Coevolution between king crabs (Paguridae: Lithodinae) and parasitic barnacles (Cirripedia: Rhizocephala)

Christoph Noever

Dissertation for the degree of philosophiae doctor (PhD)
at the University of Bergen

2017

Year: 2017
Title: Coevolution between king crabs (Paguridae: Lithodinae) and parasitic barnacles (Cirripedia: Rhizocephala)
Author: Christoph Noever
Print: AiT Bjerch AS / University of Bergen

Scientific environment

The work for this thesis was carried out in the Marine Biodiversity research group at the Department of Biology, Faculty of Mathematics and Natural Sciences, University of Bergen. The project was funded through a PhD grant from the University of Bergen. Additional funding for laboratory work and travel expenses were provided by a grand form the Meltzer Research Fund, University of Bergen, as well as from the SYNTHESYS Project which is financed by European Community Research Infrastructure Action under the FP7 "Capacities" Program.

Acknowledgements

First of all, I would like to thank Henrik Glenner, my mentor and supervisor, who has initiated this project and has been invaluable for the entire project during the last years.

I am grateful for the time I could spend with Glenn Bristow, who recently sadly passed away. Glenn was always a source of inspiration and a great motivator for research in marine parasitology.

I would like to thank Solveig Thorkildsen, Kenneth Meland, and Louise Lindblom, for providing an excellent working environment in the Biodiversity Laboratories at the Department of Biology. They were also helpful and enthusiastic during many discussions about the molecular work.

I would like to thank Andrew Olson, at the Department of Fish and Game, Alaska, for the opportunity to participate in one of their red king crab surveys.

Thanks to the crew of R/V Hans Brattström, who made sampling activities smooth and successful during numerous days on the local fjords.

The Shannon Point Marine Center (Western Washington University, Anacortes, WA, USA) helped in sampling of specimens and provided laboratory space.

Thanks to Karen van Dorp, Naturalis Biodiversity Center, Leiden, the Netherlands for providing access to the Naturalis research collection and providing work space during my visit.

Thanks to Fiina Amakali and Erich Maletzky, from the Namibian Ministry of Fisheries and Marine Resources (MFMR), who provided parasite samples from their fishery surveys.

Thanks to Christian Wirkner and Stefan Richter, University of Rostock, Germany for the opportunity to work with their MicroCT equipment.

Thanks to Ryuta Yoshida, University of the Ryukyus, Okinawa, Japan for pointing out various king crab parasite specimens which he located in museum collections, and for providing material from Japan.

Hans Tore Rapp and Nina Mikkelsen are thanked for comments on the manuscripts.

Specimens for DNA extractions were kindly loaned from the University Museum of Bergen, Norway, the NIWA Invertebrate Collection, Wellington, New Zealand, the Naturalis Biodiversity Center, Leiden, the Netherlands, the Smithsonian National Museum of Natural History, Washington D.C., USA, the Museum für Naturkunde, Berlin, Germany, and the Natural History Museum, London, UK.

Abstract

Molecular evidence has established that king crabs (Lithodinae) are gigantic hermit crabs without a gastropod shell to protect their abdomen. Secondarily, the abdomen has become calcified and flexed, in a crab-like manner. As a result, king crabs are superficially resembling brachyuran (true) crabs. Both king crabs and hermit crabs are parasitized by parasitic barnacles (Rhizocephala), which are an exclusively parasitic taxon belonging to the Cirripedia. Rhizocephalans are highly adapted to their parasitic lifestyle. Being irreversibly bound to their host, the parasites have extremely intimate relationships with their host taxa. In this thesis, the coevolutionary interplay between king crabs and parasitic barnacles has been investigated, to test, if the fascinating evolutionary origin of king crabs from a hermit crab ancestor can also be traced via the coevolution with their parasitic barnacles.

To resolve the exact placement of king crabs within the hermit crabs and identify the closest extant relatives to the Lithodinae, a phylogenetic tree of hermit crabs and king crabs was constructed via Bayesian Inference and Maximum Likelihood analyses. To achieve this goal, multiple molecular markers of mitochondrial and nuclear ribosomal genes were utilized in combination with extensive taxon sampling. Further, a molecular phylogenetic tree of parasitic barnacles from numerous hermit crabs and king crabs was produced. The phylogeny of parasitic barnacles was subsequently linked to the phylogenetic tree of hermit crabs and king crabs, via individual host-parasite associations. Cophylogeny analyses of the dataset revealed that the parasites closely followed their hosts in a coevolutionary manner, where the speciation of a host lineage is accompanied by a parallel diversification of the parasite lineage. The evolution of king crabs was accompanied by two independent parasite lineages which followed the evolution of king crabs from a hermit crab ancestor. The host-parasite cophylogeny analyses strongly corroborated the phylogenetic placement of king crabs within the hermit crab family Paguridae.

Hermit crabs were known to host a number of parasitic barnacle species, but only one species had been reported as a parasite of king crabs prior to this study. This parasite was supposed to parasitize a wide range of species, with a global distribution spanning all oceans. Detailed investigation of rhizocephalan parasites of king crabs revealed that the previously recognized single species constitutes of a rather large complex of cryptic species, each specialized to only one or few hosts. These cryptic species, of which two species new to science were described in this thesis, however, are difficult, or even impossible, to distinguish by morphology alone.

Rhizocephala solely rely on their host for nutrition. Due to their parasitic lifestyle they have evolved a highly modified morphology compared to other crustaceans, lacking almost all arthropod features like segmentation, a centralized nervous system, any alimentary tract, or appendages. The adult morphology of the female parasite can be divided into two distinct parts: a sac-shaped reproductive body which is attached to the outside of the host, called the externa; and a trophic part situated inside the host, the interna, which has a root-like appearance. The interna infiltrates the inner organs as a complicated mycelia-like structure that spreads throughout the body of the host. Its location, hidden inside the host's body, and highly structured morphology, makes this part of the organism difficult to study. Using state of the art X-ray micro computer tomography (MicroCT) and computer-aided 3D-reconstruction, the spatial organization of this root system inside the intact host was documented for parasites of king crabs and hermit crabs to investigate the parasite's adaption to a highly changed morphology in their hosts, due to the process of carcinization in the Lithodinae.

Results of this thesis are further used to evaluate the potential danger of the Northeast Atlantic red king crab population to become parasitized by a rhizocephalan parasite, with potential damaging effects for the fisheries industry. The red king crab, *Paralithodes camtschaticus,* is frequently parasitized by rhizocephalans in its native range, the North Pacific, but the introduced red king crab stock in the North Atlantic is rhizocephalan-free. The parasite grows an extensive system of green rootlets inside the crab, making infested king crabs unusable for marketing. The parasite further sterilizes its host, with a potential highly negative effect on population size and significant economic impact on the king crab fisheries.

List of publications

Paper I

Noever, C., & Glenner, H. The origin of king crabs: hermit crab ancestry under the magnifying glass. Under review at the *Zoological Journal of the Linnean Society*.

Paper II

Noever, C., Olson, A., & Glenner, H. (2016). Two new cryptic and sympatric species of the king crab parasite *Briarosaccus* (Cirripedia: Rhizocephala) in the North Pacific. *Zoological Journal of the Linnean Society*, *176*(1), 3–14. http://doi.org/10.1111/zoj.12304

Paper III

Noever, C., & Glenner, H. Host-parasite cophylogeny of Rhizocephala corroborates the origin of king crabs from hermit crabs. Manuscript

Paper IV

Noever, C., Keiler, J., & Glenner, H. (2016). First 3D reconstruction of the rhizocephalan root system using MicroCT. *Journal of Sea Research*, *113*, 58–64. http://doi.org/10.1016/j.seares.2015.08.002

Reprints were made with permission from the Zoological Journal of the Linnean Society (John Wiley & Sons publications), and the Journal of Sea Research (Elsevier).

Contents

1. **Introduction** **13**
  - **1.1 The king crabs** **13**
    - 1.1.1 A brief historic review on the concept of king crab evolution 13
    - 1.1.2 The morphology of king crabs 14
    - 1.1.3 Morphological flexibility in the Anomura 20
    - 1.1.4 Carcinization in the Anomura 21
    - 1.1.5 The fossil record 22
  - **1.2 The parasitic barnacles (Rhizocephala)** **23**
    - 1.2.1 Morphology of Rhizocephala 23
    - 1.2.2 The life cycle of the Rhizocephala 24
    - 1.2.3 Effects induced on the host 27
    - 1.2.4 Host specificity 27
    - 1.2.5 Rhizocephalan parasites of king crabs 28
  - **1.3 Host-parasite cophylogeny** **29**
  - **1.4 Rhizocephalans as biological host control agents** **30**
2. **Aims of this thesis** **33**
3. **Results and discussion** **35**
  - **3.1 Molecuar phylogeny of pagurid hermit crabs and lithodid crabs** **35**
    - 3.1.1 Rationale 35
    - 3.1.2 Main results 36
  - **3.2 Host specificity and species delimitation of the king crab parasite *Briarosaccus*** **39**
    - 3.2.1 Rationale 39
    - 3.2.2 Main results 40
  - **3.3 Phylogeny of parasitic barnacles and host–parasite coevolution** **40**
    - 3.3.1 Rationale 40
    - 3.3.2 Main results 41
  - **3.4 The internal, trophic root system of rhizocephalans from lithodids and hermit crabs** **44**
    - 3.4.1 Rationale 44
    - 3.4.2 Main results 45
  - **3.5 The type material of *Briarosaccus callosus*** **46**
  - **3.6 The Norwegian Paguridae fauna: king crab origin in a nutshell** **52**

3.7 Potential of rhizocephalans as biological control agent against invasive king crabs / Risk evaluation of parasite infection for Northeast Atlantic king crabs 55s

4. Main conclusions 63

5. Future perspectives 65
   5.1 Systematic of Paguridae 65
   5.2 Molecular work in Rhizocephala 65
   5.3 Morphological studies in Rhizocephala 66

6. References 67

Coevolution between king crabs (Paguridae: Lithodinae) and parasitic barnacles (Cirripedia: Rhizocephala)

1. Introduction

1.1 The king crabs

1.1.1 A brief historic review on the concept of king crab evolution

Lithodinae, which include the large king crabs (Fig. 1d), are anomuran crustaceans with a crab-like body, that superficially resembles that of brachyuran (true) crabs (Fig. 1i). Molecular evidence has established that king crabs, which are found in Norwegian waters as the prominent invasive red king crab, *Paralithodes camtschaticus* (Fig. 2k), and the smaller native species, *Lithodes maja* (Fig. 2j), derived from an asymmetrical hermit crab ancestor, that abandoned the use of empty gastropod shells for protection (Cunningham, Blackstone, & Buss, 1992; Tsang *et al.*, 2011; Bracken-Grissom *et al.*, 2013). Secondarily, the abdomen has become calcified and folded under the cephalothorax, resulting in a crab-like morphology. Additionally, molecular studies suggest, that king crabs actually originated within the hermit crab genus *Pagurus* (Cunningham *et al.*, 1992), which is represented in Norwegian waters by several species.

The origin of king crabs from an asymmetrical hermit crab ancestor had already been proposed in the late 19th century (Boas, 1880a,b; Bouvier, 1894), and regained considerate attention after Cunningham et al. (1992) confirmed the position of king crabs within the hermit crab family Paguridae in the first molecular phylogeny on the taxon, based on the mitochondrial 16S rRNA subunit. Numerous following molecular studies that touched the issue received corresponding results (Zaklan, 2002; Morrison *et al.*, 2002; Tsang *et al.*, 2008; Ahyong, Schnabel, & Maas, 2009; Bracken *et al.*, 2009; Chu *et al.*, 2009). But despite the increasing evidence of a hermit crab ancestry of the taxon, some of the leading taxonomist in anomuran crustaceans strongly rejected this evolutionary scenario (Mclaughlin & Lemaitre, 1997; McLaughlin & Lemaitre, 2000; Mclaughlin, Lemaitre, & Tudge, 2004; McLaughlin, Lemaitre, & Sorhannus, 2007; Lemaitre & McLaughlin, 2009). These authors proposed a rather reverse evolutionary scenario, in which the lithodid crab-like body form gave rise to the hermit crab body form through calcium loss, habitat change and consequential morphological adaptions. Therefore, at the beginning of this PhD project, the evolution of king crabs was heartily debated, and coevolutionary evidence from a host-parasite system promised to provide further evidence to remove the remaining doubts. Soon after, further molecular studies (Schnabel, Ahyong, & Maas, 2011; Tsang *et al.*, 2011; Bracken-Grissom *et al.*, 2013), as well as a phylogeny based on the morphology of the foregut in Anomura (Reimann, Richter, & Scholtz, 2011), solidified the phylogenetic position of lithodid crabs within the hermit crab family Paguridae.

