera and Diptera, have been reported from amber, the oldest from the Cretaceous (Fig. 4D, 100 mya; e.g. Grimaldi & Engel 2005, Declós et al. 2007, Pohl et al. 2012, Engel & Perrichot 2014). Beside reports of Cambrian larval pentastomids (Castellani et al. 2011), there are to the best of my knowledge only a few cases of inferring parasitism due to the phylogenetic position in representatives of eucrustaceans:

- Possible cases for infective stages (Cryptoniscus stage) of parasitic isopods (Epicaridea) in amber from the Upper Cretaceous and the Eocene has been reported (90 mya, 40 mya; Serrano-Sánchez et al. 2016, Néraudeau et al. 2017, see also chapter 2.3).
- A larval stage (in this case a nauplius) likely from a representative of Cirripedia has been reported from the Jurassic (150 mya; Nagler et al. 2017c, see also chapter 3.2).
- In the fossil representatives of another group within Thecostraca from the Devonian, parasitism is inferred primarily due to the functional morphology of the fossils and secondarily due to a phylogenetic relationship (400 mya; Nagler et al. in prep a, b, see also chapter 3.4, 3.5).

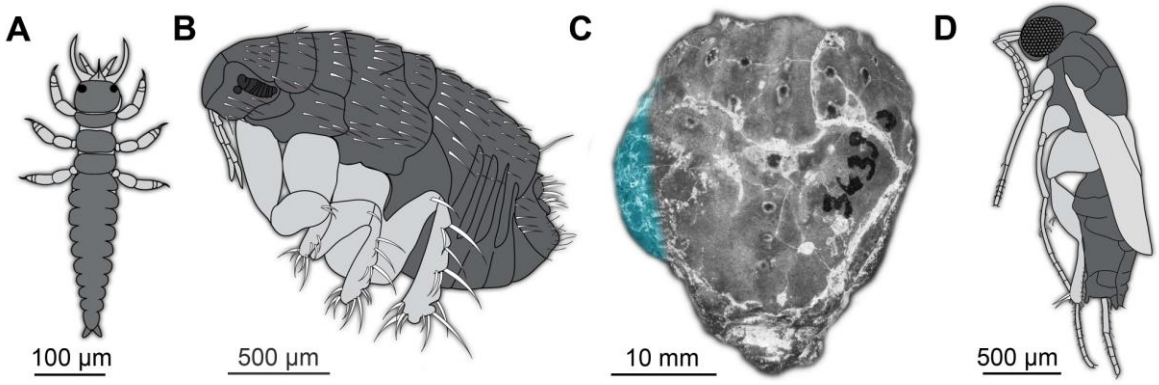

Fig. 4: Representatives of fossil parasites. A) *Mantispa styriaca* (Mantispinae), larva, modified from Ohl (2011, fig. 2b). B) *Eospilopsyllus kobberti* (Siphonaptera, Mecopterida), modified from Perrichot et al. (2012, fig. 1). C) Unknown crab with swelling in the left branchial chamber from the Eocene, NHM London, swollen area highlighted in cyan. D) *Tagsmiphron spiculum* (Stigmaphronidae, Ceraphronidea), modified from McKellar & Engel (2011, fig. 2a).

1.4 METHODS

In this thesis advanced imaging methods have been used to document and describe fossil parasites and their extant relatives. These different methods were combined to enhance the informational output. All applied methods are described in the following part.

1.4.1 SPECIMEN ACQUISITION

Fossil specimens were acquired during various visits to the Paleontological and Geological Collection of Bavaria (Munich, Germany), the Institute for Paleontology Vienna (University of Vienna, Austria), Stuttgart State Museum of Natural History (Stuttgart, Germany), Jura Museum in Eichstätt (Germany) and the private collections of Udo Resch and Roger Frattigani.

Extant specimens were acquired during visits to the Zoological State Collection of Bavaria (Munich, Germany), the Natural History Museum Berlin (Berlin, Germany), the Zoological Museum of Copenhagen (Copenhagen, Denmark) and the Natural History Museum Bergen (Bergen, Norway). During a six-month research visit in Bergen (Norway) several sampling cruises to the Norwegian Sea were attended. Beside others, specimens of the groups Thecostraca and Isopoda were sampled during these cruises.

1.4.2 DRAWING AND RECONSTRUCTION

Drawings

Drawings of specimens were obtained with the aid of camera lucida, mounted onto a dissection microscope. Some drawings were achieved by modifying already existing drawings by other authors or directly from an image, e.g. SEM photography, fluorescence photography, macro photography or microscopic photography.

The drawings were scanned and an image of the specimen was displayed in Adobe Illustrator CS5. Drawings were electronically tracked using a graphic tablet (Cintiq 12 WX, Wacom), an electronic pen (Wacom Inkling MDP—123), and the software Adobe Illustrator CS5, according to the protocol of Coleman (2003). Drawings were finally optimized in direct comparison with the original.

Reconstructions of fossil specimens

Some fossil specimens were just partly preserved. A reconstruction of these specimens was possible, if missing parts were preserved at least on one side of the specimens. To get a reconstruction of the entire specimens, the missing parts were assembled to the site of the specimens, on which they were not preserved, by mirroring missing structures in Photoshop CS5 after Haug et al. (2015a).

1.4.3 IMAGING AND IMAGE PROCESSING METHODS WITH MACRO PHOTOGRAPHY

Macro photography with different light sources

Macro photography was performed on a Canon EOS Rebel T3i camera under cross-polarized light, following e.g. (Haug et al. 2011a, 2013a). For overview images a Canon EFS (15-55 mm) lens was used. If the specimens or the area of interest had a size between 30-10 mm, one to three (depending on the size) distance rings were added between the camera and the lens to gain higher resolution. For close-up images of details or specimens smaller than 10 mm, a Canon MP-E (65 mm) macro lens was used. Illumination was provided either by 1) a set of two Canon Macro Twin Lite MT-24EX flash or a Youngnuo Digital Speedlite YNS60-II flash from opposing sides to provide even illumination without shadows, or 2) a ringflash either FVlight HDR 300 LED Ring Light for large samples (> 10 mm) or Meike LED Macro Ring Flash FC 100 for smaller samples (< 10 mm).

Macro photography with cross polarized light

Reflections and shadows would cause several artifacts in the fossil specimens (Haug et al. 2015a). Thus, the interpretation of the fossil would be biased. Cross-polarized light will prevent these artifacts. Cross-polarized light was achieved by adding a polarization film to the flashes and a polarization filter to the lens directed 90° to the polarization film on the flashes. The polarization film on the flash will force the light in one certain direction and the polarization filter on the lens will erase the indirectly reflected light. Hence, the camera detects just the light that was directly reflected by the sample (Fig.5A).

Macro photography with fluorescence

Using the auto fluorescent nature of the cuticle and heavily sclerotized or calcified areas of the specimens, an even stronger contrast could be achieved by fluorescence macro photography. In fossils fluorescence was achieved by biogenic phosphate that has been re-mineralized from cuticle and sclerotized areas. These photographs were performed with the same equipment described above in a dark room. The flashes used for macro photography did not provide light for a period that is long enough to obtain macro fluorescence. Therefore, three flashlights Vander XMLT-6 were used. The wavelength of the light emitting from the flashlights was changed by an added cyan film. The light reflecting from the sample was changed by an added red film to the lens. Thus, just red-orange light could reach the sensor of the camera and a fluorescence photograph was obtained (Fig. 5C).

Macro photography and its different methods

Photomerge

If the specimens and their details extend to a certain field of view (larger than the field of view obtained by one image) and to achieve the highest resolute final image, images of adjacent areas were taken; in this way a smaller area with a higher magnification could be recorded.

Image processing to obtain a merged image

The images were merged in Adobe Photoshop CS5 (Adobe Systems 2010) with the photo merge plug-in „interactive layout". Thus, a large high-resolute panorama image was formed.

Image stacks and composite imaging

As the studied specimens extend to a certain depth and thus the depth of field extends, stacks of single images (frames) were recorded for each specimen with different imaging methods, e.g. macro photography with cross-polarized light, photography with fluorescence, fluorescence microscopy. The first frame was recorded at a level slightly above the specimen and the last frame at a level slightly below it. Depending on the size of the specimens or details, the magnification, and the depth of field, the frames were recorded every 1-20 µm.

Image stack processing to obtain a composite image

The resulted stacks of up to 126 single frames were fused into one sharp image with the free software CombineZM (Hadley 2008) or CombineZP (Hadley 2010).

Stereo macro photography

To obtain stereo images, a rotatable rail was installed behind the camera with the rotation point at the level of the sample. At least two photographs of the samples were taken, each with a slightly different angle (6-10°) of the camera. The auto stereo effect can be observed by squinting or staring, when two photographs from different angles are positioned next to each other.

Stereo image processing to obtain stereo images

One of two images from different angles was transparently (50%) placed onto the other. After desaturating both images, the red channel of the upper image was deleted. In the bottom image the blue and green channel was deleted, resulting in red-cyan anaglyphs that can be viewed with red-cyan glasses. Other anaglyphic methods like red-green or red-blue anaglyphs can be obtained with the same method (Fig. 5B).

Stereo Depth from defocus/focus (virtual surface)

This method was used to show the relief of samples showing less depth and contrast. After recording an image stack with images every 10 µm, the stack was loaded into the software program Image Analyzer (Meesoft) to produce one sharp image of the surface. Additionally, the software created a depth map.

Depth map and image stack processing to obtain a stereo image

To reduce an exaggeration of depth and height information in the final image, the Gaussian filter was applied in Photoshop CS5. Thus, the blurriness of the depth map increased and depth and height noise was reduced. Loading this changed depth map again into Image Analyzer, a three-dimensional model of the sample could be generated with the plug in

–3D Model" based on the depth information. Changing parameters such as the scale factor, depth of the surface structure could be changed. To use these models for figures, a red-blue stereo image was obtained by applying the red-blue filter in Image Analyzer (Haug et al. 2015b, Fig. 5D).

1.4.4 FLUORESCENCE MICROSCOPY

Entire or dissected specimens were mounted in ethanol or Hydro-matrix (Micro Tech Lab, Graz, Austria) on glass slides with a cover slip. Fossils were not prepared in a special way. Fluorescence microscopy was performed on an inverse fluorescence microscope BZ-9000 (BIOREVO, Keyence, Osaka, Japan) with either a 1) DAPI filter (OP-66834, λ=360-460), 2) GFP filter (OP-66835, λ=480-510), or 3) TRITC filter (OP-66837, λ=540-650). Depending on the used lens, images, stacks and merged images of adjacent areas were recorded. 2x, 4x, 10x, 20x, 40x, 60x lenses resulted in about 20, 40, 100, 200, 400 and 600 magnification with stacks recorded every 60, 20, 5, 3, 2 and 1 µm. During usage of the 60x lens, immersion oil was applied to the lens and the cover slip. Fluorescence microscopy was combined and processed with image stacking, composite imaging and photo merging (treated in chapter 1.4.3).

1.4.5 CONFOCAL LASER SCANNING MICROSCOPY

Confocal laser scanning microscopy (CLSM) can obtain high-resolution fluorescence images of details of some specimen (Pologruto et al. 2003). It was performed on a DMRE confocal laser scanning microscope with a TCS SP scanning unit with DIC Pol (Leica, Wetzlar, Germany). The specimens were mounted in glycerin between two thin glass slides and immersion oil was used between the sample and the lens. Using a 68x lens resulted in magnifications of about *680* times. A stack of single frames was recorded with images every 0.5-1µm.

Image stack processing to obtain volume renderings

The resulting stack was loaded into ImageJ (Wayne Rasband), converted to grey values and 8bit and saved as a tiff-stack. The stack was loaded into Osirix 5.8.2 (Antoine Rosset) and volume renderings were created either by segmentation or thresholds of the grey values.

1.4.6 SCANNING ELECTRON MICROSCOPY

A scanning electron microscope (SEM) detects secondary electrons that emits from a sample that is coated with e.g. gold or platinum (Koiko & Hayakawa 1984). For scanning electron microscope (SEM) observations, specimens were dehydrated, critical point dried (BalTec CPD 030), coated in gold (Polaron Sputter Coater), and finally studied using a Leo 1430VP in the Zoological State Collection of Bavaria (Munich, Germany).

Specimens studied in the Zoological Museum in Copenhagen (Denmark) during a SYNTHESYS funded stay were already mounted and coated on stubs. They were investigated with a JEOL 6335-F scanning electron microscope with a motor-driven tilting and rotation device that makes it possible to tilt up to 90°. To obtain larger samples, composite imaging (fusion to one image out of an image stack) was applied.

1.4.7 MICRO CT

Preparing specimens for micro CT

Specimen that have been fixed in 4% Para-formaldehyde in phosphate buffered saline, were transferred via a graded series (10%, 30%, 40%, 50%, 60%, 70%, 80%, 90%, 96%, each for 24h) in absolute ethanol. Specimen from various collection stored in 70% ethanol were transferred via a graded series (80%, 90%, 96%, each for 24 h) in absolute ethanol.

Both groups of specimen were stained with 1% iodide in ethanol over night and washed in absolute ethanol two times for 20 minutes after Metscher (2009). Depending on the size of the specimen some samples were critical point dried with a Polaron E3100 (Quorum Technologies, Lewes, England) in the laboratory for Electron microscopy of the University of Bergen (Norway).

Dried specimens were attached on thin glass sticks using hot glue to receive a suitable distance in the micro CT. Not-dried specimens were fixed either between polystyrene pieces or in Agarose gel in a 5 ml tube (Eppendorf AG, Hamburg, Germany) and attached to thin glass sticks using hot glue. Fossils were attached to polystyrene cubes with modeling clay (Plasticine).

Micro CT

Micro CT scanning was performed in the Zoological State Collection of Bavaria (ZSM) with a Nanotom M Phoenix (GE Sensing & Inspection Technologies GmbH, Hürth, Germany) or in the Zoological Institute and Museum Greifswald (ZIMG) with an XRadia XCT-200 (Carls Zeiss Microscopy GmbH, Jena, Germany). Tomography scans were performed using magnifications of 0.4x and 4x objectives resulting in estimated voxel sizes between 5-20 µm. The projections were reconstructed using VGStudio MAX 2.2.6 for scans in the ZSM or XMReconstruction software for scans in the ZIMG. The resulting tiff-stacks were further processed (see reconstructions)

Reconstructions of Micro CT data sets

First, the size of the tiff stacks was reduced in ImageJ (Wayne Rasband) using the crop tool and converting them to 8bit-scale. The resulting stacks were loaded onto Osirix 5.8.2 (Antoine Rosset). Therein, surface models and volume renderings were created either by segmentation, e.g. tagging the important structures with the ROI (region of interest) tool or by thresholds, e.g. all structures with/above/below a definitive grey value were displayed. Thus, models with more than one structure could be created. Volume renderings were displayed as red-cyan anaglyphs.

Surface models were extracted to Blender 2.49 (Blender Foundation). Blender displays a mesh of the surface models. This mesh was modified, e.g. meshes were decimated to decrease the number of vertices, mesh parts and vertices that do not belong to the specimen or to the structures were manually removed, doubles in the mesh were removed, gaps in the mesh were manually filled, the surface was set smooth and different structures were displayed in different colors. In the end structures and specimens were rendered.

1.4.8 HISTOLOGICAL STUDIES

For histological studies, specimens were decalcified for 36 h in 5% acetic acid. After washing (three times for 2 h) in Sørensen‘s phosphate-buffer (0.1M) the specimens were transferred to 96% ethanol (in the following steps 10%, 30%, 40%, 50%, 70%, 80%, 90%, 96%, 1 day each). After embedding in Historesin (Technovit 7100, Heraeus Kulzer GmbH) for 2 weeks, the polymerized blocks were sectioned with a microtome (820 rotary microtome, AO Spencer) in 2 µm slices. The sections were transferred to object slides and dyed with Rüdeberg solution (0.1 g methylene blue, 0.1 g thionin, 1.42 g disodium phosphate, 70 ml distilled water, 30 ml glycerin) for 30 seconds on a heating plate (70°C). After washing with distilled water, the slides were covered with a mounting media (DPX new, Merck) and a cover slip and subsequently dried for 72 h on a heating plate (40°C). The sections were scanned and digitalized with an Olympus-dotSlide (digital virtual microscope).

1.4.9 HISTORICAL SCIENCE METHODS

Evolutionary research combined with fossils or rather paleontology is not a hypothesis driven research like experimental research fields (Cleland 2001, Cleland 2002). In other words it is a historical research based on ―Historical-Narrative Explanations" (Bock 2017). Historical analyses in evolutionary biology need comparisons and/or correlative analysis in a phylogenetic framework (Reif 2002, Bock 2017).

The elementary assumption of a comparative paleontological-zoological approach in parasitism is finding, studying and describing fossil parasites, to (1) evaluate their specific lifestyle and ecology, (2) date divergence and originating times, and finally (3) explain and reconstruct the evolution towards modern parasitic forms by using typical traits. Especially identifying morphological details can answer the functional morphology of fossils and modern relatives. Furthermore, these details are crucial to evaluate the systematic position of the fossils, to answer ecological questions and to interpret the specimens in a broader evolutionary context.

For this purpose, I worked mostly with comparative analyses between fossil and extant representatives of the respective groups in a limited phylogenetic framework. Due to the limited record of morphological details of modern parasites among arthropods, describing modern parasites in detail was often necessary. With the comparison between fossil and modern parasites, a combination of fossil and extant data was pursued to get the best possible image of the evolution of parasitism in the studied groups.

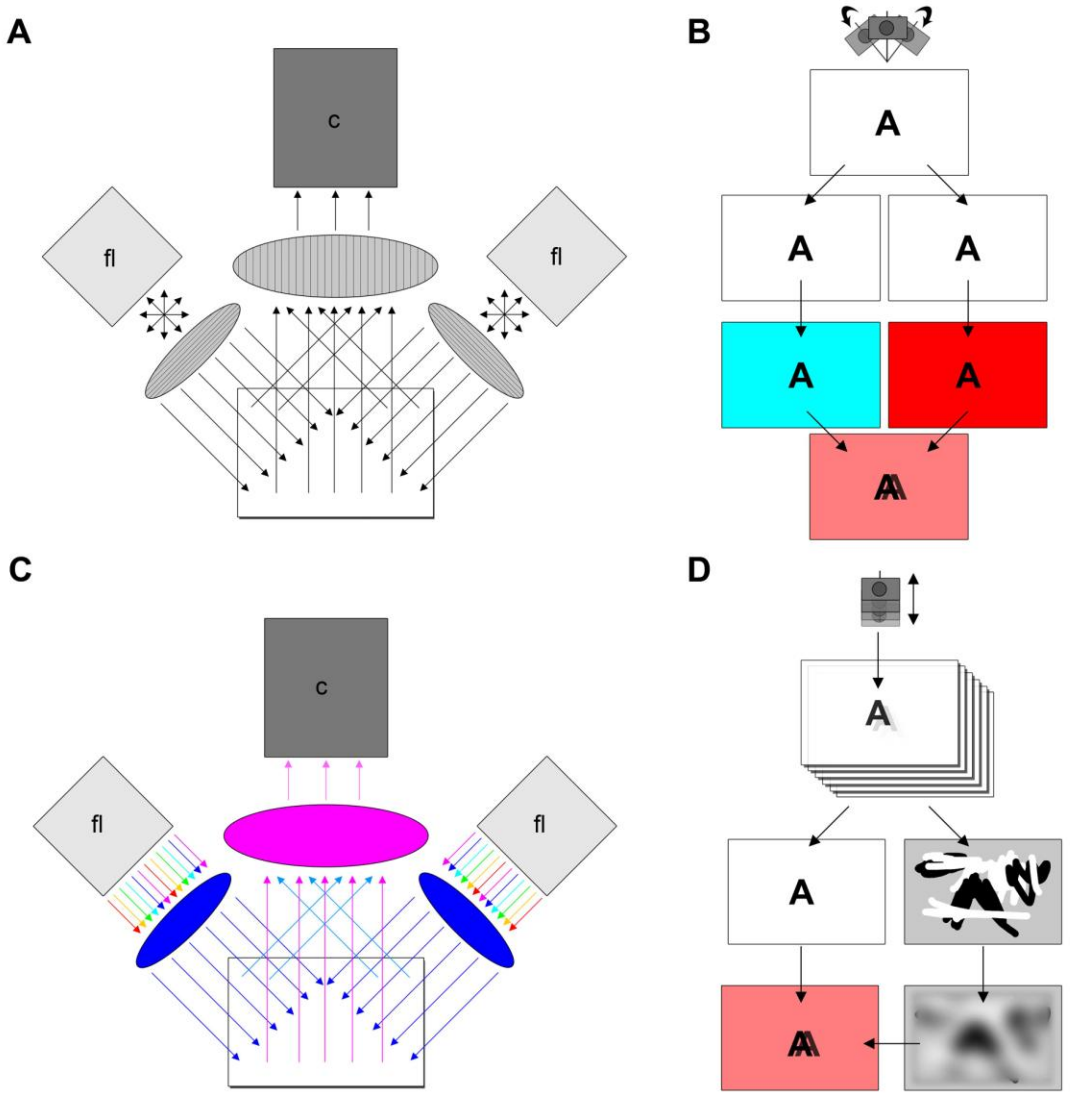

Fig. 5: Explanation of different imaging methods. A) Macro-photography with cross-polarized light. Please note that the polarization films in front of the flashes (fl) and in front of the camera (c) are directed in a 90° angle to each other. B) Stereo-photography. C) Fluorescence-imaging. Please note that the camera will not detect the reflected ~~"b~~lue" light, but the emitted ~~"r~~ed" light. D) Stereo-photography from depth map.

1.5 AIMS OF THE THESIS

Comparing fossil and modern parasites in a phylogenetic framework, I aimed at analyzing the evolutionary history of parasitism in two groups of Crustacea. Thus, the main objectives of the thesis were to study fossil parasites and their extant relatives, to reconstruct a character evolution leading towards the modern parasites and to identify crucial characters within the two different groups to evaluate their lifestyle. Having the methodological note about historical research (see chapter 1.4.9) in mind, following assumptions have been formulated:

1) Parasitic isopods, similar to modern cymothoiids, are present since the Jurassic (150 mya; see also chapter 2.1, 2.2).
2) An ontogenetic host change in epicarid isopods is present since the Eocene (50 mya; see also chapter 2.3).
3) Parasitic cymothoid isopods evolved from a scavenging ancestor (168 mya; see also chapter 2.4).
4) The fossil group *Urda* shares morphological characters with represents of Cymothoidae, Epicaridea and Gnathiidae (168 mya; see also chapter 2.4).
5) Two-organism-relationships between barnacles and other organisms are present since the Jurassic in barnacles (150 mya, see also chapter 3.1).
6) Cirriped larvae (burrowing barnacles, stalked barnacles and parasitic barnacles) are present since the Jurassic (150 mya; see also chapter 3.2).
7) Thecostraca are present since the Devonian (420 mya; see also chapter 3.4, 3.5).
8) Pre-adaptations to a parasitic lifestyle in thecostracans are present since the Devonian (420 mya; see chapter also 3.4, 3.5).

However, one objective of my thesis has been studied under the conditions of correlative research. The objective was to test, whether the volume of parasitic barnacles is linked to the volume of their hosts and whether this pattern could be linked to the proposed molecular evolution (see also chapter 3.3).

Nevertheless, a variety of morphological characters within isopods and thecostracans free from assumptions are studied. Thereafter, the results are compared between fossil representatives and their extant relatives in order to detect similarities and differences. By means of these, conclusions about the evolution, development and ecology are possible. Furthermore, aspects of the ground pattern of parasitic adaptations of isopods and rhizocephalans are elaborated. In order to elucidate the evolution of parasitism, this thesis combines functional morphology, ecology and systematics.

2. PROJECTS & RESULTS PART A: ISOPODA

2.1 PAPER I: Nagler et al. 2016.

Nagler C, Haug C, Resch U, Kriwet J, Haug JT. 2016. A 150 million year old „very hungry caterpillar–÷first fossil record of cymothoid isopods parasitizing on fishes. *Bulletin of Geosciences*, 91:1-12. DOI:10.3140/bull.geosci.1586.

http://www.geology.cz/bulletin/contents/art1586

2.2 PAPER II: Nagler & Haug 2016.

Nagler C, Haug JT. 2016. Functional morphology of parasitic isopods: understanding morphological adaptations of attachment and feeding structures in *Nerocila* as a pre-requisite for reconstructing the evolution of Cymothoidae. *PeerJ*, 4: e2188. DOI:10.7717/peerj.2188.

https://peerj.com/articles/2188/

2.3 PAPER III: Serrano-Sánchez et al. 2016.

Serrano-Sánchez M, Nagler C, Haug C, Haug JT, Centeno-García E, Vega FJ. 2016. The first fossil record of larval stages of parasitic isopods: cryptoniscus larvae preserved in Miocene amber. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen,* 279: 97-106. DOI:10.1127/njgpa/2016/0543.

https://www.schweizerbart.de/papers/njgpa/detail/279/85414/The_first_fossil_record_of_larval_stages_of_parasitic_isopods_cryptoniscus_larvae_preserved_in_Miocene_amber?l=DE

2.4 PAPER IV: Nagler et al. 2017a.

Nagler C, Hyžný M, Haug JT. 2017a. 168 million year old ―marine mallophagan" and the evolution of parasitism within isopods. *BMC Evolutionary Biology*, 17: 76. DOI:10.1186/s12862-017-0915-1.

https://bmcevolbiol.biomedcentral.com/articles/10.1186/s12862-017-0915-1

3. PROJECTS & RESULTS PART B: THECOSTRACA

3.1 PAPER V: Nagler et al. 2017b.

Nagler C, Haug JT, Glenner H, Buckeridge J. 2017b. *Litholepas klausreschi* gen. et sp. nov., a new neolepadine barnacle (Cirripedia, Thoracica) on a sponge from the Upper Jurassic lithographic limestone‘s of southern Germany. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, 284: 29-42. DOI:10.1127/njgpa/2017/0648.

https://www.schweizerbart.de/papers/njgpa/detail/284/87469/Litholepas_klausreschi_gen_et_sp_nov_a_new_neolepadine_barnacle_Cirripedia_Thoracica_on_a_sponge_from_the_Upper_Jurassic_lithographic_limestones_of_southern_Germany

3.2 PAPER VI: Nagler et al. 2017c.

Nagler C, Høeg J, Haug C, Haug JT. 2017c A possible 150 million years old cirripede crustacean nauplius and the phenomenon of giant larvae. Accepted, *Contributions to Zoology*.

A possible 150 million years old cirripede crustacean nauplius and the phenomenon of giant larvae

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Abstract
The larval phase of metazoans can be interpreted as a discrete post-embryonic period. Larvae have been usually considered to be small, yet some metazoans possess unusually large larvae, or giant larvae. Here, we report a possible case of such a giant larva from the Upper Jurassic Solnhofen Lithographic limestones (150 million years old, southern Germany), most likely representing an immature cirripede crustacean (barnacles and their relatives). The single specimen was documented with up-to-date imaging methods (macro-photography, stereo-photography, fluorescence photography, composite imaging) and compared with modern cirripede larvae. The identification is based on two conspicuous spine-like extensions in the anterior region of the specimen strongly resembling the so-called fronto-lateral horns, structures exclusively known from cirripede nauplius larvae. Notably, at 5 mm in length the specimen is unusually large for a cirripede nauplius. We therefore consider it to be a giant larva and discuss possible ecological and physiological mechanisms leading to the appearance of giant larvae in other lineages. Further findings of fossil larvae and especially nauplii might give new insights into larval evolution and plankton composition in the past.

Introduction
The larval phase of a metazoan organism, an animal, is a discrete post-embryonic period. Different authors apply various criteria what identifies a larva in comparison to a non-larval immature. Among these are, for example, 1) a morphology that is significantly different from that of the adult (Hickmann, 1999), 2) the occupation of a different ecological niche than the adult (Giese and Pearse, 1975; Young, 1999), or 3) the possession of organs that become reduced and are absent in the adult (Strathmann, 1993; Anger, 2001).

In many organisms the larval phase is comparably short, ended by a metamorphosis that produces the juvenile/adult morphology within a short period of time (Passano, 1961). As a consequence of a short larval phase in most organisms the larvae are rather small (Cowen and Sponaugle, 2009).

In classical zoological literature, we often encounter the differentiation between so-called primary and secondary larvae (although the value of this differentiation remains

questionable). The first type should represent ancestral larval types, while the second represents derived forms (Werner, 1988). Especially larval forms that are classified as primary are usually microscopic entities, more or less invisible to the naked eye. The trochophora (of annelids and molluscs) and the pluteus (of echinoids) are often given as examples (Young, 2002), although both forms are clearly derived types of larvae characterizing specific monophyletic groups (hence, could also be interpreted as secondary larvae). Yet, also many larval forms that clearly fall into the secondary larvae category are often quite small, for example, crustacean nauplii (Martin *et al*., 2014, fig. 2.3; Haug & Haug, 2015).

Despite the fact that larvae are usually small, in many lineages larvae of astonishing sizes have evolved, i.e., forms that can well be called 'giant larvae'. A rather simple case example is that of flying insects. As flying insects perform a terminal molt and can no longer grow as adults, their larval phase is comparably long and the late stages are quite large, almost as large as the adults (Truman and Riddiford, 2002). Yet, giant larvae are also known in numerous further metazoan groups.

The phenomenon of giant larvae can also be observed in the fossil record. There are cases of exceptional types of fossil preservation that seem only to preserve rather small forms. Most notably, fossils in an Orsten-type preservation include many forms of larval arthropods and larval cycloneuralians, no specimen being larger than 2 mm (Haug *et al*., 2014a). Yet, for many other types of preservation especially the large forms appear to have a higher chance to be preserved. For malacostracan crustaceans, we have fossils of especially super-sized larvae such as those of achelatan lobsters (Polz, 1971; 1972; 1973; 1995; Haug *et al*., 2011a; Haug and Haug, 2016), polychelidan lobsters (Haug *et al*., 2015a; Eiler and Haug, 2016) or mantis shrimps (Haug *et al*., 2008, 2015b), some of them in thousands of specimens (Polz, 1987; 1996), while smaller-sized larvae like those of crabs are very rare (Haug *et al*., 2015c). It seems therefore common that giant larvae occur as fossils.

With this contribution we aim at briefly reviewing the known occurrences of giant larvae. Due to the still very incomplete knowledge of Mesozoic plankton (Haug & Haug 2017), the description of a possible further case of a 150-million-year old crustacean larva that was found in the famous lithographic limestones of southern Germany add important details. Additionally, this fossil larva is of unusually large size.

Material and Methods

Material

We investigated a single slab from lithographic limestones of Southern Germany (Solnhofen area, Upper Jurassic, Tithonian, southern Germany) found in the hobby quarry near Eichstätt with a single small fossil specimen. The fossil was formerly part of the private collection of Michael Fecke, Langenberg, now transferred to the State Museum of Natural History Stuttgart (SMNS XXXWILL BE ADDED LATER).

For comparison three modern larvae were documented: a thoracican lepadomorph nauplius of the group Lepadidae from the Museum National d'Histoire Naturelle, Paris (MNHN IU-2014-5478), a thoracican balanomorph nauplius (teaching collection LMU Munich), and a rhizocephalan nauplius, *Peltogaster paguri*, from the private collection of Jens Høeg in the Zoological Museum Copenhagen.

Documentation methods

The fossil specimen was documented with macro-photography, stereo-photography and fluorescence micro-photography to extract as much information as possible from it. The lepadomorph nauplius was documented with macro-photography. The balanomorph nauplius was documented with fluorescence micro-photography. The rhizocephalan nauplius was documented with scanning electron microscopy.

Macro-photography and stereo-photography combined with composite imaging were performed (following e.g. Haug *et al*., 2012; 2013a), both under cross-polarized light. We used a Canon EOS Rebel T3i camera with Canon MP-E (65 mm) macro lens. Illumination was provided by the Canon Macro Twin Lite MT-24EX flash from two opposing sides. Fluorescence microscopy of the fossil was performed on an inverse fluorescence microscope BZ-9000 (BIOREVO, Keyence) with about 40 times magnification recording auto fluorescence under blue light (GFP, 488 nm; for details on auto fluorescence imaging, see Haug et al., 2011b). Fluorescence microscopy on the balanomorph nauplius was performed on a Zeiss AxioScope 2 with about 200x times magnification recording auto fluorescence under UV light (DAPI, 358 nm). For macro-photography and micro-photography stacks of images (of different focal planes) were recorded to overcome limited depth of field. Adjacent stacks were recorded to overcome limitations in field of view. Scanning electron microscopy of the rhizocephalan nauplius was performed on a JEOL 6335-F scanning electron microscope at the Zoological Museum in Copenhagen.

Image processing

Stacks of images were fused to sharp images using the freeware CombineZP. Resulting sharp images were stitched to panorama images using Adobe Photoshop CS3 or Elements 11. All images were optimized (sharpness, histogram, saturation) and dirt particles or background was removed manually using a lasso tool in Adobe Photoshop CS3.

Presentation methods

Interpretations of structures are presented by color-marked versions of the images. Structures apparent in the fluorescence and stereo-photography were marked with the lasso tool in Adobe Photoshop CS3 on a desaturated half image of the stereo image (Haug *et al*., 2012).

A simplified reconstruction of the fossil was assembled by mirroring missing structures (Haug *et al*., 2015d). For explaining structures, a virtual 3D model of a modern cirripede nauplius was reconstructed in Blender 2.49 (Blender Foundation), based on drawings from Miller and Roughgarden (1994).

Description of the specimen

The specimen has a maximum length of 4.7 mm. The main preserved part is an oval-shaped shield-like structure, with smaller structures protruding from it. This shield represents the maximum length of the specimen and has a maximum width of 3.1 mm.

The texture, color and fluorescence capacities of the shield (and partly the protruding structures) resemble that of crustacean cuticle from the same Lagerstätte (which is different from most remains of fish, insects, echinoderms or molluscs). Different regions of the shield can be differentiated. A very central region is apparent in the color

images as a darker area (Fig. 1A–B). This same area is also elevated in relief (Fig. 1C) and shows a stronger fluorescence (Fig. 1D). This region most likely represents the main body, partly compressed through the shield.

The central region extends latero-posterior and posterior into a thinner-appearing region. It is almost transparent under cross-polarized light; the matrix is visible (Fig. 1A–B). It appears to lack relief (Fig. 1C) and also shows a weaker fluorescence (Fig. 1D). Central region and extended region together are about 3.7 mm long and 2.5 mm wide.

Around the central region and the extended part of the shield a well set-off, ring-like region is apparent. It is set off from the central shield, i.e. in the anterior region by a distinct edge. In the posterior region the differentiation against the extended region is apparent due to a dark color of the ring (Fig. 1A–B), a slight positive relief and stronger fluorescence capacities.

The central shield bears a pair of spine-like protrusions. These spines originate antero-lateral from the edge between the central shield region and the ring. They are oriented mostly lateral, slightly anterior. They curve slightly backwards. The protrusions are slightly bellied proximally, but taper distally (Fig. 1H). The tip appears blunt; it is unclear whether this is the original condition or due to preservation. The protrusions reach slightly beyond the ring (Fig. 1A–D).

Three additional structures protrude from under the shield. The first is far anterior, also anterior to the spine-like protrusions. It is a short structure, more or less rectangular in outline. Originally, this was most likely a tube-shaped part of an appendage. It can be differentiated into two similar-appearing elements, most likely representing ringlets. Each of them bears a seta pointing antero-median. The structure can only be observed under cross-polarized light, it does not possess recognizable relief (Fig 1C) nor does it show fluorescence (Fig. 1D). It therefore differs from the preservation of the shield. The color is more orange and less glossy. Most likely it is not phosphatized (lack of fluorescence).

The second structure protrudes from under the shield laterally towards the latero-posterior (Fig. 1). The structure is preserved in different ways. Some areas resemble the preservation of the first protruding structure, show no fluorescence and appear orange. Other areas appear to be phosphatized (certain glossiness) and show fluorescence. Lastly, some areas are not at all apparent under cross-polarized light, but only under fluorescence. The central part of the structure appears elongate, originally tube-like, composed of several elements (at least eight), originally ringlets (Fig. 1G). More distal elements are narrower than more proximal ones. Also more distal ones are slightly oblique towards the main axis of the structure, as the anterior (originally median?) dimension of each ringlet appears to be slightly longer than the posterior (originally lateral?) one. The supposed median sides of each ringlet appear drawn out into setae. The more proximal ones appear to bear a pair of setae, while the more distal ones appear to bear only a single seta. Ringlets are preserved more pronounced; their edges appear to be also phosphatized. Setae are only visible under fluorescence, especially the more distal regions of the setae (Fig. 1F–G). The overall organization of the structure resembles a multi-annulated exopod.