1.1.2 The morphology of king crabs

The overall body shape of lithodid crabs is highly altered from its hermit crab ancestor and superficially rather resembles that of brachyuran crabs (Fig. 1). However, clear morphological traces of the taxon's origin from an asymmetric pagurid hermit crab ancestor can still be found. The most obvious trace of this origin is found in their asymmetric pleon (Fig. 1f-h). While male lithodids have a fairly symmetric pleon (Fig. 1h), females typically exhibit a clear asymmetric, dextrally offset abdomen (Duguid, 2010) regarding both the pleopods, which are used to carry the eggs and are only developed on the left side, as well as the tergal plates (Fig. 1e, g) (Mclaughlin & Lemaitre, 1997; McLaughlin & Lemaitre, 2000; Mclaughlin *et al.*, 2004). Asymmetrical hermit crabs are highly adapted to the use of dextrally coiled gastropod housing for protection (Fig. 1a-c). Here, bearing of the egg mass on the left body side is highly advantageous, since the egg mass only occupies the free space to the outer wall of the shell, while the right side of the pleon is twisted around the shells columella (Mclaughlin & Lemaitre, 1997). Dextral gastropod shells undoubtedly influence the direction of hermit crab asymmetries (Palmer, 2004) which are still retained in lithodid crabs.

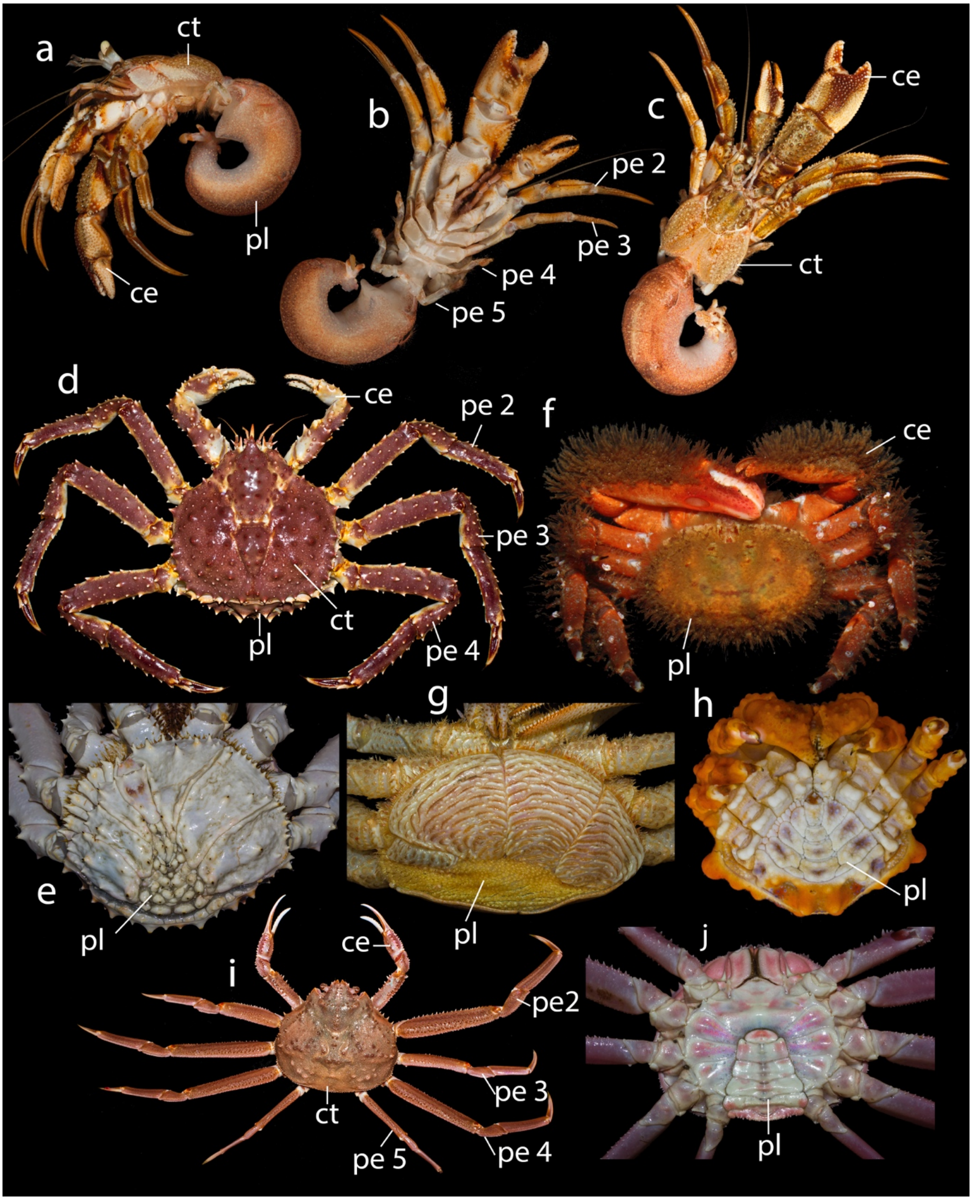

Figure 1: Morphological comparison between pagurid hermit crabs (a-c), lithodid crabs (d-h), and brachyuran crabs (I, j). a-c) *Pagurus bernhardus*. Note the large, uncalcified asymmetrical pleon, which the animal secures in empty gastropod shells, and that the 4th and 5th pair of peireopods are formed as specialized holding structures. a) Lateral, b) ventral, d) dorsal view of the hermit crab. d, e) The red king crab, *Paralithodes camtschaticus*. d) Dorsal view. Note that the 5th pair of peireopods are hidden under the carapace. e) Ventral view of a female, showing the asymmetrical pleon of the king crab. f) The small lithodid crab *Hapalogaster mertensii*, ventral view, showing the uncalcified pleon. g) The scaled

crab, *Placetron wosnessenskii*, ventral view of the highly asymmetrical pleon of a female. h) The Puged Sound king crab, *Lopholithodes mandtii*. Ventral view of a juvenile, showing the almost symmetrical pleon of a male. I-j) The brachyuran crab *Chionoecetes bairdi*. i) Dorsal view. Note the 4 pairs of well-developed walking legs. j) Ventral view, showing the highly reduced, symmetrical pleon of a male. Abbreviations: ce: chelae; ct: cephalothorax; pe 2-pe 5: 2nd-5th peieiopods; pl: pleon.

Lithodids typically also exhibit asymmetries of their chelae, with distinctive larger claws on the right body side (Fig. 2). This right-handedness is also found in pagurid hermit crabs (Fig. 1a-c) with high consistency (McLaughlin, 2003). This consistent pattern is somewhat surprising, since hermit crabs of the family Diogenidae, which also inhabit dextral housings, show the opposite pattern with a strong left-handedness. This indicates that, other than pleon asymmetry, there is not a strong selective pressure towards either left or right asymmetry regarding handedness in gastropod inhabiting hermits, but right-handedness appears to be genetically deeply implemented in the Paguridae, which has also been retained in the free living lithodids. Right-handedness in lithodids must be regarded as clear trace of their pagurid origin, with this character being homologous between lithodid crabs and pagurid hermit crabs (Tsang *et al.*, 2011). In hermit crabs the gonads and the hepatopancreas are located in the pleon, where these organs constitute the major volume of this body region (Mclaughlin & Lemaitre, 1997; Keiler, Richter, & Wirkner, 2013). This is also found in lithodids, while in other carcinized decapod taxa, which developed from ancestors with a muscular pleon used for classical locomotion, the viscera remain in the cephalothorax (Anker & Paulay, 2013). In shell-inhabiting hermit crabs, however, only little muscle tissue is situated in the pleon, used to fasten and retract the animal in its housing. The reduction of muscle mass in the pleon made space available for the voluminous hepatopancreas, which usually occupies a large volume of the cephalothorax. While the pleon in lithodid crabs is reduced, it still contains large parts of the hepatopancreas as a further heritage of their ancestry (Anker & Paulay, 2013; Keiler, Richter, & Wirkner, 2015). Further traces of the pagurid origin can for example be found in the mouthparts (Boas, 1924; Jaszkowiak *et al.*, 2015), the setation (Keiler & Richter, 2011), or the vascular system (Keiler *et al.*, 2013, 2015).

Lithodid crabs also have non hermit crab-like characters, resembling those of ancestral anomurans (Richter & Scholtz, 1994), which are related to a secondary change towards a free-living habit. A calcified body substitutes a protective housing (Fig. 2), while the 4th and 5th pereiopods lost their function of retaining the animal in the former, and re-adapted to their original function as walking- and gill-cleaning appendages. Probably the most remarkable of these features is the morphology of the 4th pereiopods. In hermit crabs these legs are developed as specialized rasp-bearing appendages, to retaining the animal inside its housing, much shorter than the two anterior pairs (Fig. 1a-c). In lithodids, not only are the 4th pereiopods developed as walking legs, but resemble the 2nd and 3rd pairs even by their spine arrangement (Fig. 1d, 2). This has led to the suggestion, that this re-development of a standard walking leg is related to the expression of hox genes (Richter & Scholtz, 1994). Also the 5th pair of thoracopods is used to retain hermit crabs in their housings, but in lithodids those are permanently hidden under the cephalothorax (Fig. 1d), where they serve as gill cleaning devices.

Lithodid crabs display a wide variability of morphological forms, corresponding to the large range of habitats and ecological adaptions of these species (Fig. 2). Morphological variety in the Lithodinae is largely corresponding to that found in the much more species rich Brachyura, the true crabs (Fig. 1i, j). Similar general body shapes of both taxa have been highlighted as prime examples for convergent evolution (Balss, 1924; Scholtz, 2014). One of these morphological adaptions related to habitat use and ecology is found in the box crab, *Lopholithodes foraminatus* (Fig. 3). This species can retract its appendages so closely to its body, that it becomes a solid box-like structure (Fig. 3a-c). The chelipeds and the first pair of walking legs have smooth, semicircular concavities, forming a respiration canal when the animal is retracted (Fig. 3b, c) (Jensen, 1995).


a
b
c
d
e
f
g
h
i
j
k
l

Figure 2. Various representatives of lithodid crabs. a) *Hapalogaster mertensii*, b) *Oedignathus inermis*, c) *Acantholithodes hispidus*, d) *Placetron wosnessenskii*, e) *Dermaturus mandtii*, f) *Lopholithodes mandtii* (juvenile), g) *Phyllolithodes papillosus*, h) *Rhinolithodes wosnessenskii*, i) *Lopholithodes foraminatus*, j) *Lithodes maja*, k) *Paralithodes camtschaticus*, l) *Cryptolithodes sitchensis* (dorsal and ventral view of the specimen). a, d, f, g, i, j, k: Living specimens, showing the natural colouration. b, c, e, h, l: Fixed museum specimens.

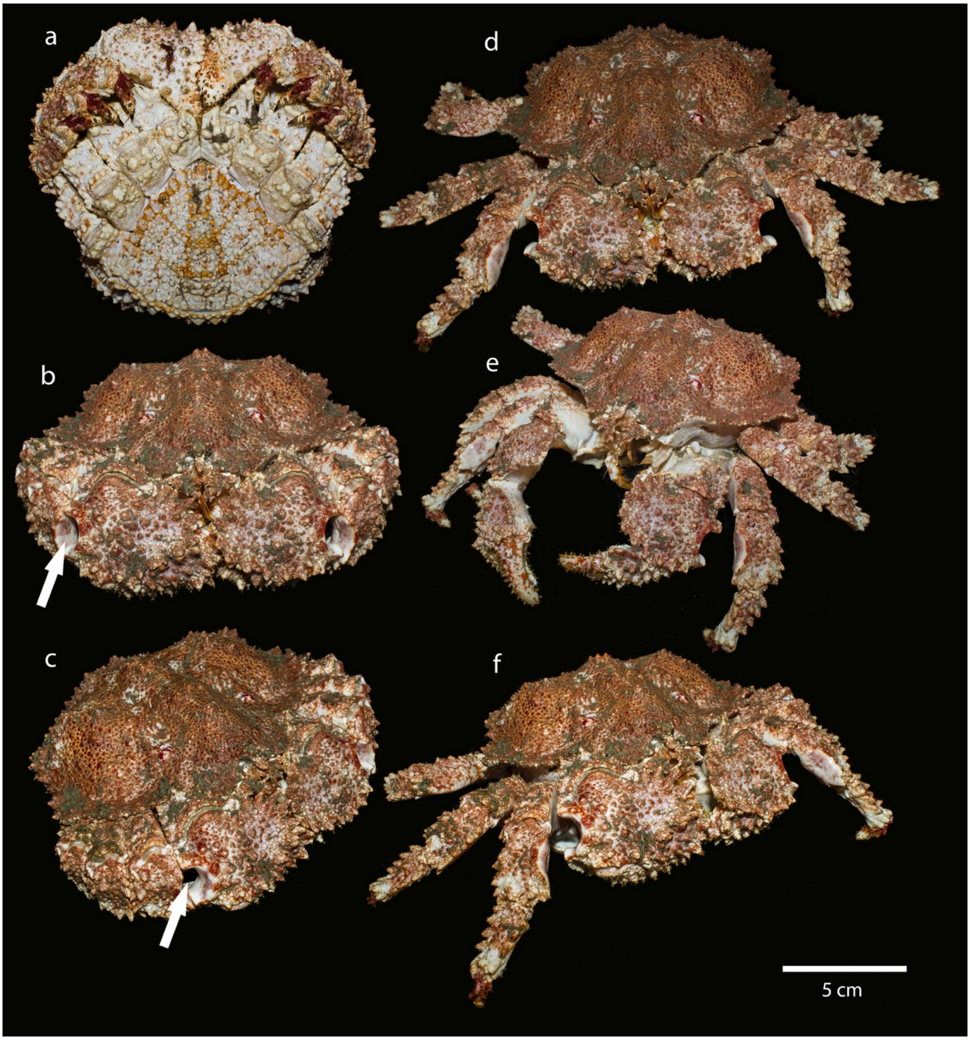

Figure 3. The box crab, *Lopholithodes foraminatus.* a-c: Animal with the pereiopods closely retracted to the body. a) Ventral view, b) frontal view, c) frontolateral view. Arrows are indicating respiration canal formed by the chelipeds and first pair of walking legs. d-f: Moving animal. d) Frontal view, e, f) frontolateral view.

1.1.3 Morphological flexibility in the Anomura

Several studies have shown that hermit crabs (Paguroidea) are paraphyletic within the Anomura, and even independent origins of asymmetrical hermit crabs have been indicated (Ahyong *et al.*, 2009; Chu *et al.*, 2009; Tsang *et al.*, 2011; Bracken-Grissom *et al.*, 2013). Different carcinized, crab-like anomuran lineages have further evolved independently from hermit crab ancestors (Ahyong *et al.*, 2009; Bracken *et al.*, 2009; Chu *et al.*, 2009; Schnabel *et al.*, 2011; Tsang *et al.*, 2011; Bracken-Grissom *et al.*, 2013). Therefore, not only the position of lithodid crabs within the Paguridae has been under debate, also internal relationships between the major taxa within Anomura, or Anomala as preferred by some authors (McLaughlin & Holthuis, 1985; Reimann *et al.*, 2011), have not reached consensus. The classification of the Anomura is in need of revision, due to current classification being largely based on superficial body forms (Tsang *et al.*, 2011). The anomuran morphology appears to be flexible in an evolutionary perspective, and different general body shapes, like crabs, hermit crabs, or squat lobsters have developed multiple times (Morrison *et al.*, 2002; Ahyong *et al.*, 2009; Schnabel *et al.*, 2011; Tsang *et al.*, 2011; Bracken-Grissom *et al.*, 2013). This morphological flexibility of the anomuran body has led to conflicting topologies within the Anomura, largely depending on whether molecular or morphological data is used in phylogenetic analyses. Phylogenies based on morphological characters used to investigate the internal relationships of Anomura, including the phylogenetic position of lithodid crabs, tended to include large amounts of characters directly linked to the general habitus and the process of carcinization (e.g. Dixon, Ahyong, & Schram, 2003; McLaughlin et al., 2007; Mclaughlin & Lemaitre, 1997) and are thus biased towards joining superficially similar taxa. Flexible morphological characters, often reflecting the lifestyle rather than the phylogenetic relationships between the taxa, are likely to give conflicting results to more independent molecular data. Dixon et al.'s (2003) results, for example, might have been influenced by what the authors considered to be the remarkably derived form of lithodid crabs. Also when molecular data is analysed in combination with morphological data sets, tree topologies tend to be shifted towards a more classical topology (Ahyong & O'Meally, 2004; Schnabel *et al.*, 2011; Bracken-Grissom *et al.*,

2013). A morphological study based on characters unaffected by the general body shape, on the other hand, has confirmed molecular genetic results (Reimann *et al.*, 2011), showing that morphological data is not necessarily contradicting molecular results, if characters included are not affected by the process of carcinization.
Not only are lithodid crabs nested within the hermit crab family Paguridae, but the latter might further be nested within the hermit crab family Diogenidae. This was first indicated when Morrison et al. (2002) included the diogenid *Paguristes turgidus* in their analyses. This species was resolved as sister taxon to Paguridae, outside of the remaining Diogenidae. *Paguristes* also stands out from other Diogenidae by its distinct mitochondrial genome arrangements (Morrison *et al.*, 2002) and morphology of the foregut (Reimann *et al.*, 2011). Paguridae were also later found in a sister relationship to *Paguristes* and its close allied genus *Areopaguristes* within the Diogenidae based on molecular data (Bracken-Grissom *et al.*, 2013). However, the relationships changed when morphological data was added to the analyses, rendering Paguridae (including lithodids) as sister group to the entire Diogenidae. A paraphyletic pattern of the Diogenidae is also found regarding the terrestrial hermit crab family Coenobitidae, which is nested within this taxon (Morrison *et al.*, 2002; Tsang *et al.*, 2008, 2011; Schnabel *et al.*, 2011; Reimann *et al.*, 2011; Bracken-Grissom *et al.*, 2013).

1.1.4 Carcinization in the Anomura

Carcinization, a morphological transformation that involves a broadening and calcification of the carapace, and reduction and underfolding of the pleon (Borradaile, 1916), is a widespread phenomenon in the Anomura, and developed independently several times in this taxon (Morrison *et al.*, 2002; Tsang *et al.*, 2011). Outside the Anomura carcinization only is present in the Brachyura, which forms the sister group to the Anomura. In the brachyuran crabs, carcinization has reached its most sophisticated form, and the high diversity of this group clearly illustrates the potential advantages of developing such a morphology (Morrison *et al.*, 2002; Tsang *et al.*, 2014). The process of carcinization from an asymmetrical hermit crab is more complex than in other anomuran taxa, since beside the broadening of the cephalothorax, and reduction and subfolding of the pleon, it also involves reorganisation and sclerotisation as the protective housing becomes abandoned (Anker & Paulay, 2013). The term “carcinization” was created by Borradaile (1916) with reference to crab-like modifications in the hermit crab genus *Porcellanopagurus*. However, the concept of carcinization originates with Boas’ hypothesis (Boas 1880a, 1880b) that king crabs represent highly derived, heavily calcified, shell-less hermit crabs (Anker & Paulay, 2013). For a critical review on the concept of carcinization see Scholtz (2014). While carcinization is widespread in the Anomura (Tsang *et al.*, 2011), king crabs represent one of the most striking example for this morphological transformation, almost resembling the degree found in brachyuran crabs. In lithodids even the uropods are lacking on the telson (Fig. 1e-h), which are retained in other carcinized anomuran taxa, making lithodids even more similar to brachyuran crabs (Fig. 1j). Most hermit crabs possess a soft and elongated pleon, which is usual protected by a gastropod shell (Fig. 1a-c). However, there are a number of cases of carcinization in hermit crabs. The most advanced example of carcinization in the Paguridae, beside lithodid crabs, is found in the recently described *Patagurus rex*. This species has a fully calcified carapace and only carries small shells to protect a greatly reduced pleon (Anker & Paulay, 2013).

1.1.5 The fossil record

Only a single fossil record exists for the Lithodinae. This species, *Paralomis debodeorum*, has been dated to the mid to late Miocene of New Zealand (Feldmann, 1998). The fossil record of hermit crabs is also relatively poor (Feldmann, 1998; Jagt *et al.*, 2006), and fossil hermit crabs are usually described only by body fractions, most importantly the chelipeds (Garassino, Angeli, & Pasini, 2009; Fraaije *et al.*, 2015). Lithodinae secondary evolved a free-living mode of life, via abandoning the inhabitation of foreign housings. But how did the shell-inhabiting lifestyle of hermit crabs evolve in the first place? Modern hermit crabs protect their soft pleon in a housing, which usually are gastropod shells, but also scaphopod shells, polychaete tubes, or bivalve shells are used by some species (Anker & Paulay, 2013). The oldest in situ fossils of a hermit crab, however, was found in an ammonite shell (Fraaije, 2003; Jagt *et al.*, 2006). This indicates that ammonites were used as housings before hermit crabs turned to gastropod shells in the late Cretaceous, when the gastropods diversified. Possibly this diversification, leading to new sources of protective housings and thus ecological niches, was subsequently followed by the diversification of the asymmetrical hermit crab lineages. Gastropods might have been used as shelter since sthe early Jurassic, but ammonites were much more frequent then. The morphology of modern asymmetrical hermit crabs is clearly adapted for inhabiting conical coiled gastropod shells. In planar-coiled ammonite shells only the outer, living chamber could be inhabited; whereas the entire coiled housing is inhabited in dextral gastropod shells. Further, ammonites were lacking a free columella to which the pleon, and in particular the telson, could be clinched to secure the animal inside the housing. As a result of their abundance, the strength and shape of their shells, and subsequent absence of ammonites, gastropods became much better suited for post-mortem occupation and transport by hermit crabs (Fraaije, 2003). Recent studies showed that the diversity of hermit crabs was already relatively high in the Jurassic (van Bakel *et al.*, 2008; Fraaije *et al.*, 2012b,a, 2013; Fraaije, 2014). From the early Cretaceous onwards, hermit crabs, and members of the families Diogenidae and Paguridae in particular, radiated across the globe (Fraaije *et al.*, 2015).

1.2 The parasitic barnacles (Rhizocephala)

1.2.1 Morphology of Rhizocephala

Rhizocephala, or parasitic barnacles, are parasites of other crustaceans, mainly Decapoda. The taxon belongs to the Cirripedia, in which they form the sister group to the Thoracica. Thoracican barnacles, which for example contain the well-known rock barnacles from the intertidal, or the stalked goose barnacles that drift on flotsam, are suspension feeding. But rhizocephalans solely rely on their host for nutrition. Due to their parasitic lifestyle they have evolved a highly modified adult morphology compared to other crustaceans, lacking almost all arthropod features like segmentation, a centralized nervous system, any alimentary tract, or appendages (Høeg & Lützen, 1995; Walker, 2001; Glenner & Hebsgaard, 2006). The adult morphology of the female parasite can be divided into two distinct parts: a sac-shaped reproductive body which is attached to the outside of the host, usually on the pleon, called the externa (Fig. 4c-k); and a trophic part situated inside the host, the interna, which has a root-like appearance. The externa is lined with a cuticular mantle and consists of a mantle cavity, in which the eggs are breed, and a visceral mass, which contains the ovaries, colleteric glands, and usually a pair of receptacles in which the male larvae settle and subsequently serve as functional testes (Høeg & Lützen, 1995; Walker, 2001).

While the adult organism cannot be identified as crustacean, or even arthropod, by its morphology, the affiliation to the Cirripedia was already discovered in the description of the first species, *Sacculina carcini*, since the characteristic nauplius larvae (Fig. 4a) were observed (Thompson, 1836). These closely resemble those of conventional barnacles. Interestingly, the second described species, *Peltogaster paguri*, was described as a worm (Rathke, 1842), since no larvae were observed and the author was apparently not aware of the description of *S. carcini*. However, the understanding of the rhizocephalan morphology, life cycle, as well as the impact on their hosts, was puzzling biologists for much longer (Høeg & Lützen, 1995; Walker, 2001). Even the interna, which is a crucial part for the understanding of the parasites biology, was only discovered almost two decades after the discovery of the taxon (Anderson, 1858). The interna of the Rhizocephala is a unique organ in Arthropoda. Similar structures are only found in the thoracican barnacles *Anelasma*, parasitic on lantern sharks, and *Rhizolepas*, parasitic on polychaetes (Day, 1939; Rees et al., 2014), as well as in some parasitic copepods (Boxshall and Harrison, 1988).

1.2.2 The life cycle of the Rhizocephala

The life cycle of rhizocepalans includes planktonic larvae of separate sexes. These lecitotrophic larvae are released from the mantle cavity of the externa, where the eggs are bred. The planktonic phase consists of a series of nauplii stages (Fig. 4a), which transform into a cypris larva (Fig. 4b). These larvae are typical for the entire Cirripedia.