The third structure is preserved at an area, where apparently a part of the shield is broken off, with this revealing the structure, which would have been otherwise concealed. The preservation is rather weak, the structure only being apparent under fluorescence (Fig. 1E–F). It is elongate, most likely originally tube-shaped, tapering distally. It is curved, or partly folded or kinked. Proximal and distal region are both concealed by the shield. The

surface appears to some degree granulose, with weakly outlined rings. Possibly the structure was rather weakly sclerotized originally, not being subdivided into discrete sclerites.

Discussion

A possible interpretation of the fossil

Although the specimen is small in comparison to other fossil larvae, at least from this Lagerstätte, and may not appear to bear many details, some of these details that are present allow a well-founded interpretation on the identity of the specimen. Texture and fluorescence capacities of the fossil resemble crustacean remains from the same deposits. Also from a structural point of view many interpretations that could come into mind, such as a fish scale, can be easily discarded. Specimens distantly resembling the fossil have been interpreted as possible remains of crustacean larvae (Haug *et al*., 2011a; 2014b). This seems also a likely interpretation of the new fossil.

When comparing the specimen to small-sized eucrustaceans it shows similarities to larval forms of barnacles and their relatives (Cirripedia). The pelagic larvae of cirripedes (nauplius larvae) are characterized by a pair of spine-like extension of the anterior shield region, generally termed fronto-lateral horns (Høeg, 1987; Walker, 1992, Høeg and Møller, 2006; Pérez-Losada *et al*., 2009; 2012; Høeg *et al*., 2015). Historically, these fronto-lateral horns are an important character that was first recognized by Thompson (1830). For a long time these structures were the only argument for the monophyly of Cirripedia (Høeg *et al*., 2015). Shape and relative position of the two spine-like extensions of the fossil (Figs. 1D, F, H, 2A) strongly resemble these fronto-lateral horns (Fig. 2B–E).

The preserved presumed appendage remains of the fossil would also well fit into this interpretation. Cirripede nauplii have three functional pairs of appendages: antennulae, antennae and mandibles (Fig. 2B–E; Chan *et al.*, 2014; Høeg *et al*., 2014a; b; Kolbasov *et al.*, 2014).

The second structure protruding from underneath the shield of the fossil specimen (Fig. 1D, F) strongly resembles the setose swimming exopods of antennae or mandibles of modern cirripede nauplii (Fig. 2B–E; e.g. Walossek *et al.*, 1996). Due to the number of ringlets and setae, the structure on the fossil could represent an antenna, although an interpretation as a mandible cannot entirely be excluded.

The appendage remain on the other side of the fossil specimen (third structure; Fig. 1D) could represent the less well preserved antenna of the other body side, although it remains unclear whether it could then represent the endopod or the exopod. The further anterior, very incomplete appendage (first structure, Fig. 1D) is more difficult to interpret. The distinct ringlets could be understood as another exopod. The position would argue more for an interpretation as an antennula, yet, an antennula would not be organized into such discrete ringlets. In conclusion, the observed structures are compatible with the interpretation of the fossil as a cirripede nauplius.

Difficulties with the interpretation

When interpreting the fossil as a larval form of a barnacle or one of its relatives, three possible aspects need to be discussed:

1) Size: The fossil is comparably large, at least for a nauplius, as most eucrustacean nauplii are rather small. Nauplii of representatives of Cirripedia are mostly in a size range

between 200 µm and 1 mm (Walossek *et al.*, 1996; Walker, 2001; Høeg *et al.*, 2004). Yet, also nauplii reaching astonishing sizes have been reported (Rybakov *et al.*, 2003). In fact, shield sizes well over 1 mm seems not to be uncommon among modern forms (Fig. 2), resulting in total lengths of about 6 mm in *Lepas anatifera* (Moyse, 1987) or in *Lepas pacifica* (Ryusuke Kado, unpublished data).

The only fossil example of a possible cirripede larva is that of *Rhamphoverritor reduncus* (Briggs *et al.*, 2005; see also further below). This larval specimen is not a nauplius, but may represent a settling stage, a so-called cypris, hence the stage following the last nauplius stage. Among modern forms the lengths of cypris larvae are difficult to infer from the literature. The fossil cypris has a total length of 4 mm.

Crustaceans usually increase their size by up to 30 % within a single molt (see discussion in Kutschera *et al.*, 2012). The largest known cirripede eggs can reach up to 400 µm (Korn *et al.*, 2004). All extant representatives of Cirripedia develop through at most six naupliar stages (nauplius I – nauplius VI; Høeg *et al.*, 2015). By calculating this example, the possible maximum size of a nauplius VI would result in an overall size of about 2 mm.

However, the 30% rule seems to be less strict in certain crustaceans. The size increase between nauplius I and nauplius II in e.g. *Lepas pectinata*, is in average 150% (Moyse, 1987). Consequently, nauplius VI could reach overall lengths of more than 7 mm. Taking this into account, a shield length of 4.7 mm in the fossil specimen described herein is quite reasonable (but see also further below).

2) Position of the fronto-lateral horns: In most cirripede nauplii the fronto-lateral horns arise right from the fronto-lateral corners of the shield (Fig. 2 B–C, E). This seems not to be the case in the fossil specimen. Here the shield rim is further drawn out, forming a set-off ring. Interpreting the horns differently is difficult, other possible structures such as frontal filaments, which occur within Thecostraca in all representatives (Walker, 1974; Grygier, 1987), are tiny and soft and hence unlikely to be preserved in a fossil. Also they are not horn like. In some naupliar stages, e.g. of the rhizocephalan *Peltogaster paguri,* the fronto-lateral horns are fully covered by a round extension of the shield (Fig. 2D; Høeg, unpublished data). These structures in the fossil specimen described herein are blunt at the tip and might therefore end in a pore as do true fronto-lateral horns. This observation supports the interpretation of the spine-like extensions as fronto-lateral horns and not as frontal filaments.

3) Interpretation of the set-off ring: Examples of extensions of the shield, so-called 'floating collars', occur in some ingroups of Cirripedia, more precisely of Rhizocephala (exclusively parasitic forms). Such a floating collar has been considered as floatation device, enhancing the buoyancy of the nauplii (Veillet, 1943; Høeg *et al*., 2004). Such a type of floating collar (Fig. 2D) is known from the rhizocephalan ingroups Peltogastridae and Lernaeodiscidae, but could be part of the rhizocephalan ground pattern (Høeg *et al.*, 2004; Glenner and Hebsgaard, 2006; Høeg *et al.*, 2009).

The floating collar in rhizocephalans is shed separately from the rest of the cuticle and is made of exceedingly thin cuticle (Fig. 2D; Høeg *et al.*, 2004). This seems to be quite different in the fossil specimen. Also in the fossil the possible floating collar seems to be positioned under the horns, while in modern forms it is over these. Still the

structure and position of the ring in the fossil could still indicate an at least comparable function in the fossil. It could also be speculated that this could be indicative of a closer relationship to Rhizocephala.

Other possible interpretations:
Malacostracan affinity: Most fossil larvae from the Solnhofen limestone have been identified as malacostracan larvae (see below). The fossil specimen described herein resembles in certain aspects a supposed malacostracan larva from the Solnhofen limestone (Haug *et al.*, 2011a; 2014 b, fig. 32.2K). The specimen has been suggested to represent the remains of a shield of a decapod zoea. Could this interpretation also apply to the specimen described here? This is unlikely. The supposed fronto-lateral horns could be interpreted as lateral spines for example of a brachyuran zoea. In such a case we would expect additional spines, especially a rostral spine and a postero-dorsal spine (Wear, 1968; Martin, 1984; Haug *et al.*, 2011a; Martin, 2014a). Also in other decapod zoeas especially a pronounced rostral spine should be expected. No breakage indicators are apparent that could indicate an absence due to preservation. Also the shape of the spines and their blunt tips would be unusual for a zoea larva. Therefore an interpretation of the new fossil as a zoea appears unlikely to us. Notably, already Haug *et al.* (2014b, p. 176) stated that the ~~"s~~systematic affinities remain uncertain until better-preserved specimens are found". The specimen from Haug *et al.* (2014b) could in the light of the new fossil described here also represent the conspecific cypris larva. The specimen should be reinvestigated for this aspect.

Branchiopod affinity: There is also a certain resemblance of the fossil to the nauplius larva of representatives of Laevicaudata, an ingroup of Branchiopoda. These have a kind of spine-like extensions that represent the still immobile antennulae (Olesen, 2005). In contrast to larval representatives of Laevicaudata, in which these horns protrude from the ventral side of the head (Olesen, 2005; 2007), it seems that the horns in the fossil specimen described herein protrude from the dorsal site of the head shield, indicated by the relative position of the appendages (Fig. 1). Additionally, laevicaudatan nauplii have a distinct triangular shape of the anterior head which should be expected to be seen in the fossil if present. Yet, this is not the case. Also other characteristic features, such as a large, rounded labrum or caudal lobes, which are spine-like extensions posterior from the shield (Olesen, 2005; 2007) are not present in the fossil specimens. Yet, these could be more difficult to be visible, as the labrum is a soft ventral structure and the caudal lobes are comparably small. Lastly, most branhciopod are fresh water forms, only few groups of raptorial cladocerans have re-entered the marine realm, yet the original lagoons of the Solnhofen lithographic limestones must have represented a marine environment. Thus, a laevicaudatan or even a branchiopod affinity is very unlikely.

Summarizing: From the morphological point of view it seems likely that the here described fossil indeed represents a cirripede nauplius. It appears to possess a kind of floating collar that may point to a closer relationship to rhizocephalan cirripedes. The ~~"m~~main" shield would then measure about 3 mm and could molt into a cypris larva of the size as it is known for the fossil *Rhamphoverritor reduncus* with 4 mm length (Briggs *et al.*, 2005). While the new larva is well in a possible size range for cirripede larvae, it clearly represents a giant form.

Early fossil record of Cirripedia

Cirripedes have a comparably good fossil record, at least concerning their adults. *Rhamphoverritor reduncus* from the Silurian (420 mya) is exceptional as only a possible cypris larva and a juvenile are known (Briggs *et al.*, 2005). The species most likely represents the sister group to all other cirripedes (Høeg *et al*., 2009). There is generally a distinction of three groups within Cirripedia: Acrothoracica, Thoracica and Rhizocephala, with the latter two groups representing sister groups. The monophyly of each of the three groups is generally well supported. Yet, Thoracica is not as well characterized by morphological characters. It is therefore possible that any pedunculated fossil barnacle older than the presumed split between Rhizocephala and Thoracica (see below) might be situated phylogenetically below this point.

Representatives of Acrothoracica have been reported as trace fossils from the Devonian (380 mya; Glenner *et al.*, 1995). Molecular analyses give support for the origin of Thoracica in the Early Carboniferous (340 mya; Pérez-Losada *et al.*, 2008). Based on the reconstruction of a co-evolution between rhizocephalans and anomalan crabs and molecular reconstructions of thoracican barnacles, representatives of Rhizocephala have been estimated to be present also since the Carboniferous (Walker, 2001; Boyko and Williams, 2009). As a consequence, all pedunculated fossil thoracicans older than 340 million years could be considered as representatives of the unnamed sister group to Acrothoracica. The first more direct fossil indications of rhizocephalans are feminized male crabs from the Miocene (4–23 mya; Feldmann, 1998). Also important to mention in this aspect: fossils of cirripedes are well known to occur in the lithographic limestones of southern Germany (Barthel *et al*., 1990; Nagler *et al.*, 2017).

With this fossil record an interpretation of the here described fossil as the nauplius of a cirripede and even as a possible relative of Rhizocephala seems reasonable; at least it is not contradicted. The fossil, therefore, most likely represents the first fossil record of a cirripede nauplius. It also follows the general pattern that we seem to be more likely able to find especially giant larval forms as fossils.

Giant larvae in metazoans

The phenomenon of oversized larval forms has been reported from various metazoan groups. Yet, in many cases 'giant' is a matter of relation. An overview of giant larvae can be seen in Tab. 1.

As pointed out above, larvae of *flying insects (Pterygota)* are in their final larval stage often as large, sometimes larger, than the adult. Yet, as almost all insects have such comparably large larvae it is somehow difficult to consider any of them as a giant. Comparably larger larval size is mostly coupled to larger adult size.

Larvae of *corals, sea anemones and others (Cnidaria)* – planula – have an average maximum size of about 1 mm (Leloup, 1932). Yet, also specimens of up to 11 mm have been reported. Some of the even larger specimens with larva-like morphology already possess gonads (Molodtsova 2004; Stampar *et al.*, 2015) are therefore no longer larvae in the meaning of being immature.

The planktic larvae of marine *snails and slugs (Gastropoda)* – veliger – are usually below 1 mm in size before settling to a pelagic life. Yet, in some groups significantly larger forms are known. Veliger larvae of strombiids, coniids and cypraeiids have extremely elongated structures, the velum lobes. With these structures they reach sizes of

about 5 mm (Hickman, 1999). Even larger forms of about 6–7 mm have been reported by Dawydoff (1940).

The early larval stage of *ringed or segmented worms (Annelida)* is plesiomorphically the trochophora. These are mostly below one millimeter in size before they metamorphose into forms with few body segments that carry appendages (chaetigers; often three such segments). Exceptions are special forms of phyllodocid larvae. Here the trunk grows significantly longer from the trochophora before undergoing metamorphosis. The spherical anterior region (hence the original trochophora) can reach sizes of up to 2 mm; the trunk with up to 120 rudimentary segments can reach 10 mm. Hence, the total length of these larvae reaches up to 12 mm (Tzetlin, 1998).

Larvae of *peanut worms (Sipunculida)* – pelagosphaera – have an average size of 300 µm (Rice, 1967). Yet also significantly larger forms of up to 3.2 mm can sometimes be found in the plankton of open ocean regions (Rice, 1973).

Larvae of *horseshoe worms (Phoronida)* – actinotrocha – reach in general a maximum size of 0.7–0.9 mm. An unusually large phoronid larva has been reported by Temereva *et al.* (2006). This larval specimen measured 3.5 mm long, thus 4–5 times larger than a ~~"n~~ormal" actinotrocha larva.

Larvae of *echinoderms (Echinodermata)* are generally small, below 1 mm (e.g. Pawson, 1971). Yet, certain larvae of abyssal sea cucumbers (Holothuroidea) – auricularia – can reach sizes between 3 and 15 mm (Ohshima, 1911; Mortensen, 1913; 1921; Garstang, 1939). Also, the larva of the deep-sea starfish *Luidia sarsi* (Asteroidea) – bipinnaria – can reach body lengths of up to 25–35 mm (Domanski, 1984).

Larvae of *acorn worms (Enteropneusta, Hemichordata)* – tornaria – reach usually about 0.5–1 mm (Stiasny, 1928). Giant tornariae (*Planctosphaera pelagica*) with a length of up to 28 mm have been found in the Atlantic and Pacific Ocean (Spengel, 1932; Hadfield and Young, 1983). Thus the found giant larvae are at least 20 times bigger than the ~~"n~~ormal" larvae of Hemichordata. Yet, it is still controversial if *Planctosphaera pelagica* represents an ingroup of Enteropneusta (Hadfield and Young, 1983) or a separate group of hemichordates (Van der Horst, 1936).

Larvae of *teleost fishes (Teleostei)* are often quite large; few centimeters length is not uncommon. A very notable size is reached by larval eels (Anguilliformes) – leptocephalus – which regularly reach 300 mm in length (Miller, 2009), but sometimes even giant larvae longer than 1800 mm have been reported (Aron and McCrery, 1958; Tabeta, 1970; Kurogi et al., 2016).

Amphibian tadpoles (Lissamphibia) are all large compared to many other metazoan larvae, being in the range of several centimeters. Tadpoles of the frog *Pseudis paradoxa* reach sizes of up to 230 mm (Emerson, 1988). Also other species of *Pseudis* can reach quite a large tadpole sizes with up to 180 mm (Fabrezi *et al.*, 2009). In these species the larva is also significantly larger than the adult. Fossil tadpoles with a size of up to 150 mm have been reported from the Miocene (Roček *et al.*, 2006) and from the Lower Cretaceous (Chipman and Tchernov, 2002).

Giant larvae in crustaceans

Among numerous crustacean groups giant larvae have been reported, especially among decapods. Decapods usually have (at least) two larval phases: The pelagic zoea larvae swim with the outer locomotion branches (exopods) of their thoracopods. This phase may

include up to ten stages. The zoea is followed by the megalopa, which mediates the transition between the pelagic larva and the benthic juvenile. Most megalopae have lost their exopods on the thoracopods and swim with their pleopods. In many groups there is only a single megalopa stage. Sometimes larvae show a kind of mixed morphologies somewhere ~~"b~~etween" zoea and megalopa. The latest zoea as well as the megalopa usually measure only few millimeters in total length. Yet, there are quite some exceptions:

Zoea larvae of *prawns (Dendrobranchiata)* are usually small with shield lengths rarely reaching 1 mm. Yet, within Aristidae zoea larvae formerly addressed as ~~"C~~*erataspis monstrosa*" reach shield lengths of almost 12 mm (Bracken-Grissom *et al.*, 2012).

Polychelidan lobsters (Polychelida) only have a short zoea phase (Torres *et al.*, 2014), but have several megalopa stages that reach astonishing sizes. These eryoneicus larvae reach sizes of more than 100 mm in length (Martin, 2014b; Eiler *et al.*, 2016). Fossil forms that show some similarities to modern forms and also an increased size have been reported from the Jurassic Solnhofen limestones (Eiler and Haug, 2016), and from the Cretaceous limestones of Lebanon (Haug *et al.*, 2015a).

Achelatan lobsters (Achelata) develop through a characteristic type of zoea larva, the phyllosoma (Palero *et al.*, 2014). Phyllosoma larvae have been recognized as giant larvae frequently in the literature. They can reach up to 80 mm in body length, with their thin legs extending even longer (Guérin, 1822; Richters, 1873; Johnson, 1951; Sims, 1964; Sims and Brown, 1968). Phyllosoma larvae most likely represent the largest decapod larvae (Palero *et al.*, 2014). As a consequence, also the megalopa larvae of achelatans (nisto and puerulus larvae) are significantly larger than other types of megalopa larvae. Giant phyllosoma larvae have been reported from the fossil record with body length up to 100 mm. Besides ~~"t~~ypical phyllosoma larvae (Polz, 1972; 1973; 1984; 1987; 1995; 1996; Haug *et al.*, 2009; 2011a), large nisto larvae (Audo *et al.*, 2014; Haug and Rudolf, 2015), but also transitory forms with a ~~"m~~ixed" morphology of phyllosoma and post-phyllosoma stages have been reported (Haug *et al.*, 2013b; Haug and Haug, 2013, 2016).

Larvae of *false sand crabs (Hippidae)* usually reach a total length of 2 mm. A single specimen has been reported to have reached 15 mm in total (Martin and Ormsby, 1991). Yet recently more material turned up demonstrating that reaching such a size may be quite more common among false sand crabs than expected (Rudolf *et al.*, 2016).

While *mantis shrimps (Stomatopoda)* are not decapods, they show certain similarities to them including various aspects of their larval development. Their later larva can be roughly seen as the functional equivalent to the megalopa larva in decapods. Depending on the specific ingroup these larvae are of the alima-type or of the erichtus-type. Both reach sizes of several centimeters. Alima-type larvae have been known to reach up to 5 mm (Ahyong *et al.*, 2014). Just recently new very large erichthus-type larvae have been described (Haug *et al.*, 2016). Erichthus-type larvae have also been described from the Jurassic lithographic limestones from Germany with up to 18 mm (Haug *et al.*, 2008; 2015b). Notably, giant fossil larvae from the Triassic Hallstatt limestone from Austria with shield lengths of 13 mm show certain characters of the mantis shrimp larvae, and also similarities to the false sand crab larvae (Hyžný *et al.*, 2016).

The possible function of giant larvae

Generally, we can distinguish between two types of giant larva: Type one are facultative giant larvae, type two are obligate giant larvae.

Type one giant larvae occur in species that usually have „normal-sized" larva, but in which from time to time giant individuals occur. Here 'giant' is meant in comparison to individuals of the same species. Such giant larvae must be understood as caused by external factors. A rather simple and probably widespread case for causing such instances is the simple absence of a settling trigger. Many larvae need specific chemical environmental cues that indicate an advantageous habitat for the benthic juvenile/adult. If such cues are absent, larvae can simply continue to grow without metamorphosing. Also other abiotic factors have been suggested to be important in this aspect. For example, temperature and shifts in photoperiod length seem to influence the development of tadpoles in the direction to giant tadpoles (Emerson, 1988; Fabrezi *et al.*, 2010).

It has also been suggested that giant size of larvae may be a consequence of a physiological defect. Such larvae often already develop adult organs, e.g., primordial gonads (Temereva *et al.*, 2006). A disruption in thyroid hormone production before metamorphosis has been suggested as reason for this phenomenon (Emerson, 1988; Shi and Hayes, 1994; Schreiber *et al.*, 2001; Yun-Bo *et al.*, 2001; Ogielska and Kotusz, 2004; Rot-Nikcevic and Wassersug, 2004; Roček *et al.*, 2006).

Parasites have also been identified as causes of suppressing a metamorphosis trigger, with this leading to giant-sized larval forms. Insect larvae infected with parasites molt more often than non-parasitized larvae and die as giant larvae (Fisher, 1963). Hormones increasing the juvenile activity of the host cause this exceptional development. In this way, the parasite gets a larger host by its hormone manipulation (Dawkins, 1990).

Type two giant larvae are cases in which representatives of all individual species (or larger group) develop through larval forms that grow significantly larger than the larvae of closely related groups (Fabrezi and Goldberg, 2009). This also leads to a prolonged larval phase. Such a prolonged larval span can enhance the capability for long-distance dispersal in the planktic phase of some species of different molluscs, echinodermatans, or achelatan lobsters (Domanski, 1984).

In this context, one could think of abyssal gigantism (Herring, 2001) also as explanation for giant larvae. Mainly crustaceans have been reported to reach a larger size in deep-sea environments than their relatives in shallow waters (King and Butler, 1985; Mauchline, 1995; Chapelle and Peck, 1999). Low temperature and restricted food availability in deep seas are thought to decrease growth rates, but to increase longevity and the time span to reach sexual maturity (Nybakken, 2001). Hence, it seems to affect juvenile instead of larval development, not necessarily leading to large larvae. Abyssal gigantism has been proposed for the loriciferan Higgins larvae by Gad (2005). Yet, these forms are in fact paedomorphic and therefore not larvae.

Giant larvae of type two often bear structural specializations. In many giant crustacean larvae spines or extensions of the shield are necessary to increase the buoyancy (Eiler *et al.*, 2016; Haug *et al.*, 2016). Eel larvae deposit large amounts of glycosaminoglycans in their musculature increasing their swimming ability due to the enhanced skeletal stability (Bishop and Torres, 1999). Giant acorn worm larvae are adapted to a prolonged larval span by relatively larger feeding structures to process more food (Damas and Stiasny, 1961; Strathmann and Bonar, 1976).

Interestingly, we can even identify combined cases of type one and type two giant larvae. Eel larvae are in some species 300 mm in average and with this significantly larger than many other fish larvae and representing cases of giant larvae of type 2. Yet, among these even larger larval individuals are known of 1800 mm, with this being cases of type 1, representing a kind of super-giant larva.

Interpretation of the present case

Cirripede nauplius larvae represent dispersal and growth stages that can last short or long (Høeg *et al.*, 2015). A short larval span is only possible if the larvae find a suitable habitat in close distance to their parents (Buhl-Mortensen and Høeg, 2006). In environments that have a patchily distributed settlement habitat, it is more likely that larger larvae are adapted for long-distance and long-time dispersal as it has been reported for some deep-sea cirripedes (Buhl-Mortensen and Høeg, 2006; Yorisue *et al.*, 2013). The Solnhofen limestone Lagerstätte represents a Jurassic back-reef lagoon (Barthel *et al.*, 1990), where suitable habitats for cirripedes might have been rare and nauplii must have searched for a long time for their settlement site. Additionally, in modern cirripedes, lecithotrophic nauplii are more rounded and larger than planctotrophic nauplii, but show more simple setae and reduced development of the appendages and the labrum (Anderson, 1965; 1987; Høeg *et al.*, 2004). However, the fossil specimen described herein is generally large and rounded, but show at the same time well developed appendages and a well developed labrum (Fig. 1D). Hence, it is likely that the fossil specimen described herein could store lipids and ingest food for its metabolic needs at the same time to survive a long-term dispersal phase. As pointed out above, modern cirripedes seem to be restricted in the number of molts as a nauplius. It seems therefore most likely that the larva represents a case two, i.e. an obligate dispersal larva. This is also in accordance with a supposed floating rim of the shield.

It might be seen as special that we have a highly specialized nauplius larva as the first fossil report of a cirripede nauplius. Yet, it is in overall concordance that we tend to find giant larvae. Moreover, the finding is also important because it provides us a rare look into the Mesozoic plankton of which our knowledge is still very incomplete.

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Table

Tab. 1: Overview of giant larvae with larval terms and reported maximum sizes of their respective group or close relatives.

Metazoan group (Representatives of)	**Name of the larva**	**Maximum reported size**	**Average "usual" size**
Cnidaria	planula	11 mm	1 mm
Gastropoda	veliger	7 mm	1 mm
Annelida	trochophora	12 mm	3 mm
Sipunculida	pelagosphaera	3 mm	0.3 mm
Phoronida	actinotrocha	3.5 mm	0.7 mm
Echinodermata (Holothuroidea)	auricularia	15 mm	1 mm
Echinodermata (Asteroidea)	bipinnaria	35 mm	1 mm
Hemichordata	tornaria-like	28 mm	0.7 mm
Teleostei	leptocephalus	300/1800 mm	1 cm
Lissamphibia, extant	tadpole	230 mm	few cm
Lissamphibia, fossil	tadpole	150 mm	few cm
Achelata, extant	zoea (phyllosoma)	80 mm (body)	few mm
Achelata, fossil	zoea (phyllosoma-like)	100 mm (body)	few mm
Polychelida, extant	megalopa (eryoneicus)	100 mm	few mm
Polychelida, fossil	megalopa (eryoneicus-like)	40 mm	few mm
Stomatopoda, extant	erichthus, alima	50 mm	few mm
Stomatopoda, fossil	erichthus	18 mm	few mm
Anomala (Hippidae)	megalopa	15 mm	few mm
Dendrobranchiata (Aristidae)	zoea (cerataspis)	12 mm	1 mm
Thecostraca (Facetotecta)	y-nauplius	0.7 mm	0.4 mm
Thecostraca (Ascothoracida)	a-nauplius	0.7 mm	0.4 mm
Thecostraca (Cirripedia)	c-nauplius	7 mm	0.5 mm

Figures

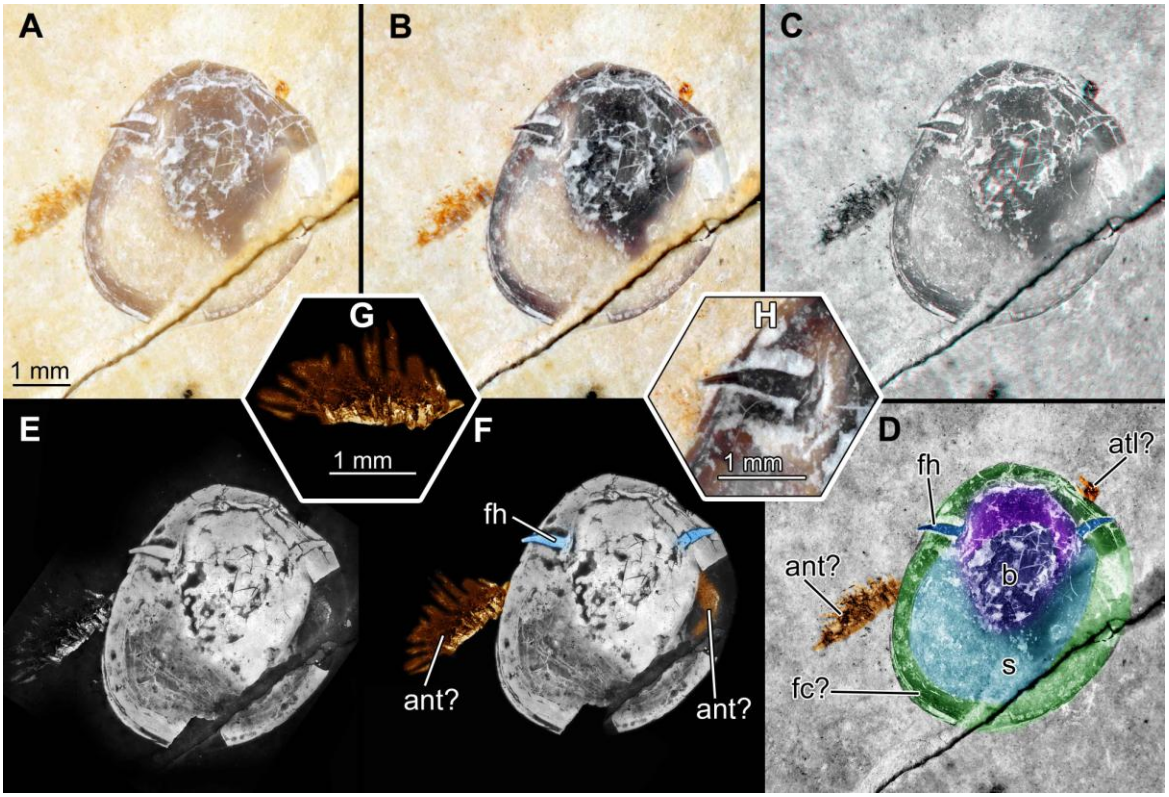

Figure 1: Different photographic methods applied to the fossil specimen (SMNS XXXWILL BE ADDED LATER). A) Macro-photography under cross-polarized light, scale bar = 1 mm. B) Like A, but with optimized histogram. C) Stereo-photography, please use red-cyan glasses. D) Highlighted version of C. E) Fluorescence photography. F) Highlighted version of E. G) Detail of appendage, scale bar = 1 mm. H) Detail of horn, scale bar = 1 mm. Abbreviations: ant? = antenna (orange); atl? = antennula (orange); b = body under the shield (dark blue); fc? = floating collar (green); fh = fronto-lateral horn (blue); s = shield rim (light blue).

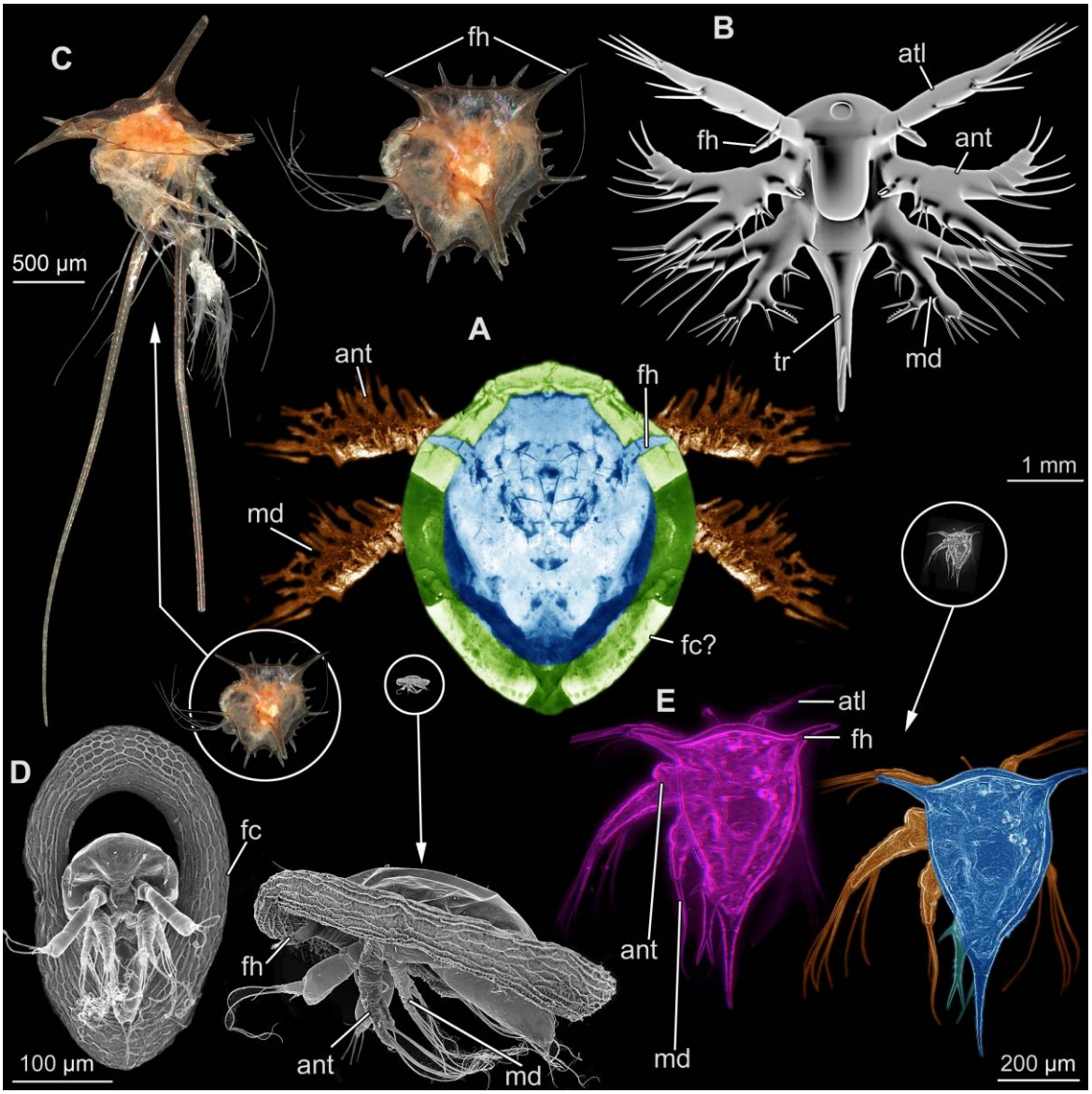

Figure 2: Fossil and modern cirripede nauplii. A) Reconstruction of the fossil nauplius (center) and size comparison to modern counterparts (in circles), scale bar = 1 mm. B) Model of a modern cirripede nauplius, not to scale. C) Macro-photography under cross-polarized light of modern lepadomorph nauplius (MNHN IU-2014-5478), lateral and dorsal view, scale bar = 500 µm. D) Scanning electron microscopic photography of a modern rhizocephalan nauplius, please note the floating collar, lateral and ventral view, scale bar = 100 µm. E) Fluorescence photography of modern balanomorph nauplius, stereo-projected (left, please use red-cyan glasses) and colour-marked version (right), dorsal view, scale bar = 200 µm. Abbreviations: atl = antennula; ant = antenna; fc = floating collar; fh = fronto-lateral horn; md = mandible; tr = (initial) trunk.

3.3 PAPER VII: Nagler et al. 2017d.

Nagler C, Hörnig MK, Haug JT, Noever C, Glenner H. 2017d. The bigger the better? Volume measurements of parasites and hosts: parasitic barnacles (Cirripedia, Rhizocephala) and their decapod hosts. *PLoS ONE*, 12: e0179958. DOI: 10.1371/journal.pone.0179958.

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3.4 PAPER VIII: Nagler et al. in prep a

Nagler C, Wagner P, Olesen J, Kerp H, Waloszek D, Haug JT, Haug C. The 400-million-year old eucrustacean *Ebullitiocairs oviformis* re-evaluated: a thecostracans with a parasite-type morphology in the Rhynie chert. In preparation, *Palaeontology*.

The 400-million-year old eucrustacean *Ebullitiocaris oviformis* re-evaluated: a thecostracan with parasite-type morphology in the Rhynie chert

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Abstract
The 400 million years old Rhynie chert Lagerstätte together with the nearby Windyfield chert represents a very special type of fossil deposit. The original ecosystem has been reconstructed as having been dominated by hot springs and a large fluvial system, comparable to the Yellowstone National Park in the USA. Due to these conditions, numerous metazoans have been preserved in Rhynie chert, although being outnumbered by finds of plants and fungi. Especially various arthropods have become "frozen" in their natural position, partly associated with other organisms such as terrestrial plants. We present new morphological details of one of three known eucrustacean species: *Ebullitiocaris oviformis*. Specimens have been documented with up-to-date imaging methods in three dimensions revealing also small details such as setae and setulae. Contrary to earlier studies we reject an interpretation as representative of Cladocera (water fleas, ingroup of Branchiopoda). Anterior structures include a pair of large appendages, each with a prominent distal suction disc. Trunk appendages appear to be specialized for swimming. Specific arrangement of the trunk in combination with the morphology of the appendages indicates a close relationship to Ascothoracida within Thecostraca s.str.

Keywords
Windyfield chert, plantparasitism, fossil thecostracan, suction discs, functional morphology

Introduction
The Devonian Rhynie chert Lagerstätte together with the nearby Windyfield chert, Scotland, represents a ~~–~~Site of Special Scientific Interest" as it provides an insight into one of the earliest terrestrial ecosystems and therefore it is of scientific importance for studying terrestrialisation (Rice et al. 2002). It has been suggested that the ecology of these chert deposits was originally comparable to the hot springs and geysers in the Yellowstone National Park in the USA (Trewin & Wilson 2004). With about 400 million years, it is the oldest and best preserved support for non-marine and terrestrial life habitats (Trewin &

Rice 2004; Channing & Edwards 2009a) that reports the evolution of terrestrial and freshwater structures as well as physiological adaptations necessary for this environment (Taylor et al. 2003).

The Rhynie (and Windyfield) chert is also an important Lagerstätte for arthropods. Reports include arachnids (Dunlop 1994), aquatic eucrustaceans (Scourfield 1926; Anderson et al. 2003; Haug et al. 2012; Womack et al. 2012), but also insects and myriapods (Hirst & Maulik 1926; Whalley & Jarzembowski 1981; Engel & Grimaldi 2004; Ross & York 2004; Fayers & Trewin 2005). It has been proposed that arthropods found in chert represent the most diverse arthropod assemblage from the Devonian (Anderson & Trewin 2003)

Finds from the Rhynie and Windyfield chert provide a important sources for understanding the evolution of several interactions between metazoans, plants, and micro-organisms (Taylor & Kerp 1995; Channing & Edwards 2009b) including predation (Anderson & Trewin 2003; Fayers & Trewin 2004), parasitism (Taylor et al. 1992), mutualism (Remy et al. 1994), herbivory (Habgood et al. 2004) and detrivory (Habgood et al. 2004; Tayler et al. 2004). Due to permineralisation of the silica-rich geothermal fluids, specimens are exceptionally well preserved in three dimensions including their original anatomy (in many aspects) and position. Therefore, their life habits and even structures down to a length of 200 nm, e.g. cells and setae, can be observed (Trewin 1994, 1996; Haug et al. 2012).

Within Eucrustacea sensu Walossek (1999) different lineages invaded non-marine environments, e.g. copepods, ostracods, branchiopods and several lineages of malacostracans (Schram 1986). Beside the eucrustaceans *Lepidocaris rhyniensis* Scourfield 1926 and *Castracollis wilsonae* Fayers & Trewin 2002, *E. oviformis* Anderson et al. 2003 has been descriebd from the cherts. Another fossil attributed to *Ebullitiocaris*, the species *elatus* Womack et al. 2012, has been reported from Sandsend cobble, however, the differences in the deposition sites and morphology of the species *elatus* and *E. oviformis* (Sandsend cobble vs. Rhynie chert, respectively) cast several doubts on the phylogenetic position of this fossil (Van Damme & Kotov 2016). All three fossil eucrustaceans from the Rhynie-Windyfield Cherts have been interpreted branchiopods (the group including modern, mostly ephemeral forms such as brine shrimps, tadpole shrimps or water fleas). This interpretation was probably partly based on their occurrence under the specific environmental conditions, reconstructed for the chert Lagerstätten. Additionally, eucrustacean, non-branchiopod nauplii, probably closely related to maxillopodans have been reported from Windyfield chert (Haug et al. 2012). All crustacean specimens from Rhynie and Windyfield chert represent one of the earliest known non-marine eucrustaceans.

The phylogenetic position of *E. oviformis* is still controversial and the originally suggested branchiopod affinity could to date not be finally evaluated due to the absence of sufficient morphological characters (Hegna & Kotov 2016; Van Damme & Kotov 2016). Here we present new material of *E. oviformis* from Windyfield chert. Based on the morphological details reported herein as well as the functional morphology and ecology of this species, we were able to re-evaluate the phylogenetic position of *E. oviformis*.

Material & Methods

Material

Fossil material

Specimens of *Ebullitiocaris oviformis* are preserved in chert samples from the Windyfield locality, about 300 m northwest of the village of Rhynie, Aberdeenshire, Scotland. The chert was cut into thin slices of approximately 50–150 µm; these were polished on both sides and glued onto unfrosted glass slides for studying with a light microscope (Hass & Rowe 1999). The investigation included 18 thin sections, most of the included specimens being fragments representing single legs or leg assemblages; only in rare cases entire animals are preserved. The micro slides have the collection numbers M-3701, M-3703, M-3704, M-3706–M-3708, M-3711, M-3712, M-3715, M-3717–M-3720, M-3722, M-3742, M-3780, M-3792, M-3798 and are deposited in the Paleobotanical Collection in the Forschungsstelle für Paläobotanik, Westfälische Wilhelms-Universität, Münster, Germany. Stereo images of the individual specimens are deposited in MorphDBase under the accession numbers C_Nagler_EDIT-M29–M126.

Comparative material

The fossils described herein were compared to the following representatives of maxillopod eucrustaceans:

Argulus foliaceus (Branchiura): one adult specimen, former teaching collection University of Ulm, Germany, dissected; slide is deposited in the Zoological State Collection of Bavaria (ZSMA20170024).

Ascothorax gigas (Ascothoracida): one ovigerous female, Southern Ocean (50°48.02`S, 39°23.96`W), endoparasitic in *Ophiura* sp., SYSTCO II Expedition, Laura Würzberg 2012, dissected, slide is deposited in the Zoological State Collection of Bavaria (ZSMA20170025a & b).

Ulophysema sp. (Ascothoracida): brooded embryo, deposited in the zoological collection of the University Mueseum of Copenhagen (ZMUC XXXWILL BE ADDED LATER XXX)

Caligus sp. (Copepoda): one copepodit stage II, Cross Bay, Rovinj, Croatia (45°7.06`N 13°3.99E), ectoparasitic on a reef fish (Mugilidae), Roland Melzer 2014 (ZSMA20159001).

Documentation methods

Microscopy

The specimens preserved in chert were studied using a Zeiss Axioskop 2 and documented using an AxioCam digital camera. Objectives used were either of 10x or of 20x magnification, resulting in 100x or 200x magnification in total. As the fossils extend to a certain depth into the matrix, a stack of single images (= frames) was recorded for each specimen, the first frame at a level slightly above the specimen and the last frame at a level slightly below it. The camera then recorded a frame every 4 µm for 10x magnification and every 2 µm for 20x magnification in z-axis. From these stacks stereo images were processed with the software packages ImageJ (Wayne Rasband) and OsiriX (Antoine Rosset) (following Haug et al. 2009, 2012).

Extant specimens were investigated with composite autofluorescence imaging and scanning electron microscopy. Fluorescence microscopy of *Caligulus* sp., and *Ascothorax gigas* was performed on an inverse fluorescence microscope BZ-9000 (BIOREVO,

Keyence). The microscope was equipped with a DAPI filter (λ = 358 nm) recording autofluorescence and 4x and 10x objectives resulting in total in about 40x and 100x magnification (Haug et al. 2011). Stacks of images were processed with the freeware packages CombineZP, ImageJ and ImageAnalyzer (Meesoft). Scanning electron microscopy and photography of *Ulophysema* sp. was performed on a JEOL 6335-F scanning electron microscope with 10 kV at the Zoological Museum of the University of Copenhagen. Confocal fluorescence microcopy of *Argulus foliaceus* was performed on an Observer Spinning Disk Z1 (Zeiss). The microscope was equipped with an Axiocam.

Measurements

Measurements were performed using Adobe Acrobat 7.0 Professional. The software offers two different measurement tools. The distance tool allows measuring the linear distance between two points, which was used for example, to measure the diameter of the antenna. Some structures, such as the outline of the entire antenna, are bent or curved and as a consequence are not measurable by a linear distance. Therefore, the second tool, the perimeter tool, using more than two points to measure curved structures, was used. The values are mean values of different specimens, because not all parts are visible at all specimens.

Drawings

Drawing of a cypris larva of Cirripedia was performed in Adobe Illustrator CS2. Images were electronically tracked using a graphic tablet (Cintiq 12 WX, Wacom), an electronic pen (Wacom Inkling MDP—123), and the software Adobe Creative Suite 2, according to the protocol of Coleman (2003). Drawings were finally optimized in Adobe Illustrator while comparing directly to the original light-microscope image from Høeg & Møeller (2006).

Stratigraphy

Information on the geology, sedimentology and setting of the Lagerstätte Rhynie chert can be found in Rice et al (2002) and Trewin & Rice (2004).

Based on palynomorph assemblages (Richardson 1967), radiometric dating (Rice et al. 1995) and spores (Wellman 2006) the age of the chert generally is considered to be Pragian (Early Devonian). Based on radiometric studies a 40Ar/39Ar age of 403.9 ±2.1 Ma has been obtained by on K-feldspar from a quartz-feldspar vein that is part of the hydrothermal system that was responsible for the formation of the Rhynie chert (Mark et al. 2011).

Results

Description of adult Ebullitiocaris oviformis

Overall arrangement (Fig. 1)

The fossil specimens have a body enveloped by a large shield. The body within the shield is organized into three major regions: The most anterior region most likely equivalent to the head, with three structures: a tube-shaped extension, a prominent structure with a distal suction disc, and a third smaller structure. The ill- delineated head is distinctly sett off from the trunk with 10 segments. These are further subdivided into two sets; an anterior one (six segments, at1–6) bearing six pairs of appendages, and a posterior one (four segments, pt1–

4) without appendages (Fig. 1E–F). The trunk articulates to the telson with two furcal rami (Fig. 1F).

The extended shield (length: 1000 µm, width: 550 µm, height: 600 µm) has no apparent dorsal hinge. It is drawn out in all directions enclosing the entire body. The shield has the overall shape of an elongated spheroid which opens ventrally from anterior to posterior end with the attachment site supposedly around the head or anterior trunk region (the posterior trunk region is not attached to the shield, Fig. 1A–E). The preservation indicates a strongly structured surface covering the entire shield (Fig. 1A, D, G).

Head (Figs. 2-4)

The head region bears three pairs of structures.

The most anterior ventral structure (pp, length: 700 µm, width: 70 µm, presumable on the ocular segment) is a long, slender, tube-shaped and unbranched extension without any visible elements or subdivisions (Fig. 2A, B).

The second prominent structure from anterior (presumably post-ocular segment 1) is a prominent appendage, possibly the antennula. It is composed of three distinct regions, a proximal functional peduncle, an armoured middle region, and a distal suction disc (Figs. 3, 4). The functional peduncle (length: 100 µm, width at widest point: 40 µm) has an elongated tube-like shape, being narrower at the proximal part (width: 25 µm) and becoming wider distally at the transition to the armoured region (Fig. 3B–E). This armoured middle region (length: 130 µm, width at widest point: 75 µm) bears numerous small spines, arranged in at least 8 concentric rings, with around 25 spines per ring. These spines (length: 5 µm, width at basis around 3 µm) have a triangular shape with a distal tip and are orientated with the tip pointing to the proximal end of the appendage (Fig. 3D, indicated by black arrows). At the most distal part of the armoured region, two small hemispherical humps are visible (Fig. 3B, D–F, 4A). Each hump (length: 25 µm, width: 30 µm) bears approximately four setae, one hump is positioned posterior-laterally to the suction disc and one posterior-medially to the suction disc (Fig. 3D, E). Distally a round, cup-like suction disc (diameter: 75 µm) is connected to the armoured region. The wall of the disc shows two concentric rings of rays (diameter of outer ring of rays: 70 µm, diameter of inner ring of rays: 60 µm, length of one ray: 5 µm, width of one ray: 2 µm; in other species, e.g. fish lice, rays often also called rods), which appear to function as rim supporting structure. Each of these rings features around 60 rays in equal distance to each other (Fig. 3, 4A–E).

The third structure is a pair of a structure composed of three, equally sized elements (length of one element: 60 µm, width: 30 µm) located postero-laterally to the second structure, they are possibly unbranched, elongated and tube-shaped, but are composed of a minimum of three elements (Fig. 2C). Unfortunately, these appendages either do not show a good preservation or are covered by overlying structures. Hence a more detailed description and thus identification is not possible.

Trunk (Figs. 1, 4)

The trunk (length: 400 µm) has an elongated, tube-like shape and features ten visible segments. The first six segments (at1-6, total length: 180 µm) bear a pair of trunk appendages each (Fig. 1A–C, E, F), either indicated by insertion areas or the actual appendages. These trunk appendages are biramous, with a basipod (width: 40 µm, Fig. 4F,

G), carrying endo- and exopod. Both endo- and exopod are truncated cone-shaped and similar in length (length endo- and exopod: around 250 µm). The endopod is composed of four elements and bears a minimum of four setae (each element bearing one seta). The exopod is composed of three to four elements and bears six setae (one on each element and two additional terminal setae, Fig. 4F–I). Posterior four trunk segments (pt1–4, length: 220 µm) bear no appendages. These segments are elongated with a cylindrical shape getting narrower to the posterior end of the trunk; they are longer than the appendage-bearing trunk segments.

Telson (Fig. 1)
The trunk posteriorly articulates to the telson (length: 100 µm, width: 60 µm), which has an elongated rectangular shape bearing a furca. The telson is about twice as long as the most posterior trunk segment. The two distal furcal rami are small, about half of the length of the telson. They have paddle-shaped terminal ends and appear to be articulated (Fig. 1A–C, E–F).

Discussion

Systematic interpretation
Although we could not study the type material of *Ebullitiocaris oviformis*, the morphological details point to conspecifity with the original material. The outline of the carapace and the ~~t~~ube" (Anderson et al. 2003, p. 357, figs. 1–5), which seems more compatible with an interpretation as the trunk (Fig. 1A–C, E–F, 4F), and the attachment to plants with cup-like structures originating from the head (Fig. 1A, D, 2A, 4A–D; Anderson et al 2003, p. 362, fig. 4) suggest that the specimens studied herein are indeed representatives of *Ebullitiocaris oviformis*.

Ebullitiocaris oviformis has been interpreted as a representative of Cladocera, the group including all water fleas. This interpretation was based on the morphology of the shield, although the authors were aware of the lack of diagnostic details (Anderson et al. 2003). The cladoceran affinity of *Ebullitiocaris oviformis* has been drawn into question recently (Hegna & Kotov 2016; Van Damme & Kotov 2016; see introduction).
Besides branchiopodans, other small eucrustaceans could be assumed for a closer relationship with *E. oviformis*, such as cephalocaridans, remipedians and maxillopodans. Yet, a close relationship to the first two groups is unlikely due to their completely different overall morphology. The following characters support a maxillopodan affinity:
(1): Modern representatives of Maxillopoda bear five head segments, followed by six trunk segments with biramous appendages, followed by five trunk segments without appendages and the telson carrying the furcal rami (5-6-5 pattern; Schram 2013). The proposed tagmosis pattern in the ground pattern of Maxillopoda is five head segments, seven trunk segments with appendages and four trunk segments without appendages followed by the telson (5-7-4 pattern; Newman 1992; Walossek & Müller 1998; Schram & Koenemann 2004). The number of the posterior trunk segments is not in all groups of maxillopods fixed and variations are common, e.g. in ascothoracidans (Fig. 5; Grygier 1984). Although the exact segment composition of the head of *E. oviformis* is unclear due to preservational constraints, we can observe the general maxillopodan tagmosis of the trunk for the fossil

specimens described herein. The fossils have six trunk segments with appendages, followed by four trunk segments without appendages and a telson carrying the furcal rami (hence a pattern of X-6-4) (Figs. 1, 4E–G, 6A). The posterior pattern of 6-4 fits well into the tagmosis pattern of maxillopodans. In contrast, cladoceran branchiopodans possess five to six trunk segments with biramous appendages (Van Damme & Kotov 2016) followed by a short trunk without appendages of about one fifth of the length of the anterior trunk (in the fossil specimens the posterior four segments are slightly longer than the anterior trunk part with appendages).
(2): The specimens studied herein have six pairs of ppendages at the trunk, clearly expressed as swimming appendages similar to the adaptation of legs in maxillopods (Newman 1992). This modification is exemplified by the long setae arising from these legs and the absence of endites (Fig. 4E–I). In adult branchiopods, the trunk appendages retain their ancestral feeding function and do not bear long setae for swimming (Olesen 2007).

Based on tagmosis and functional morphology of trunk appendages and parts of the animal that are freely overhung by the shield (the entire animal in the fossil specimens (Fig. 1, 6A) versus only the poster part of the body in cladocerans (Olesen 1998)), a cladoceran affinity of E. ovifomis seems very unlikely.

Although the monophyly of Maxillopoda is controversial (Martin & Davis 2001, Regier et al. 2010; Reumont et al. 2012), there are morphological characters that support their monophyly, (e.g. Newman 1992; Walossek & Müller 1998; Haug & Haug 2015). As the fossil specimens described herein have a tagmosis compatible with maxillopodan affinities (X-6-4; Figs. 1, 4E–G, 6A), we compare the morphology of the fossils with that of the maxillopodan groups. These include here: Copepoda, Thecostraca (sensu Grygier 1987a) with Facetotecta, Ascothoracida and Cirripedia as well as the partly problematic groups Ostracoda and Branchiura the latter two especially for functional comparison.

Overall body organization and morphology of the shield

As discussed above, the overall body organization indicates a maxillopodan affinity with head, six trunk segments with appendages, four trunk segments without appendages and a telson carrying the furcal rami. This is also the case in other maxillopodans, e.g. Thecostraca and Copepoda (Figs. 5, 6B). Representatives of Branchiura have a head, but a shorter a trunk with four appendage-bearing segments and an unsegmented posterior trunk articulated with a telson carrying the furcal rami (Fig. 6C; Møller et al. 2008; Møller 2011).

The shield of the fossil specimens is extended and enclosing the entire body (Figs. 1, 6A), similar to the shield of adult ascothoracidan thecostracans (Figs. 5, 6D; Wagin 1946) or the cypridoid larvae of thecostracans groups, such as Ascothoracida, Thoracica and Rhizocephala. In contrast to the cypridoid larva of Cirripedia and Ascothoracida, the shield of the facetotectan cypridoid larvae is not enclosing the entire body of these animals (Høeg & Kolbasov 2002, p. 69, fig. 1A). In endoparasitic or symbiotic adult representatives of Thecostraca *s. str*., such as Rhizocephala and Acrothoracica, the shield is either not properly developed (Glenner et al. 2010; Nielsen et al. 2016), or in representatives of Thoracica there is no real shield but rather shell plates (Glenner & Hoeg 1993), or it is not known for the adult stage as in Facetotecta (Glenner et al. 2008). Contrary to the fossil specimens studied herein, the shield of branchiurans (Fig. 6C) and

copepods (Fig. 6B) is extending only over about two thirds of the body without a wide lateral extension (Møller 2011).

The shield of the specimens described herein has a golf ball-like surface with irregular shaped deep indents (Fig. 1A, D, G indicated by arrows). Such a surface structure of the shield is rare in eucrustaceans. Nevertheless, various groups of ostracods (Liebau 1977) and cypridoid larvae of some thecostracans, such as the y-cypris of facetotectans (Høeg & Kolbasov 2002), show a similar structure. Given the similarities outlined above an ingroup position of *E. oviformis* to Thecostraca seems likely.

Head structures

Usually, morphological details are very well preserved in chert (Haug et al. 2012). However, the head structures in the fossil specimens described herein are difficult to discern, especially the order and partly the morphological details of the head appendages.

First structure on the head of the fossil specimens: One of the most anterior, prominent structures in eucrustaceans is usually the antennula with several elements, ringlets. For example parasitic representatives of Copepoda bear an antennula composed of six elements and a length of about 30 % of the length of the shield (Boxshall & Jaume 2013; Brazenor & Hutson 2013). In contrast, the most anterior elongated, tube-shaped structure of the fossil specimen described herein seems not subdivided into several elements, but in any case in relation to the shield length, this extension is very long, reaching about 50 % of the length of the shield (Fig. 2A, B).

A structure, similar to the fossils‘ first structure, is known from representatives of Facetotecta and Ascothoracida (Grygier 1984; 1987a, b). Representatives of these groups, such as of *Parascothorax,* possess a so-called para-ocular process that has a tube-like shape without subdivisonal elements, sometimes with aesthetascs (Grygier 1987b). This process is similar to the one seen in the fossil specimens described herein (Grygier 1984 fig. 2.6). Therefore, we interpret the tube-shaped extension as para-ocular process.

Second structure on the head of the fossil specimens: This structure of the fossil specimens bears at the distal end a kind of suction disc (Fig. 3, 4A–E). Suction structures with an at least distantly comparable morphology are known from some groups of eucrustaceans:

1) ostracods with suction structures (Smith 2011)
2) copepods with lunulae (Huys et al. 2012; Kaji et al. 2012)
3) thecostracans with attachment discs (Grygier 1984)
4) branchiurans with oral suckers (Møller et al. 2008; Kaji et al. 2011)
5) larval isopods with oral suckers (Shimomura et al. 2005)
6) and tantulocarids with oral disc (Mohrbeck et al. 2010)

The morphology of the fossil specimens shows no similarity to isopods or tantulocarids. Due to the similar overall morphology and the morphology of the suction disc, copeopods, branchiurans and thecostracans are discussed in the following.

So-called lunulae of ectoparasitic copepods, e.g. caligids and caligiform copepods (Fig. 6E), are formed by the ventral part of the head shield and/or one or more pairs of swimming legs and/or their setae to a membranous cup-like structure. These structures are an additional attachment organ and help the copepods to attach and to stay attached to their

hosts (Huys et al. 2012; Kaji et al. 2012). However, due to the order of the head structures, the prominent structure with the suction disc in the fossil specimens described herein is not formed by the head shield (Figs. 2–3).

In ostracods, the suction structures are disk-like suckers, developed from the setae at the antennulae (Tanaka & Tsukagoshi 2010; Tanaka et al. 2010). Male ostracods use this suction structure for attachment to the females during copulation (Vannier & Abe 1993). The fossil specimens show rather a ~~"t~~rue" suction disc than curled setae (Fig. 3), therefore, we have no indication for an ostracodan affinity.

The suction disc in branchiurans develops from the proximal element of the maxillula during the larval development (Rushton-Mellor & Boxshall 1994; Møller et al. 2008). With this suction disc fish lice attach to their host fishes. The suction disc in *Argulus foliaceus* has a large area of articulation and is bordered by closely arranged setae (Gretsy et al. 1993). Inside the suction disc is one layer of 60 rays, each composed of three sclerites (Fig. 6F). The fossil specimens described herein bear a prominent appendage that is clearly differentiated into a non sub-divided proximal part with two humps bearing several setae and a distal suction disc with one row of 60 rim-supporting rods composed of two sclerites each (Fig. 3). Interestingly, the suction disc in the sixth larval stage of *Argulus foliaceus* is composed of four elements: the suction area at the now distal end, former most proximal end, followed by remains of three proximal (former distal) elements, the most distal one bearing two spines (Møller et al. 2008; Kaji et al. 2011). If the suction disc in the fossil specimens would originat also from the maxillulae, it could be possible that the humps with setae (Fig. 3B, D–F, 4A) represent remains from other maxillulary elements like in the sixth larval stage of *Argulus foliaceus*.

However, the positional arrangement of the head structures in the fossil specimen described herein argues for an interpretation of the prominent second structure with a suction disc as an antennula. The antennulae of Branchiura have four distinct elements: a basal part with two elements with hooks and a distal part with two elements with setae, each element just about 1–5 % as long as the shield, whereas the third element is modified into a hook (Fig. 6C; Rushton-Mellor & Boxshall 1994; Boxshall & Jaume 2013; Lutsch & Avenant-Oldewage 1995).

Notably, the cypridoid larvae of representatives of Cirripedia and Ascothoracida show an attachment disc-like or hook-like structure at the distal end of the third element of the antennulae, composed of four elements. The structure is used to attach to the settlement habitat, either a host or any surface, before metamorphosis into an adult (Glenner et al. 1989; Moyse et al. 1995; Kolbasov et al. 1999; Lagersson & Hoeg 2002; Hoeg et al. 2009). Especially, the disc-like third element of representatives of Cirripedia is morphologically similar to the suction disc in the fossil specimens described herein (Fig. 7). Similar to the antennulae of cypridoid larvae of Thecostraca, the structure with the suction disc is divided into four elements, while the fourth element is a small hump with setae, situated laterally to the third element in the fossil specimens versus a small element with several setae and aesthetascs, situated laterally to the third element in Thecostraca (Grygier 1987a; Korn et al. 2000; Høeg & Møller 2006; Al-Yahya et al. 2016). The shape of the attachment device at the distal end has been proposed to depend on the habitat (Al-Yahya et al. 2016). Barnacles, such as *Chthamalus* that settle on plants show a cup-shaped third element with a circular attachment disc and an extended rim (Young 1981; Yan & Chan 2001 fig. 6) that looks very similar to the third element in the prominent structure of the fossil specimen

described herein. The interpretation of the second structure with the suction disc as an antennula is highly compatible with a possible ingroup position within Thecostraca *s. str.*

Hence, the pattern and morphology of the antennula of Thecostraca *s. str.* and Branchiura is similar, thus indicating a common evolutionary origin (Grygier 1987a, b)

Third structure on the head of the fossil specimen: In maxillopodans the structure posterior to the antennula (antenna) is usually biramous, consisting of coxa and basipod, the latter bearing the exopod and endopod. The endopod is composed of three elements in copepods and two elements in thecostracans where such a structure is present, while the exopod usually bears nine to ten elements (Grygier 1987b; Huys & Boxshall 1991; Boxshall & Jaume 2013). The fossils described herein have preserved just three elements (Fig. 2C). Hence, the morphology of the third structure in the fossil specimen studied herein argues not against a close relationship to Thecostraca *s. str.*

Trunk appendages

Branchiurans have four pairs of biramous trunk appendages that are differentiated into basipod, endo- and exopod (Fig. 6C). The endopod is composed of two elements and the exopod consists of one element in *Argulus foliaceus*. The endo- and exopod are similar in length, bearing in total at least 15 setae (Fig. 6C). The six trunk appendages of ascothoracidans (Fig. 5) are biramous (basi-, endo-, exopod), but the exo- and endopod are both composed of two elements. Due to the swimming function of the trunk appendages in ascothoracidans, they are formed as leaf-shaped paddles in the adults (Grygier 1984). The exopod is slightly longer than the endopod with a minimum of three setae (Fig. 5). Beside ascothoracidans, cypridoid larvae of representatives of the other thecostracan groups (Facetotecta, Cirripedia) bear also six swimming legs (Fig. 7; Peresz-Losada et al. 2012).

The six trunk appendages in the fossil specimens are also biramous, bearing basi-, endo- and exopod (Fig. 4F, G). In contrast to branchiurans and ascothoracidans, the endopod is composed of four elements and bears a minimum of four setae. The similarly long exopod is composed of either three or four elements and bears six setae, additionally there are no endites or extensions (Fig. 4H, I), hence modified for swimming movement. Thus, trunk appendages modified for swimming argue again for a maxillopodan affinity of the fossil specimen studied herein. Moreover, the similar long endo- and exopod of the trunk appendages of the fossil specimen argue for an ingroup position within Thecostraca *s. str.*

Broodcare

Additional to the remarkable morphological characters, some of the studied specimens carry eggs with nauplii beneath their shield (Haug et al. in review). Also other groups, e.g. copepods, branchiopods and ostracods, carry their eggs under their shields, but not on the dorsal side of the posterior trunk (Horne et al. 1998). Only extant ascothoracidans carry their eggs in a similar or even the same way as reported in the fossil specimens described herein (Fig. 5D, Grygier 1984). The similar broodcare behaviour in the fossil specimen and Ascothoracida support the interpretation of the fossil specimens as closely related to Ascothoracida.

The discussed morphological details, especially the similar tagmosis, the shield, the extended tube-like first structure, the possible antennula with a suction disc and the trunk appendages indicate not only an affinity to maxillopodans, but moreover a possible ingroup position within Thecostraca *s. str*. Within Thecostraca *s. str.*, the earliest offshoot is the group Facetotecta. Within the unnamed sistergroup to Facetotecta, Ascothoracida represents the sistergroup to the remaining thecostracans (Acrothoracica + (Thoracica + Rhizocephala) (Høeg et al. 2009). The attached, parasitic adult ascothoracidan is similar to a thecostracan cypridoid larva (Høeg et al. 2009). Although the fossil specimens studied herein share many morphological characters with thecostracans cypridoid larvae, the fossils specimens are more similar to adult ascothoracidans, because of the behavioural similarities (see above; Fig. 7). In other words, the morphological and behavioural similarity between the fossil specimens described herein and extant ascothracidans is remarkable and indicates either a sistergroup relationship to (Ascothoracida + Cirripedia), to Cirripedia, or to Ascothoracida. Due to the morphological similarities to adult ascothoracidans, a sistergroup relationship to Ascothoracida seems most likely.

Thecostracans in non-marine environment

In the chert, non-marine aquatic facies from fluvial systems, hot springs and material from sub-aerial systems have been preserved. The chemical composition of the aquatic systems has been heavily debated (Trewin & Wilson 2004; Channing and Edwards 2009a, b; Dotzler et al. 2009). Due to the contradictory view of the environmental settings and especially concenring the water chemistry, we used mainly morphological characters of the here investigated specimens to elucidate their phylogenetic position. Nevertheless, we want to highlight non-marine habitats as possible environment for thecostracans. Although the prevalent view is that extant representatives of Thecostraca are mainly marine, some thecostracans are able to live in non-marine and survive even in freshwater habitats (Høeg & Lützen 1995; Anger & Schubart 2005; Töttrupp et al. 2010; Li et al. 2011). Moreover, cirripeds have been reported to survive and live in rivers, streams and ballast water tanks (Foster & Willan 1979; Høeg & Møller 2006; Riedel et al. 2006). Due to the variety of non-marine habitats, the invasion into freshwater happened several times independently in thecostracans (Glenner, unpublished data). In other words, thecostracans may invade every kind of wet habitat (Høeg & Møller 2006). Thus, it is not unlikely that the fossil specimens described herein represent early thecostracans. Furthermore, the fossil nauplii reported from Windyfield chert seem to represent ascothoracidan nauplii (Haug et al. 2012). Due to the close geographical distance between the finding sites of the fossil nauplii and the fossil specimens reported herein, they likely even represent the same species. This interpretation is backed up by exceptionally preserved adults with brooding larvae beneath their shield (Haug et al. in review).

Similarity to Branchiura

Representatives of Branchiura were used for a functional comparison to the morphology of the fossil specimens described herein. Due to the unclear phylogenetic position of branchiurans and the morphological similarity of the suction disc of the fossils and branchiuarns, we want to add some notes.

After separating Branchiura from Copepoda and thus from maxillopodans (Martin 1932; Stekhoven 1937), the phylogeny of Branchiura is unclear (Møller et al. 2008, Regier

et al. 2010 Pinnow et al. 2015). Based on spermatology and molecular analysis, Pentastomida has been proposed as sitergroup to Branchiura, further complicating the story (Wingstrand 1972, Abele et al. 1992).

Notably, there are some morphological similarities to the fossil specimens studied herein, Thecostraca *s. str.* and Branchiurans (see above). The morphology of the antennula of Branchiura is similar to the one of Thecostraca s. str., indicating a common ancestor (Grygier 1987a, b). The overall morphology of the presumably antennula (e.g. four elements with a distal suction disc) of the fossil specimen supports a close relationship between the fossils and Ascothoracida, although the distal suction itself is more similar to the one of Branchiura (see above). Hence, a convergent evolution of such a suction disc, adapted for attachment to either a host or sediment, might be conceivable, similar to the convergent evolution of the infective stages in Facetotecta (ypsigon) and Rhizocephala (kentrogon).

However, we cannot fully exclude that the suction disc in the fossil specimens originates from the maxillula. If such a suction disc is then more than a convergent character, the phylogenetic placement of branchiurans might need to be re-evaluated.

Ecology and lifestyle

Feeding

We described and discussed above that the trunk appendages bear long setae for swimming and show no sign of food-processing structures (Fig. 4F–I). Like in all representatives of Maxillopoda (Newman 1992) the trunk appendages of the fossil specimens represent swimming legs. We cannot observe other head structures than a tube-like extension, a possible antennula with a suction disc and fragments of a third structure (Fig. 1–4).

Notably, the first structure is very long and seems to be flexible in contrast to the other appendages (Fig. 2). Parts of the para-ocular process of Ascothoracida and Facetotecta have also a flexible appearance and serve as sensory structure (Grygier 1987b). Due to the soft structure and the possible interpretation as para-ocular process, the first structure might function as a sensory organ.

Eucrustacean antennulae have been proposed to usually identify, locate, deposit and process food particles in most cases (Boxshall & Jaume 2013). A feeding function of the antennula has been proposed for adult copepods and adult thecostracans (Grygier 1987b; Yen & Nicholl 1990). A similar function of the antennula has been suggested for the „Orsten"-type fossil *Bredocaris admirabilis*. Interestingly, *B. admirabilis* is considered to represent an early maxillopodan crustacean as sitsergroup to Thecostraca *s. str. (*Müller & Walossek 1988). However, the presumably antennula in the fossil specimen described herein represents an attachment device, similar to a thecostracans cypridoid larva, and does not show any morphology adapted to any feeding process.

Notably, most non-parasitic cirripeds are suspension feeders by their thoracic appendages. However, there have been many, independent transitions from thoracic appendages to other food-processing structures within Cirripedia (Rees et al. 2014). Due to the lack of food-processing structure, a hemi-sessile suspension feeding lifestyle would be rather unlikely possibility for the fossil specimens studied herein.

The third structure in the fossil specimens studied herein, could be a part of a possible mouthcone, similar to the mouthcone of adult Ascothoracida. The fossils might have fed on the plants, onto which they have been attached. Due to preservational aspects,

these structures are not accessible. Also other food-processing appendages at the head of the fossil specimen are not accessible or lacking.

Due to the lack of food-processing structures, the fossil specimens studied herein might have been non-feeding, similar to adult Gnathiidae (an ingroup of Cymothoida, parasitic isopods). While larval representatives of Gnathiidae are temporary ectoparasitic on fishes, adult representatives of Gnathiidae are non-feeding and free-living, non-parasitic in sponges, tunicates and tubes of sepulid worms (Smit et al. 1999). Thus, the fossil specimens studied herein might have been non-feeding as adults.

Attachment

The fossil specimens are attached with their suction discs to plant material (Fig. 3, 4A–E). To the best of our knowledge, a similar behaviour in crustaceans has been reported for a few copepods, barnacles and some insects (Gorb 2001; Boxshall & Halsey 2004; Ohtsuka & Boxshall 2004). In contrast to the fossil specimens described herein these copepod groups use not a pair of suction discs for attachment, but attach to plants or their host with the help of several ‗button setae' on their maxilla and maxilliped (Matsuura & Nishida 2000). The structure of these specialized setae indicates that the surface, e.g. prey and plants, has a smooth surface (Matsuura & Nishida 2000). This assumption can be concluded for the suction disc of the fossil specimens described herein (Fig. 3, 4A–D) and observed for branchiurans (Fig. 5B, F) and the exploration walk of cirripedes (Fig. 7; Lagerrson & Høeg 2002; Maruzzo et al. 2011). Furthermore, all true sucking structures are adapted for attachment to smooth surfaces either for parasitism, phoresy, predation and copulation or just to keep the position (Gorb 2001). The prominent appendage in the fossil specimens described herein could be applied for keeping their position onto the plants.

Water plants have been suggested to slow the water flow and raise the water turbulence, resulting in an increased residence time of possible nutrient particles (Gili & Coma 1998). Thus, the fossil specimens could take advantage of the slowed water currents caused by the plants by an increased duration of particles residence. Furthermore, plants have been proposed to provide a vertical substratum and new microhabitats (Barthel & Gutt 1992), offering new shelter and space. The fossil specimens could have been attached to the plants to prevent being floated and for a suitable spot for suspension-feeding in the same way as extant barnacles attach to corals, plants and other surfaces (Kolbasov 1993).