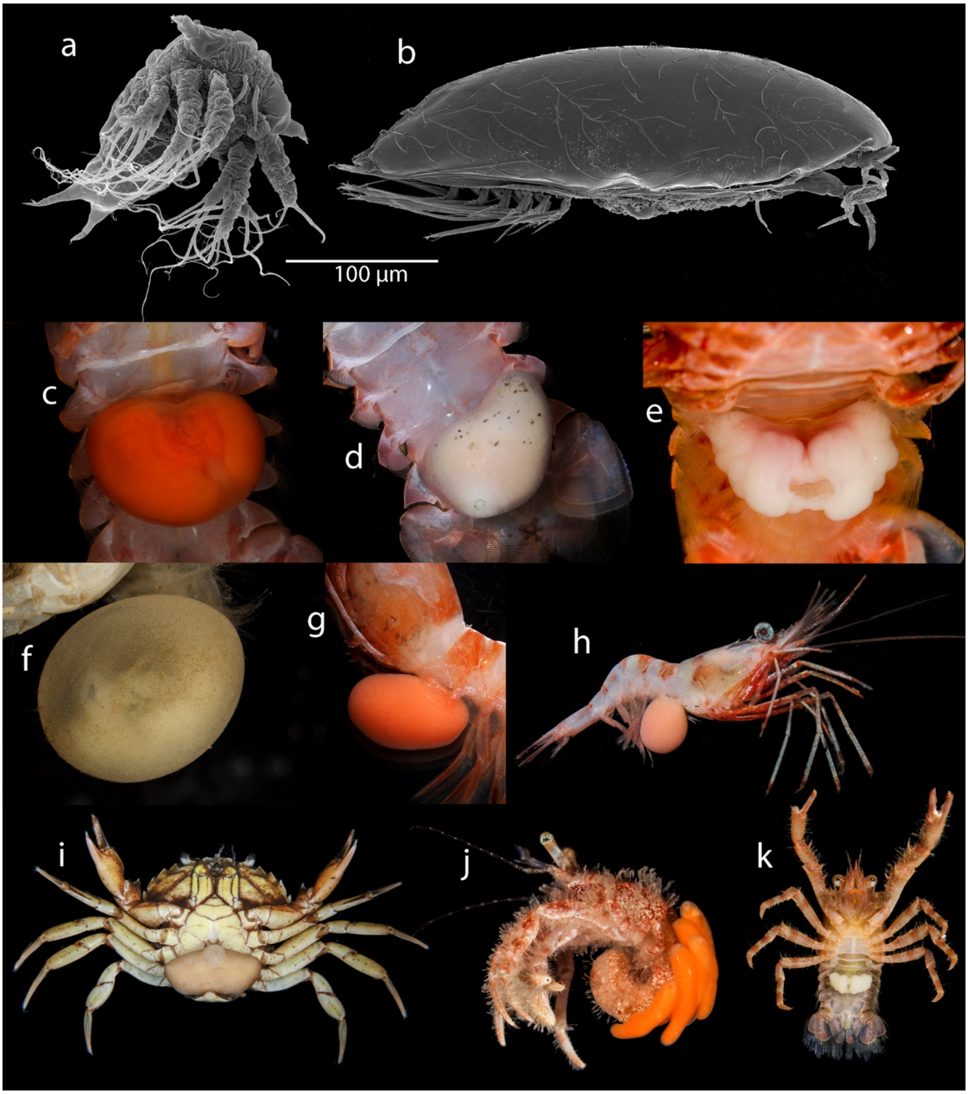

Figure 4: The parasitic barnacles (Rhizocephala). a-c) SEM photographs of the pelagic larvae stages. a) Nauplius of *Tortugaster boschmai*. b) Cypris of *Peltogaster paguri*. **c-g) Light photographs of living externae attached to their hosts.** c) *Triangulus munidae*, d) *Tortugaster boschmai*, e) *Lernaeodiscus ingolfi*, f) *Sacculina gerbei*, g) *Sylon hippolytes*. **h-k) Light photographs of living hosts parasitized by rhizocephalans.** h) *Sylon hippolytes* on the shrimp *Atlantopandalus propinqvus*. I) *Sacculina carcini* on the green crab, *Carcinus maenas*. j) *Peltogasterella sulcata* on the hermit crab *Pagurus cuanensis*. k) *Lernaeodiscus squamifera* on the squat lobster *Galathea dispersa*.

The female cypris has to find a suitable host, to which it attaches. At the settlement site, which is depending on the species, usually on the base of a seta or on the gills, the cypris moulds into a further larval stage, the kentrogon (Høeg, 1995). This kentrogon is the injection stage of the parasite, which penetrates the hosts cuticle with a hollow stylet and inserts parasite material into the host. The early internal phase is a discrete vermiform body, called the vermigon (Glenner & Høeg, 1995; Glenner *et al.*, 2000; Glenner, 2001). The internal phase grows to an extensive root system, which is ramifying the hosts body. Eventually the externa emerges through the hosts integument. Once the juvenile externa is in contact with the seawater, it has to attract a male cypris larva before the parasite can proceed to mature (Høeg, 1995). The male cypris larva settles on the mantle opening of the juvenile externa, where it moulds into a motile trichogon larva, homologous to the female kentrogon. The trichogon migrates into one of the female receptacles, where it sheds its spiny, outer cuticle, that serves as a plug, enabling further male larvae to enter (Høeg, 1987; Glenner & Høeg, 1994). The males, once implanted in the female externa, serve as functional testes of the parasite (Høeg & Lützen, 1995).

Due to the only very few morphological features of the adult parasites, the internal phylogeny of the Rhizocephala has long been ambiguous. While the phylogeny of the taxon is still not fully resolved, molecular methods have yet significantly increased our understanding of the evolution of this highly diverged group of crustaceans. The Rhizocephala have been divided into two orders: Kentrogonida and Akentrogonida. Members of the Akentrogonida, which are lacking both the kentrogon and trichogon stages, have long been seen as the basal rhizocephalan taxon. However, molecular phylogenies showed that akentrogonids are the most derived members of the Rhizocephala, and that the presence of the kentrogon is the plesiomorphic state in Rhizocephala. The molecules further showed that the Akentrogonida are nested within the Kentrogonida, and here even within the family Sacculinidae (Glenner, Lützen, & Takahashi, 2003; Glenner *et al.*, 2010; Glenner & Hebsgaard, 2006). In the Akentrogonida various modifications in the life cycle occur. Such are the larvae not released as nauplii, but at the cypris stage from the mantle cavity. The receptacles in some akentrogonids are completely lacking, and the male cypris injects spermatogenetic cells directly into the female externa (Høeg, 1990; Høeg & Lützen, 1995).

1.2.3 Effects induced on the host

Rhizocephalans are exerting both physiological and morphological effects on their hosts, and can also induce behaviour changes (e.g. Høeg, 1995; Kristensen et al., 2012; Li et al., 2014; Rasmussen, 1959; Sloan, 1984). Rhizocephalans can sterilize their hosts, feminize the morphology of male hosts, and arrest the hosts moulting cycle (Høeg, 1995), however, not all species induce all of these effects. Further, some species induce behavioural changes in their hosts, resulting in the host taking care of the parasites externa, as if it was its own offspring (Rasmussen, 1959; Ritchie & Høeg, 1981). The externa is in most species situated in the same location where the female host carries its own eggs. The parasite thereby mimics a brood of eggs, and parasitized hosts do not damage the externa, even if they have the potential to do so. Instead, the hosts may show brood caring behaviour, which seems vital to some species. It has also been observed that the host performs its natural spawning behaviour, which assists the dispersal of parasite larvae (Ritchie & Høeg, 1981; Høeg, 1995).

1.2.4 Host specificity

Rhizocephalans have extremely intimate relationships with their hosts. They have adapted to such a level that they can grow an extensive trophic structure inside their host without being attacked by the hosts immune system. Not surprisingly, most rhizocephalan species display a high host specificity. However, many species have been reported on more than one host species (Høeg & Lützen, 1985; Høeg & Rybakov, 1992; McDermott, Williams, & Boyko, 2010; Hirose, Hirose, & Yoshida, 2014). But only for few rhizocephalans, species identities of parasites from different host species have been investigated using molecular markers (Gurney, Grewe, & Thresher, 2006; Yoshida *et al.*, 2012; Kruse, Hare, & Hines, 2012; Hirose *et al.*, 2014). Rhizocephalan taxonomy, and in particular species delimitation, relies heavily on very crude morphological characters, and species records from different hosts might often represent cryptic species, which cannot be distinguished by morphology alone (Høeg, 1995). Cryptic species, which are defined as a group of species previously identified as one, can constitute an important part of biodiversity (Bickford et al., 2007; Nygren, 2014). Species delimitation by morphological means is not always sufficient, since speciation is not necessarily accompanied by morphological change (Bickford et al., 2007), which must be considered of special importance for Rhizocephala, considering the near absence of proper morphological characters in this taxon.

Host taxa highly differ between the larger taxonomic groups within the Rhizocephala. The families Peltogastridae (Fig. 4j) and Lernaeodiscidae (Fig. 4c-e, k) are exclusively parasitic on anomuran crustaceans, like hermit crabs, squat lobsters, or porcelain crabs (Boyko & Williams, 2009). Members of the family Sacculinidae (Fig. 4f, i) are usually parasitic on brachyuran crabs (Lützen *et al.*, 2016), and the family Parthenopeidae is parasitic on mud shrimp (Upogebiidae) (Rybakov & Høeg, 2013). All hitherto mentioned families are members of the rhizocephalan order Kentrogonida. The other order, Akentrogonida (Fig. 4g, h), on the other hand parasitize a broad range of crustaceans. Here, hosts are not restricted to the Decapoda, but various crustacean groups, such as Stomatopoda, Anomura, Caridea, Isopoda, and Cumacea are parasitized. Species of the akentrogonid family Chthamalophilidae are even parasites of other Cirripedia; balanomorph barnacles (Høeg, 1990; Høeg & Rybakov, 1992; Lützen & Takahashi, 1996). Host specificity appears not to rest with the cyprid stage, since experiments showed that larvae settle and metamorphose on species that do not carry externae in the field (Ritchie & Høeg, 1981; Høeg, 1995; Høeg & Lützen, 1995). Such normally unsuccessful, fatal host choices might occasionally lead to successful establishments of rhizocephalans on new hosts (Høeg, 1995).

1.2.5 Rhizocephalan parasites of king crabs

Hermit crabs are hosts to a number of parasitic barnacle species from different genera, but only one genus, *Briarosaccus*, is a parasite of lithodid crabs. Prior to this thesis, the genus had been recognized to consist of only two species: *B. callosus,* parasitizing the large king crabs, and *B. tenellus*, which parasitizes the small lithodid crab *Hapalogaster mertensii* (Boschma, 1970; Guzman, Moreno, & Moyano, 2002; Lützen, Glenner, & Lörz, 2009). The rhizocephalan *B. callosus* had been reported to parasitize a large number of king crab species on a global scale (Boschma, 1930, 1962; Haynes & Boschma, 1969; Hawkes, Meyers, & Shirley, 1985; Pohle, 1992a,b; Cadien & Martin, 1999; Agnew *et al.*, 2001; Guzman *et al.*, 2002; Shukalyuk *et al.*, 2005; Ahyong & Dawson, 2006; Watabe, 2007; Lützen *et al.*, 2009; Anosov *et al.*, 2015). Either *B. callosus* consist of number of cryptic species, which have not been possible to separate by morphological traits, or the species *B. callosus* demonstrates an exceptional broad host specificity and distribution range. Beside a global distribution, the single parasite species would consequently have a habitat stretching from the shallow subtidal to the deep-sea (Boschma, 1962; Pohle, 1992a; Lovrich, Roccatagliata, & Peresan, 2004), including such diverse habitats as kelp forests (Cárdenas *et al.*, 2007) and hydrothermal vent systems (Lützen *et al.*, 2009). *Briarosaccus* grows an extensive root system of green colour throughout the internal tissue of the king crab host. Not only does the parasite make the crab unsuitable for commercial marketing, but the crab is also irreversible sterilized (Boschma, 1970; Sloan, 1984b; Sparks & Morado, 1986; Hoggarth, 1990; Shukalyuk *et al.*, 2005). In some king crab populations, the prevalence of the parasite reaches over 50%, greatly impacting the fishery (Sloan, 1984a; Hawkes *et al.*, 1986b; Watabe, 2007).

1.3 Host-parasite cophylogeny

The evolution of parasites is highly influenced by that of their host taxa. Co-speciation between host and parasite occurs when the divergence and diversification of a host lineage triggers a parallel divergence of the parasite lineage. If strictly followed, this scenario would lead to mirroring phylogenies of both hosts and parasites, known as the Farenholz’s rule (Hafner & Nadler, 1988; Klassen, 1992). However, several other factors have to be considered in these coevolutionary scenarios, such as host-switching, failure of a parasite to diverge together with its host, speciation of a parasite within a host species, or parasite loss (Paterson & Poulin, 1999; Paterson, Wallis, & Lise, 2000; Desdevises, 2007). The association between host and parasite taxa is thus the result of an interplay of processes, and a coevolutionary signal can be disrupted by these factors (Paterson & Poulin, 1999). Analyses of such coevolutionary relationships are extremely difficult due to the complex interplay of events (Paterson & Banks, 2001). Programs have been developed to test for these coevolutionary events, comparing host and parasite phylogenies and their associations (Page, 1994; Conow *et al.*, 2010). These programs reconcile host and parasite phylogenetic trees via event-cost methods to test if the number of co-speciation events is higher than expected by chance.

Many host-parasite systems only show weak signals of cophylogeny, since other evolutionary pathways, like host switches, are predominant (Caira & Jensen, 2001; Desdevises *et al.*, 2002; Summers & Rouse, 2014). Further, evidence for cophylogeny is more likely found in parasites with restricted hosts (Boyko *et al.*, 2013). Most host-parasite cophylogeny studies have been conducted on mites and parasitic insects of vertebrates (e.g. Banks, Palma, & Paterson, 2006; Demastes et al., 2012; Hafner et al., 1994; Hendricks, Flannery, & Spicer, 2013; Štefka, Hoeck, Keller, & Smith, 2011; Weckstein, 2004), and only few systems have been closely investigated in a marine environment (Paterson & Poulin, 1999; Hoberg & Klassen, 2002; Lanterbecq, Rouse, & Eeckhaut, 2010). Cophylogeny studies have the potential to support evolutionary theories of host relationships. Cestoda, for example, sustained the independent lineages of sharks and rays (Olson *et al.*, 2010). Høeg (1995) noted that rhizocephalan parasites sometimes seems to have followed the host through an evolutionary specialization. As an example, Høeg (1995) stated that *Briarosaccus* parasitizes exclusively lithodids, while most peltogastrids occur on true hermit crabs. The potential of parasites, in particular rhizocephalans, to provide phylogenetic signals that support or refute hypotheses of decapod evolution has been highlighted by Boyko and Williams (2009).

1.4 Rhizocephalans as biological host control agents

Rhizocephalans are inducing parasitic sterilization of their hosts (Høeg, 1995), and their potential use as biological control agents against introduced marine species has been discussed. In particular, the use of *Sacculina carcini* (Fig. 4i) as a parasitic castrator of the European green crab, *Carcinus maenas*, has been in focus of research (Lafferty & Kuris, 1996; Thresher *et al.*, 2000; Goddard *et al.*, 2005; Kuris *et al.*, 2007). *C. maenas* is an invasive species in many regions around the globe and causes huge impacts on marine ecosystems (Goddard *et al.*, 2005). But if an introduced parasite would, in addition to the target, parasitize native, non-target crab species, the introduction of a parasite might have further negative impacts on the ecosystem. Therefore, host specificity of the potential control agent is a crucial factor when a parasite is considered to be released as such an agent (Thomas & Willis, 1998; Strong & Pemberton, 2000). For *S. carcini*, molecular analyses showed that this parasite is indeed parasitizing a rather wide host range in nature (Gurney *et al.*, 2006), and experiments indicated that also native crab species outside its distribution might be additional suitable hosts when exposed to the parasite (Thresher *et al.*, 2000; Goddard *et al.*, 2005).

But even if a rhizocephalan is host specific to its target species, a successful reduction of the targets impact on the ecosystem is uncertain. So far, biological control agents have not been used in the marine environment (Lafferty & Kuris, 1996; Kuris *et al.*, 2007). A key factor of effective host control is that the parasite reduces the population size of its host. Rhizocephalans sterilize their hosts, preventing infested specimens from reproduction. Rhizocephalans might, therefore, be capable of reducing the size of their host population, if this is limited by the total reproductive output, via the amount of larvae released into the water. Other factors, like intraspecific competition, might however in many cases be the crucial factor for upper population limits. Crab populations with high prevalences of rhizocephalan infections have shown to be stable (Innocenti & Galil, 2007; Innocenti *et al.*, 2009), and the practical use of rhizocephalans as biological control agents is, therefore, ambiguous. Further, prevalence levels of parasite infections cannot be controlled in a natural environment.

The king crabs comprise one species, *Paralithodes camtschaticus*, which is invasive in parts of its current distribution range. Other than most invasive species in the marine environment, *P. camtschaticus* was introduced intentionally into the Barents Sea during the 1960s by Russian scientists, to establish a target fishery on this species

(Orlov & Ivanov, 1978). While native to the North Pacific, the red king crab has since established a self-sustaining population in the Northeast Atlantic, including northern Norwegian waters (Hjelset, Sundet, & Nilssen, 2009; Sundet & Hoel, 2016). The red king crab (Fig. 1d) is a valuable resource for commercial exploitation, but also causes impacts on the native benthic fauna (Jørgensen & Primicerio, 2007; Oug *et al.*, 2011; Fuhrmann *et al.*, 2015). Therefore, fisheries management of the red king crab in Norwegian waters is highly controversial.

P. camtschaticus is host to *Briarosaccus* in its native range, the North Pacific (Haynes & Boschma, 1969; Hawkes *et al.*, 1986b), but the introduced red king crab stock in the North Atlantic is rhizocephalan-free. Approximately 3,800 adult and 10,700 juvenile *P. camtschaticus* specimens were introduced into the Barents Sea in the 1960s (Zelenina *et al.*, 2008). If these king crab specimens were screened for *Briarosaccus* infections, or if some parasites were introduced together with their hosts but could not successfully develop a parasite population, is unknown.

Since rhizocephalans have been highlighted as potential candidates for biological control against invasive species in the marine environment (Lafferty & Kuris, 1996), *Briarosaccus* might have the potential to function as such for the red king crab in its non-native range. On the other hand, in the North Pacific, the native range *of P. camtschaticus*, the parasite accounts for a substantial economic loss in king crab fisheries (Hawkes, Meyers, & Shirley, 1986a; Shukalyuk *et al.*, 2005). The rhizocephalan-free king crab stock in the Northeast Atlantic is, therefore, without a doubt the most desired situation for the target fisheries on this species. Risk evaluation of the Atlantic red king crab stock becoming exposed to a fishery damaging rhizocephalan parasite appears, therefore, of higher relevance in this context than the possibility of a rhizocephalan being used as control agent. Results of this thesis aims to shed light on both of these questions concerning the introduced red king crab.

2. Aims of this thesis

To investigate the coevoluionary relationships of king crabs and hermit crabs with their rhizocephalan parasites, in paper I an extensive molecular phylogeny of lithodid crabs and pagurid hermit crabs has been constructed to reveal the exact phylogenetic position of lithodid crabs within the hermit crabs. The detailed knowledge of phylogenetic relationships between host taxa is a crucial factor for the study of host-parasite cophylogeny.

In paper II the diversity and host specificity of the king crab rhizocephalan *B. callosus* was investigated in a restricted geographical range, the Northeast Pacific. In this paper, two species new to science are described. These species showed a high host specificity, and this study indicated that *B. callosus* may in fact consist of a rather large complex of cryptic species on a global scale.

In paper III, investigation of rhizocephalan parasites is extended on a global scale, including parasites from a large number of both hermit crabs and lithodid hosts. A molecular phylogeny of these rhizocephalan parasites was produced. Via species delimitations of parasitic barnacles and individual host-parasite associations, this parasite phylogeny was linked to that of their hosts from paper I, to test for co-speciation between the taxa.

In paper IV, the trophic organ of Rhizocephala, the interna, is investigated using X-ray micro computer tomography (MicroCT) and computer-aided 3D-reconstruction. This allowed the visualization of the spatial organization of this highly structured organ, which is usually hidden inside the hosts body. Parasites of lithodid crabs and hermit crabs were studied, to investigate the morphological response of the parasite to a highly altered morphology of king crab hosts.

Main questions of this PhD project were:

- Where are the king crabs phylogenetically placed within the hermit crabs, and which are the closest extant relatives?
- Are all rhizocephalan parasites of king crab representing only a single species, *B. callosus*, or is this species representing a complex of cryptic species?

- How host specific are rhizocephalan parasites of king crabs?
- Can the evolution of king crabs from a hermit crab ancestor be traced in the evolution of their parasites?
- How did the internal root system of parasitic barnacles adapt to the strong morphological transformation of their lithodid hosts?
- Would rhizocephalans have the potential to serve as a biological control agent against invasive king crabs?
- Is the rhizocephalan-free red king crabs stock in the Northeast Atlantic in danger of becoming parasitized by a fisheries-damaging parasite?

The following section aims to synthesise and provide a holistic view of the major results from these publications and address some additional topics that are not covered in the publications. Detailed discussions can be found in the respective papers.

3. Results and discussion

3.1 Molecuar phylogeny of pagurid hermit crabs and lithodid crabs

3.1.1 Rationale

To investigate cophylogeny patterns between host and parasite taxa, solid phylogenies of both taxa are crucial (Brooks, 1988). Therefore, as a first step towards a cophylogenetic analyses between king crabs and hermit crabs, and their rhizocephalan parasites, a molecular phylogeny of the hermit crab family Paguridae with the containing lithodid crabs was constructed (paper I). While the descent of king crabs from an asymmetrical hermit crab predecessor had already been proposed in the late 19th century (Boas, 1880a,b), and became highly supported by molecular studies (Cunningham *et al.*, 1992; Morrison *et al.*, 2002; Ahyong *et al.*, 2009), at the starting point of this thesis this phylogenetic position had still been under debate (Lemaitre & McLaughlin, 2009). And while a pagurid hermit crab origin of the taxon became generally accepted in the course of this thesis, due to ever increasing evidence from both molecular and morphological studies (Reimann *et al.*, 2011; Tsang *et al.*, 2011; Bracken-Grissom *et al.*, 2013), the internal relationships within the Paguridae were largely unknown. Key questions included the exact phylogenetic position of lithodid crabs within the Paguridae, and which hermit crabs constitute the closest extant relatives within the taxon. Also our knowledge about phylogenetic relationships within the lithodids were ambiguous, including the status of the two subfamilies Lithodinae (Fig. 2f-l) and Hapalogastrinae (Fig. 2a-e). Not only were answers to these questions crucial for a cophylogenetic analyses, in which the host phylogeny must serves as a solid backbone to that of their parasites. Also for the understanding of the underlying factors behind the fascinating body transformation from a small sized, shell-inhabiting hermit crab to the gigantic king crabs, detailed knowledge about phylogenetic relationships is crucial. To construct a comprehensive, species rich phylogeny, we utilized both genetic sequences that were available online, at GenBank and the Barcode of Life Data Systems (BOLD), as well as new sequences obtained from fresh collected material and museum collections. Molecular markers were chosen in order to correspond to a broad range of previously published sequences. Further, included markers should cover a broad range of sequence deviations, allowing the resolution of both deep and recent nodes in the phylogenetic tree. Sampling of fresh material focused on species from the North Pacific. This region harbours a rich fauna of pagurid hermit crabs, and lithodid crabs evidently evolved in this region (Hall & Thatje, 2009). Further, beside three lithodid genera that have a global distribution via the deep-sea, all other lithodid genera are restricted to the North Pacific. As the phylogenetic position of these, often monotypic, genera are important to understand the early evolution within the lithodid crabs, efforts were taken to include molecular data from those taxa.

3.1.2 Main results

The phylogenetic trees obtained in this study resulted in today's most comprehensive molecular phylogeny of pagurid hermit crabs and lithodid crabs (paper I). The lithodids were found deeply nested within the hermit crab family Paguridae. Our analyses further revealed a distinct clade of pagurid hermit crabs as closest relatives to lithodid crabs within the Paguridae. Hermit crabs included in this clade have a predominant shallow water distribution in the North Pacific, agreeing with a proposed origin of lithodid crabs in this region. Included in this hermit crab clade, which we refer to as "pagurid-lithodid sister (PLS) clade", are few minor genera, which are exclusive to the North Pacific, as well as various species of the genus *Pagurus* (Fig. 5).

Species of the genus *Pagurus,* which is by far the most species rich genus within the Paguridae, are also found outside this PLS clade, and are found widespread throughout the phylogenetic tree of the Paguridae. The usage of *Pagurus* as a lump genus for pagurid hermit crabs with a rather standard morphology is thus well illustrated in our phylogeny. However, species of the genus are found grouped in distinct clades, which generally correspond to previously established informal species complexes.

Figure 5. Various representatives of the hermit crab group which comprises the closest extant relatives to lithodid crabs, the PLS clade. a) *Pagurus pubescens* inhabiting in an empty gastropod shell. c) 2 individuals of *Discorsopagurus schmitti* inhabiting empty polychaete tubes on a rock (arrows are pointing to specimens). c) *D. schmitti*. Note the almost symmetrical pleon. d) *Elassochirus gilli*, e) *Elassochirus cavimanus*, f*)* *Pagurus beringanus*, g) *Pagurus caurinus*, h) *Pagurus kennerlyi*, i) *Pagurus hirsutiusculus*, j) *Pagurus granosimanus*, k) *Pagurus bernhardus*, l) *Pagurus aleuticus*, m) *Pagurus ochotensis*.