Many of the representatives of extant maxillopodans are parasitic. Furthermore, ascothoracidans have been proposed to attach to their hosts with different structures, e.g. claws at the antennula, claws at other mouthparts, attachment discs at different mouthparts, cement pads at the antennula, claws and spines at the shield (Grygier 1984). Notably, early ascothoracidan groups are not sessile and can move within their hosts (Grygier & Høeg 2005). Also the fossil specimens studied herein can move due to their functioning swimming legs. It has been proposed that the group Ascothoracida ―has survived through adoption of a parasitic mode of life" (Grygier & Høeg 2005, p. 150). Having this in mind and the close morphological similarity between the fossil specimen studied herein and representatives of extant Ascothoracida, the question arises if the described suction disc in the fossil specimens is such a possible adaption to a parasitic lifestyle.

The new details observed in *E. oviformis* stress the importance of the Devonian Rhynie and Windyfield chert. The high quality preservation of specimens from these Lagerstätten is exceptional and provides vital answers for early evolutionary questions. Also insights into

developmental processes, ecological circumstances and even interactions of animals with their environment are possible. All these aspects allowed the re-evaluation of *E. oviformis* in this study and lead to a more detailed morphological description and a stronger support for their phylogenetic placement. *E. oviformis* therefore represents not only one important finding for early non-marine crustaceans, but also the possible first non-marine thecostracans fossil.

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Author contribution
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Data archiving
Raw stereo images of all fossil specimens studied herein are deposited at MorphDBase under the access numbers: C-Nagler_EDIT-M29–M33 for slide M3703, C-Nagler_EDIT-M34–M39 for slide M3701, C-Nagler_EDIT-M40–M43 for slide M3704, C-Nagler_EDIT-M44–M50 for slide M3706, C-Nagler_EDIT-M51–M54 for slide M3707, C-Nagler_EDIT-M55–M57 for slide M3708, C-Nagler_EDIT-M58–M62 for slide M3711, C-Nagler_EDIT-M63–M75 for slide M3712, C-Nagler_EDIT-M76–M80 for slide M3715, C-Nagler_EDIT-M82–M83 for slide M3717, C-Nagler_EDIT-M64–M88 for slide M3718, C-Nagler_EDIT-M89–M94 for slide M3719, C-Nagler_EDIT-M95–M96 for slide M3720, C-Nagler_EDIT-M97–M107 for slide M3722¸ C-Nagler_EDIT-M108–M112 for slide M3742¸ C-Nagler_EDIT-M114–M124 for slide M3780¸ C-Nagler_EDIT-M125–M126 for slide M3798.

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Figures

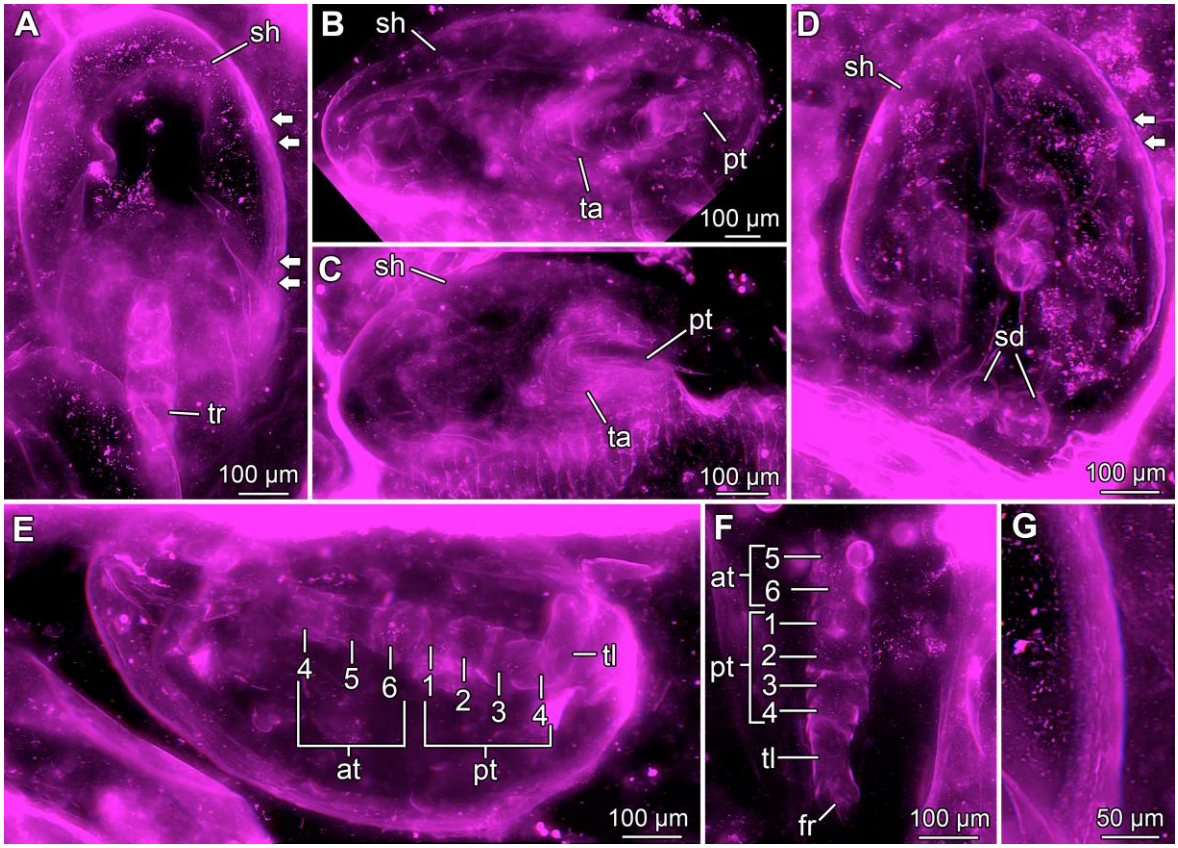

FIG. 1. General overview and body organization of *Ebullitiocaris oviformis*, stereo images; A, Dorsal view of shield and trunk; B, Latero-ventral view of insights into the shield, with trunk appendages and posterior trunk; C, Lateral view of shield, trunk appendages and posterior trunk; D, *E. oviformis* with shield and suction discs from an anterior angle; E, F, Dorsal view of trunk and telson; G, Detail of shield structure; at, anterior trunk; fr, furcal rami; pt, posterior trunk; sd, suction dics; sh, shield; ta, trunk appendages; tl, telson; white arrows, surface structure of the shield; at 4-6, anterior trunk segments 4-6 bearing appendages; pt 1-4, posterior trunk segments 1-4 without appendages.

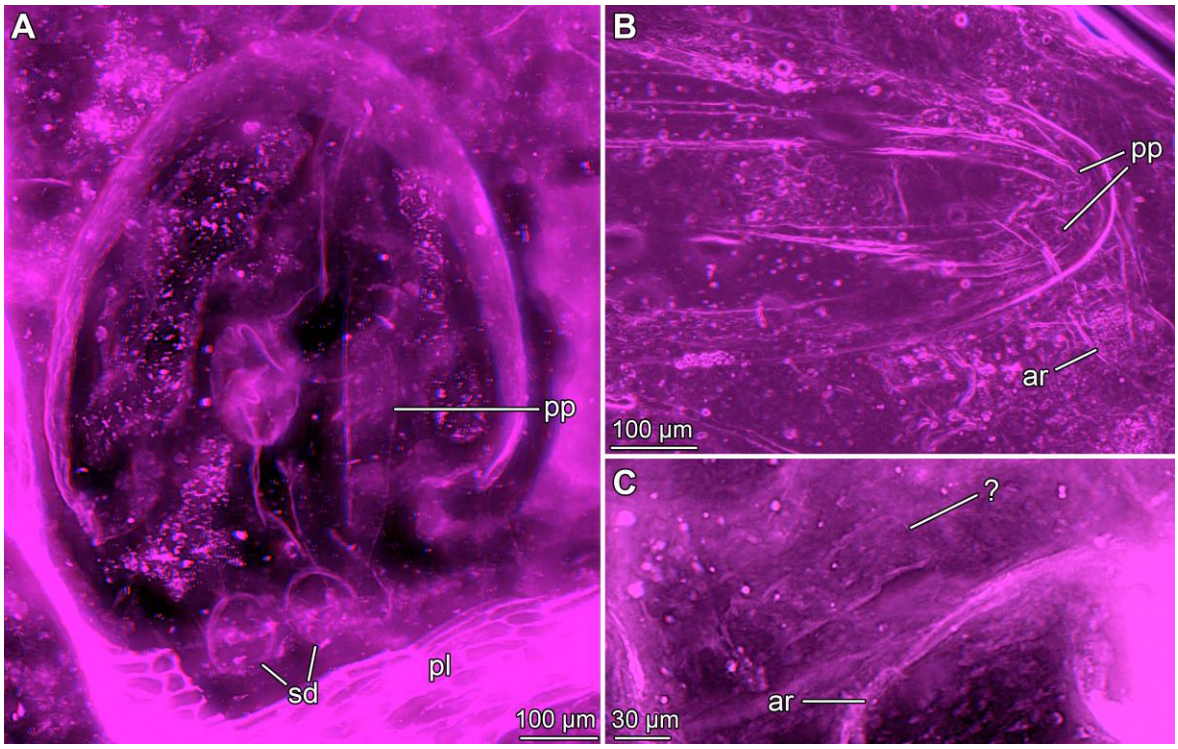

FIG. 2. Head appendages of *Ebullitiocaris oviformis*, stereo images; A, Anterior view of the head region of *E. oviformis* with suction discs and paraocular process (associated with plant material), same specimen as Fig. 1D, image taken from the other side of the slice; B, Head region of *E. oviformis* with paraocular process and articulation of one suction disc (find edges); C, Detail of the head region with unknown structure and parts of the articulation of one suction disc; ar, armored region; pl, plant material; sd, suction disc; te, tube-shaped extension; ?, third structure.

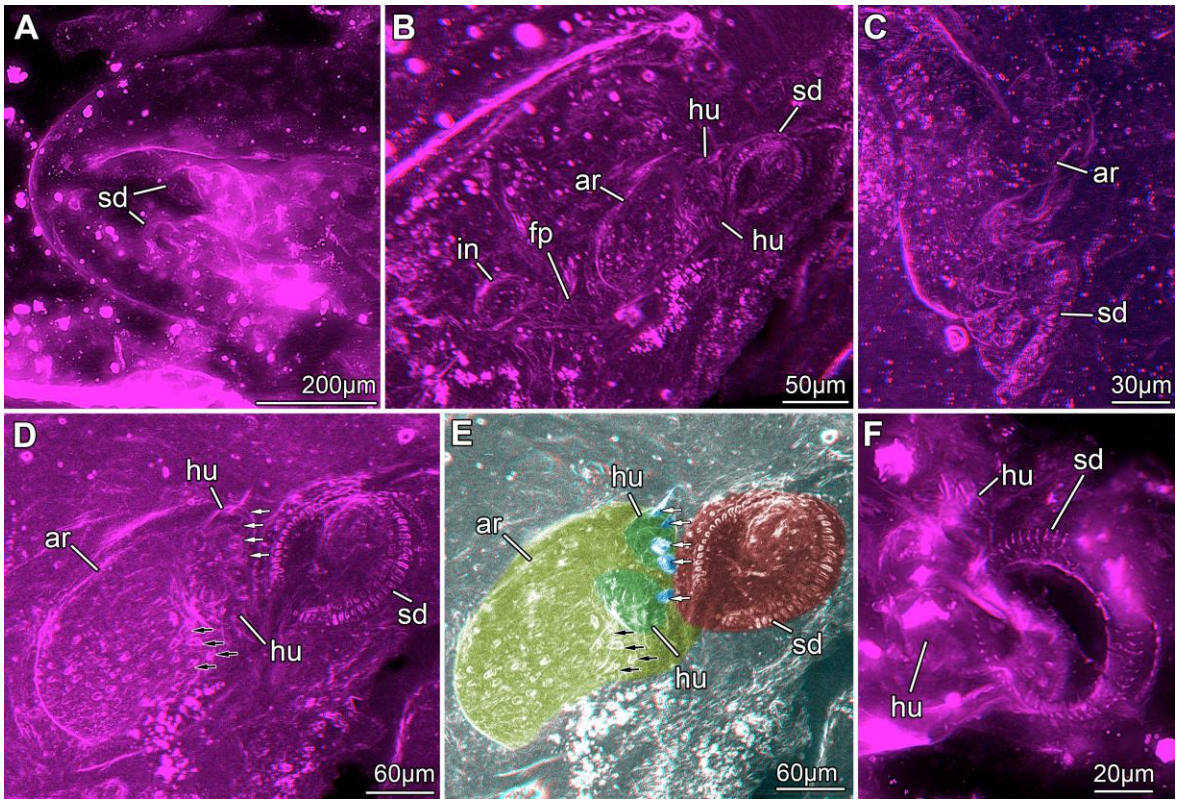

FIG. 3. Prominent appendage of *Ebullitiocaris oviformis*; A–D, F, Stereo images; E, Maximum intensity projection of *E. oviformis*; A, Head region of *E.is oviformis* with both suction discs; B, General organization of the prominent appendage with insertion area, functional peduncle, armoured region, humps and suction disc (find edges); C, Detail of prominent appendage with armoured region and suction disc (find edges); D, Detail of prominent appendage with armoured region, humps with setae and suction disc (find edges); E, Detail of prominent appendage (areas labelled) with armoured region, humps, setae and suction disc; F, Detail of prominent appendage with humps and suction disc; ar, armoured region; fp, functional peduncle; hu, hump; in, insertion area; sd, suction disc; black arrows, small spines on surface of armoured region; white arrows, setae; blue area, seta; green area, hump; red area, suction disc; yellow area, armoured region.

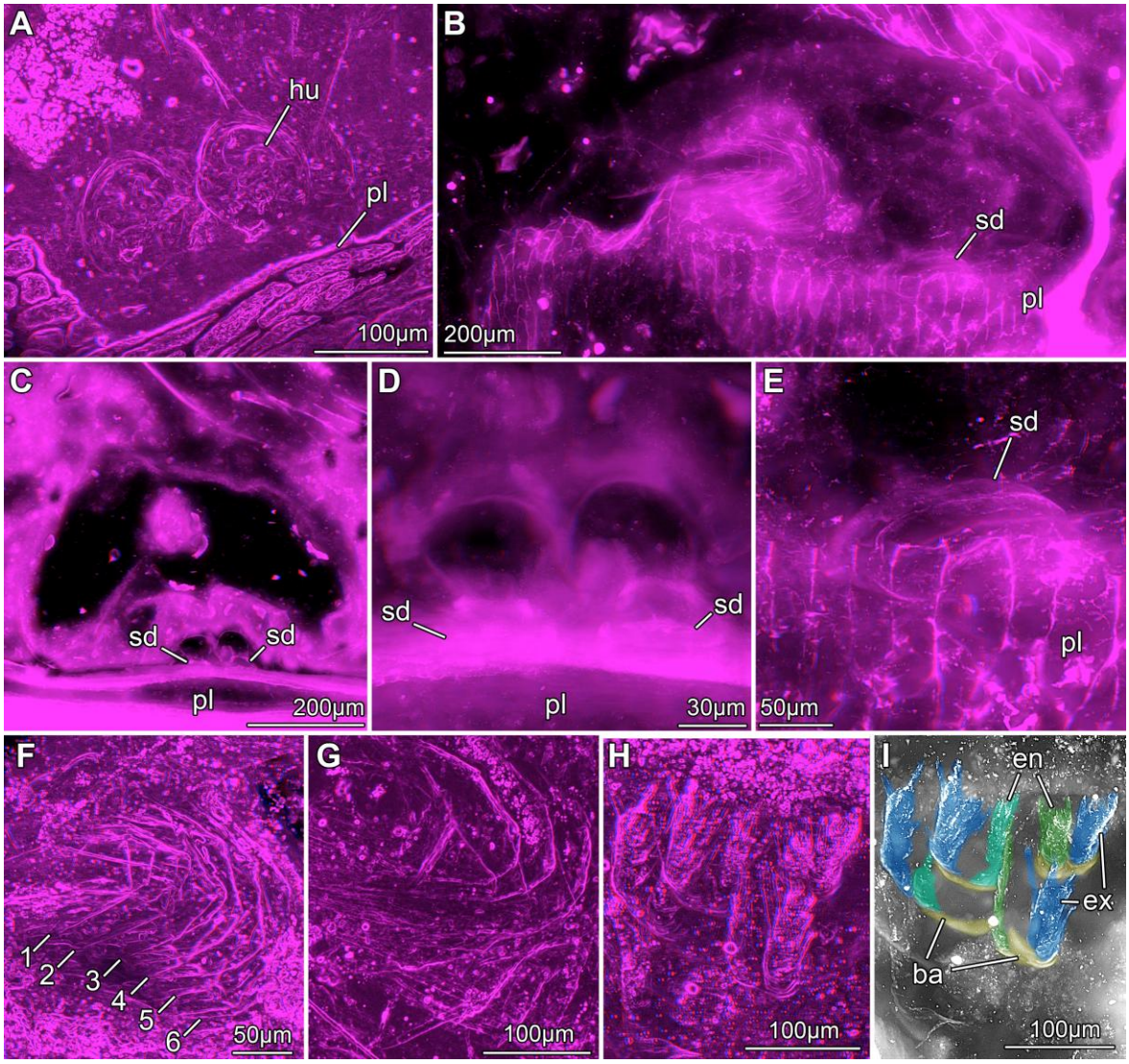

FIG. 4. Suction discs associated with plant material and trunk appendages of *Ebullitiocaris oviformis*; A–H, Stereo images; I, Maximum intensity projection; A, Detail of suction disc with humps associated with plant cells; B, *Ebullitiocaris oviformis* with one suction disc associated with plant material in lateral view; C, *Ebullitiocaris oviformis* with both suction discs associated with plant material in an anterior view; D, Detail of both suction discs associated with plant material; E, Detail of one suction disc associated with plant cells; F, Trunk appendages in lateral view (find edges); G, Detail of trunk appendages in lateral view (find edges); H, Detail of trunk appendages in ventral view (find edges); I, Labelled trunk appendages in ventral view; ba, basipod; en, endopod; ex, exopod; hu, hump; pl, plant material; sd, suction disc; blue area, exopod; cyan and green areas, endopods of different appendages; yellow area, basipod; 1-6, anterior trunk segments 1-6 bearing appendages.

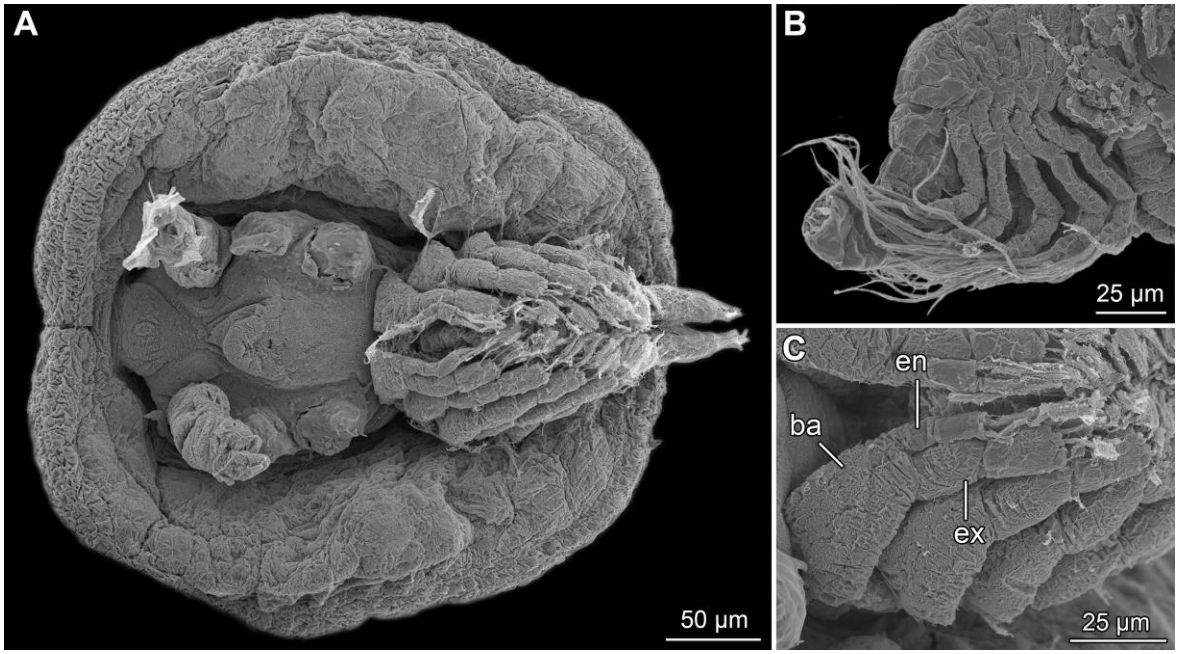

FIG. 5. Comparison to Ascothoracida, scanning electron microscope images; A, *Ulophysevma* sp. in ventral view with antennula, antenna, mandible and trunk appendages; B, Trunk appendages of *Ulophysema* sp. in lateral view; C, Detail of trunk appendages of *Ulophysema* sp. with basipod, exopod and endopod; ant, antenna; atl, antennula; ba, basipod; en, endopod; ex, exopod; mdb, mandible; ta, trunk appendages.

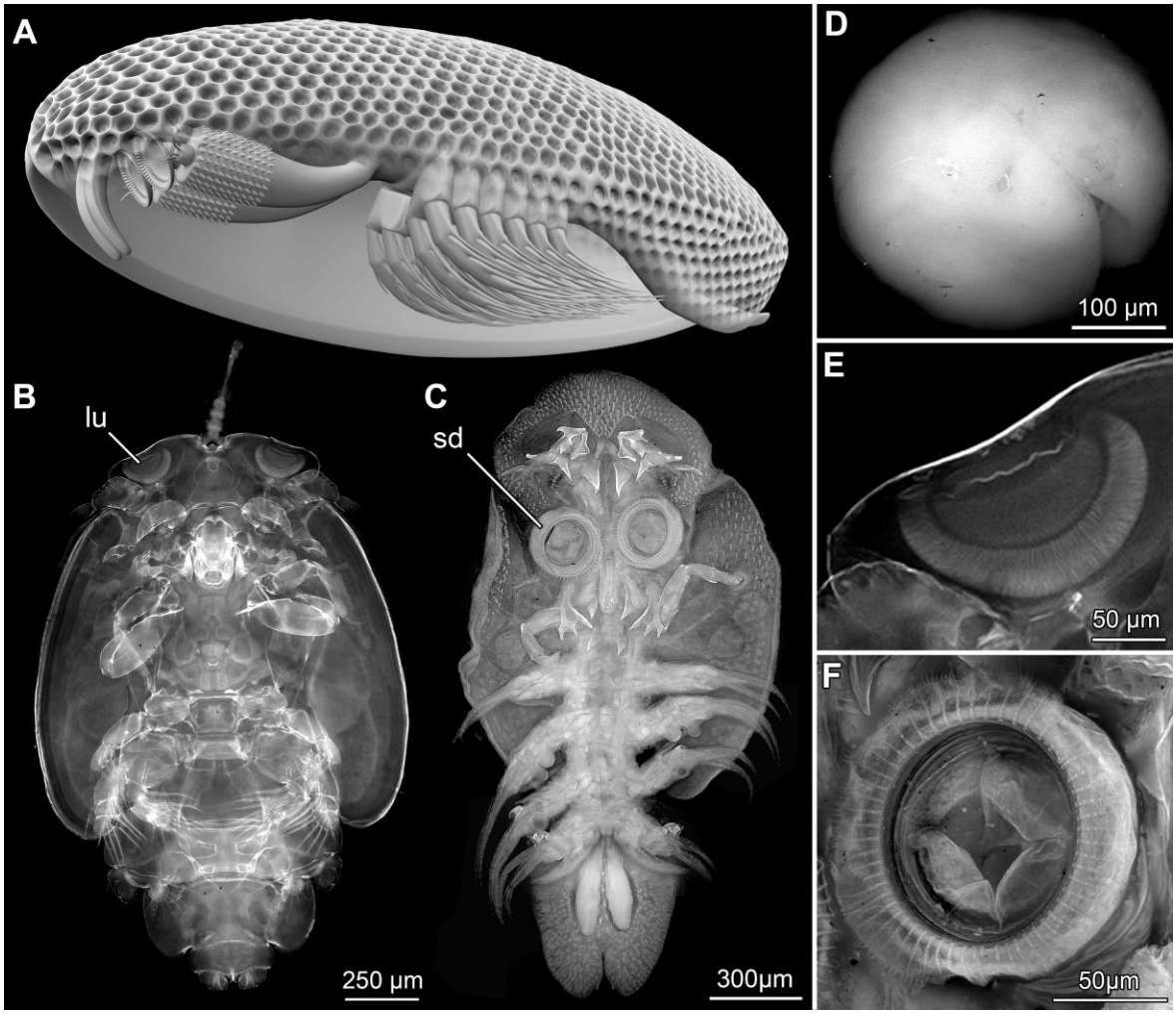

FIG. 6. Reconstruction of *Ebullitiocaris oviformis* and comparison to other metazoans; A, Model of *Ebullitiocaris oviformis*; B–F, Fluorescence images; B, *Caligus* sp. (Copepoda) in ventral view; C, *Argulus foliaceus* (Branchiura) in ventral view; D, *Ascothorax gigas* (Ascothoracida) in dorsal view; E, Detail of copepod lunulae; F, Detail of suction disc of *Argulus foliaceus* (Branchiura) in ventral view; lu, lunulae; sd, suction disc.

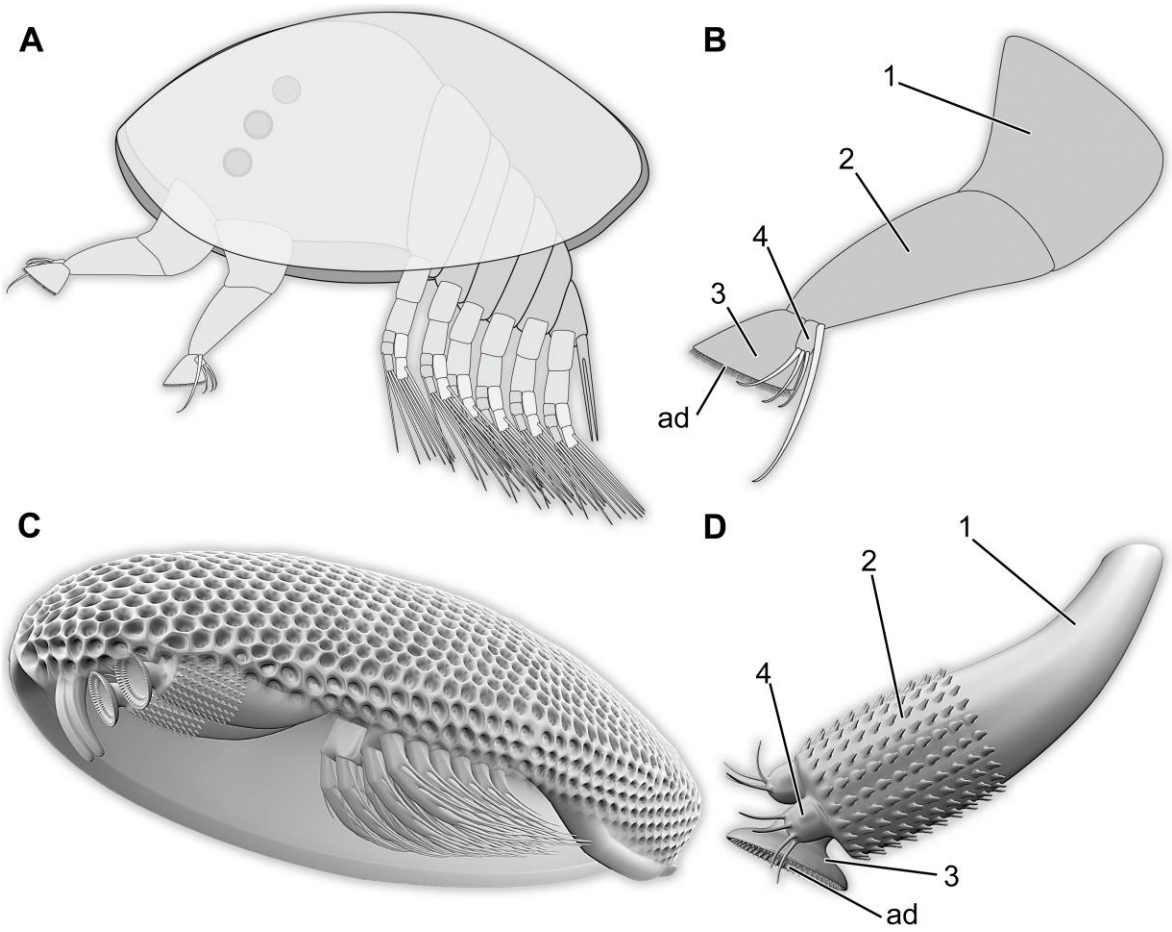

FIG. 7. Cirripede cypris and reconstruction of *Ebullitiocaris oviformis in comparison*; A, Drawing of cypris larva of Cirripedia, lateral view. B, Detail drawing of antennula of cirripede cypris, redrawn after Høeg & Møller (2006, fig. 7b). C) Model of *E. oviformis*, lateral view. D) Detail model of second structure, presumably antennula of *E. oviformis*. Not to scale. 1–4 indicating 1–4 elements of the antennula, ad, attachment device.

3.5 PAPER IX: Nagler et al. in prep b

Nagler C, Wagner P, Olesen J, Kerp H, Hagen H, Waloszek D, Haug JT, Haug C New maxillopodan nauplius from the Rhynie Chert. In preparation, *Palaeontology*.

Re-evalution of nauplius larvae from Rhynie Chert supports a phylogenetic affinity to Thecostraca

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Abstract
Crustacean larvae are still rarely reported in the fossil record. However, some fossil marine and non-marine environments reveal frequently crustacean larvae. Chert Lagerstätten are known for their abundance of branchiopod larvae. Yet, different naupliar larvae with a possible maxillopodan affinity have been reported from chert. By using advanced imaging methods, this study describes new morphological details of these naupliar larvae, such as a small canal posterior to the mouth opening and maxillular limb buds. By measuring morphometric characters, this study adds a further naupliar stage (stage IV) to the described ones (stages I-III). Furthermore, the fossil larvae are compared to naupliar larvae from probably closely related groups, e.g. fossil *Bredocaris admiribilis*, extant Copepoda, extant Thecostraca and extant Branchiopoda. The comparison, as well as the additional morphological characters, supports a close affinity to the parasitic Ascothoracida.

Introduction
Notably, crustacean larvae represent still a rarity in the fossil record (Haug et al. 2014a, Haug et al. 2012, Haug et al. 2014b). A great diversity and abundance of exceptionally preserved fossil crustacean larvae is known from the Orsten. Beside others, larvae of the early lineage towards modern eucrustaceans (Mueller & Walossek 1986, Walossek & Mueller 1990, Mueller et al. 2009, Haug, et al. 2009a, Haug et al. 2010a, Haug et al. 2010b) as well as larvae of the likely thecostracans representatives *Bredocaris admiribilis* Mueller & Walossek 1988 and *Wujicaris muelleri* Zhang et al. 2010 have been reported from the Cambrian (about 500 mya and 520 mya respectively) and additionally a closer relationship to Maxillopoda has been proposed (Mueller and Walossek 1988, Walossek 1993, Zhang et al. 2010). Furthermore, barnacle larvae have been reported from the Devonian (400 mya) and the Jurassic (150 mya) (Briggs et al. 2005, Nagler et al. 2017) and an ostracod larva from the Jurassic (150 mya) (Gramann 1962).

A special crustacean larva is the phyllosoma larva of achelatan lobsters. These giant phyllosoma larvae, which can reach body length up to 100 mm, despite their size, show a high preservation potential and are common in the limestone of Solnhofen from the

Jurassic (Polz 1971, Polz 1972, Polz 1973, Polz 1984, Polz 1987, Polz 1995, Haug et al. 2011a, Haug et al. 2013, Haug & Haug 2013). Additionally one specimen was described from the Cretaceous from Brazil (Tanaka et al. 2009). From the same Lagerstätten larvae of stomatopods, crabs and polchelidan lobsters have been reported (Haug et al. 2008, Haug et al. 2009b, Haug et al. 2010a, Haug et al. 2015a, Haug et al. 2015b, Luque 2015, Eiler & Haug 2016, Haug & Haug 2017). Recently, the first fossil peracarid larvae have been described from Cretaceous amber (Serrano-Sánchez et al. 2016, Néraudeau et al. 2017).

Notably, most representatives of Eucrustacea *sensu* Walossek (1999) occur exclusively in marine environment. Only some crustaceans, e.g. copepods, ostracods, branchiopods und numerous lineages of malacostracans inhabit non-marine environments (Schram 1986). A detailed preservation-potential is especially important to get a hint for the systematic position of crustaceans that inhabited the non-marine environments of chert. Beside the fossil representatives of *Lepidocaris rhyniensis* Scourfield 1926 and *Castracollis wilsonae* Fayers & Trewin 2003, two species of *Ebullitiocaris*, *E. oviformis* Anderson et al. 2003 and *E. elatus* Womack et al. 2012 have been found in chert. These fossil crustaceans have been considered as branchiopods, probably due to an ~~–e~~nvironmental bias". Additionally, eucrustacean, non-branchiopod nauplii, probably closely related to maxillopods have been reported from the Devonian Rhynie and Windyfield chert (400 mya) (Haug et al. 2012, Haug et al. 2014c). These specimens represent the earliest known non-marine crustaceans. We present here new material of naupliar larvae from the same location. Due to the exceptionally well preservation of the specimen, we add new morphological details with this study. Additionally, the specimen reported herein can be linked to an adult (Haug et al. in prep). With our material we can build on the proposed discussions about the phylogenetic position (Haug et al. 2012, in prep, Nagler et al. in prep a) and provide an evolutionary reconstruction of maxillopod larvae excluding branchiurans, tantulocarids, pentastomids and mystacorids.

Material and Methods

Material

Fossil Material

Specimens of larvae are preserved in chert samples from the Windyfield locality, near (700 m northwest) the village of Rhynie, Aberdeenshire, Scotland. The chert was cut into thin slices of approximately 50–150 µm and these were polished on both sides and glued on unfrosted glass slides for studying with a light microscope (Hass & Rowe 1999). The investigation included three thin sections containing probably between 10 and 14 specimens, most of them being fragments representing single legs or leg assemblages; only in rare cases whole animals are preserved. The micro slides have been assigned to the collection numbers G_2010_16, G_2004_2822 and G_2004_2823 and are deposited in the Science Collections of the National Museum of Scotland, Edinburg, Scotland.

Microscopy, documentation and image processing

The specimens were studied using a Zeiss Axioskop 2 and documented using an AxioCam digital camera. Objectives used were either of 10×, 20× or of 40x magnification, resulting in 100×, 200× or 400x magnification.

The specimens were documented by using a technique referred to as 'optical tomography' (Sutton 2008, see also Haug et al. 2009c, 2012). As the fossils extend to a

certain depth into the matrix, a stack of single images (=frames) in different focus layers was recorded for each specimen, the first frame at a level slightly above the specimen and the last frame at a level slightly below it. The camera then recorded a frame every 1 µm in z-axis, resulting in image stacks of up to 130 single frames.

These stacks were processed with free available software. Due to the three-dimensional preservation of the specimens within the chert three-dimensional images were created to prevent loosing information, because two-dimensional images do not provide enough information neither for the orientation of the specimen within the matrix nor for their morphology. Image J was used to find sharp edges within every frame of the stack. These stack were projected in three dimensions from which stereo images were produced with the program Osirix 5.8.2b. For specimens located deep within the matrix an alternative method was applied, using „minimum intensity projection" or „maximum intensity projection", to get the best possible result (for a detailed description of this method see Haug et al. 2012). The resulting images were finally processed (level, sharpness, saturation) in Adobe Photoshop CS2 (Figs. 1-3). Stacks of images were processed with the freeware packages CombineZP (Alan Hadley), ImageAnalyzer (Meesoft) and ImageJ (Wayne Rasband).