In previous studies, closest relatives to king crabs resolved were largely based on which pagurid taxa were included in the analyses. Generally, species found in our PLS clade were also found as closest relatives in these studies. But with only one or few species of this group included in the analyses, previous authors largely based their discussion on species that were included in their analyses, e.g. *Discorsopagurus schmitti* (Bracken-Grissom *et al.*, 2013), or the nested position of king crabs within the genus *Pagurus* (Cunningham *et al.*, 1992).

Our analyses revealed, that instead of only few species being closest relatives to the lithodid crabs, the PLS clade is species rich and includes a number of genera and several informal *Pagurus* groupings. Based on the parallel diversification of hermit crabs and lithodid crabs in the same region we suggest that the advances of abandoning a shell-inhabiting lifestyle, rather than limitations of such shelters, played a central role for the origin of the Lithodidae.

Phylogenetic relationships within the Lithodidae reveal its two subfamilies to be polyphyletic. Instead of a division between taxa with a soft pleon, and with a calcified pleon, small sized, shallow water taxa are found basal in the phylogenetic tree, while an increase in size and following deep-sea distribution occurred later in the evolution of the group.

Recently, lithodid crabs had been proposed to be elevated to the rank of a superfamily, Lithodoidea, placed outside the hermit crabs (McLaughlin *et al.*, 2007). Contradicting both molecular and morphological evidence, this rendering of the taxon caused large taxonomic confusion, since different authors used various taxonomic rankings for lithodid crabs following this rendering. This applies especially regarding the two lithodid subfamilies, Lithodinae and Hapalogastrinae, which following McLaughlin et al. (2007) were elevated to family ranks.

Due to the apparent polyphyletic status of both Hapalogastrinae, characterized by a soft pleon (Fig. 2f, g), and Lithodinae, characterized by a calcified one (Fig. 2e, h, 3l, 4a), and the nested position of lithodid crabs within the family Paguridae, we suggest a different taxonomic rendering of the taxon: here, all lithodid crabs are included in a subfamily Lithodinae, placed within the family Paguridae. In this taxonomic hierarchy, which is rather opposite to that of McLaughlin et al. (2007), true phylogenetic relationships between the taxa are reflected.

3.2 Host specificity and species delimitation of the king crab parasite *Briarosaccus*

3.2.1 Rationale

To investigate the host specificity of parasitic barnacles from king crabs, and a possible complex of cryptic species within the single recognized rhizocephalan species of king crabs, *B. callosus*, the next study (paper II) aimed to investigate these questions on a regional level, namely the coast of Southeastern Alaska, in the North Pacific. In this highly structured coastline, consisting of numerous fjords and islands, a high number of lithodid species co-occur, including three king crabs which have been target for fisheries: the red king crab (*Paralithodes camtschaticus*), which has been introduced to the Northeast Atlantic, the blue king crab (*Paralithodes platypus*), and the golden king crab (*Lithodes aequispinus*). All these three species host rhizocephalan parasites, which had previously been identified as *B. callosus* (Haynes & Boschma, 1969; Hawkes *et al.*, 1985, 1986b). While the two *Paralithodes* species appear to be closely related, sibling species, *L. aequispinus* belongs to one of the species rich deep-sea lineages, that also includes the native North Atlantic king crab species *Lithodes maja*. The Alaska Department of Fish and Game, which performs king crab stock assessment surveys, and in addition has fishery observers on commercial vessels, kindly supplied rhizocephalan parasites from these hosts in sufficient numbers to investigate both molecular and morphological variations between specimens from the different host species. I also had the opportunity to participate in one of their red king crab surveys, allowing the study of living parasitized crabs. This gave the opportunity to investigate the molecular and morphological variation of *Briarosaccus* specimens from different hosts with a sympatric occurrence. Further, this host-parasite system is of high relevance regarding the invasive red king crab in the Northeast Atlantic, as host specificity of *Briarosaccus* in the natural distribution range of *P. camtschaticus* must be identified to enable conclusions about both the risk of the North Atlantic red king crab population to become parasitized with a rhizocephalan, as well as the potential of *Briarosaccus* being used as a biological control agent against invasive king crabs.

3.2.2 Main results

Comparing *Briarosaccus* specimens from three king crab hosts in Southeastern Alaska (paper II), no consistent morphological differences could be detected between specimens taken from the different hosts, neither using gross morphology, dissection, or SEM. The molecular markers, COI and 16S, however, revealed that two distinct parasite species were present in the samples. One of the species, which we described as *Briarosaccus regalis* n. sp., parasitizes the two *Paralithodes* species *P. camtschaticus* and *P. platypus*. The other species, *Briarosaccus auratum* n. sp., parasitizes *Lithodes aequispinus*. These two newly described rhizocephalan species have a sympatric occurrence, but each species has a distinct host specificity. Comparing the morphology of the two described *Briarosaccus* species to that of *B. callosus* from the original description (Boschma, 1930), a number of significant morphological differences were found. This enabled a delimitation of the two new species from *B. callosus*, to which they previously had been assigned to.

This study revealed that not all rhizocephalan parasites of king crabs can be assigned to the single species *B. callosus* as it previously had been assumed. Instead of having a global distribution and utilizing a broad range of king crab hosts, the study suggested that *B. callosus* likely consists of a rather large complex of cryptic species on a global scale.

3.3 Phylogeny of parasitic barnacles and host–parasite coevolution

3.3.1 Rationale

After investigating the diversity of king crab rhizocephalans on a regional scale (paper II), the species delimitation of the previously assumed single rhizocephalan species of king crabs, *B. callosus*, was extended on a global scale, including a considerable number of reported hosts for this parasite (paper III). A molecular phylogeny of rhizocephalans parasitic on hermit crabs and king crabs was constructed, with an emphasis on the genera *Peltogaster* and B*riarosaccus*.

All described species of Rhizocephala parasitic on lithodid crabs were included in the molecular phylogeny. Parasites previously had been assigned to *B. callosus* taken from various king crab species and a global range were sequenced. These included specimens from the type's host, *Neolithodes agassizii*. Further, we included the two species described in paper II (*B. regalis* n. sp. and *B. auratum* n. sp.), as well as *B. tenellus*, parasitic on the small lithodid crab *Hapalogaster mertensii*, which was sampled at spring low tide in Southeastern Alaska.

Of the genus *Peltogaster*, which is parasitic on hermit crabs of the family Paguridae and Diogenidae (McDermott *et al.*, 2010), we included new sequences from four species, of which two were represented by specimens from different hermit crab hosts, with the potential to contain cryptic species. The identification of cryptic parasite species was a crucial part of the study, since besides solid phylogenies of both hosts and parasites, also true associations between species of these two taxa are required. Additional sequences from two *Peltogaster* species were downloaded from GenBank, provided by studies from Yoshida et al. (2012, 2015). Special effort was taken to include parasites from hermit crabs that were resolved as closest extant relatives to the Lithodinae in paper I, and in particular those which had, in addition, been forwarded as such in previous studies (Cunningham *et al.*, 1992; Bracken-Grissom *et al.*, 2013). In a following step, the parasite phylogeny was analysed for co-speciation with their hosts (paper III). The host phylogeny utilized for this analyses was taken from paper I.

3.3.2 Main results

Briarosaccus specimens taken from 11 different lithodid hosts were sequenced, from which eight distinct *Briarosaccus* species were discriminated using the genetic markers (paper III). Beside *B. tenellus*, which parasitizes the small lithodid crab *Hapalogaster mertensii* (former subfamily Hapalogastrinae), all these species had been assigned to the single species *B. callosus* prior to this thesis. As the local study from Southeastern Alaska (paper II) indicated, what was known under *B. callosus* turned out to represent a rather large complex of cryptic species, instead of this species having a global distribution and utilizing a broad range of host species.

Also in the genus *Peltogaster*, parasitic on hermit crabs, a number of cryptic species were identified. Ten *Peltogaster* species were included in the phylogenetic analyses. Of those, four represent cryptic species, of which three had previously been assigned to *P. paguri*, and one had been recognized as *P. curvata*.

Identifying species boundaries and host associations was a crucial step to investigate coevolutionary pattern between rhizocephalan parasites and their hosts. Resolving these cryptic species complexes also indicated, that the species diversity of rhizocephalans might be highly underestimated.

The phylogenetic analyses of rhizocephalan parasites of king crabs and hermit crabs revealed some highly interesting patterns. The genera *Briarosaccus* and *Peltogaster*, which had been recognized as closely related (Boschma, 1930, 1962), together form a highly supported clade. Further, *Briarosaccus* is in fact nested within *Peltogaster*. The genus *Briarosaccus* in addition is composed of two distinct lineages, each containing several of the identified cryptic species that were previously recognized as *B. callosus*. Both of these two *Briarosaccus* lineages originated independently within the genus *Peltogaster*, which parasitizes hermit crabs. *Peltogaster* was found separated into three distinct genetic lineages, of which to clades formed direct sister clades to the two independent *Briarosaccus* lineages.

The finding that species of *Briarosaccus* are nested within the genus *Peltogaster* might be of little surprise, given the absence of distinguishing morphological characters between the genera. A polyphyletic *Briarosaccus*, with two independent origins, on the other hand, is quite astonishing. But between the two genetic lineages of *Briarosaccus,* consistent morphological differences can be found, that are also present in the respective *Peltogaster* sister lineages.

As species of *Briarosaccus* are found nested within the genus *Peltogaster*, we transferred species assigned to *Briarosaccus* to the latter genus. This taxonomic transformation is not only justified by the molecular evidence, but also by the lack of morphological characters to distinguish between the two genera. A distinction of

Briarosaccus based on its hosts, namely lithodid crabs, further appears much less justified then when it was highlighted by Boschma (1962, 1970), based on current phylogenetic knowledge (see paper I). In this thesis, the name *Briarosaccus* is still used throughout, to avoid confusion.

A reconciliation analyses conducted with the software Jane 4 (Conow *et al.*, 2010) resulted in a significant correlation between host and parasite phylogenies, showing that coevolution between the two taxa did occur.

The most significant node, in the context of the evolution of king crabs from hermit crabs, is the divergence node between Lithodinae and their closest relatives, the PLS clade, within the remaining Paguridae (paper I). This divergence in the host tree is accompanied by two cophylogeny events in the parasite tree, each leading to one *Briarosaccus* and one *Peltogaster* lineage (paper III).

Each of the *Peltogaster* clades that represent sister clades to the *Briarosaccus* lineages have hosts that have been identified as closest relatives to the Lithodinae within the Paguridae, as members of the PLS clade (paper I), or host which have not been included into phylogenetic analyses, but which likely belong to this group. This implements, that the last common ancestor (LCA) shared by hermit crabs and lithodid crabs within the Paguridae was parasitized by two distinct rhizocephalan species. These co-speciated with both the hermit crab and lithodid crab lineages from this LCA, leading to duplicate parasite lineages.

The cophylogeny analyses further suggest that the divergence of the two lineages leading to *Briarosaccus* did occur early in the evolution of the Paguridae. The analyses not only confirm the nested position of lithodid crabs within the Paguridae, but also strongly support a sister relationship of lithodids with a clade of predominantly North Pacific hermit crabs within the Paguridae (paper I).

As lithodid crabs are nested within the hermit crab family Paguridae, also parasites of Lithodinae are nested within parasites of pagurid hermit crabs. The parasite phylogeny not only corroborates the position of Lithodinae within the Paguridae with one coevolution event, but two independent lineages followed the divergence between hermit crabs and lithodid crabs from their LCA.

3.4 The internal, trophic root system of rhizocephalans from lithodids and hermit crabs

3.4.1 Rationale

The morphology of the adult female parasite can be divided into two parts: the externa and the interna. The externa, which is attached to the outside of the crustacean host, is a sac-like structure, which contains the reproductive organs and a voluminous cavity in which the eggs are breed until the offspring is released as larvae into the water. This structure is generally in focus of taxonomy, and species descriptions are largely based on this part of the parasite (Høeg & Lützen, 1985, 1995). The interna, which is the sole trophic organ of the parasite, is situated inside the host, and infiltrates the inner organs as a complicated root-like structure. Its location, hidden inside the host's body, and highly structured morphology, makes this part of the organism difficult to study, and only few studies have investigated the rhizocephalan interna in detail (Lützen, 1981; Shukalyuk, Baiborodin, & Isaeva, 2001; Bresciani & Høeg, 2001; Shukalyuk, 2002; Isaeva, Akhmadieva, & Shukalyuk, 2012).

The lithodid crabs have undergone a remarkable morphological transformation from their hermit crab predecessor, especially regarding the size, shape, and location of the pleon. A rhizocephalan parasite, which follows this morphological transformation in a coevolutionary manner, must be able to adapt to this changed morphology. This adaption accounts not only for the orientation of the externa on the hosts pleon, but in particular to the structural organization of the interna.

To investigate the spatial organization of the rhizocephalan interna of parasites from hermit crabs and lithodid hosts, micro-computed tomography (MicroCT) and computer-aided 3D-reconstruction was utilized, which produces 3D x-ray imaging of the specimens (paper IV). Using this method, the internal parasite can be visualized in situ inside the hosts body. We studied various species of the genus *Peltogaster*, from pagurid hermit crab hosts, as well as *Briarosaccus tenellus*, which due to the moderate size of its lithodid host, *Hapalogaster mertensii*, was suitable for MicroCT.

3.4.2 Main results

Using MicroCT and computer-aided 3D-reconstruction, we documented the spatial organization of the interna inside the intact host and also demonstrated its use for morphological examinations of the parasites reproductive part, the externa (paper IV). The study was the first that used MicroCT to demonstrate the in situ organization of a rhizocephalan interna inside the integument of an intact crustacean host.

The gross morphology of the internae of *Peltogaster* spp. observed in paper IV is in agreement with the earlier descriptions of *Peltogaster paguri* (Pérez, 1931, 1937; Bresciani & Høeg, 2001). The interna can be divided into a main trunk, situated in the pleon of the hermit crab, and a network of irregularly branching rootlets, which are spreading between the organs of the cephalothorax. The main trunk, previously described as resembling a horse's tail (Bresciani and Høeg, 2001; Pérez, 1937), has numerous side branches, giving the interna a large surface area to absorb nutrition. The roots are highly interwoven into the crab's organs, in particular the tubular hepatopancreas, which takes up the main volume of the hermit crabs pleon. The roots do not penetrate into the muscles of the hermit crab host. The characteristic horse's tail structure of the *Peltogaster* interna is not found in *Briarosaccus,* but also here the main volume of the interna is present in the pleon of the host, highly interwoven into the tubules of the hepatopancreas, and the interna is not penetrating the muscles. The absence of the clear split of the interna of *Briarosaccus* into an anterior and posterior trunk inside the pleon appears to be related to the morphological change of its hosts due to the carcinization in the evolution of the Lithodinae, and the subsequent reduction of the pleon. As in the hermit crabs, the pleon of king crabs houses the main portion of the hepatopancreas (Anker & Paulay, 2013; Keiler *et al.*, 2015). The hepatopancreas appears to be the target for the major part of the interna, both in *Peltogaster* and *Briarosaccus*. The structural organization of the interna between these two genera is thus directly comparable and structural differences appear to merely reflect the hosts anatomy due to the carcinization of the Lithodinae.

3.5 The type material of *Briarosaccus callosus*

B. callosus was described based on one single specimen from the host *Neolithodes agassizii*, sampled from the Atlantic US coast by the United States Fish Commission Steamer *Albatross*. The specimen was collected in May 1886, either on station 2666, off Fernandina, Florida, 494 m depth, or on station 2677, off Cape Fear, North Carolina, 864 m depth (Boschma, 1930). The specimen was registered under the catalogue number 62304 at the Smithsonian National Museum of National History, Washington D.C, USA.

Boschma described this single specimen in detail for the description of *B. callosus*. In course of the morphological investigation of the specimen, the mantle cavity of the externa was opened, and the visceral mass detached from the mantle. Parts of the visceral mass, containing the receptacles and colleteric glands, were embedded in paraffin and thin sectioned on a microtome. Further, parts of the mantle were cut for detailed microscopic investigation (Boschma, 1930). Resultantly, the type specimen was left largely destroyed following the species description.

In a later publication, Boschma (1962) reported and illustrated a second specimen of *Briarosaccus,* which was sampled together with the specimen used for the species description. This specimen was not mentioned in the original species description, and was morphological quite different from the type specimen, especially regarding the position and shape of the mantle aperture.

The remains of the dissected specimen that Boschma based his description on could not be located, neither in the Smithsonian National Museum of National History, Washington D.C, USA, where Boschma received the specimen from, nor in the Naturalis Biodiversity Center, Leiden, the Netherlands, which houses the majority of Boschma’s material.

At the Smithsonian Institution, a note was found in an old ledger under the catalogue number of the type specimen that stated “reserved for Boschma, type in his hands” (Rafael Lemaitre, pers. com.), and likely the specimen had not been returned.

But the specimen of the second parasite from the type locality, which was not included in the species description, could be found in the Smithsonian collection.

This specimen had at some point be dissected and is largely destroyed, but could clearly be identified as the specimen illustrated by Boschma (1962). This specimen also had a label containing the two possible station data from the type's lot. A new collection number (USNM 1148190) was assigned to this specimen in 2010. The specimen also contained a label stating "Rhizocephala reg. no. 329B. H. Boschma", which refers to Boschma's personal notebook. While the whereabouts of this notebook is unknown (Karen van Dorp, pers. com.), the number 329B of the second specimen from the type lot suggested that the type specimen had Boschma's personal ID number 329A.

Boschma's extensive collection of serial sections are stored in the Naturalis Biodiversity Center. These slides are marked with Boschma's personal ID numbers, but are unfortunately lacking other information. Under specimen number 329A I was in fact able to find the serial sections made from the type specimen of *B. callosus*. These sections are mounted on 116 individual glass slides, with each slide containing 9 thin sections (RMNH.CRUS 13377 – 13493). Due to the large size of the parasite, only parts of the slides were finally stained and mounted, while the main part remained unmounted, and only embedded in paraffin. Also the particular slides from which the drawings in the species description are based on could be found (RMNH.CRUS 13466 (Box BE 127612)/ RMNH.CRUS 13400 (Box BE 127611)) (Fig. 6).

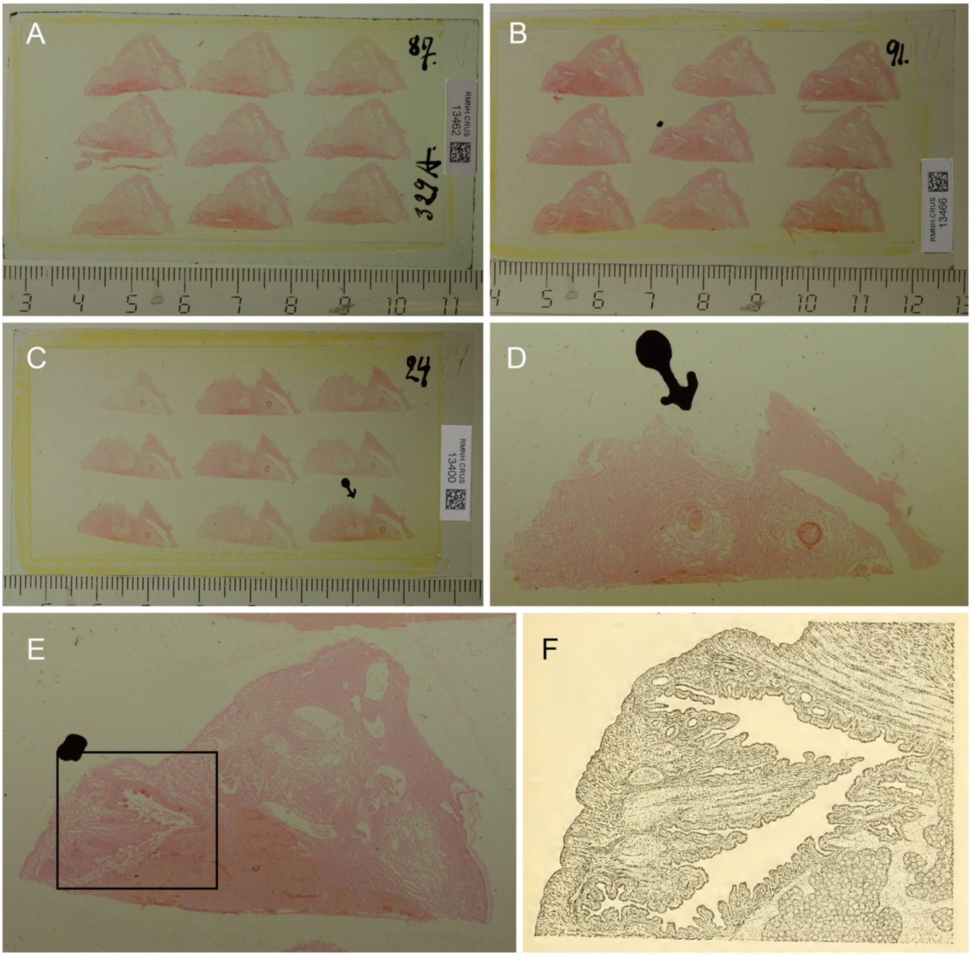

Figure 6: Serial sections of the type specimen of *B. callosus*. A: Slide number 87, with Boschma's ID number for the specimen (329A) (RMNH.CRUS 13462). B: Slide number 91, with a mark at the section used to illustrate the colleteric gland in the original description (RMNH.CRUS 13466). C: Slide number 24, with a mark at the section used to illustrate the receptacles in the original description (RMNH.CRUS 13400). D. Detail of the section from C. Note the Mars symbol drawn by Boschma. E: Detail of the section from B. Black box indicating the part used in Boschma's illustration. F: Figure 6 from the species description of *B. callosus*, with part of a transverse section, showing one of the colleteric glands. Drawing from Boschma (1930). Scales in A-C are in centimetres.

Boschma classified all rhizocephalans of king crabs as *B. callosus* (Boschma, 1970). This was largely due to the fact that his samples, which steadily increased over the years, showed high morphological variations, but from most hosts only very few specimens were available to him. Lacking modern species delimitation methods, Boschma did not find another solution than classifying all records as a single species. Following authors had little other choice than following Boschma's practice when new king crab hosts to rhizocephalan parasites were discovered (e.g. Arnaud & Do-Chi, 1977; Abelló & Macpherson, 1992; Pohle, 1992a; Lützen, Glenner & Lörz, 2009; Pino et al., 2010).

To discriminate cryptic species of king crab rhizocephalans that have been classified as *B. callosus*, it was crucial to clearly identify the "true" *B. callosus*. Therefore, a genetic identification of *B. callosus* s. str. was needed. Naturally, *Briarosaccus* samples for this had to be obtained from the type's host, *N. agassizii*. The presence of *Briarosaccus* specimens with two highly deviating morphologies from this host, and even from the types sample lot, further requested genetic sequences from both morphotypes from this king crab host.

Neolithodes agassizii is rarely sampled due to its deep-sea habitat and a lack of fisheries for this species. I was, therefore, unable to acquire fresh samples of *Briarosaccus* from this host species. It was, however, possible to extract DNA from museum material of *Briarosaccus* taken from this host. The mitochondrial 16S marker could be successfully amplified from three specimens parasitic on *N. agassizii*.

One of these specimens was collected in the Caribbean Sea, off the north coast of Colombia at a depth of 1318-1299 meters in 1968. This specimen, which belongs to a lot of three externae, was reported and sketched by Boschma (1970), and was located at the Naturalis Biodiversity Center (RMNH.CRUS.C.1884). Those specimens were of much smaller size then the type specimen, but the external morphology largely resembled that of the type.

I located a further specimen of *Briarosaccus* in the Naturalis collection, situated on a large specimen of *N. agassizii* (RMNH.CRUS.D.36147) collected off the Bahamas Islands at a depth of 1378 meter in 1974. This specimen had a highly similar external morphology and size to the type specimen of *B. callosus*.

It was also possible to obtain a genetic sequence from the specimen that was sampled together with the type specimen (USNM 1148190). This was quite remarkable, since sampled in 1886, this specimen was almost 130 years old!

Encouraged by the possibility to obtain PCR products from a specimen that was sampled together with the type specimen of *B. callosus*, I also attempted to extract DNA from some of the thin sections made by Boschma from the type specimen of *B. callosus*. Only every 5th slide, each containing nine sections, was stained and mounted permanently, while the remaining sections were only paraffin embedded and uncovered. Samples were taken from five individual sections, each located in the middle of an individual glass slide, and DNA extractions were performed following a protocol for paraffin embedded tissue. However, the PCR's were unsuccessful to amplify neither 16S nor COI from these samples.

The 16S marker revealed that the *Briarosaccus* specimens from *N. agassizii* are actually belonging to two separate species. One of these two species is represented by the specimen that was sampled together with the type specimen. The other species by the specimens from the Caribbean and the Bahamas Islands. The latter ones are morphologically similar to the type specimen, and therefore must be considered to represent *B. callosus* s. str. The other specimen, that is morphologically aberrant to the type, represents a further, cryptic species. This is remarkable, since it shows that the two *Briarosaccus* specimens sampled at the type locality of *B. callosus* are belonging to two separate species. The two species from the type locality of *B. callosus* are further found in each of the two distinct *Briarosaccus* clades (see paper III). This rather distant relationship between these species also explains the morphological differences between the *Briarosaccus* specimens from the type locality of *B. callosus*.