Measurements

Measurements of the specimen were obtained following the method of Haug et al. (2012). The produced stereo images and in some cases the plain minimum/maximum intensity projections, depending on where the structures could be detected in the best way, were used. Measurements were performed using the measuring instrument of Adobe Acrobat 7.0 Professional (values were rounded the following way: $x < 2.5 \rightarrow 0$, $2.5 \geq x < 7.5 \rightarrow 5$, $7.5 \geq x < 12.5 \rightarrow 10$ …). Four different measurements were taken:

- diameter of the antennal exopod (d2, N=15) and endopod (d3, N=7),
- length of the antennal coxa (in median-lateral axis) (l, N=11)
- diameter of the mandibular exopod (d1, N=9)

Additionally, the diameter of exopods with unclear affinities (exopods which could not be subscribed to antenna or mandible, N=14), the diameter of the antennal coxas hight (in proximal-distal axis, N=3) and the diameter of the mandibular endopod (N=4) were measured.

Limitations of the measurement method:

Due to the three-dimensional preservation of the specimens within the matrix, measurements in a two-dimensional orientation in most cases do not provide reliable results. This makes it difficult to measure for example the length of a bended exopod that expands in three dimensions. Thus, performed two-dimensional measurements would always miss the distance of the third dimension of the structure and thus, are not reliable. To measure the length of an exopod it is necessary that this structure of a specimen is orientated from proximal to distal in a 90° angle to the light beam of the microscope. Only, such an orientation allows to measure the length using a two dimensional measuring technique, but as explained above most of the structures described herein are preserved three-dimensional. To obtain reliable values for the diameter of the coxa of the antennula and exopod and endpod of the antenna and the mandible, the distance was measured at the proximal part in each case.

However, circular cross sections (which represent a two-dimensional structure) of exopods and endopods allow measurements of the diameter of these. These elliptical sections (exopods not sectioned orthogonal to the proximal-distal axis) allow a plain measurement of the diameter. In such cases the minor axis, which is the shortest diameter was measured. Also length of the coxa could be measured, given that the coxa is orientated in the right way. Due to preservation and diagonal sections of the coxa it was not possible to measure the height of the coxa, like Haug et al. (2012) did.

Processing of data

Measurements were collected and plotted (d1/d2, d3/d2, d2/l) using the spreadsheet application (Calc) of Apache OpenOffice 4.1.3. Additionally the data collected by Haug et al. (2012) were added to the spreadsheet and to the plots for comparison (Fig. 4). Finally clusters were positioned equally to the mean value of each cluster.

Drawings

Drawings of the antennula, antenna and the mandible of all specimens were performed in Adobe Illustrator CS2. Images were electronically tracked using a graphic tablet (Cintiq 12 WX, Wacom), an electronic pen (Wacom Inkling MDP—123), and the software Adobe Creative Suite 2, according to the protocol of Coleman (2003). Drawings were finally optimized in Adobe Illustrator while comparing directly to the original.

Stratigraphy

Information on the geology, sedimentology and setting of the Lagerstätte Rhynie chert can be found in Rice et al. (2002) and Trewin & Rice (2004). Based on palynomorph assemblages (Richardson 1967), radiometric dating (Rice et al 1995) and spores (Wellman 2006) the age of the chert generally is considered to be Pragian (Early Devonian). Based on radiometric studies , a hydrothermal system has been proposed to be responsible for the formation of the Rhynie cherts (Mark et al. 2011).

Results

Size cluster

Diameter of the mandibular exopod (d1) versus the diameter of the antennal exopod (d2)

The measured specimens lie within four size clusters. Cluster 1 includes 1 specimen, cluster 2 includes 2 specimen, cluster three includes 4 specimen, cluster 4 includes 1 specimen (Fig. 4A).

Diameter of the antennal endopod (d3) versus the diameter of the antennal exopod (d2)

The measured specimens lie within three size clusters. By comparing the clusters with the one formed by the plot d1/d2, they begin in the second size cluster. Cluster 2 includes 1-2 specimen, cluster 3 includes 2-3 specimen, cluster 4 includes 3 specimen (Fig. 4B).

Diameter of the antennal exopod (d2) versus the length of the antennal coxa (l)

The measured specimens lie within three size clusters. By comparing the clusters with the one formed by the plot d1/d2, they begin in the second size cluster. Cluster 2 includes 4 specimens, cluster 3 includes 2 specimens, cluster 4 includes 3 specimens (Fig. 4C).

Amended description:
Following Haug et al. (2012), who provided a detailed description of the morphology of the naupliar larvae, we herein describe gross morphological features and add new morphological details. None of the specimens examined is entirely preserved; all specimens only show different parts of the nauplius. In some cases it was not possible to assign pieces of exopods to antennula or mandible (Figs. 2F, 3D, G, H).

Overall morphology
The anterior margin of the body seems to be rounded (Figs. 1A, B, 2A, C, 3I). The anterior region of a cephalic shield seems to be as wide as the maximum body width and slightly domed, made of cuticle with small, similar sized and regular indentations (Fig. 1H). The rest of the shield is not accessible. The posterior end of the fossil specimen is not accessible.

Structures
Labrum (Figs. 1A, B, 2A, C, E, G, 3I): Labrum prominent, wide and elongated; slightly covering the mouth opening (Figs. 1B, F, 2A, 3C, I).

Pair of appendages of post-ocular segment 1 (antennula, Figs. 1A, B, G-J, 2D, G): Situated antero-lateral to the labrum, uniramous, comprising at least seven elements, similar shape and more or less equally long (Fig. 1H). Insertion area not accessible. Two most proximal elements without setae. Third to sixth elements with possibly one seta. Four, possibly five terminal setae on seventh element.

Pair of appendages of post-ocular segment 2 (antenna, Figs. 1A-D, G-J, 2A, C-E, G, 3A, B, E, F): Antenna situated posterolateral to labrum, biramous, with coxa, basipod, endopod and exopod. Coxa articulated with body, its cross section more or less oval. Coxa with two median spines (naupliar process, Figs. 1C, D). Basipodit oval, in diameter smaller than coxa, with two slender spines. Endopod comprising three elements, with the first one being the largest, the third one being the smallest, with four setae at the distal element. Exopod comprising 12 elements or annuli, getting smaller distally, each carrying one seta, small spines at the base of each element and additionally with four to five very small spines at the basis of each seta. Terminal element with additional terminal setae.

Pair of appendages on post-ocular segment 3 (mandibles, Figs. 1A, B, E-G, 2C, D, 3A, B, E, F, I): Mandible situated posterior to antenna, biramous, with coxa, basipod, endopod and exopod. Coxa articulated with the body, with oval shape but not as elongated as the antennal coxa. In cross section flattened in longitudinal axis. Coxa with three spines medially. Basipod with four spines medially, ovaly shaped, smaller than coxa. Endopod comprising one element with at least four setae terminally. Exopod comprising at least seven elements or annuli getting smaller distaly, Setation similar to antennal exopod, but with two short and two long setae at the tip, small spines at the base of each element and additionally with four to five very small spines at the basis of each seta. (Figs. 2C, 3I).

Pair of morphological structure posterior to the mouth opening (Fig. 3I): semioval plate with continuous edge, pair forming a small canal, which extends posteriorly.

*Pair of appendages of post-ocular segment 4 (*maxillula, Figs. 1A, B, E, F, 2A, B): Knob-like structures slightly posterior and median to the mandible, with two small setae and a small rounded endit with an additional seta. (length without setae = 35µm, width = 25µm, length of endit = 15µm, width of endit = 15µm, length of setae ≈ 20 µm)

Discussion

Interpretation of size clusters

Most arthropods have to molt to increase in size (Chang et al. 1993, Hopkins 2001, Fusco et al. 2003). In naupliar larvae molting is linked to molting stages or instars (Jones 1978, Fink 1983, Martin et al. 2014). Hence, our results in combination with the results in Haug et al. (2012) show four clusters which we interpret as representing four size classes of naupliar larvae (Fig. 4).

Brooks's law states that during early development, growth factors should be approximately constant (Fowler 1909, Gore 1985, Kutschera et al. 2012). In other words, between the different growth stages should be approximately the same increase of size, if the four detected size clusters represent consecutive growth stages. However, a significant gap between stage three and four seems to be larger than between stage one and two and stage two and three (Fig. 4). This could indicate another stage, not being represented in the material, laying between stages three and four, filling this gap. Subsequently, the stage described herein as stage four would be stage five, following the ~~"m~~missing" stage. Therefore we calculated the growth factors between the four stages using the mean diameter of the antennal and mandibular exopod as well as the antennal endopod for each stage (assuming the new stage represents stage four and not five; Tab. 1).

Tab. 1: Growth factors between stages one to four for diameters of different appendages.

	Growth factor between stages 1 and 2	Growth factor between stages 2 and 3	Growth factor between stages 3 and 4
ø of mandibular exopod	1.34	1.33	1.26
ø of antennal exopod	1.38	1.28	1.32
ø of antennal endopod	1.36	1.34	1.23

The growth factors nearly stay the same (around 1.3) between all four stages, even being slightly smaller between stages three and four regarding the mandibular exopods and antennal endopods diameter. Assuming a missing stage, like described above, and a constant growth factor following Brock`s law, stage 5 should be larger. Thus, it is most likely that the fossil specimen of the larger size represent a fourth growth stage, following stage one to three already described by Haug et al. (2012). By comparing the results of the first size cluster, calculated herein, to embryos that can be definitely linked to the fossil nauplius larvae, described herein (Haug et al. in prep.), it is unequivocal that the first size cluster represent the first free living nauplius larva.

Interpretation of morphological structures

It is well known, that the consecutive naupliar stages of Maxillopoda are similar to each other (Newmann 1983, Haug & Haug 2015). This is also the case in our example. As already described, the three first growth stages, stage 1-3, are morphologically similar to each other (Haug et al. 2012). In contrast, the fossil specimens of stage 4 show some new morphological characters. Besides a larger number of elements in the antennula and mandibular exopod, following characters have been observed:

(1)Pair of morphological structure posterior to the mouth opening: Representatives of growth stage 4 show a pair of morphological structure posterior to the mouth opening, which forms a small canal, extending posteriorly (Fig. 3I). They could be interpreted as plate of the post-ocular segment 3, where also the mandible is situated. This canal has not been described before by Haug et al. (2012) and is not apparent in specimens of stages one to three. The canal is located posteriorly to the mouth opening and possibly is incorporated in food processing. The shape of the canal may allow a better transportation of food particles from posterior regions towards the anterior situated mouth opening. Forming those structures for the transportation of food particles is a common feature and are known from several lineages within the arthropods, for example within the cephalocarids (Sanders 1963) and trilobites (Fortey & Owens 1999, Hegna 2010) but also from non crustacean lineages for example from gastropods (Yonge 1946, Strathmann et al. 1972, Romero et al. 2010). Within Eurustacea, branchiopods show a very distinct food processing structure. They possess a postmandibular filter-feeding apparatus showing a sternitic food groove. This deep food groove is V-shaped and allows the transportation of food particles driven by the beat of the limbs (Walossek 1995, Fortey & Owens 1999, Dumont & Negrea 2002). We cannot clearly state which structure forms the canal in our specimens. It is not V-shaped as described for Branchiopods (Walossek 1995) and rather short. We think the canal does not represent a real food groove, like in branchiopods but rather represents a functional protrusion of the mouth opening allowing a better processing of food.

(2) Pair of appendages of post-ocular segment 4: The two knob like shaped humps, each carrying two distal setae and an endit with an additional pair of setae, following antennula, antenna and mandible are the fourth appendage of the nauplius (Fig. 1A, B, E, F, 2A, B). As seen in representatives of the fossil *B. admiribilis* (5 instars, Müller &Walossek 1988), of extant Facetotecta (5 instars, Ito 1990, Ponomarenko & Korn 2006, Høeg et al. 2014a), Ascothracida (up to 6 instars, Grygier 1984, Høeg et al. 2014b) and Copepoda (6 instars, Huys 2014), the fourth nauplius stage shows always a knob-like structure with two setae, similar to the fossils specimen described herein (Grygier 1984, 87a, Ito 1986, Dahms 2004, Müller & Walossek 1988). Position and morphology of this structure argues for representing the anlagen of the maxillula, again as seen in other thecostracans groups. Furthermore, the structure is not apparent in growth stage 1-3 althought he region is usually well preserved. There it seems likely and firstly appears in growth stage four. Notably, such a pattern is known as limb bud delay (Grygier 1987b, Newman 1992, Walossek 1995, Haug & Haug 2015). Concerning this ontogenetic pattern, it is likely that these fossil naupliar larvae show a limb bud delay, similar to that in (other) thecostracans (see below).

Possible limb bud delay?

Limb bud delay describes a condition, where the development of naupliar posterior segments is more advanced than the development of the appendages (Walossek and Müller 1998; Haug & Haug 2015). One segment is added per molting stage in the ancestral pattern of Eucrustacean nauplius development. This segment shows a pair of limb buds, which develop to appendages in the next molting stage. The following molting stage again shows a new segment, again with limb buds (Grygier 1987b, Haug & Haug 2015). However, the fossil naupliar larvae described herein show a limb bud delay by adding one segment per molting stage without developing already limb buds. These are delayed and are developed in later molting stages (Haug & Haug 2015). Hence, segments are visible in earlier stages, but without limb buds. This pattern is only known from representatives of Maxillopoda (Newman 1983, Grygier 1987b, Walossek and Müller 1998; Høeg et al. 2009; Haug et al. 2011b). The ontogenetic pattern of Branchiopods in general is very gradual and does not show a limb bud delay (Claus 1873, Pai 1958, Martin 1992, Fryer 1996, Møller et al. 2003, 2004, Olesen & Grygier 2003, 2004, Pabst & Richter 2004, Olesen 2005, Haug & Haug 2015). Thus, the pattern seen here in the fossil specimens strongly points towards an assignment to the Maxillopoda.

Further support for phylogenetic interpretation

Due to the overall morphology and the detected limb bud delay, we will compare the fossil specimens described herein (Fig. 5G) to representatives of some groups within Thecostraca; the fossil *B. admiribilis* (Fig. 5A), Copepoda (Fig. 5B), Facetotecta (Fig. 5C), Ascothoracida (Fig. 5D) and Cirripedia (Fig. 5E). Most crustacean larvae found in chert were described to represent Branchiopods (Trewin et al. 2003, Scourfield 1926, 1940, Anderson et al. 2003, Fayers & Trewin 2003, Dumont & Negrea 2002, Lindholm 2014). Hence we will compare the fossil specimens described herein to representatives of Branchiopoda (Fig. 5F), additionally. For this comparison we took one representative of each group. We are aware of generalizing in respect to numbers of setae, segments, ringlets and more, because the variation within one group can be very large, e.g. in copepods.

Branchiopoda

First of all, representatives of Branchiopoda develop directly, similar to the supposed eucrustacean pattern by adding segments step by step and not via a limb bud delay (Claus 1873, Pai 1958, Martin 1992, Fryer 1996, Møller et al. 2003, 2004, Olesen & Grygier 2003, 2004, Pabst & Richter 2004, Olesen 2005, Haug & Haug 2015). This argues most against a branchiopod affinity of the fossil specimen described herein (see above). Additionally, naupliar representatives of Branchiopods bear always short and non-elemented antennulae (Figs. 5F, 6F, Olesen 1999, Olesen & Høeg 2014) in contrast to longer antennulae with elements in the fossil specimen described herein (Fig. 6G). Furthermore, naupliar representatives of Branchiopoda possess large antennae with a very large naupliar process with two characteristic setae originating from the coxa (elongated part of the coxa with setae, used for feeding) and in which the length of the basipod together with the coxa is more than twice as long as the entire limb (Figs. 5F, 7F; Møller et al. 2003). This is different to the pretty short coxa and basipod in z-axis in representatives of the fossil specimen described herein (Fig. 7G). Branchiopod naupliar larvae bear mandibles with a very short endopod (Figs. 5F, 8F; Møller et al. 2004, Olesen 2005,

2007). Although the endopod in the fossil specimen described herein is short in relation to the exopod (Fig. 8G), a branchiopod affinity is rather unlikely due to the different morphological characters described above.

Maxillopoda

In the following we will discuss the crucial appendages (antennula, antenna, mandible, maxillula) from anterior to posterior:

Antennula: B. admiribilis has an antennula with many segments (Fig. 6A, Müller & Walossek 1988). Grygier (1987b, c) has proposed that representatives of the ground pattern of Thecostraca show an antennula with eight elements as in certain outgroups (e.g. in mystacocarids). Only representatives of Ascothoracida show either eight or many more elements in the antennula (Fig. 6D, Grygier 1984, 1987b, c). Representatives of Facetotecta (Fig. 6C) and Cirripedia (Fig. 6E) bear always six elements in their antennula (Grygier 1987b, Ito 1986, 1987, Anderson 1965, Yan & Chan 2001, Moyse 1984, Høeg & Møller 2006). In contrast, the antennula of representatives of Copepoda bear less segments and a very short coxa (Fig. 6B, Dahms 1990, 2004). Thus, the morphology of the antennula in the fossil specimens described herein with at least seven similar shaped elements with several setae (Fig. 6E) argues for close relationship to Thecostraca. Besides the number of and ratio between antennular elements, the two proximal elements of the antennula bear no setae in representatives of Thecostraca and *B. admiribilis*, as well as in the fossil specimen described herein, contrary to representatives of Copepoda (Figs. 6A-E, G).

*Antenna:*Antennae of the groups for comparison are all biramous: coxa and basipod bearing an endopod and exopod (Figs. 7A-G). The coxa of representatives of *B. admiribilis* is stout and two times as long as the basipod (Fig. 7A, Müller & Walossek 1988). This is also the case in the fossil specimen described herein (Fig. 7G, Haug et al. 2012). In contrast, the coxa of representatives of Copepoda is much smaller than the basipod (Fig. 7B, Dahms 1990). The coxa of representatives of Thecostraca is roughly as long and wide as the basipod (Figs. 7C-E, Izawa 1986, Grygier 1984, Yan & Chan 2001, Moyse 1984). Notably, most of the groups discussed herein show two setae at the coxa (Fig. 7). This ~~"n~~aupliar process" is presumably important for the feeding process and therefore important for planctotrophic species (Fritsch et al. 2013, Dahms et al. 2006). Due to the inconsistency of the morphology of this process (Dahms 1991, 2004, Fritsch et al. 2013, Semmler et al. 2006), we will not focus on this character. However, this process seems to be similar in representatives of *B. admiribilis* (Fig. 6A), Thecostraca excluding Facetotecta (Figs. 7D-E) and in the fossil specimen described herein (Fig. 7G).

More crucial seems the length and elemental ratio between the endopod and the exopod. In contrast to all other group discussed herein, representatives of Copepoda show one element in the endopod and at least four in the exopod (Fig. 7B, Dahms 1991, Dahms et al. 2006, Izawa 1986, 1973). In representatives of *B. admiribilis*, Facetotecta, Ascothoracida, Cirripedia and the fossil specimen described herein show a different pattern with at least two, but not more than three elements in the endopod and several elements in the exopod (Figs. 7A, C-E, G; Grygier 1987a, b, 1991, Haug et al. 2012, Müller & Walossek 1988, Hoeg et al. 2004, Ito 1986, 87). Following Hoeg et al. (2004, 2009) and

Grygier (1987c), bearing not more than three elements in the antennal endopod is one of the characterizing traits of representatives of Thecostraca. However, the state in representatives of Facetotecta with two endopodal elements is apomorphic (Fig. 7C, Grygier 1987b, 1991).

Concerning the morphology of the antennal exopod, *B. admiribilis*, representatives of Thecostraca and the fossil specimen described herein show many exopodal elements (Figs. 7a, C-E, G) in contrast to at maximum four elements in representatives of Copepoda and Branchiopoda (Figs. 7B, F). Taken together the antenna of the fossil specimen described herein (Fig. 7G) (supports a sistergroup relationship to) is most similar to that of representatives of Ascothoracida (Fig. 7D)

Mandible: Mandibles of the groups for comparison are all biramous: coxa, and basipod bearing an endopod and exopod (Figs. 8A-G). The coxa of representatives of *B. admiribilis* is prominent and robust, medially extended into large gnathobase, already in the first naupliar stage (Fig. 8A, Müller & Walossek 1988). Only representatives of Branchiopoda show also a distinct gnathobase (Fig. 8F). Representatives of Copepoda (Fig. 8B), Facetotecta (Fig. 8C), Ascothoracida (Fig. 8D) and Cirripedia (Fig. 8E) bear a coxal, which is similare to the antennal coxa in shape and relation to the basipod. In contrast to the antennal coxa, the mandibular coxa in these groups bear no masticatory process with two setae, but some are armored with one seta. The coxa of the fossil specimen described herein (Fig. 8G) seems to be medially extended, but less than in *B. admiribilis*. Additionally, the fossil specimen described herein show three spines medially at the coxa. With this, the fossil specimens described herein share a median extension of the coxa with *B. admiribilis* and the ratio between the coxa and basipod with Copepoda, Facetotecta, Cirripedia.

Again the number of elements in the endopod and the ratio between the endopod and exopod seems to be characteristic for representatives of Thecostraca. Grygier (1987b, 1991) has proposed that an endopod with three elements represents a plesiomorphic condition for representatives of Thecostraca and Copepoda. This character is retained in *B. admiribilis* (Müller & Walossek 1988), Ascothoracida (Grygier 1984, Ito 1986) and Cirripedia (Grygier 1987b, c). The endopod with two elements in representatives of Facetotecta (Grygier 1987c, 1994, Ito 1986, 87), Copepoda (Izawa 1973, Dahms 1990) would represent independent apomorphies. One element in the mandibular endopod of the fossil specimen described herein (Fig. 8G) is likely also an apomorphic condition. Notably, all groups discussed herein, show a rather short endopod and long exopod, except in representatives of Copepoda, in which the endopod is similar in length to the exopod (Fig. 8B). Hence, the mandible of the fossil specimen described herein (Fig. 8G) is very similar to the mandibles of representatives of *B. admiribilis*, Facetotecta, Ascothoracida and Cirripedia.

Ontogeny: As discussed above the detected limb bud delay argues for a maxillopodan affinity. The lack of post-maxillular limb buds in the following naupliar stages is characterizing for representatives of Copepoda, Facetotecta, Ascothoracida, Cirripedia and the fossil *B. admiribilis* (Müller & Walossek 1988, Grygier 1987c, Høeg et al. 2009, Izawa 1973, 1986). Looking closer at the ontogenetic pattern of different maxillopodan groups, the fossil specimen described herein show an ontogenetic pattern similar to thecostracans

in which the Anlagen for the appendage on the fourth postocular segment (maxillula) develops in the fourth naupliar stage (Fig. 1E, F, 2A, B). Similar to representatives of Facetotecta (Ito 1986, 1987, 1990), Ascothoracida (Grygier 1987b) and Cirripedia (Høeg & Møller 2006, Yan & Chan 2001), maxillular limb buds in the fossil specimen described herein develop in the fourth naupliar stage with a similar shape. However, in representatives of Copepoda and *B. admiribilis* the maxillular limb buds develop in earlier or later naupliar stages (Grice 1971, Izawa 1973, Müller & Walossek 1988). Due to the morphology of the maxillular limb buds, the fossil specimen described herein is most similar to representatives of Facetotecta, Ascothoracida and Cirripedia.

Conclusion

Taken together, the naupliar morphology (no setae at the proximal two elements of the antennula, three elements in the endopod of the antenna and one element in the endopod of the mandible) and larval development without post-maxillulary limb buds of the fossil specimens described herein strongly support a close relationship to representatives of Thecostraca. Furthermore, linking these fossil nauplii to adult representatives of *E. oviformis* (Haug et al. in prep, Nagler et al. in prep a), support a sistergroup relationship between *E. oviformis* and Ascothoracida. Especially the adult tagmosis, a shield, which covers the whole body and taking care for their brood by carrying the eggs within the shield, argues for a sistergroup relation between *E. oviformis* and Ascothoracida (Grygier 1984, Wagin 1946). Additionally, the most anterior, long slender appendage in adult representatives of *E. oviformis* (Nagler et al. in prep a, figs 1-2*)* could represent an aesthetasc, similar to that associated with the paraocular process of Facetotecta and Ascothoracida (Bresciani 1965, Grygier 1984, 1987a, b, Ito 1985, Ito & Takenaka 1988, Walker 1974). The second head structure with the distal suction disc of *Ebullitiocaris* could represent the antennula, similar to the attachment devices in other representatives of Thecostraca. Thus, an attachment device on the antennula would be not only characterizing Facetotecta, Ascothoracida and Cirripedia, but these groups together with *E. oviformis*. All other apomorphic characters uniting Thecostraca (e.g. lattice organs or eyes with tripartite cones (Jensen et al. 1994, Høeg & Kolbasov 2002, Hallberg & Elofsson 1983, Hallberg et al. 1985)) are not accessible in the fossil *E. oviformis*. If the long slender appendage represents an aesthetasc and the appendage with the distal suction disc represents the antennula of the fossil *E. oviformis*, a sister group relation between *E. oviformis* and Ascothoracida is supported.

Similar to the fossil *B. admiribilis* (Müller & Walossek 1988), the fossil *E. oviformis* is proposed to live at a level when the group was not yet parasitic. Furthermore, the modification of the distal end of one head appendage into a suction disc can be seen as a pre-adaptation for parasitism (Nagler et al. in prep a).

As all representatives of Thecostraca show either a reduction of the naupliar phase or of the post-naupliar phase (Haug & Haug 2015), a metamorphic stage, e.g. cypridoid larva would be missing in the fossil specimen described herein. In contrast to other thecostracans groups, representatives of Ascothoracida show not an extreme metamorphosis. Hence, the ascothoracidan parasitic adults are very similar to their cypris larvae (Grygier & Høeg 2005, Høeg et al. 2009, Kolbasov et al. 2008, Grygier 1984). Thus, it is likely that *E. oviformis* developed also via a metamorphic stage, likely similar to a cypridoid larva.

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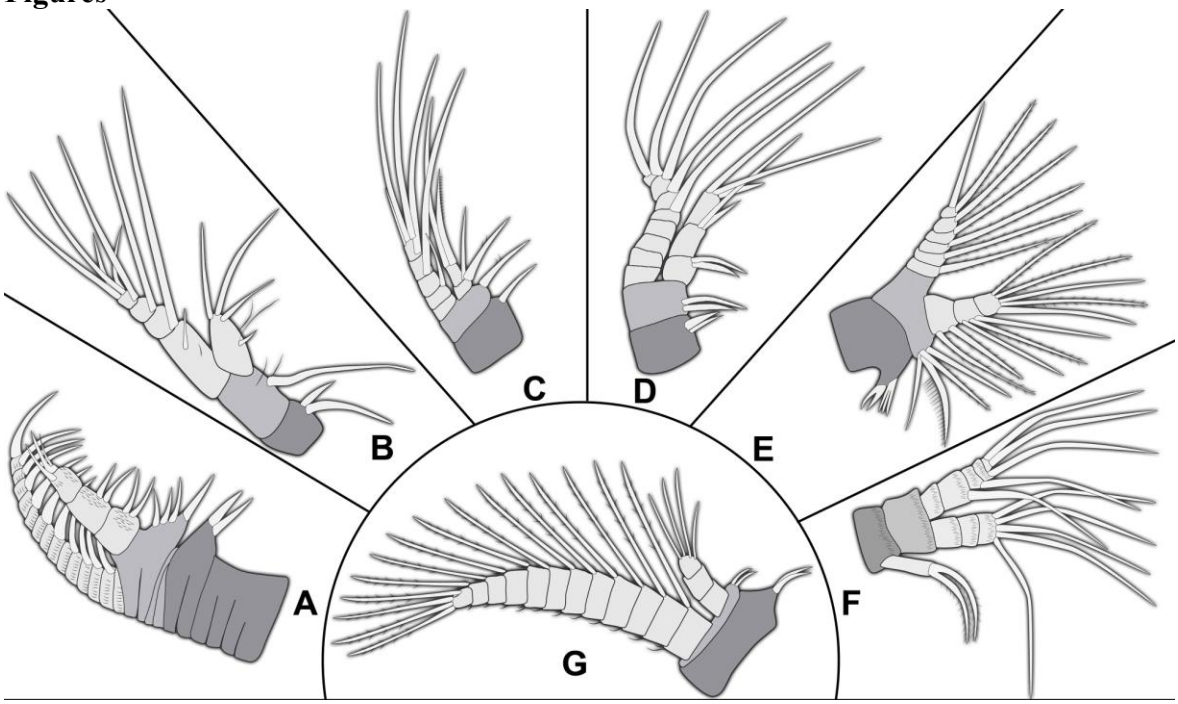
Author contribution

Conceptualization, C. N, P. W., J. T. H. and C. H.; Methodology, C. N., P. W., J. T. H., C. H.; Formal Analysis, C. N., P. W.; Investigation, C. N., P. W., J, T. H., and C. H.; Resources, Science Collections of the National Museum of Scotland; Data Curation, C. N.; Writing – Original Draft, C. N. and P. W.; Writing – Review & Editing, J. O., J. T. H. and C. H., Visualization, C. N., P. W., C. H., Supervision, J. O. and C.H., Project Administration, C. N., P. W. and C. H., Funding Acquisition, C. N., J. O., J. T. H. and C. H.

Figures



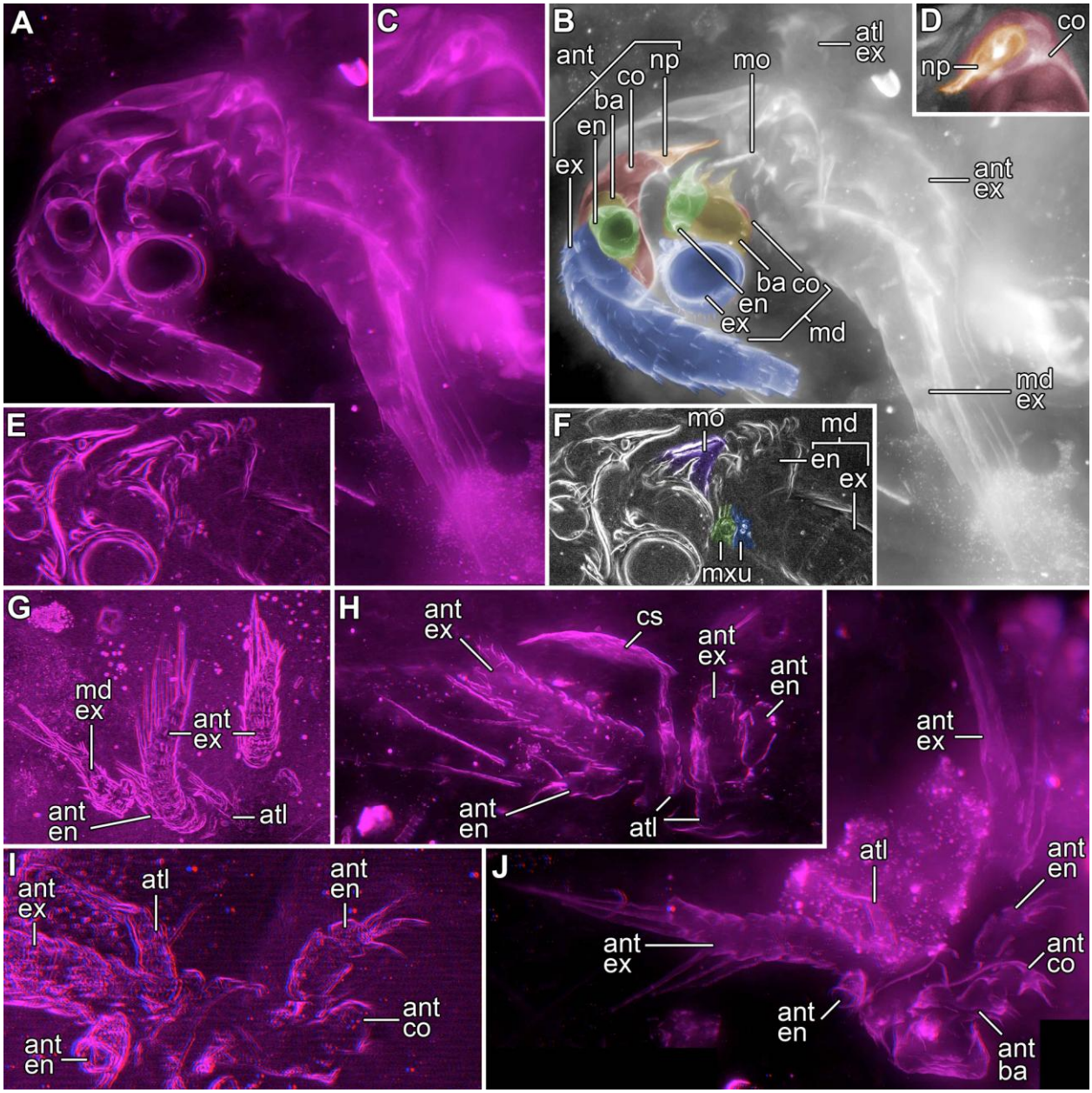


Figure 1: Red-blue stereo images of naupliar larvae of *Ebullitiocaris oviformis*. A) E_G_2010_16_2_1_S5; B) E_G_2010_16_2_1_S5; C) E_G_2010_16_2_1_S5; D) E_G_2010_16_2_1_S5; E) E_G_2010_16_2_1_S5; F) E_G_2010_16_2_1_S5; G) E_G_2010_16_2_1_S15; H) E_G_2010_16_2_1_S20; I) E_G_2010_16_2_1_S22; J) E_G_2010_16_2_1_S22; ant, antenna; atl, antennula; ba, basipodit; cs, cephalic shield; en, endopodit; ex, exopodit; co, coxa; np, naupliar process; md, mandible; mo mouth opening; mxu, maxillula.

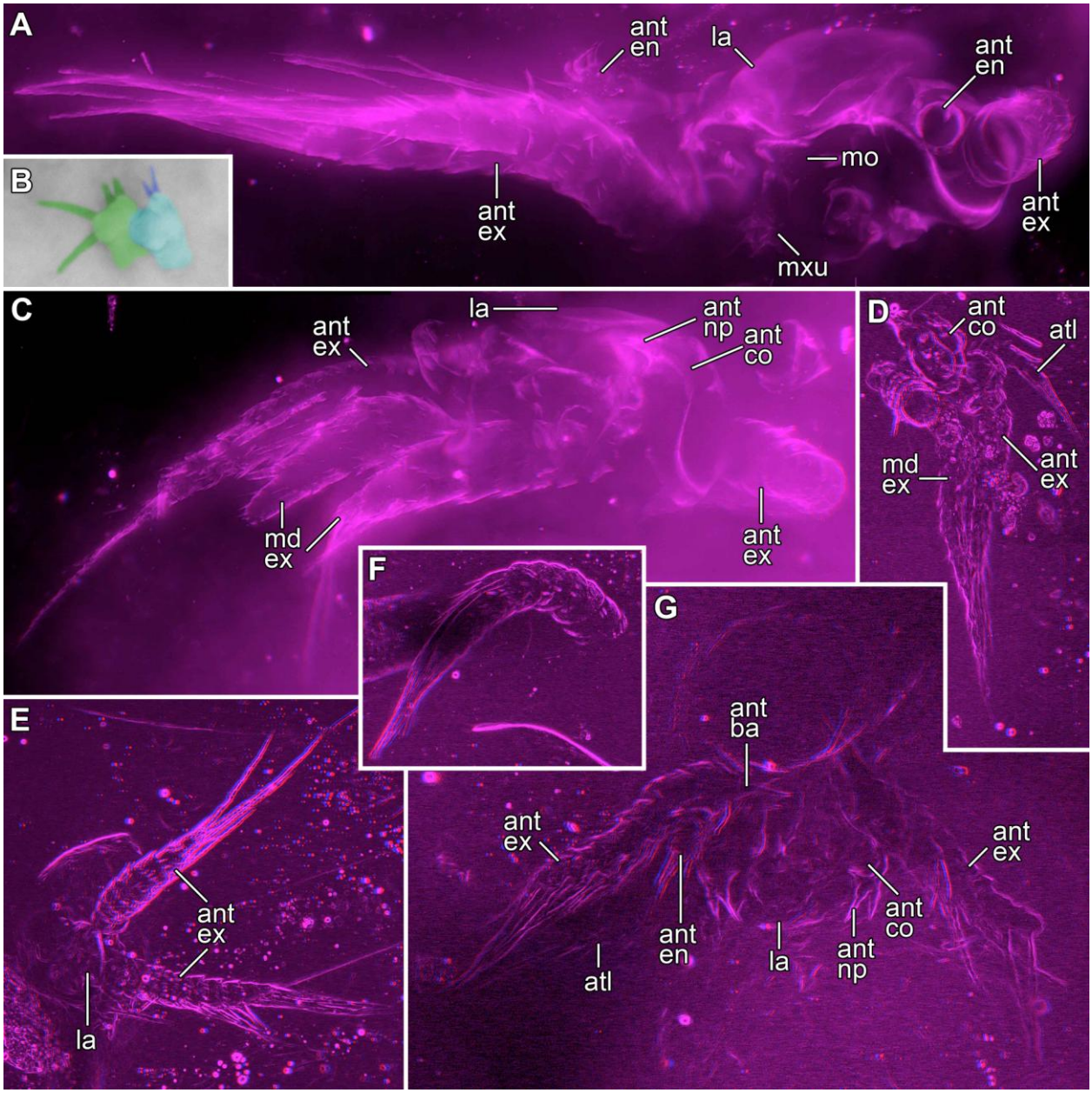


Figure 2: Red-blue stereo images of naupliar larvae of *Ebullitiocaris oviformis*. A) E_G_2010_16s19_2_1_S4; B) E_G_2010_16_2_1_S4; C) E_G_2010_16_2_1_S7; D) E_G_2010_16_2_1_S23; E) E_G_2010_16_2_1_S18; F) E_G_2010_16_2_1_S17; G) E_G_2010_16_2_1_S13; ant, antenna; atl, antennula; ba, basipodit; en, endopodit; ex, exopodit; co, coxa; la, labrum; np, naupliar process; md, mandible; mo mouth opening.

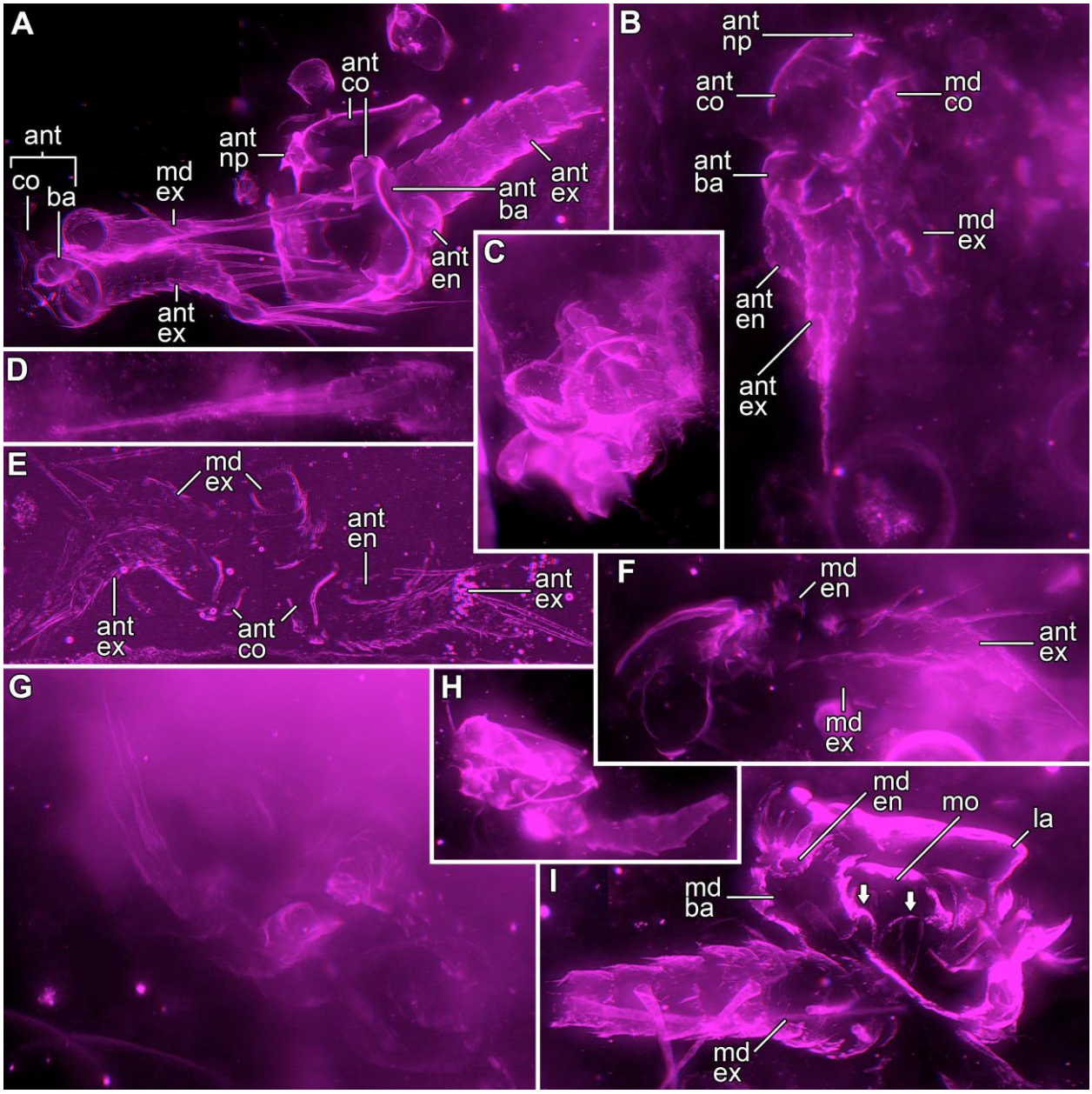


Figure 3: Red-blue stereo images of naupliar larvae of *Ebullitiocaris oviformis*. A) E_G_2004_2823_S10; B)E_G_2010_16_2_1_S24; C) E_G_2004_2822_S8; D) E_G_2010_16_2_1_S19; E) E_G_2010_16_2_1_S25; F) E_G_2010_16_2_1_S8; G) E_G_2010_16_2_1_S9; H) E_G_2004_2822_S9; I) E_G_2004_2822_S6; ant, antenna; ba, basipodit; en, endopodit; ex, exopodit; co, coxa; la, labrum; np, naupliar process; md, mandible; mo mouth opening; white arrows; sternal plate with canal extending posteriorly.

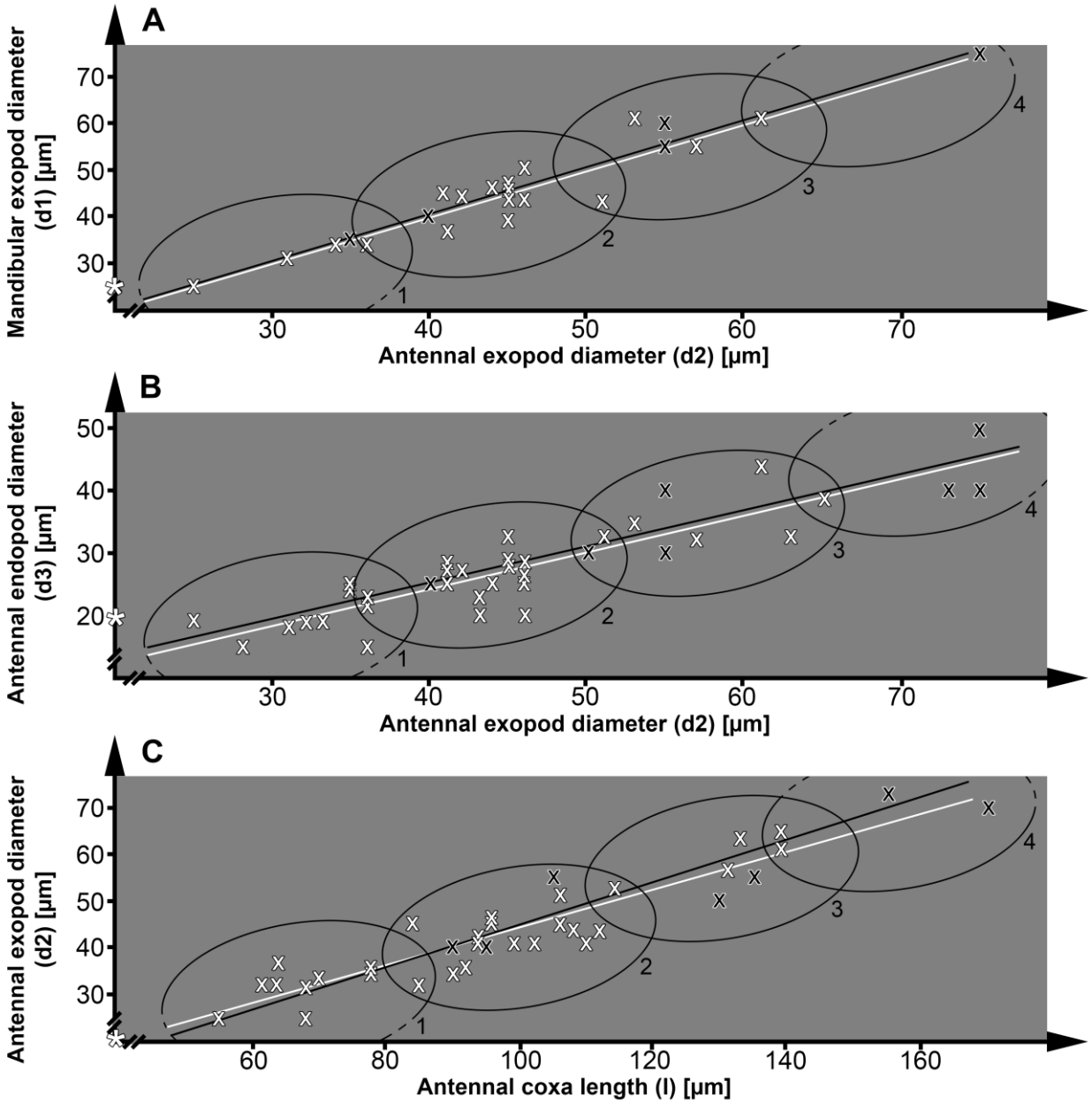


Figure 4: Scatter plots of the measured parameters (black, this study; white, Haug et al. 2012, *, Haug et al. in prep.). A) Diameter of the mandibular exopod (d1) versus the diameter of the antennal exopod (d2), $f_{(Haug\ et\ al.\ 2012)}$= 0.998x-0.125, $f_{(this\ study)}$=1.003x+0.373; B) Diameter of the antennal endopod (d3) versus diameter of the antennal exopod (d2), $f_{(Haug\ et\ al.\ 2012)}$=0.590x+0.816, $f_{(this\ study)}$=0.579x+2.079; C) Diameter of the antennal exopod (d2) versus the length of the antennal coxa (l), $f_{(Haug\ et\ al.\ 2012)}$=0.407x+3.570, $f_{(this\ study)}$=0.455x-0.784. Oval clusters 1-4, growth stages (size classes) 1-4.

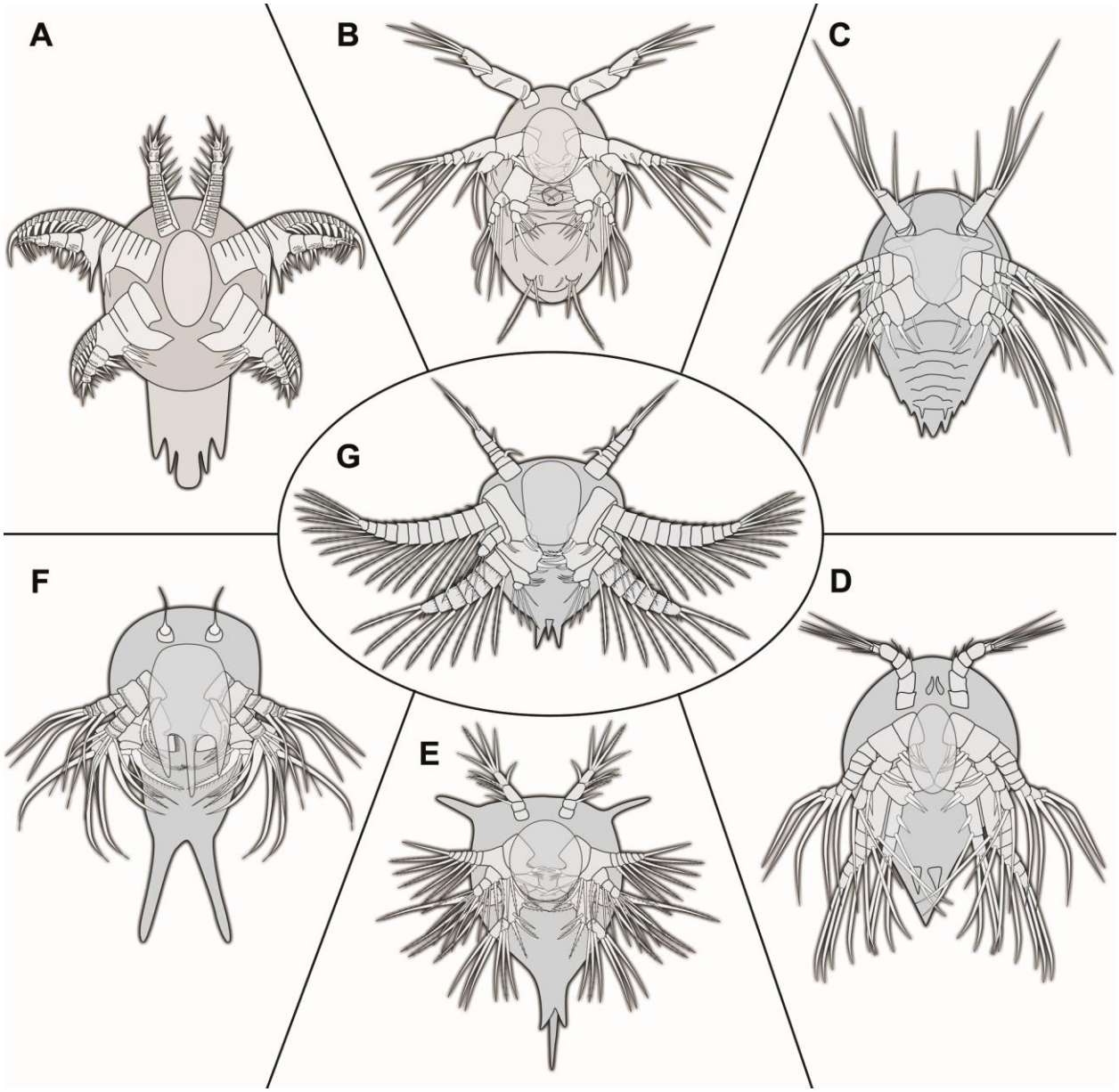


Figure 5: Drawings of naupliar larvae from different species. A) *Bredocaris admiribilis* (Orstenocarida) modified after Müller & Walossek 1988. B) *Philoblenna arabici* (Copepoda) modified after Izawa 1986. C) *Hansenocaris furcifera* (Facetotecta) modified after Ito 1990. D) *Laura bicornuta* (Ascothoracida) modified after Grygier 1984, 1987b. E) *Tetraclita rubescens* (Cirripedia) modified after Miller & Roughgarden 1994. F) *Lynceus biformis* (Branchiopoda) modified after Olesen et al. 2013. G) *Ebullitiocaris oviformis* modified after Haug et al. 2012.

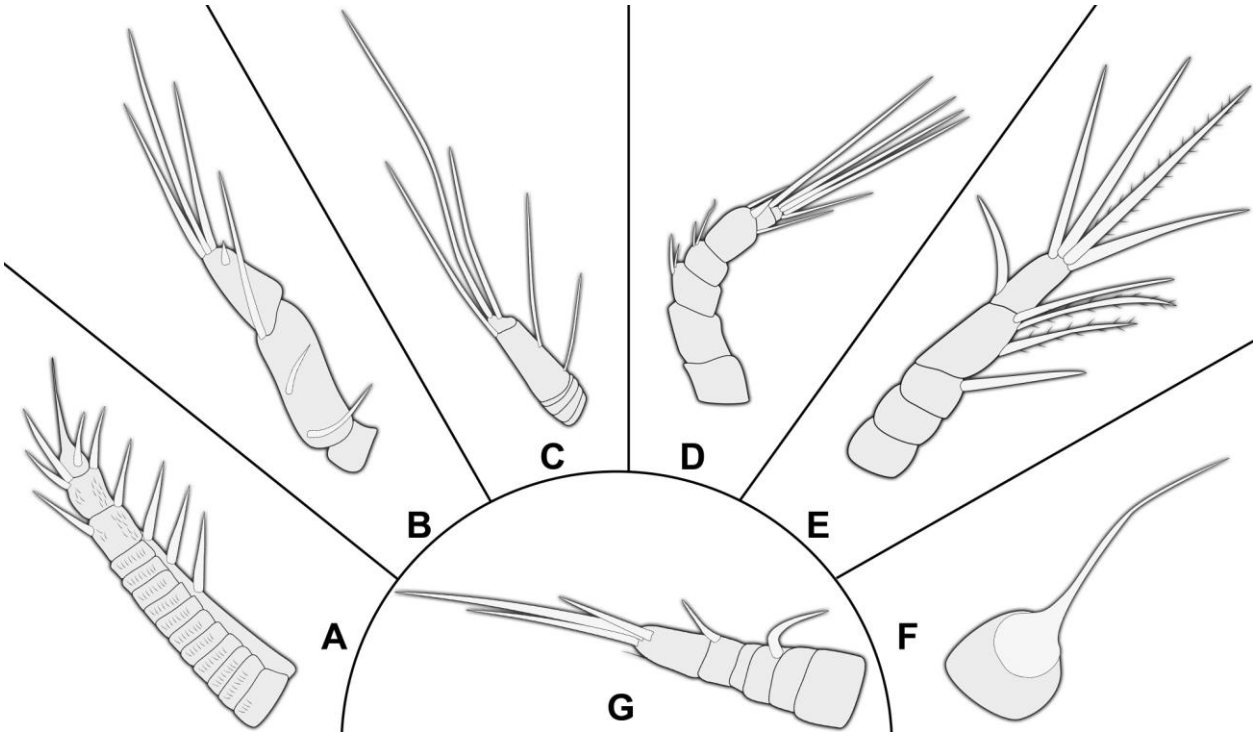


Figure 6: Drawings of antennula of naupliar larvae from different species. A) *Bredocaris admiribilis* (Orstenocarida) modified after Müller & Walossek 1988. B) *Philoblenna arabici* (Copepoda) modified after Izawa 1986. C) *Hansenocaris furcifera* (Facetotecta) modified after Ito 1990. D) *Laura bicornuta* (Ascothoracida) modified after Grygier 1984, 1987b. E) *Tetraclita rubescens* (Cirripedia) modified after Miller & Roughgarden 1994. F) *Lynceus biformis* (Branchiopoda) modified after Olesen et al. 2013. G) *Ebullitiocaris oviformis* modified after Haug et al. 2012.

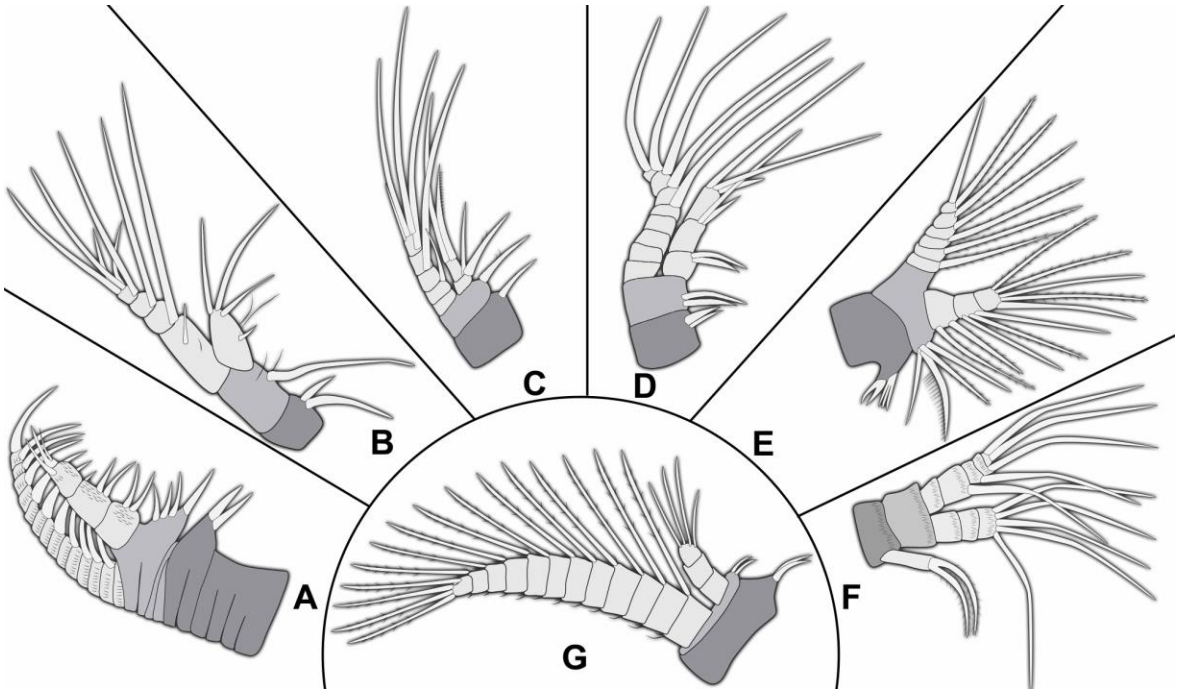


Figure 7: Drawings of antenna of naupliar larvae from different species. Coxa = darkgrey, basipod =lightgrey. A) *Bredocaris admiribilis* (Orstenocarida) modified after Müller & Walossek 1988. B) *Philoblenna arabici* (Copepoda) modified after Izawa 1986. C) *Hansenocaris furcifera* (Facetotecta) modified after Ito 1990. D) *Laura bicornuta* (Ascothoracida) modified after Grygier 1984, 1987b. E) *Tetraclita rubescens* (Cirripedia) modified after Miller & Roughgarden 1994. F) *Lynceus biformis* (Branchiopoda) modified after Olesen et al. 2013. G) *Ebullitiocaris oviformis* modified after Haug et al. 2012

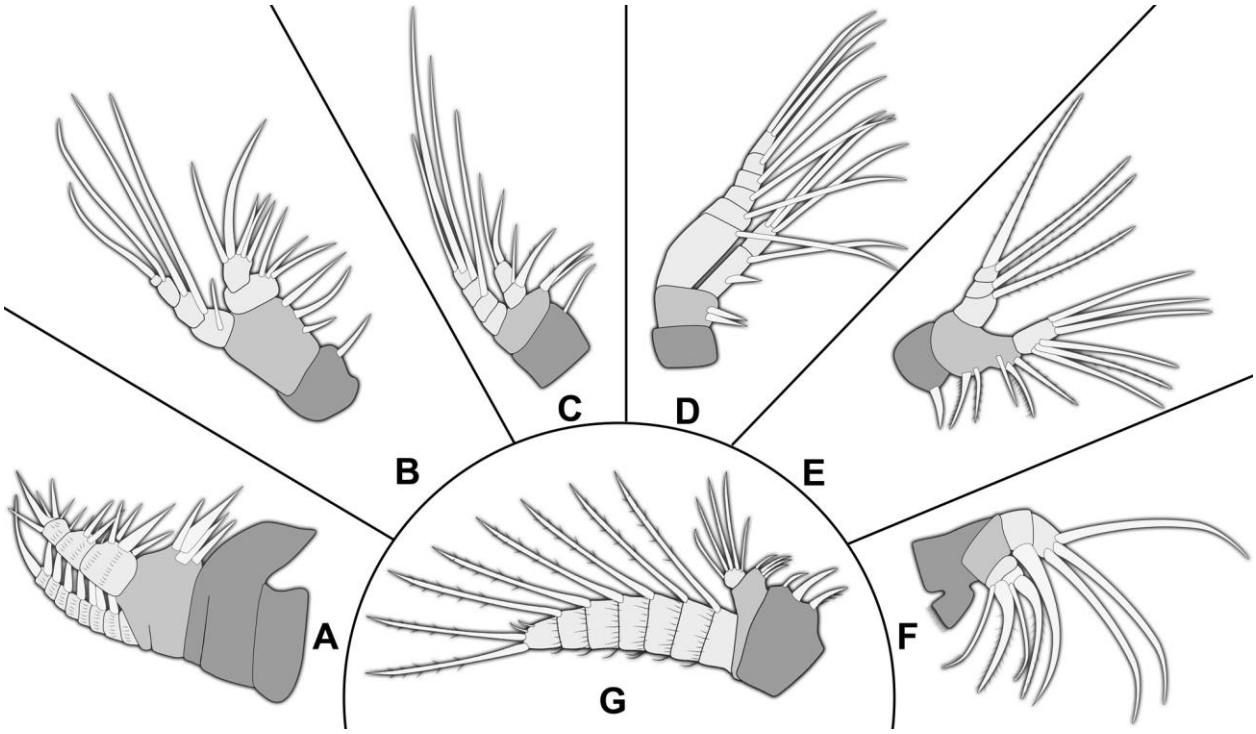


Figure 8: Drawings of mandible of naupliar larvae from different species. Coxa=darkgrey, basipod = lightgrey. A) *Bredocaris admiribilis* (Orstenocarida) modified after Müller & Walossek 1988. B) *Philoblenna arabici* (Copepoda) modified after Izawa 1986. C) *Hansenocaris furcifera* (Facetotecta) modified after Ito 1990. D) *Laura bicornuta* (Ascothoracida) modified after Grygier 1984, 1987b. E) *Tetraclita rubescens* (Cirripedia) modified after Miller & Roughgarden 1994. F) *Lynceus biformis* (Branchiopoda) modified after Olesen et al. 2013. G) *Ebullitiocaris oviformis* modified after Haug et al. 2012.

4. DISCUSSION

Parasites are found in all habitats and occur all over the world in most major groups of metazoans. There are numerous examples of parasites within crustaceans. This study was focused on parasitic isopods (Cymothoida) and parasitic barnacles and their relatives (Thecostraca). Thus, I will discuss the character evolution of parasitism first of Cymothoida and second of Thecostraca. Finally, I will compare the two groups to each other and to other parasitic groups by focusing on convergent aspects.

4.1 EVOLUTION OF PARASITISM WITHIN CYMOTHOIDA

Studying the evolution of parasitism, Cymothoida, a specific group within isopods, is especially interesting, because different ingroups within Cymothoida evolved different parasitic strategies. Similar to most parasitic groups within metazoans, there was a shift from non-parasitic to parasitic lifestyle within Cymothoida. This evolutionary shift was followed by a large adaptive radiation, most likely in the Jurassic (see fossil reports below and chapter 2.1, 2.3), and a diversification of different parasitic groups and strategies within Cymothoida. By mapping morphological characters linked to parasitism, e.g. mouthparts and thoracopods, on a combined phylogeny proposed by Wägele (1989) and Brusca & Wilson (1991), we could tell the evolutionary history of the different groups within Cymothoida (Nagler et al. 2017a). In the following, I will explain this stepwise evolution.

The reconstructed morphology of the ground pattern of Cymothoida is characterized by mouthparts adapted to a carnivorous lifestyle by sharps cusps, spines, teeth and robust setae, additionally, by thoracopods adapted for swimming (Fig. 6A; Hansen 1890, Kensley 1978, Bruce 1986, Wägele 1989, Brusca & Wilson 1991, Brandt & Poore 2003). As demonstrated by some fossils from the Jurassic and the Cretaceous (Polz 2004, Wilson et al. 2011, Hyžný et al. 2013), representatives of fossil Cirolanidae had a scavenging and predatory lifestyle on fishes and water bugs (Fig. $6A_1$; Hyžný et al. 2013, in prep), similar to modern representatives of Cirolanidae (Fig. $6A_2$; Briones-Fourzan & Lozano-Alvarez 1991, Wong & Moore 1995, Lowry & Dempsey 2006, Thomson 2010).

The reconstructed morphology of the ground pattern of the unnamed sister group to Cirolanidae – (Corallanidae + (Aegidae + (Cymothoidae + (Epicaridea, Gnathiidae, *Urda*)))) – is characterized by at least one hook-like dactylus at the first pair of free thoracopods at least during a specific stage of their life (Fig. 6B). Molecular and morphological data support the sistergroup status of modern Corallanidae to all other obligatory parasitic representatives of Cymothoida (Wägele 1989, Dreyer & Wägele 2001, Brandt & Poore 2003, Wetzer et al. 2013, Nagler et al. 2017a). Although some modern representatives of Corallanidae still live as predators, they have longer, thinner and more pointed mouthparts than representatives of Cirolanidae (Fig. $6B_1$; Schiodte & Meinert 1879, Bruce 1982, Bruce et al. 1982, Guzman et al. 1988, Bunckley-Williams & Williams

1998, Morris & Akins 2009). Together with the morphological modification of the first free thoracopod into a ~~–h~~ook leg", the modified mouthparts were later transformed into a specialized morphology, highly adapted for parasitism as seen in obligate parasites within Cymothoida, e.g. Cymothoidae, Epicaridea

The reconstructed morphology of the ground pattern of the unnamed sister group to Corallanidae – (Aegidae + (Cymothoidae + (Epicaridea, Gnathiidae, *Urda*))) – is characterized by hook-like dactyli on the first three pairs of free thoracopods at least during a specific stage of their life (Fig. 6C; Dreyer & Wägele 2001, Brandt & Poore 2003, Wetzer et al. 2013, Nagler et al. 2017a, see also chapter 2.4). Concurrently, representatives of this group share a specialization of the mouthparts by forming a mouth cone (sealed by the labrum, paragnath, maxilla, maxilliped, and maxillula and mandible are used for piercing and cutting pieces of the host) that allows piercing and sucking (Günther 1931, Wägele 1989, Brusca & Wilson 1991, Nagler & Haug 2016, see also chapter 2.2). Modern representatives of Aegidae are adapted to a temporary parasitism on fishes, like a ~~–m~~arine mosquito", based on well-developed eyes, the modification of the mouth parts to a mouth cone and the hook like dactyli (Fig. $6C_{1-2}$; Bunckley-Williams & Williams 1998, Nagler et al. 2017a).

The reconstructed morphology of the ground pattern of the unnamed sister group to Aegidae – (Cymothoidae + (Epicaridea, Gnathiidae, *Urda*)) – is characterized by hook-like dactyli on all pairs of free thoracopods at least during a specific stage of their life (Fig. 6D; Brusca 1981, Wägele 1989, Brusca & Wilson 1991, Nagler & Haug 2016, Nagler et al. 2017a, see also chapter 2.2 & 2.4). With this transition, the group retained a mouth cone adapted for piercing and sucking, but the seven free thoracopods are modified for attachment to the host. All dactyli show a hook-like shape and therefore provide a more stable attachment on the host. Modern representatives of Cymothoidae, additionally, show further adaptation to parasitism on fishes; the anterior four free pairs of thoracopods are oriented from the outside towards the inside, whereas the latter three pairs of thoracopods are oriented almost parallel to the anterior-posterior axis of the isopod and inclined from the inside towards the outside. This is linked to the biphasic molting behavior in isopods: First the anterior part (functional head + first four free pairs of thoracopods), secondly the posterior part (last three free pairs of thoracopod + pleotelson) (Fig $6D_{2-6}$; Günther 1931, Fogelmann & Grutter 2008, Smit et al. 2014, Nagler & Haug 2016, see also chapter 2.2). Notably, larval representatives of Cymothoidae are only temporary parasitic and change their hosts all the time, similar to adult and larval representatives of Aegidae, the ~~–m~~arine mosquitoes" (Sandifer & Kerby 1983, Mladineo 2003, Lester 2005, a context between ontogeny and evolution will be discussed in chapter 4.3). Representatives of Cymothoidae have been reported to be present at least since the Jurassic (150 mya) (Fig. $6D_1$; Nagler et al. 2016, see also chapter 2.1).

The reconstructed morphology of the ground pattern of the unnamed sister group to Cymothoidae – (Epicaridea, Gnathiidae, *Urda*) – is characterized by a reduced mandibular palp and maxillula, the labrum is smaller and not covering the other mouthparts, thus they possess a less tight mouth cone than the groups discussed before (Wägele 1989, Brusca & Wilson 1991). Larval representatives of this group retain hook-like dactyli on all pairs of free thoracopods (larvae of representatives of Cymothoida possess only six pair of free thoracopods) (Fig. 6E; Dale & Anderson 1982, Williams & Boyko 2012, Boyko et al. 2013, Boyko & Williams 2015). The relationship between these three groups is still

equivocal, because of the character cluster compromising the looser mouth cone and hook-like dactyli only in larval representatives. Due to this ambiguous phylogeny, a monophyletic group – including Epicaridea, Gnathiidae and *Urda* – as sister group to Cymothoidae might be possible.

Representatives of Epicaridea show a host change during their ontogenetic stage, as further adaptation to a parasitic lifestyle: larval representatives of Epicaridea will be released as free-swimming epicaridium larva that attach to an intermediate host, mainly to a copepod, and develops into a microniscus larva. Once developing into a cryptoniscus larva, these larvae detach from the intermediate host and seek for a final host. In contrast to other groups within Cymothoida, representatives of Epicaridea parasitize not on fishes, but on decapods (Fig. 6E_2; Giard & Bonnier 1887, Sars 1899, Danforth 1963, Sadoglu 1969, Anderson & Dale 1981). Due to fossil findings of cryptoniscus larvae in amber, this host change must have been present since the Cretaceous (Fig. 6E_1; Serrano-Sánchez et al. 2016, Néraudeau et al. 2017, see also chapter 2.3). Although it is a more indirect support for fossil Epicaridea, swellings in the branchial chamber of crabs have been reported from the Jurassic (Klompmaker et al. 2014, Klompmaker & Boxshall 2015).

Representatives of Gnathiidae are characterized by an incorporation of the first thoracopod into the head (Fig. 6F; Smit et al. 1999, Smit & Basson 2002, Smit et al. 2003, Smit & Davies 2004, Hispano et al. 2014). Gnathiidae was a ~~„p~~roblematic" group concerning their phylogenetic position for a long time (Wägele 1989, Brusca & Wilson 1991, Dreyer & Wägele 2001, Brandt & Poore 2003, Wilson 2009, Wetzer et al. 2013). However, due to their larval morphology with a loose mouth cone, reduced mandibular palp and maxillula, as well as the hook-like dactyli on all free pairs of thoracopods in larval representatives, the group Gnathiidae fit well in the proposed phylogenetic system as closely related to Epicaridea and *Urda*, although adult representative of Gnathiidae show quite a different morphology (Fig. 6F_1; Monod 1926, Brusca & Wilson 1991, Nagler et al. 2017a, see also chapter 2.4). These praniza larvae are temporary parasitic on fishes. As an additional novelty, adults lose their parasitic life style and are non-feeding (Monod 1926, Smit & Davies 2004, Tanaka 2007).

Adult representatives of the fossil group *Urda* are characterized by a looser mouth cone than in representatives of Cymothoidae, but a tighter mouth cone than in representatives of Epicaridea and larval Gnathiidae. They share the lack of a mandibular palp with representatives of larval epicarideans and larval gnathiids and the incorporation of the first thoracopod partly into the head with larval representatives of Gnathiidae. The dactyli retain hook-like on all free pairs of thoracopods (Fig. 6G; Nagler et al. 2017a). Sharing morphological characters with modern representatives of Cymothoidae and Gnathiidae, it seems that *Urda* is either closely related to Gnathiidae and Epicaridea or to Cymothoidae. Based on an unclear mouth part (either maxillula or elongated paragnaths), the phylogenetic position of *Urda* is ambiguous. However, the loose mouth cone together with the incorporation of the first free thoracopod partly into the head, supports a closer relation to Gnathiidae (Fig. 6G_{1-4}; Nagler & Haug in prep.). Although, there is no direct implication for the life style of *Urda*, the functional morphology of the mouth parts and the thoracopods indicate well-founded that *Urda* was permanent parasitic on fishes.

Summing up, the highly specialized parasitic lifestyle, mainly on fishes and the diverse morphology of modern representatives within parasitic Cymothoida (Gnathiidae, Epicaridea, Cymothoidae, Aegidae) originated stepwise from non-parasitic representatives of Cirolanidae with a scavenging life style on fishes. These steps include

- a scavenging and predatory life style in representatives of Corallanidae via
- a temporary parasitic life style on fishes in representatives of Aegidae via
- a permanent parasitic lifestyle on fishes in representatives of Cymothoidae to finally
- an extremely specialized and modified morphology and life cycle including a permanent parasitism on fishes with an incorporation of the first free thoracopod into the head in adult representatives of *Urda*,
- a larval stage parasitic on fishes and a secondary loss of parasitism in adult representatives of Gnathiidae, and
- an ontogenetic host change and parasitism on decapods in adult representatives of Epicaridea.

Finally, it seems that the group Cymothoida radiated very soon after the first occurrence of it. This radiation seems linked to the switch to a parasitic lifestyle. Considering the similarity of fossil and modern representatives of Cymothoida, their evolutionary history led to one of the most successful and hyper diverse groups among malacostracan crustaceans containing about 2700 species (Ahyong et al. 2011).

Taken together, the proposed evolutionary reconstruction represents a robust framework for further studies. Additional morphological details of all groups within Cymothoida, especially groups that are not well studied, e.g. Epicaridea, can add important data for the significance of the proposed evolutionary reconstruction. Future investigations of additional fossil specimens might resolve the precise position of *Urda* and add crucial data for the support of the proposed evolutionary reconstruction (Nagler & Haug in prep.).

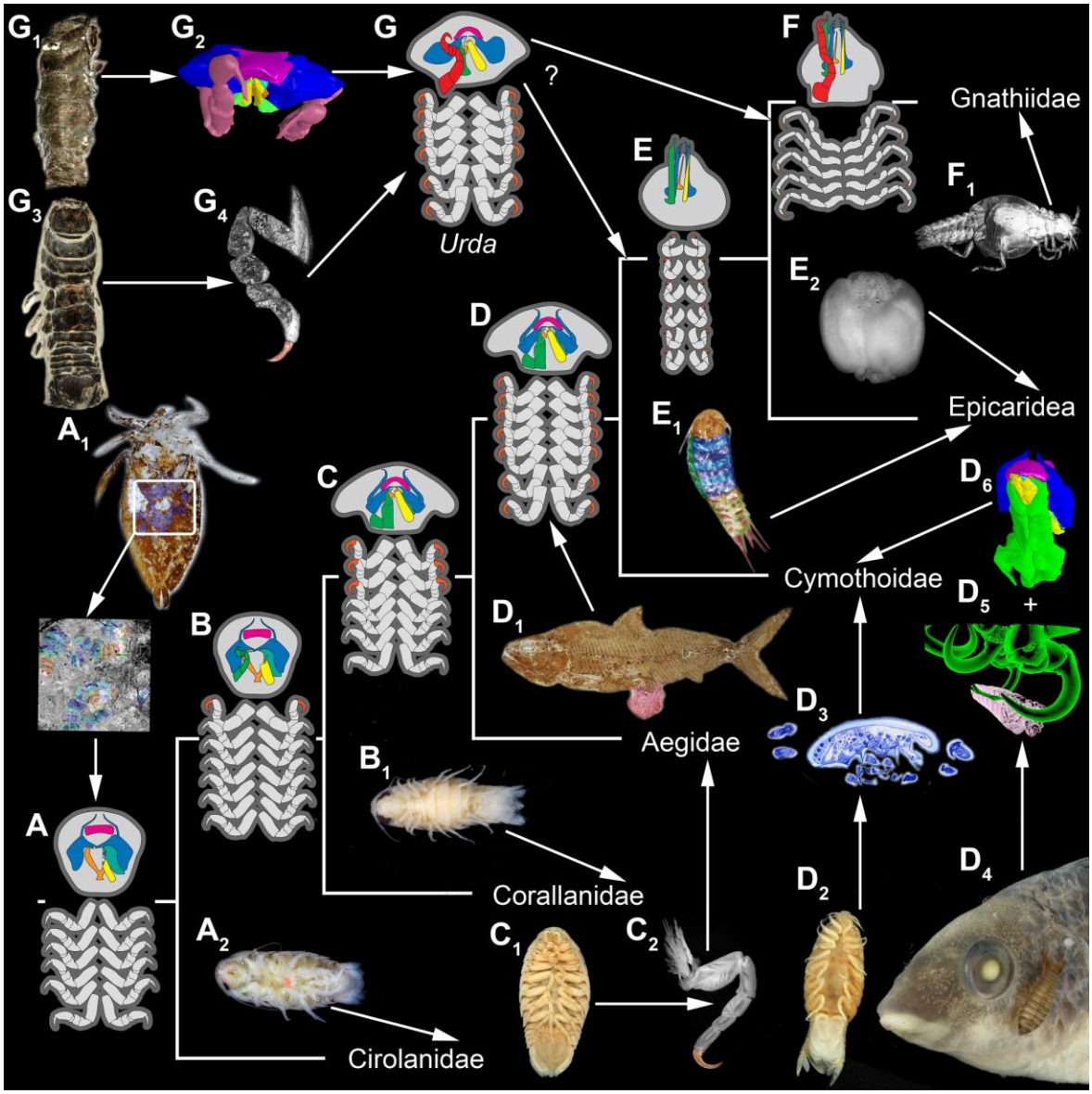


Fig. 6. Reconstructed relationship of major groups within Cymothoida with support from extant and fossil data. A-G) Schematic character evolution of the mouthparts and thoracopods. Color-marks: labrum= purple, mandibles = blue, paragnaths = orange, maxillula = cyan, unclear mouthpart = white, maxilla = yellow, maxilliped = green, first free thoracopod = red, claw-like dactyli on thoracopods = dark orange. A_{1-2}) Representatives of Cirolanidae. A_1) Fossil specimen scavenging on a water bug, from the Jurassic (150 mya). A_2) Modern specimen. B_1) Modern representative of Corallanidae. C_{1-2}) Modern representative of Aegidae, ventral view and detail of third free thoracopod. D_{1-6}) Representatives of Cymothoidae. D_1) Fossil specimen (red mark) parasitizing a fish from the Jurassic (150 mya). D_{2-3}) Modern specimen, ventral view and histological section of functional head. D_{4-6}) Modern specimen parasitizing a fish and detail of surface model of thoracopods and mouthparts. E_{1-2}) Representatives of Epicaridea. E_1) fossil larva from the Miocene. E_2) Modern specimen. F_1) Larval representative of Gnathiidae. G_{1-4}) Fossil representatives of *Urda*, dorsal view with detail of surface model of mouthparts and volume rendering of sixth free thoracopod. Not to scale. Please see chapter 4.1 for more information.

4.2 EVOLUTION OF PARASITISM WITHIN THECOSTRACA

Due to the parasitic lifestyle of most representatives in the group Thecostraca *sensu lato* and their morphological diversity, the evolutionary reconstruction of the group Thecostraca is especially interesting. Together with *B. admirabilis*, Thecostraca *sensu stricto* (Grygier 1987a) forms the group Thecostraca *sensu lato* (Høeg et al. 2009).

Thecostraca *sensu lato* is characterized by a post-embryonic delay of post-cephalic limb development and segment expression in the thorax region caused by the heterochronic event ~~–a~~cceleration" (Walossek & Müller 1998, Høeg et al. 2009, Haug et al. 2011b, c, Haug & Haug 2015b). In other words, posterior limbs, e.g. thoracopods, will be developed as limb buds during the naupliar phase. In the metanauplius phase the post-maxillulary limbs persist as limb buds and develop to limbs at once during the molt between the last nauplius stage and the first cypris stage (Grygier 1987a). Such a metamorphic event can be observed already in the Orsten fossil *Bredocaris admirabilis* (500 mya, Müller & Walosseek 1988) and in the chert fossil *Ebullitiocaris oviformis* (400 mya, see chapter 3.4, 3.5). Recent morphological and molecular studies suggest following relationship within Thecostraca *s. str.*: Facetotecta + (Ascothoracida + (Acrothoracica + (Thoracica + Rhizocephala))) (Pérez-Losada et al. 2002, Høeg et al. 2009, Pérez-Losada et al. 2009, 2012).

Furthermore, a possible ingroup position of Branchiura (fish lice) and the parasitic Tantulocarida within Thecostraca *sensu lato* has been discussed based on morphological studies (Boxshall & Huys 1989). Especially fish lice have been ~~–s~~hifted around" the crustacean phylogeny (Martin 1932, Stekhoven 1937, Møller et al. 2008, Møller 2009, Møller & Olesen 2010, Neethling & Avenant-Oldewage 2016); a closer relationship to Pentastomids (Wingstrand 1972, Abele et al. 1989, 1992), Ostracods (Pinnow et al. 2016) or Thecostraca (Grygier 1987a, b) has been proposed. In the general discussion of the character evolution within Thecostraca *s. l.* (see chapter 4.2.3), Branchiura will be included. Even though an ingroup position of the fossil *Wujicaris muelleri* within Thecostraca is not finally evaluated, this fossil metanaupliar larva will be included into this reconstruction (Zhang et al. 2010).

Below, I follow the proposed phylogenetic relationship for Thecostraca *sensu lato* (Høeg et al. 2009), but will discuss some other possibilities, also in the light of the uncertain phylogenetic position of Tantulocarida, Branchiura, the fossil *Wujicaris muelleri* and the fossil *Ebullitiocaris oviformis.*

4.2.1 PROPOSED PHYLOGENY WITHIN THECOSTRACA *S. STR.*

The reconstructed ground pattern of Thecostraca *s. str*. has six naupliar stages, followed by a cypridoid larva and the adult (Fig. 7A; Høeg et al. 2004a, Haug & Haug 2015b). The groups within Thecostraca *sensu stricto* are united only by their unique cypridoid larva *sensu* Høeg et al. (2004a). The cypridoid larva represents the transition stage between a free-living nauplius to a sessile adult (Grygier 1987a, Høeg et al. 2004a, Høeg et al. 2009). Most morphological studies about Thecostraca *sensu stricto*, especially about the parasitic groups Facetotecta, Ascothoracida and Rhizocephala, are based only on larval characters (Grygier 1987a-c, Høeg & Kolbasov 2002, Høeg et al. 2004a, Pérez-Losada et al. 2009). This is probably biased by the lack of knowledge about adult representatives of many groups of Thecostraca *s. str.* together with the lack of characters in the known adult representatives of some Thecostraca *s. str.* due to their modified morphology. Nevertheless, the naupliar larva is characterized by (a) two unarmed basal elements in the antennula, (b) a fusion of the distal elements of the antennula during metamorphosis and c) not more than three elements of the endopod of the antenna and mandible (Grygier 1987c, Høeg et al. 2004a, 2009). The cypridoid larva is characterized by (a) antennula modified for mechanical attachment (Grygier 1987a-c, Høeg et al. 2004a, 2009), (b) five pairs of chemosensory lattice organs in the head shield with a posterior terminal pore in a keel-shaped elongated depression, separated from the cuticle (Jensen et al. 1994, Høeg et al. 1998, Høeg & Kolbasov 2002, Rybakov et al. 2003, Kolbasov & Høeg 2007, Kolbasov et al. 2008, Høeg et al. 2009, Pérez-Losada et al. 2009) (c) not more than three endopod and two exopod elements in the thoracopods (Grygier 1987c), (d) soft body completely or partly covered with a head shield, that is drawn down on either side (Høeg et al. 2014), and (e) where eyes are present, they show tripartite crystalline cones (Hallberg & Elofsson 1983, Hallberg et al. 1985, Grygier 1987a, Ax 2000, Semmler et al. 2008). Høeg et al. (2004a) has proposed that the cypridoid larva of representatives of Facetotecta is called y-cypris, of Ascothoracida a-cypris and of Cirripedia cypris.

Naupliar representatives of Facetotecta are characterized by (a) cephalic shield continuous with free trunk dorsum, (b) a strong sculptured shield due to a number of notches in a specific position (c) ventral side of the head shield is rather flat, round and bears a wide rim, and (d) two-elemented endopods of antenna and mandible (Fig. 7A$_{1-2}$; Ito 1986a, Grygier 1987a, Ito 1987, Grygier 1991b, 1994). Cypridoid representatives of Facetotecta are characterized by (a) a labrum modified into a spiny lobe and lack of functional mouthparts (b) two- elemented endopods of thoracopods, (c) a hook at the second element and an aesthetascs on the fourth element of the antennula, (d) three abdominal segments, excluding the telson (Ito 1986b, Grygier 1987a, Kolbasov et al. 2007, Høeg et al. 2009). Due to missing information in outgroups of Thecostraca *s. str.*, it remains unclear if the character ‗three abdomincal segments excluding the telson' represents an autapomorphic character for Facetotecta (see below). Inducing metamorphosis of a facetotectan cypridoid larva, a worm shaped, unsegmented stage without appendages (―ypsigon") develops. This ypsigon is morphological similar to the infesting stage of rhizocephalans (vermigon). Thus, it has been proposed that representatives of Facetotecta are endoparasitic (Glenner et al. 2008).

The reconstructed morphology of the ground pattern of the unnamed sister group to Facetotecta – (Ascothoracida + Cirripedia) – is characterized by (a) a reduced musculature

in the distal part of the antennula in the cypridoid larva, (b) a fusion of the genital appendages on trunk segment 7 to a median penis (notably, the reproductive process in Facetotecta is not known), (c) an adductor muscle that connects the two halves of the head shield in the cypridoid larva and (d) frontal filaments (Fig. 7B; Bresciani 1965, Walker 1974, Grygier 1983a, 1985, Høeg 1985, Ito 1986b, Grygier 1987a, c, Glenner et al. 1989, Ito & Grygier 1990, Grygier 1991a, b, Høeg & Lützen 1993, Høeg & Rybakov 2007, Kolbasov et al. 2008, Høeg et al. 2014, Obukhova et al. 2015).

In contrast to other thecostracans groups, representatives of Ascothoracida show not an extreme metamorphosis. Hence, the ascothoracidan parasitic adults are very similar to their cypridoid larvae (Grygier & Høeg 2005, Høeg et al. 2009, 2012). Some of them, e. g. *Ulophysema oeresundense*, develop into a cypris already in the egg and thus hatch as cypridoid larvae (Fig. $7B_{1\text{-}2}$; Grygier 1984, Bresciani & Jespersen 1985, Grygier 1996, Høeg et al. 2005). Others have two consecutive cypridoid larvae and only the second one infests the host (Kolbasov et al. 2008). These cypridoid larvae are characterized by (a) a head shield with a distinct hinge line, (b, unclear if apomorphic) a well developed abdomen with five segments, and (c, unclear if apomorphic) more than seven elements in the antennula expressed in the entire life cycle (Grygier 1983c, Grygier 1984, 1987a, Høeg et al. 2009). As parasites on echinoderms and cnidarians, representatives of Ascothoracida have mouthparts modified to a piercing mouth cone and a truly bivalve shield (Pérez-Losada et al. 2009). Although some representatives of Ascothoracida, e.g. of Dendrogastridae, show extreme modification of the morphology with long root-like extensions of the body and absorption of nutrients through the body surface, they retain always the maxillopodan body segmentation and appendages (Bresciani & Jespersen 1985, Grygier 1996). Adult Ascothoracidan carry their eggs within the truly bivalve shield and care for their brood (Wagin 1946, Grygier 1984).

The reconstructed naupliar morphology of the ground pattern of Cirripedia is characterized by the presence of fronto-lateral horns that are antero-ventrally extensions of the head shield with distally glands and represent sensory structure (Fig. 7C, C_1; Thompson 1836, Walker 1973, Høeg 1987a, b, Glenner et al. 1989, Walker 1992, Anderson 1994, Rybakov et al. 2002, Høeg & Møller 2006, Semmler et al. 2009). Their function is still unknown (Høeg& Møller 2006, Walker 1992). The cypridoid larvae retain these glands (Glenner et al. 1989, Høeg 1985, Høeg et al. 2009, Walker 1974). The fossil finding of a putatively cirripede nauplius with fronto-lateral horns from the Solnhofen limestone support the presence of Cirripedia already in the Jurassic (Fig. $7C_2$; 150 mya, Nagler et al. 2017c, see also chapter 3.2). Adult and cypridoid representatives of Cirripedia have been reported already from the Silurian (Glenner et al. 1995, Briggs et al. 2005).

The reconstructed cypridoid morphology of the ground pattern of Cirripedia is characterized by (a) the lack of the digestive organs and mouthparts, e.g. antenna, maxillula, maxilla, mandible, due to their non-feeding lifestyle (b) a reduced abdomen with less than four segments, (c) the shift of the terminal pore of the second anterior most lattice organ from the posterior to the anterior, (d) a modified morphology of the third element of the antennula as a non-movable attachment organ associated with specific multicellular glands that secret cement, and (e) setae and/or aesthethascs on the fourth element of the antennula (Høeg 1985, Grygier 1987a, Glenner & Høeg 1993, Høeg & Kolbasov 2002, Lagersson & Høeg 2002, Blomsterberg et al. 2004, Kolbasov & Høeg 2007, Høeg et al. 2009, Kolbasov 2009, Chan et al. 2014a). This attachment disc has been proposed to play

an major role in the evolutionary success of representatives of Cirripedia, as their cypris larvae can settle on all kind of substrates, e.g. rocks, wood, floating objects, crustaceans, whale skin, corals, in almost every marine environment, e.g., hydrothermal vents, deep sea, intertidal zone and employ different lifestyles as suspension feeders or parasites (Moyse et al. 1995, Høeg et al. 2004a, Høeg & Møller 2006, Bielecki et al. 2009). Additionally, representatives of Cirripedia are characterized by a complex metamorphosis resulting in a sessile juvenile that is morphologically distinct different to the cypridoid larva and beside others characterized by a suspension feeding lifestyle as their thoracopods are transformed to a basket of food-collecting cirri (Walley 1969, Walker 1974, Anderson 1994, Høeg et al. 2012, Maruzzo et al. 2012, Chan et al. 2014a). Cirripedia can be further differentiated into Acrothoracida (burrowing barnacles), Rhizocephala (parasitic barnacles) and Thoracica (stalked and sessile barnacles) (Pérez-Losada et al. 2002).

Representatives of Acrothoracica hatch mostly as cypridoid larva, while the naupliar phase is passed in embryonic form within the egg (Kolbasov et al. 1999, Kolbasov 2009, Chan et al. 2014b). Thus, characters of naupliar larvae are hardly accessible and not commonly used for identifying representatives of Acrothoracica (Fig. $7C_3$; Høeg et al. 2009). The cyprioid larva of representatives of Acrothoracica is characterized by a distinct, but small abdomen with less than four segments (Kolbasov & Høeg 2001). Adult representatives of Acrothoracica are symbiotic and live in burrows of carbonate sediments and skeletons of marine molluscs and thus, lack mineralized plates (Anderson 1994, Kolbasov 2000, Chan et al. 2012, 2014b).

The reconstructed cypridoid morphology of the ground pattern of the unnamed sister group to Acrothoracica – (Cirripedia + Rhizocephala) – is characterized by (a) lack of an abdomen, (b) a shift of the terminal pores of the anterior most lattice organ from a posterior position to an anterior position and the transformation of the lattice organ in a broad oval pore-field, and (c) thoracopods with a two-elemented endopod (Fig. 6D; Grygier 1987a, Høeg & Kolbasov 2002, Kolbasov & Hoeg 2007, Høeg et al. 2009, Kolbasov 2009).

Cypridoid larvae of representatives of Thoracica are characterized by (a) a specialized morphology of the attachment disc that is modified for exploratory walking while searching a suitable habitat for irreversible settlement (Lagersson & Hoeg 2002, Maruzzo et al. 2011, Aldred et al. 2013). Naupliar larvae of representatives of Thoracica are planktotroph and thus, bear many, long setae (Fig. $7D_1$; Desai & Anil 2002, Desai et al. 2006, Watanabe et al. 2008). In contrast to other cirripedian groups, representatives of Thoracica have a modified mode of growth, because their soft body is protected by a number of mineralized shell plates. After settlement, the cypridoid larvae molt and develop primordial plates, which are cuticular formations. These primordial plates represent the base for the shell plates. The shell plates are not shed during molts, but increase in size by subsequently cuticular molts in a special cuticular zone on the external surface, while the soft body is molted in the usual eucrustacean way (Glenner & Høeg 1995a, Glenner et al. 1995, Hoeg et al. 1999, Pérez-Losada et al. 2004, Blomsterberg et al. 2004, Buckeridge & Newman 2006, Pérez-Losada et al. 2009, Maruzzo et al. 2012). Within Thoracica, there is a great diversity of morphology, ecology and lifestyles. Representatives of Thoracica colonize any type of substratum with different life strategies, from intertidal to deep-sea, from floating objects and sponges to vertebrates and from epibiotic to parasitic (Chan & Høeg 2015). It has been proposed that parasitism evolved several times independently

within Thoracica, but every time from a sessile suspension-feeding ancestor probably via an epibiotic ancestor (Nogata & Matsumura 2006, Leung 2014, Rees et al. 2014). Fossil findings of barnacles infesting a sponge from the Solnhofen limestone, support the presence of a close relation between barnacles and sponges – either parasitic or commensalistic – already in the Jurassic (150 mya, Fig. 7D_{2-5}; Nagler et al. 2017b; see also chapter 3. 1).

Cypridoid larvae of representatives of Rhizocephala settle on the gill of a prospective host and are characterized by (a) a large aesthetasc on the third element of the antennula and (b) spinous process on the attachment disc restricted to male representatives (Glenner et al. 1989, Glenner & Høeg 1995b, Høeg & Møller 2006, Høeg et al. 2009). Naupliar larvae of representatives of Rhizocephala are lecitotroph, lack all setae for suspension feeding and might be characterized by a kind of cuticular ring (floating collar) (Fig. 7E, 7E_1; Thompson 1836, Høeg et al. 2004b, Høeg & Møller 2006). However, representatives of Rhizocephala show an additional metamorphosis between the cypridoid larva and the sessile juvenile to an infective stage with a stylet. This infective stage is called kentrogon in female representatives and trichogon in male representatives. These inject a slug-shaped infesting stage into the host (vermigon stage) or into the matured female (Høeg 1985, 1987a, b, Glenner & Høeg 1994, 1995b, Glenner et al. 2000, Glenner 2001). The formation to kentrogon or trichogon has been lost in representatives of the monophyletic Akentrogonida (as ingroup to the remaining representatives of Rhizocephala) likely linked to a more r-strategic lifestyle with faster development of more offspring (Fig. 7E_{2-5}; Høeg 1982, Glenner & Hebsgaard 2006, Glenner et al. 2010, Nagler et al. 2017d, see also chapter 3.3). This additional metamorphosis has been proposed as adaptation to avoid of the hosts` defense for finally a successful infection (Ritchi & Høeg 1981, Høeg et al. 2005). Adult representatives of Rhizocephala show no retains of arthropod morphology or organization and consist of an external reproductive sac and internal root-like extension that absorb nutrients directly from the host (Høeg 1995b, Bresciani & Høeg 2001, Walker 2001, Høeg et al. 2005). Additionally, adult male representatives of Rhizocephala display dwarf males reduced to their simplest form, the testes (‚cryptogonochoric'; Ichikawa & Yanagimachi 1958, Yanagimachi & Fujimaki 1967, Lützen 1981, Høeg 1982, Høeg 1985, Lützen 1985, Glenner et al. 1989, Bower & Boutilier 1990, Høeg et al. 1990, Klepal 1990). Different studies have proposed that the unique parasitism in Rhizocephala originated from sessile suspension-feeding relatives (Glenner & Hebsgaard 2006, Glenner et al. 2008, Høeg et al. 2009, Pérez-Losada et al. 2009, Glenner et al. 2010, Pérez-Losada et al. 2012).

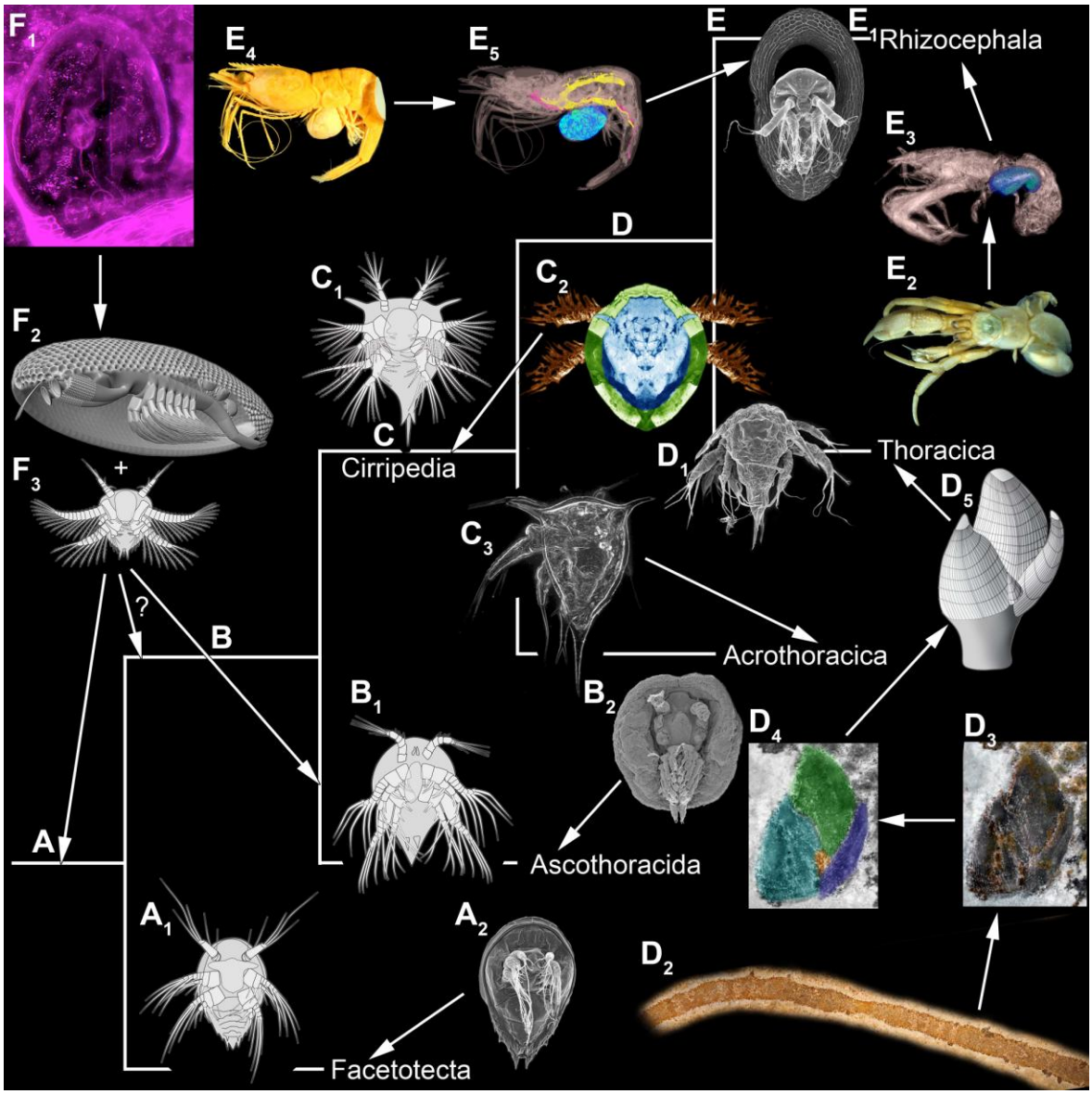


Fig. 7. Reconstructed relationship of some groups within Thecostraca *s.str*. with support from extant and fossil data. A-E) Different character state transitions. A_{1-2}) Naupliar larvae of representatives of Facetotecta, schematic and SEM image, ventral view. B_{1-2}) Representatives of Ascothoracida, schematic drawing of nauplius and SEM image of just hatching cypris, ventral view. C_1) schematic drawing of naupliar larvae of representatives of Cirripedia. C_2) fossil specimen. C_3) naupliar larva of representatives of Acrothoracica, fluorescence-photograph. D_1) naupliar larva of representatives of Thoracica, SEM image. D_{2-5}) fossil representative of Thoracica parasitizing a sponge, detailed macro photography, highlighted image (color-marks: blue = carina, turquoise = scutum, green = terga, orange = lateral plate) and reconstructed drawing. E_1) Naupliar larva of representatives of Rhizocephala, SEM image. E_{2-3}) Representative of ~~"K~~entrogonida" parasitizing their host crab, macro photograph and volume rendering. E_{4-5}) Representative of Akentrogonida parasitizing their host shrimp, macro photograph and volume rendering. F_{1-3}) Fossil representative of *Ebullitiocaris oviformis*, stereo photograph, three-dimensional model and reconstructed drawing of a naupliar larva *of E. oviformis*. Please note that the phylogenetic position of *E. oviformis* is not evaluated. Not to scale. Please see chapter 4.2 for more information.

ALTERNATIV PHYLOGENETIC POSITION OF FACETOTECTA

Besides the position proposed above, one alternative phylogenetic position of Facetotecta would be a sister group relationship to Ascothoracida (Fig. 8A). One character for the cypridoid larvae that would unite Ascothoracida and Facetotecta is the paraocular process with an aesthetasc and posterior filamentary tuft (several setae) (Fig. 8AI; Bresciani 1965, Newman 1974, Walker 1974, Grygier 1981a, 1983b, 1984, Ito 1985, Grygier 1987b, c, Ito & Takenaka 1988). With this pattern it would be likely, that the ancestor of Thecostraca *s. str.* was non-parasitic. The highly specialized morphology of the slug shaped infective stage (ypsigon, vermigon) known from Facetotecta and Rhizocephala would have evolved convergent (Pérez-Losada et al. 2012).

A third possibility would be a sister group relation between Ascothoracida and (Facetotecta + Cirripedia) (Fig. 8B). Facetotecta and Cirripedia would be united by a reduced gut, reduced mouthparts and a reduced abdomen (less than five segments) in the cypridoid larva (possibly plesiomorph characters; Fig. 8BI; Grygier 1987a-c, Jensen et al. 1994). Considering that adult representatives of Ascothoracida look like thecostracans cypridoid larvae, a heterochronic event might have taken place within Thecostraca *s. str.* This –adultised" appearance of the cypridoid larva of Facetotecta and Cirripedia is caused by peramorphosis, more specifically by hypermorphosis, likely together with pre-displacement (McNamara 1986). Thus, growing faster and –further" might represent a character that unites Facetotecta and Cirripedia.

As a fourth possibility, the similarity between the facetotectan ypsigon and the vermigon in representatives of rhizocephalan Kentrogonida, could indicate a sister group relationship between Rhizocephala and Facetotecta (Fig. 8C). The cypridoid larvae of Cirripedia with Facetotecta as ingroup could be characterized by a reduced gut, reduced mouthparts and a reduced abdomen with less than four segments (Fig. 8CI). Representatives of Rhizocephala and Facetotecta would be united by their highly specialized morphology, modified for a parasitic lifestyle (Fig. 8CII). Representatives of early Rhizocephala (e.g. *Lernaeodiscus*) have a cuticular stylet midventrally of the ventral site of the head, where one would expect a labrum. With this stylet, they pierce through the host and release the vermigon stage into the host (Høeg 1985, Glenner et al. 1989, Høeg 1992, 1995b, Chan et al. 2005, Glenner et al. 2000). This is similar in representatives of Facetotecta, in which the ypsigon is released through a hole between the bases of the antennules, through a spiny lobe median in the labrum (Grygier 1987a, Ito 1990, Belmonte 2005, Ponomarenko 2006, Glenner et al. 2008). As a consequence of this relation, representatives of Facetotecta would have secondary lost the fronto-lateral horns in the naupliar larvae and would have re-evolved an abdomen in the cypridoid larva (Høeg & Kolbasov 2002, Pérez-Losada et al. 2002, Høeg et al. 2004a, 2009, Pérez-Losada et al. 2009).

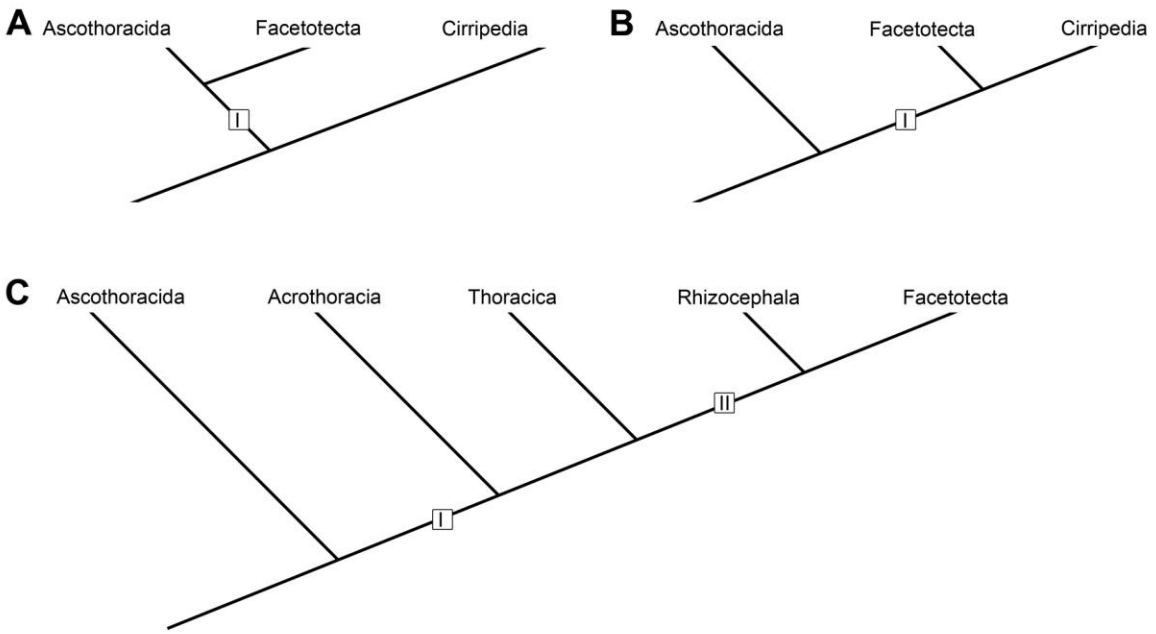


Fig. 8: Three different possible relationship of some groups within Thecostraca *s. str*. A) Facetotecta as sistergroup to Ascothoracida, (I) paraocular process and posterior filamentary tuft. B) Facetotecta as sistergroup to Cirripedia, (I) peramorphosis. C) Facetotecta as sister group to Rhizocephala, (I) peramorphosis, (II) blob-like infective stage. For explanation please see chapter 4.2.1.

4.2.2 ALTERNATIVE RELATIONSHIPS WITHIN THECOSTRACA *S. L.*

In the following, I will focus on the relationships of the different group within Thecostraca *s. l.* (Thecostraca *s. str.*, Tantulocarida, *Ebullitiocaris oviformis*). Due to the proposed outgroup position of *Bredocaris admiribilis* to the remaining groups of Thecostraca *s. l.* (Walossek & Müller 1998), I will exclude *B. admiribilis*. Furthermore, I assume the widely accepted phylogeny for Thecostraca *s. str*.: Facetotecta + (Ascothoracida + (Cirripedia)), while discussing the phylogenetic position of *E. oviformis* and Tantulocarida.

Phylogenetic position of Ebullitiocaris oviformis

One possible option for the phylogenetic affinity of *E. oviformis* is a sister group relation between *E. oviformis* to the other groups in Thecostraca s. str. (Figs. $7F_{1-3}$, 9A). Crucial characters for this relation would be the distinct limb bud delay in the naupliar stages, no setae at the proximal two elements of the antennula, three elements in the endopod of the antenna and mandible of naupliar stages, adult tagmosis, shield which covers the whole body and its structure in adult representatives (Fig. 9AI; Grygier 1987a, Haug et al. 2012,

see also chapter 3.4, 3.5). *Ebulitiocaris* is characterized by one paired head-appendage with suction discs at the distal end (Fig. 9AII; Nagler et al. in prep a). Thecostraca *s. str.* is characterized, beside others, by a metamorphosis including a cypridoid stage with its antennula modified for mechanical attachment. However, the most anterior, long slender appendage in adult representatives of *E. oviformis* could represent a part of a paraocular process, similar to that associated with the paraocular process of Facetotecta and Ascothoracida. The second head appendage with the distal suction disc of *Ebulitiocaris* could represent the antennula, similar to the attachment devices in other representatives of Thecostraca *s. str.* This suction discs are very similar to the suction discs of fish lice, although the suction discs of fish lice develop from the maxillula (see chapter 3.4). Thus, this character would be not an autapomorphy. All other autapomorphic characters uniting Thecostraca *s. str.* (e.g. lattice organs or eyes with tripartite cones, see above) are not accessible in the fossil *E. oviformis*.

If the long slender appendage represents a part of a paraocular process and the appendage with the distal suction disc represents the antennula of the fossil *E. oviformis*, a sister group relation between *E. oviformis* and Ascothoracida is likely (Fig. 9B). The uniting character is taking care for their brood by carrying the eggs within the shield as well as a less expressed metamorphosis (Fig. 9BI; Grygier 1984, see chapter 3.4, 3.5). The modification of the distal end of the possible antennula into a suction disc can be seen as a adaptation for parasitism. Characters uniting representatives of Ascothoracida is a bivalved shield with a distinct hinge line, in that both halves are fixed by a muscle (Fig. 9BII), whereas a univalved shield without a hinge line probably represents the plesiomorphic character for Thecostraca *s. str.* including *E. oviformis*. Thus, a free-living or plant-parasitic life style is likely for *Ebuliticaris oviformis* (Fig. 9BIII; Nagler et al. in prep a, see also chapter 3.4).

Phylogenetic position of Tantulocarida

Tantulocarida are the most likely sistergroup to Thecostraca *s. str.* (Fig. 9C; Bradford & Hewitt 1980, Boxshall & Lincoln 1987, Boxshall and Huys 1989, Walossek 1993, Boxshall 2005b, Høeg et al. 2009, Petrunnia & Kolbasov 2012). Possible apomorphies are (a) the position of male gonopores on the seventh trunk segment, (b) the general body tagmosis covered by an univalved shield and (c) the metamorphosis from free-living to sessile including a cypridoid larva with an attachment device either on the antenna in Thecostraca *s. str.* or from an unknown origin in Tantulocarida (Fig. 9CI; Boxshall & Lincoln 1987, Grygier 1987a, Boxshall and Huys 1989, Boxshall et al. 1989, Boxshall 1991, Huys et al. 1993). However, the position of male gonopores in Facetotecta is unknown. Thus, the apomorphic view of the position of the male gonopores is equivocal. Representatives of Tantulocarida are united by a parthenogenetic reproduction stage in their life cycle and by the lack of antennulae (Fig. 9CII; Boxshall 2005b). Representatives of Thecostraca *s. str.* are again united by compound eyes with tripartite cones and the lattice organs in the cypridoid larvae (Fig. 9CIII). Due to a comparison with Tantulocarida as outgroup to Thecostraca *s. str.*, the ground pattern of Thecostraca *s. str.* would have been parasitic.

Recent molecular analysis and morphological studies have proposed an ingroup position of Tantulocarida within Thecostraca *s. str.* (Fig. 9D; Newman 1992, Petrunnia et al. 2014). Characters uniting representatives of Tantulocarida and Cirripedia are (a) the attachment to a suitable habitat by secretion from muliticellular glands leading to one or two canals by four tubular ducts (cement gland in paired antennula in Cirripedia vs. cement glands in a unpaired proboscis in Tantulocarida), (b) a stylet-like appendage through that they infesting their host) and (c) both develop a nutrient absorbing system of rootlets inside the host (by a own stage in Rhizocephala, kentrogon, that infest the host in the haemolymph vs. the attached parasites stay and the rootlet grows through the whole punctured by the stylet in tantulocarids) (Fig. 9DI; Delage 1884, Boxshall & Lincoln 1983, Høeg 1985, 1987a). Representatives of Tantulocarida are characterized by a parthenogenetc lifestage (Fig. 9DII). Representatives of Cirripedia are characterized by fronto-lateral horns (Fig. 9DIII; see above). However, an ingroup position of Tantulocarida within Thecostraca *s. str*. would entail that the lattice organs have been lost secondarily (Petrunnia et al. 2014). Due to the ontogenetic development of the lattice organs from setae in representatives of Ascothoracida, Facetotecta and Cirripedia, it is possible that the remaining setae situated in pores at the dorsal surface of the shield in Tantulocarida, represent the plesiomorphic condition of the lattice organs (Høeg & Kolbasov 2002, Savchenko & Kolbasov 2009, Kolbasov & Savchenko 2010, Petrunina & Kolbasov 2012).

4.2.3 CONCLUSION (ALTERNATIVE POSSIBILTY) ABOUT PHYLOGENY OF THECOSTRACA *S. L.*

Taken all these possibilities together, it is extremely difficult to argue for the phylogenetic position of one of the discussed groups, because neither molecular nor morphological data are unequivocal. In order of a combination of morphological characters, lifestyles and fossil data, I propose following relationship: Branchiura + ((Ascothoracida+*E. oviformis*) + (*W. muelleri* + (Facetotecta + (Tantulocarida + Cirripedia)))) (Fig. 9E).

The ground pattern of the unnamed group Branchiura + ((Ascothoracida + *E. oviformis*) + (*W. muelleri* + (Facetotecta + (Tantulocarida + Cirripedia)))) would be characterized by (a) an attachment device (hook, disc) at the third element of the antennula, (b) not more than three elements in the endopod and two elements in the exopod of the thoracopods, (c) adult stages that look like post-naupliar stages, and (d, probably plesiomorph) an abdomen with at least five segments in larval stages after the naupliar phase (Fig. 9EI; Grygier 1987a, c, Rushton-Mellor & Boxshall 1994, Møller et al. 2007, 2008, Møller & Olesen 2010, 2014). Comparing this group with a possible outgroup, such as Copepodoida, parasitism would have occured in the ground pattern of this group.

Representatives of Branchiura are characterized by a modification of the maxillula into muscular suction cups or strong hooks that are used for attachment to their fish hosts (Fig. 9EII; Møller et al. 2008, Kaji et al. 2011). However, I cannot exclude an ingroup position of Branchiura within Thecostraca *s. str*. as sistergroup to Facetotecta + (Tantulocarida + Cirripedia), because some representatives of Branchiura bear a pre-oral

spine, formed by the labrum as seen in Facetotecta, Tantulocarida and Rhizocephala (Madsen 1964, Swanepoel & Avenant-Oldewage 1992, Gretsy et al. 1993).

The reconstructed morphology of the ground pattern of the unnamed sister group to Branchiura – ((Ascothoracida + *E. oviformis*) + (*W. muelleri* + (Facetotecta + (Tantulocarida + Cirripedia))) – is characterized by a transition from free-living, actively swimming larvae to sessile adults including a cypridoid larva (Fig. 9EIII). The reconstructed naupliar morphology of the ground pattern of this group is characterized by (a) two unarmed basal elements in the antennula, (b) a fusion of the distal elements of the antennula during metamorphosis and (c) not more than three elements of the endopod of the antenna and mandible (Fig. 9EIII; Grygier 1987a, Huys et al. 1993, Høeg et al. 2004a, 2009, Zhang et al. 2010, see also chapter 3.5). The reconstructed cypridoid morphology of the ground pattern of this group is characterized by (a) five pairs of chemosensory lattice organs (or at least setae) in the head shield with a posterior terminal pore in a keel-shaped elongated depression, separated from the cuticle, (b) a wholly or partially cover with a head shield, that is drawn down on either side, and (c) where eyes are present, they show tripartite crystalline cones (Fig. 9EIII; Hallberg & Elofsson 1983, Hallberg et al. 1985, Grygier 1987a, Jensen et al. 1994, Høeg et al. 1998, Ax 2000, Høeg & Kolbasov 2002, Rybakov et al. 2003, Kolbasov et al. 2007, 2008, Høeg et al 2009, Pérez-Losada et al. 2009, Høeg et al. 2014).

The reconstructed morphology of the ground pattern of the group containing Ascothoracida and *E. oviformis is* characterized by (a) a reproduction strategy linked to brood care within the shield, and (b) a parasitic lifestyle either on echinoderms or on plants (Fig. 9EIV). The reconstructed morphology of the ground pattern of the sistergroup to (Ascothoracida + *E. oviformis*) – (*W. muelleri* + (Facetotecta + (Tantulocarida + Cirripedia)) – is characterized by (a) an elongated labrum into a stylet-like appendage, (b, probably plesiomorph) the position of the male gonopore at the seventh trunk segment and (c) a most likely parasitic lifestyle (Fig. 9EV). The reconstructed morphology of the ground pattern of the sistergroup to *W. muelleri* – (Facetotecta + (Tantulocarida + Cirripedia)) – is characterized by (a) the lack of mouthparts and a gut in the cypridoid larva, (b) an abdomen with less than five segments and (c) and a highly derived adult morphology due to a heterochronic event (acceleration + hypermorphosis) in the metamorphosis between the cypridoid larva and the adult (Fig. 9EVI, see above). Representatives of Facetotecta are characterized by (a) two elements in the endopods of naupliar antenna and mandible, (b) a strongly sculptured shield, and (c) three abdominal segments in cypridoid larvae (Fig. 9EVII, see above). The reconstructed morphology of the ground pattern of the unnamed sister group to Facetotecta – (Tantulocarida + Cirripedia) – is characterized by a chemical attachment to the settle habitat by secretion from multicellular glands (Fig. 9EVIII, see also chapter 4.2.2).

Taken together important steps in the evolution of parasitism of the discussed group containing Branchiura, Ascothoracida, the fossil *E. oviformis*, the fossil *W. muelleri*, Facetotecta, Tantulocarida and Cirripedia are:

1) Transition to parasitism in the stem species of Thecostraca *s. l.* (Fig. 9EI).
2) Transition to a more specialized parasite due to the development of an elongated labrum modified for piercing or attaching to the host in the stem species of the unnamed group (*W. muelleri* + (Facetotecta + (Tantulocarida + Cirripedia))) (Fig. 9EV).

3) Transition to a highly adapted parasite with a completely different adult morphology caused by a heterochronic event (acceleration + hypermorphosis) in the stem species of the unnamed group (Facetotecta + (Tantulocarida + Cirripedia)) (Fig. 9EVI).
4) Transition to an obligate sessile adult (either parasitic or suspension feeding) by irreversible attachment to a suitable habitat by secretion of cement through glands in the stem species of the unnamed group (Tantulocarida + Cirripedia) (Fig. 9EVIII).

Following this evolutionary reconstruction, parasitism in Rhizocephala, Facetotecta and Tantulocarida would either have evolved convergent or have been lost secondarily in Acrothoracica and Thoracica. Due to the similar morphology of the feeding apparatus in Acrothoracica and Thoracica, it is more likely that parasitism in Rhizocephala evolved convergent to parasitism in Facetotecta and Tantulocarida. The group Thecostraca *s. str*. could be extended for the fossil *E. oviformis* as sistergroup to Ascothoracida , the fossil *W. muelleri* as sistergroup to Facetotecta + Tantulocarida + Cirripedia, as well as Tantulocarida as sistergroup to Cirripedia. The evolution of the morphology of the cypridoid larva displays a crucial innovation for the evolutionary success of the ~~"n~~ew" Thecostraca *s. str.* Furthermore, the heterochronic event, adding a morphological completely re-arranged adult in the same time span, could explain the larger evolutionary success by representatives of Facetotecta, Tantulocarida and Cirripedia.

Possible limits for this evolutionary reconstruction

There are morphological as well as molecular characters that argue for specific phylogenetic positions of each of the discussed groups. I am not able to value these characters, but I think that an assemblage of different characters is harder to evolve than single characters. Thus, the proposed evolutionary reconstruction might be possible. However, the long scientific history of the phylogenetic position of the large ingroups within Maxillopoda and especially within Thecostraca is ever since ambiguous.

As most groups within Thecostraca have a parasitic lifestyle and therefore an accelerated evolutionary tempo measured by molecular clocks (Dowton & Austin 1995; Page et al.1998), it might be harder to understand their evolution. Additionally, parasites tend to lose their own genes or gain hosts` genes. This might be one reason, why molecular data of parasitic groups are less significant and harder to interpret with current molecular methods (see chapter 4.3).

Furthermore, a unique ontogenetic pattern within all the discussed groups is the abundant frequency of heterochronic events (Haug & Haug 2015b). If representatives of a specific group tend to heterochronic events a comparison between single stages is almost not achievable, because these stages are either not developed, skipped or accelerated. Especially, the lack of knowledge in different groups, especially in the fossils, in Facetotecta and in Tantulocarida, impedes any evidence for a precise phylogeny. Based on current data, I conclude the above proposed phylogeny (Fig. 9E).

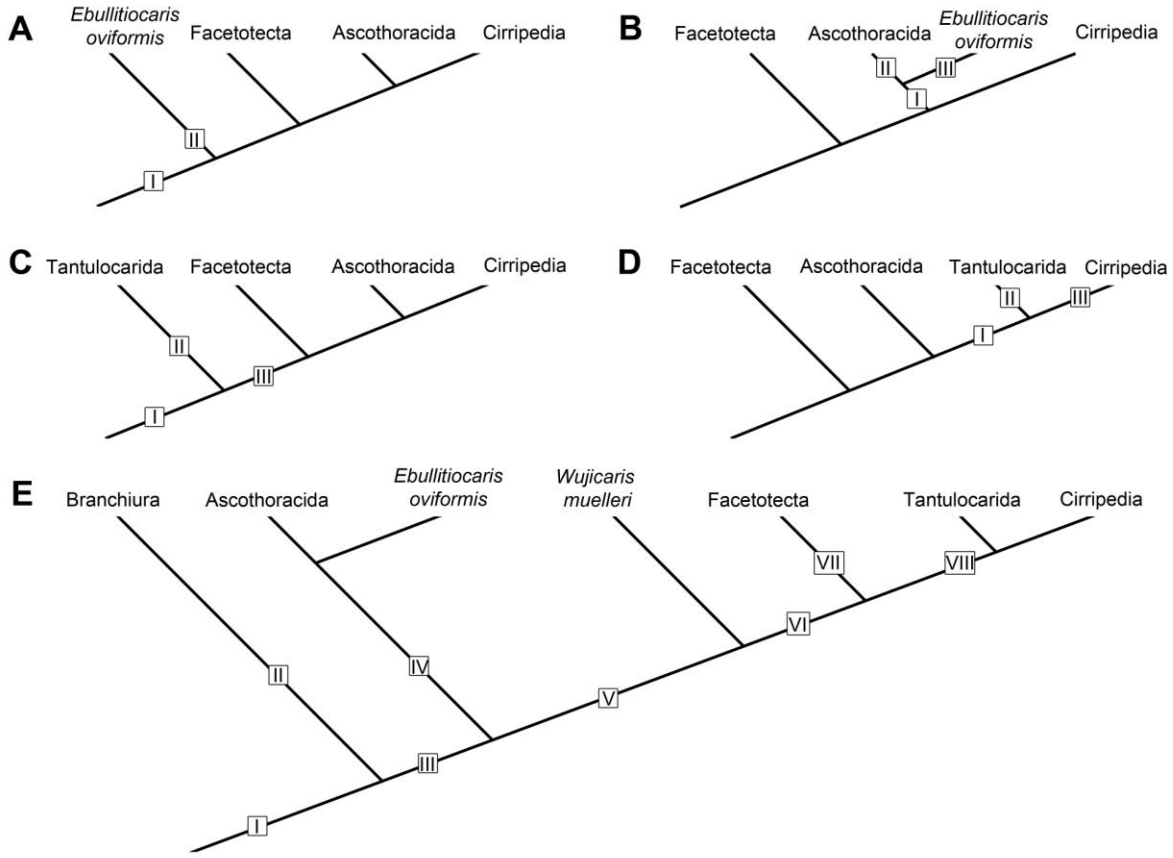


Fig. 9: Different possible relationship of some groups within Thecostraca *s. l*. A) Fossil *Ebullitiocaris oviformis* as sistergroup to Thecostraca *s. str*., (I) overall tagmosis, (II) paired head-appendage with suction discs at the distal end. B) Fossil *Ebullitiocaris oviformis* as sistergroup to Ascothoracida, (I) broodcare, (II) bivalved shield, (III) plantparasitism. C) Tantulocarida as sistergroup to Thecostraca s. str., (I) metamorphosis from free-living to sessile including a cypridoid larva with an attachment device, (II) parthenogenetic reproduction, (III) lattice organs. D) Tantuloacrida as sistergroup to Cirripedia, (I) attachment by chemicals, secreted from multicellular glands, (II) parthenogenetic reproduction, (III) fronto-lateral horns. E) Possible relationship of some groups within Thecostraca, (I) attachment device at antennula, (II) maxillula modified to suction discs, (III) metamorphosis from free-living to sessile, (IV) broodcare, (V) labrum modified into a stylet-like appendage, (VI) peramorphosis, (VII) three abdominal segments, (VIII) chemical attachment. For explanation of A-D and E, please see chapter 4.2.2 and 4.2.3, respectively.

4.3 COMPARISON BETWEEN THE EVOLUTION WITHIN CYMOTHOIDA AND THECOSTRACA

4.3.1 CONVERGENCE

Convergent evolution towards similar strategies, morphologies or behavior can be caused either because the number of possible combinations is limited by genetic and developmental factors (Orr 2005) or adaptation of possible combinations by different genetic changes (Arendt & Reznick 2008). In other words, genetic evolution differs from phenotypical evolution. Nevertheless, in the end there are only a limited number of solutions for the evolution of characters in different groups, which underlay a similar evolutionary pressure (Wright 1984, Poulin 2009, 2011). This is especially true for arthropods, because all arthropods have similar structured and legs and use them for everything, e.g. feeding and locomotion (Boxshall 2013). It is crucial to note, that morphologically similar structures in distantly related groups indicate not always a homology, but a structure with similar function (Stevens 1984, Richter 2005). These similar characters might be caused ~~-b~~y different cellular and physiological processes during development and be the ultimate expressions of completely different genetic architectures. Therefore, the convergent evolution of parasites at the phenotypic level is not necessarily reflected at the genomic level." (Poulin & Randhawa 2015, pp. 6-7). Due to the ambiguous view in parasitic groups of a correlation between morphology loss or gain and genetic loss or gain, respectively and the other way around (Reinsmith et al. 1974, Visser et al. 2001, Frank et al. 2002, Cavalier-Smith 2005, Huyse et al. 2005, Blaxter 2007, Corradi et al. 2010, Kikuchi et al. 2011, Cafasso & Chinali 2012, Heinz et al. 2012, Mueller et al. 2012, Gloeckner & Noegel 2013, Heinz & Lithgow 2013, Kishore et al. 2013, Rödelsperger et al. 2013, Tsai et al. 2013), I am going one step further: In my opinion the molecular phylogenies for parasitic groups fail, because first most studies (excluding phylogenomic studies) are looking for single genetic characters and not for a genetic combination, and second a correlation between molecular and morphological phylogenies is rarely possible, because molecular phylogenies are based on the genotype and morphological phylogenies are based on the phenotype. Selection affects the actual phenotype (Doolittle & Sapienza 1980). Due to the gap between molecular and morphological analyses, an integrative phylogeny is always problematic. Furthermore, I even speculate that the gain of hosts` genes in parasites, such as in nematodes, fungi or plants (Davis & Wurdack 2004, Butler et al. 2009, Paganini et al. 2012), can be the reason that Pentostomida and Branchiura are closely related in molecular phylogenies, while Branchiura are considered as maxillopodans in morphological studies (Grygier 1981b, 1987a, c, Boxshall & Huys 1989, Newman 1992, and see chapter 4.2).

4.3.2 MORPHOLOGICAL CONVERGENCE

One of the most distinct forms of phenotypic convergence among parasites is the loss or reduction of morphological characters. Interpretation of this loss of characters as „degenerative" evolution or secondarily simplification (Dodson & Dodson 1985) is not held anymore. In fact it is contrary; parasites are more specialized to their lifestyle by gaining innovative characters, e. g., attachment structures, specific mouthparts, and sensory structures, although they may lose their entire body structure (Osche 1966, Rohde 1989, Brooks et al. 1993, Lucius et al. 2017). These characters can be interpreted as adaptations, if the character evolved in response to a specific selective agent (Harvey & Pagel 1991). Additionally, as shown above, a loss of characters is not typical for free-living infective stages of parasites, as seen in the cryptoniscus or cypridodid larvae (see chapter 4.1 & 4.2). In order to describe the morphology of representatives of the rhizocephalan parasite *Sacculina*, a specific term („sacculinization") has been introduced to describe the loss of morphological characters in parasites compared to their non-parasitic relatives (Lorenz 1988; for challenges with such a term see Scholtz 2014).

Notably, some derived groups discussed herein, e.g. Epicaridea, Rhizocephala, Tantulocarida, and possibly also Facetotecta are extremely simplified by loss of almost all morphological characters, e.g. segmentation, cephalic sensory structures and appendages, which would be typical for Eucrustacea (Nielsen & Strømberg 1973, Boxshall & Lincoln 1983, Lützen & Jespersen 1992, Høeg & Lützen 1993, Høeg 1995b, Glenner et al. 2008, Boyko & Williams 2015). However, it has been proposed that the evolutionary development of new sensory, feeding and attachment structures speaks louder than the loss of plesiomorphic characters (Poulin & Randhawa 2015). Taken together, parasitic representatives of Cymothoida and of Thecostraca have convergent evolved towards a simpler morphology following their transition to a parasitic mode of life. Following recent studies (Poulin 2011, Poulin & Randhawa 2015), the convergent characters among parasitic groups appears at a more complex functional and ecological level, therefore, I discuss not single morphological adaptations, but a connected character complex consisting of the site of infestation, feeding and attachment structures, and partly the life cycle and reproductive pattern.

Representatives of ectoparasitic Cymothoidae, Epicaridea and juvenile Gnathiidae attach to the host always at easily penetrable areas, e.g. insertion of the fins of fishes, if at the fish' fins, between the fin rays, the gills of fishes, between segments of crustaceans, between the eyes of crustaceans, branchial chambers of crustaceans. These ectoparasitic isopods attach to their hosts with their thoracopods and pierce through the hosts` tissue to suck the hosts` body fluids or bite pieces of the host (Koehler 1911, Field 1969, Anderson & Dale 1981, Williams & Williams 1985a, b, 1987, 1986, Bashirullah 1991, Shields & Gómez-Gutiérrez 1996, Al-Zubaidy & Mhaisen 2013, Klompmaker & Boxshall 2015, Nagler & Haug 2016). This pattern of site infection can also be seen in ectoparasitic representatives of Tantulocarida and Thoracica. While representatives of Tantulacarida show a similar feeding apparatus by piercing through the crustacean host, representatives of Thoracica still show their non-functional cirri and feed through the surface of their root-like stalk that is embedded into the host fish (Johnston & Frost 1927, Boxshall & Huys 1989, Huys et al. 1993, Long & Waggoner 1993, Yano & Musick 2000, Rees et al. 2014).

Representatives of Rhizocephala settle mostly on the dorsal left side between segments of crustaceans‘ abdomen or again on the gills of other crustaceans before they inject the infesting stage. The infesting stage migrates through the hosts` body and develops until the externa can break through the host, always between the thorax and pleon of the host during a molt (Ritchi & Høeg 1981, Høeg 1982, Bower & Boutillier 1990, Høeg 1990, Glenner & Høeg 1995b, Høeg 1995b, Glenner et al. 2000, Glenner 2001). A similar infective pattern is known from representatives of endoparasitic Epicaridea, such as Bopyridae or Entoniscidae. They enter the crustacean host through the gills during a specific infesting stage, the cryptoniscus larva. In contrast to representatives of Rhizocephala they are often surrounded by a hosts` membrane, thus not migrating in the host‘s body and not so extremely reduced in their morphology (Veillet 1945, Kuris 1971, Kuris et al. 1980, Pascual et al. 2002). Representatives of such endoparasitic Epicaridea release their eggs through a created pore in the hosts` gill or produce even a stalk that extends to the external environment of the host through the hosts branchial chamber (McDermott et al. 2010). Due to their highly modified and reduced morphology into a non-segmented body without appendages, but with a brood chamber (Williams & Boyko 2012) and their similar lifecycle, they seem to be convergent evolved to Rhizocephalans. Endoparasitic representatives of Epicaridea show a shorter evolutionary history than Rhizocephala, thus, Epicaridea might evolve also an external sac and a motile infesting stage, because of the same evolutionary pressure caused by the internal environment of crustaceans.

Interestingly, representatives of Epicaridea show some similarities to representatives of Ascothoracida. Some representatives of Ascothoracida are surrounded by hosts` membrane; the still segmented males live like in endoparasitic representatives of Epicaridea within the mantle cavity of the morphological reduced females (Wagin 1946, Hickman 1959, Grygier 1984, 87b). After hatching within the females mantle, the mantle breaks and the larvae of Ascothoracida penetrates the host`s stomach and leave it through the mouth opening (Hickmann 1959, Grygier 1984). Representatives of Ascothoracida feed either by absorption through their surface or by piercing and biting (Lacaze-Duthiers 1880, Wagin 1976, Bresciani & Jespersen 1985). Although representatives of Epicaridea feed mainly by piercing and biting the host, there has been absorption of nutrients reported (Reinhard 1956, Holdich 1975, Pascual et al. 2002, Izdebska & Rolbiecki 2010). Due to the still unresolved phylogeny within Ascothoracida (Poulin & Hamilton 1997) and within Epicaridea (Boyko et al. 2013), I cannot imply any evolutionary convergence between the feeding apparatus in Ascothoracida and Epicaridea. Nevertheless, it seems that feeding by absorption of nutrients through the parasites surface evolved independently more than one time within Ascothoracida and within endoparasitic Epicaridea.

Although representatives of Cymothoida are always hermaphrodites (mainly sequentiell hermaphrodites and protandrous), within Cymothoida it can be observed the same evolutionary direction towards an extreme sexual dimorphism often linked with dwarf males than in representatives of Thecostraca. In ectoparasitic and highly adapted forms, such as Ascothoracida and Epicaridea, this character reaches a milestone by a highly, morphological reduced females and still segmented males. However, the cryptochrononistic reproductive system in representatives of Rhizocephala with a male reduced to testes living in a completely different arranged female represent a highly specialized sex system (Raibaut & Trilles 1993).

4.3.3 HETEROCHRONIC CONVERGENCE

Heterochrony has been proposed to be one driving force of evolution (Gould 1977, Haug et al. 2009). Although in most cases heterochronic events are rather local, e.g. certain structures, than global, e.g. an entire organism (Haug et al. 2009), I detected global heterochronic events in both studied groups by applying the methods of phylogenetic systematics (following Haug et al. 2009, Ramsköld 1988). Due to the proposed phylogenies (for Cymothoida chapter 4.1, for Thecostraca chapter 4.2), we have a solid base for the detection of heterochronic events.

Representatives of Cymothoida show no global heterochronic event in their evolutionary phylogeny towards Gnathiidae until to the ground pattern of the unnamed sister group to representatives of Aegidae. At this state, the stem species of the group (Cymothoidae + (Epicaridea + Gnathiidae)) is characterized by a peramorphosis by a combined hypermorphosis and acceleration (same starting point, same duration and number of stages, but different additional end point), because the reconstructed juvenile morphology of the ground pattern of the group (Cymothoidae + (Epicaridea + Gnathiidae)) is similar to adult representatives of Aegidae in morphology and behavior. Additionally, the reconstructed adult morphology of the ground pattern of the group (Cymothoidae + (Epicaridea + Gnathiidae)) is characterized by a permanently attachment to their host fishes and a highly adapted morphology for their permanent parasitism (Nagler & Haug 2016, Nagler et al. 2017a, see also chapter 2.2, 2.4). Following the evolutionary reconstruction, in the ground pattern of the unnamed sister group (Epicaridea + Gnathiidae) to Cymothoidae a second global peramorphic event occurs. There a pre-displacement (later starting point, same duration and same numbers of stages, same end point) occurs, because the larvae, juveniles and adults of representatives of this ground pattern of the group (Epicaridea + Gnathiidae) are similar to adult representatives of Cymothoidae. Looking into the endoparasitic groups within Epicaridea, additionally, a hypermorphosis combined with acceleration occurs in the female adult representatives by ~~a~~dding" a new morphological adapted stage, while adult males retain more or less the larval morphology. Due to the protandrous hermaphrodism, reported for all representatives of Cymothoida (Brandt & Poore 2003), this pattern is not unusual. In contrast, representatives of Gnathiidae evolved a hypermorphosis by adding a non-feeding adult stage. Notably, the morphological differentiation between male and female adult representatives of Gnathiidae differs significantly; the female representatives of Gnathiidae are rather similar to juveniles, while male representatives of Gnathiidae are extremely modified (Smit & Davies 2004, Smit et al. 2003). Taken together, there have been at least three heterochronic events, always a peramorphic event, within the evolution of Cymothoida towards the highly adapted group Gnathiidae and Epicaridea.

Detecting Heterochronic events is less clear in the evolutionary reconstruction of Thecostraca due to the lack of knowledge in certain groups. Thus, referring to Thecostraca *s. l.* it is hard to make any statement about Heterochronic events, because we cannot correlate certain groups due to their modified (very abbreviated) ontogeny, e.g. Branchiura. However, one heterochronic event, a combination of hypermorphosis and acceleration is obvious. This specific type of peramorphosis occurs in the ground pattern of the group (Facetotecta + (Tantulocarida + Cirripedia)) by ~~a~~dding" a morphological different adult compared to representatives of Ascothoracida (see also chapter 4.2). Reconstructing the

ground pattern of Cirripedia, it seems that there occurs a paedomorphism within the male representatives. All representatives of Cirripedia have dwarf males that are similar to the cypridoid larva (Klepal 1985, Høeg 1995a, Kolbasov 2002). However, it is not possible to test this hypothesis, because there is no knowledge about adult males in representatives of Facetotecta. Within Rhizocephala, again, acceleration occurs at the transition from Kentrogonida to Akentrogonida, because representatives of Akentrogonida skip the infesting kentrogon stage (Høeg 1990, Glenner & Høeg 1994, Nagler et al. 2017d, see also chapter 3.3). In conclusion, there have been at least two Heterochronic events, again peramorphic events, within the evolution of Thecostraca towards the highly adapted group of akentrogonid Rhizocephala. To study heterochronic events in the evolution of Thecostraca *s. l.* the method of studying developmental, or rather ontogenetic sequences of a specific group can be used (Smith 2002, Fritsch et al. 2013).

Regarding the convergence in the abundance or occurrence of heterochronic events, it seems that mainly peramorphic events are favored by parasitic groups. In contrast to non-parasitic groups, like the achelatan decapods, it is likely that within parasitic groups, there is more selective pressure on the adult, thus the parasitic stage, than on the juvenile representative of parasitic groups, at least in the two studied groups, Cymothoida and Thecostraca *s. l.*

In conclusion, there seem to be several convergent characters between the parasitic groups within Cymothoida and Thecostraca *s. l.*, although it is hard to draw any major conclusion due to the shear vastness of parasites within these groups. Due to the lack of knowledge in some ingroups of Thecostraca *s. l.*, it is hard to discuss these characters. Nevertheless, it seems that there is a general evolutionary convergence to a ~~–s~~implified" morphology, absorption of nutrients through the surface of the parasite, sexual dimorphism and peramorphic events. These characters obviously correlate to the degree of adaptation and dependence of the parasite to the host. This parallel or at least convergent evolution of different pattern in Cymothoida and Thecostraca *s. str.* can be enlightened by a closer comparison between these groups in reference to their ontogenetic, morphological, ecological and life-history traits. Including more fossil data and data about extant Thecostraca *s. l.* will help to elucidate the evolution of parasitism between and in these two groups.

4.4 COMPARISON IN A WIDER SYSTEMATIC CONTEXT, CONCLUSIONS & OUTLOOK

Comparing parasitic groups, it is especially interesting to examine the origin of parasitism within these groups. It is well known, that most, if not all parasitic groups originated from non-parasitic relatives by morphological, physiological or ecological adaptations to parasitism and consequently major evolutionary shifts in their life history strategies. The evolution of parasitism is displayed as a stepwise process, for example via scavenging stages, saprotrophic stages or epibiotic stages. Such a stepwise evolution has been proposed to occur independently in several groups at different times in their own evolutionary history, e.g. nematodes, several ingroups of insects, mites, flatworms, Acantocephala (Osche 1956, 1958, 1966, Piekarski 1973, Price 1991, Ronquist 1994, Blaxter et al. 1998, Littlewood et al. 1999, Strand 2000, Near 2002, Mironov et al. 2005, Dietrich & Sommer 2009, Poulin 2011, Blaxter & Koutsovoulos 2015).

Concerning the evolution of parasitism, especially insects are interesting, because it seems that some insects developed adaptations, like elongated mouthparts or a habitat that is close to their future hosts, early in their evolutionary history (Nagler & Haug 2015). One model example for studying the evolution of parasitism and co-evolution between parasite and host are lice due to their stepwise adaptation to obligatory parasitism: Modern book lice, the suggested sistergroup to true lice, are known free living from nests and pelage of mammals and birds, had simple chewing mouthparts (Mockford 67, 71, Yoshizawa & Lienhard 2010). Later in their evolutionary history, they adapted from associates to parasites by feeding directly from their hosts; hence, representatives of true lice developed more specialized mouthparts for specific hosts and consequently a large diversity of forms (Light et al. 2010, Nagler & Haug 2015). Modern true lice, e.g. chewing and sucking lice (mallophagan and anopluran respectively) are obligatory ectoparasitic on birds and mammals (Yoshizawa & Johnson 2010). With this, the evolution displays a stepwise process via saprotrophism and phoresy to obligate ectoparasitism.

The evolution of parasitism within Cymothoida (see chapter 4.1) shows a similar pattern at least towards the obligate ectoparasitic representatives of Cymothoidae via scavenging and temporary parasitism (Nagler et al. 2017a). The step to endoparasitism in some representatives of Epicaridea would thus display one step further. The next step resembles the one that has been proposed for representatives of endoparasitic nematodes.

Due to the well-studied evolution of parasitism in nematodes, several steps have been proposed from free-living relatives to obligatory parasitic, partly endoparasitic representatives of nematodes (Osche 1956, 58, 66, Blaxter et al. 1998, Blaxter & Koutsovoulos 2015). The first evolutionary event led to saprotrophic nematodes that live in the ground and have the ability to produce resting stages to outlive unfavorable environmental conditions. Later saprotrophic nematodes evolved phoretic behavior on scavenging or saprotrophic insects, such as dung beetles. With the next step, they evolved an endoparasitic lifestyle due to an eventually contact of the resting stage to another metazoan, e.g. by feeding; thus, there are parasitic juvenile stages within the host, but free living adults that produce resting stages. A next evolutionary event led to parasitic adults, but still a resting stage outside the host that will be feed by a host. The climax of the evolutionary history of some nematode groups is the reduction of all free living stages and the addition of intermediate hosts, due to the ingestion of the resting stage within an

intermediate host by the final host (Osche 1956, 58). Furthermore, in the case of nematodes it has been proposed that a saprobic environment complies with all requirements for endoparasitism due to the similar abiotic factors (Osche 1966)

Again, the evolution of parasitism within Thecostraca *s. l.* is more difficult to interpret due to the lack of knowledge about certain groups resulting neither in a clarified phylogeny nor the sister group is unambiguously known. Following the here proposed phylogeny for Thecostraca *s. l.* (see chapter 4.2), it is likely that parasitism originated in the ground pattern. One important step of the evolutionary success of parasitic representatives of Thecostraca is definitely the origin of the cypridoid larva, which displays the transition from a free living nauplius larva to a morphologically specialized adult (Crisp 1984, Høeg 1995a, b, Høeg & Møller 2006). Looking closely at representatives of Cirripedia, a stepwise evolution might be detected towards the highly modified representatives of Rhizocephala. It has been proposed that representatives of Thoracica that are epizoic at a wide range of invertebrates and vertebrates, e.g. turtles, whales, crustaceans, molluscs, evolved via representatives that obligatory parasitize their hosts with their ramified peduncle to the obligatory parasitic representatives of Rhizocephala (Day 1939, Loven 1845, Osche 1966, Raibaut & Trilles 1993). However, recent molecular and morphological studies about the phylogenetic relationship between Rhizocephala and Thoracica have proposed more than one independent origin of parasitism within Cirripedia (Pérez-Losada et al. 2002, Leung 2014, Rees et al. 2014, Chan & Høeg 2015). Concerning the proposed lifestyle at the transition to the stem species of Cirripedia as suspension feeder sessile at any kind of substratum, several independent origins or parasitism within Cirripedia are possible.

In summary, there are many different transitions to parasitism in the evolutionary history of arthropods (Poulin 2011). As seen for Cymothoida and Thecostraca, fossils can provide direct evidence for parasitism and in comparison to their extant relatives these fossils can reveal important aspects of the origins and diversification of parasitism with different grading. Notably, even with all the fossil examples we only get a phenomenological insight. Combining several methods, e.g. biogeographics, taphonomy, geochemical studies, molecular studies, phylogenetics, fossil record and extant species, we might enlighten and understand the evolution, biology, ecology and morphology of fossil parasites. In other words, only combining approaches with an elaborated concept of mutual views between fossil and extant species, can supply a more detailed understanding of the evolutionary processes leading to modern parasitic forms. As shown, my thesis presents such an approach (minimum ages of fossils, divergence times, clarifying life styles based on functional morphology, comparison between fossil and extant representatives) to study and reconstruct the evolution of parasitism within Cymothoida and Thecostraca. The presented results about the character evolution of parasitism within these two groups illustrate that such a methodological combination is worth to pursue. Finally, by pursuing such an approach also while studying other lineages, we will be able to tell the evolutionary success story of parasitism within these different lineages.

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