While this finding might surprise at first, it explains why all rhizocephalans of king crabs had been considered as a single species, namely *B. callosus*. While Boschma described *B. callosus* based on one single externa, the sample containing this specimen was a lot of two externa. This second externa has, in rhizocephalan terms, a striking different morphology, making the morphological differences between the two parasite specimens on the type's host species as large as between the type and any other rhizocephalan found on a king crab. Due to the rarity of two rhizocephalans of the same genus parasitizing the same host, the solution that the type's lot consisted of two *Briarosaccus* species obviously did not appear to Boschma. With very few specimens available for comparison, and lacking modern species delimitation methods, he had to assume that those belong to a single species.

This apparently high morphological variation of *B. callosus* samples taken from the same host made parasite specimens from other host species and regions apparently fitting into the large morphological variability of *B. callosus*, as Boschma stated that in many instances the variation was more striking between two specimens from one host than between two specimens from different hosts (Boschma, 1962). Following, all rhizocephalan records on king crabs were classified as a single species; *B. callosus* (Boschma, 1970).

The most significant morphological difference between the two *Briarosaccus* species from *N. agassizii* is found in the position and shape of the mantle aperture. In *B. callosus* s. str., this is not exactly located at the anterior pole, but slightly on the right side of the median plane (see paper III Fig. 4), resulting in a not fully bilateral symmetry of the externa. Only one of the investigated museum specimens of *B. callosus* s. str. was still located in situ on its host. This specimen, from the Bahamas Islands (RMNH.CRUS.D.36147), was parasitizing a large female host. The mantle aperture of the parasites externa was exactly located at the indentation of the outer edge of the hosts pleon, formed at the joint between the left tergal plates of the 3rd and 4th abdominal somites. While this pattern needs confirmation from additional specimens, the shifted position of the mantle aperture in *B. callosus* s. str. is likely a highly specialized adaption to the pleon morphology of its host king crab. Protected under the broad abdomen of the female king crab, the exact placement of the parasites mantle aperture under the indentation in the hosts pleon, allows an optimal supply of fresh, oxygenized water to the voluminous mantle cavity, where the parasite breeds its eggs.

3.6 The Norwegian Paguridae fauna: king crab origin in a nutshell

Hermit crabs are represented in Norwegian waters by seven species belonging to two genera of the family Paguridae: *Anapagurus* and *Pagurus*. *Anapagurus,* which can be distinguished from the latter genus by the presence of sexual tubes in males (McLaughlin, 2003), is present with two species; *A. chiroacanthus* (Fig. 7g) and *A. laevis* (Fig. 7h). *Pagurus* is represented by *P. cuanensis* (Fig. 7f), *P. alatus* (Fig. 7d), *P. prideaux* (Fig. 7a), *P. pubescens* (Fig. 7b, e), as well as *P. bernhardus* (Fig. 7c), the type species of the genus. Lithodid crabs are represented in the Norwegian fauna by one native king crab species, *Lithodes maja* (Fig. 7j), which has the Norwegian name “trollkrabbe” (troll crab), and the more prominent, introduced red king crab, *Paralithodes camtschaticus* (Fig. 7i), which reaches the largest size of all lithodid crabs (Stevens & Lovrich, 2014). A molecular phylogeny of species present in the Norwegian fauna was constructed using Bayesian inference analyses, using the same markers and methodology as described in paper I (Fig. 8). Part of the data compiled for paper I was used for this analyses.

Figure 7: Photographs of living specimens of all Paguridae taxa found in the Norwegian fauna. a) *Pagurus prideaux* with its symbiotic sea anemone *Adamsia palliata*. Note the purple coloured acontia which are protruded from the anemone as a defence response. b) *Pagurus pubescens* inhabiting a broken gastropod shell. c) *Pagurus bernhardus*, d) *Pagurus alatus*, e) *Pagurus pubescens*, f) *Pagurus*

cuanensis, g) *Anapagurus chiroacanthus*, h) *Anapagurus laevis* carrying externae of the rhizocephalan genus *Peltogasterella* on its pleon. i) The red king crab, *Paralithodes camtschaticus*, j) *Lithodes maja*, the native king crab species.

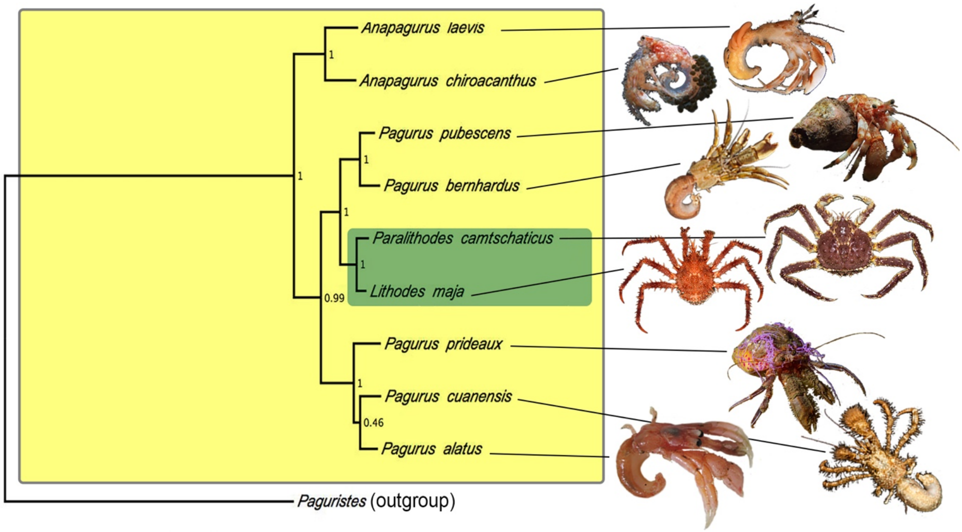

Figure 8: Phylogenetic tree of the Norwegian Paguridae fauna. Bayesian majority rule tree for the five-gene concatenated data set. The hermit crab genus Paguristes (family Diogenidae), not present in the local fauna, is used as outgroup taxon. Bayesian posterior probabilities are given on the nodes. The Paguridae are marked in the yellow box. The nested Lithodinae, represented by the native *L. maja* and the invasive *P. camtschaticus*, are highlighted in the green box. Specimens not to scale.

Even in this phylogenetic tree, containing a much smaller number of species than in paper I, the king crabs are found nested within the pagurid hermit crabs. Further, the polyphyly of the genus *Pagurus* is also found in this dataset, with the lithodids being nested within this genus as currently recognized. *P. bernhardus* and *P. pubescens* were found as sister group to the king crabs. These two species are some of the few hermit crabs of the PLS clade that are found outside the North Pacific, where lithodid crabs evolved from a hermit crab ancestor (see paper I). Both species have close relatives in the North Pacific, belonging to the informal *Pagurus* morpho-groups "*bernhardus*" and "*trigonochirus*" respectively. Predecessors of both species must have independently entered the Atlantic Ocean through the Bering Strait. The remaining *Pagurus* species, *P. alatus*, *P. cuanensis*, and *P. prideaux,* which were grouped into the informal *Pagurus* subdivision I by Ingle (1985), form a second, distinct *Pagurus* clade. This small scale phylogeny of Paguridae from Norwegian waters illustrates the astonishing pattern, that some hermit crabs have a more recent last common ancestor with king crabs than with other hermit crabs, which are morphologically so similar that they are assigned to the same genus. While the exact phylogenetic position of lithodids within the Paguridae, and answers to the evolutionary origin of the taxon required a comprehensive, species-rich phylogeny as constructed in paper I, this regional restricted analyses aims to highlight the fascinating morphological transformation of king crabs from a hermit crab ancestor.

3.7 Potential of rhizocephalans as biological control agent against invasive king crabs / Risk evaluation of parasite infection for Northeast Atlantic king crabs

One aim of this thesis was to evaluate the potential of using rhizocephalan parasites as biological control agents against the invasive red king crab in the Northeast Atlantic. Or, depending on the point of view, evaluating the risk of the rhizocephalan-free red king crab stocks in the introduced range to become parasitized by rhizocephalans, and thereby decrease the commercial valuable king crab population (see 1.4).

The red king crab, *P. camtschaticus*, is commonly parasitized by *Briarosaccus* in its native range, the North Pacific (Haynes & Boschma, 1969; Hawkes *et al.*, 1986b). But no rhizocephalan parasites have been recorded from the red king crab in its introduced range. Also another king crab species, *Lithodes maja*, which is native in the invasive distribution range of *P. camtschaticus,* does not host rhizocephalan parasites. But while no rhizocephalan has been recorded from lithodids in the Northeast Atlantic, *Briarosaccus* is present in the Northwest Atlantic (Pohle, 1992a,b), as well as in the Mid-East Atlantic, off the coast of Africa (Abelló & Macpherson, 1992).

Knowledge about host specificity is of crucial importance to provide answers to both of these questions. If all rhizocephalans recorded from king crab hosts in fact only represent a single species as previously recognized, red king crabs could potentially become infested by parasites transmitted from any kind of king crab species that hosts a rhizocephalan. If *B. callosus*, on the other hand, represents a complex of cryptic species, parasite transfer from other, distantly related king crab species would be unlikely. Likewise, if a rhizocephalan would be introduced as biological control agent against invasive king crabs, native species, represented by *L. maja* in the Northeast Atlantic, would potentially be simultaneously exposed to the parasite, if *B. callosus* has a broad host range. A parasite which only parasitizes *P. camtschaticus* and congeneric species, on the other hand, could more likely be considered as a safe agent for the native Northeast Atlantic king crab fauna.

A further potential threat to the Northeast Atlantic red king crab stocks might also come from a rather unexpected source, namely rhizocephalans of hermit crabs. Previous molecular studies indicated that king crabs are not only nested within the hermit crab family Paguridae, but even within the hermit crab genus *Pagurus* (Cunningham *et al.*, 1992; Bracken-Grissom *et al.*, 2013). Species of this genus are host to a number of parasitic barnacles of the genus *Peltogaster* (McDermott *et al.*, 2010), which appeared to be closely related to the king crab parasite *B. callosus* (Boschma, 1962). In fact, consistent morphological differences between the two genera are lacking, and the genus *Briarosaccus* has largely been erected due to the exceptional large size of the type specimen and its host choice (Boschma, 1930, 1962). In the light of molecular phylogenies (Cunningham *et al.*, 1992; Morrison *et al.*, 2002; Tsang *et al.*, 2011; Bracken-Grissom *et al.*, 2013), host choice (pagurid hermit crab vs. lithodid crab) appears to be even less significant that at the time of Boschma's description of *B. callosus* (Boschma, 1930), even though an evolutionary origin of king crabs within the Paguridae had been forwarded much earlier on (Boas, 1880a,b, 1924; Bouvier, 1897). In the introduced distribution range of *P. camtschaticus*, two species of *Peltogaster* had been reported to occur: *P. paguri* and *P. curvata.* Both of these parasites have been reported from a number of hosts, including different species of the genus *Pagurus* (Høeg & Lützen, 1985; Øksnebjerg, 2000). Hosts to both *Peltogaster* species are found in different informal *Pagurus* morpho-groups, indicating a rather distant relationship between some of the hosts of a single parasite species (Ingle, 1985; García-Gómez, 1994). If these two species indeed have a host range that includes hermit crabs which are more distantly related to each other than some are to the king crabs, the surprising conclusion would be, that Norwegian waters possess a natural occurring biological control agent against invasive king crabs, in the form of rather anonymous parasites of local hermit crabs. These parasites may consequently have the potential to extend their host range to the red king crab. For the Norwegian target fishery of the red king crab, this would be alarmingly news, indicating that there is no need to be on watch for the fishery damaging rhizocephalan parasite *B. callosus*, since the local fauna already includes parasitic barnacles with the potential to infest king crabs.

Prior to this thesis, all rhizocephalans from king crabs were recognized as only a single species. This species, namely *B. callosus*, had been reported from a large range of king crab species and with a global distribution (see paper III). To provide answers to both the potential use as biological control agent, as well as a risk assessment for the king crab fisheries, it is crucial to understand the true host specificity of the parasites. To investigate if rhizocephalans of king crabs really consist of only a single species, or if they represent various cryptic species with individual higher species specificities, we first investigated *Briarosaccus* specimens from different host king crabs from the native range of *P. camtschaticus*, the North Pacific (paper II). In this study, we showed that two sympatric species of *Briarosaccus* occur on three investigated king crab species in this region. One of these two parasites, *Briarosaccus regalis* n. sp., was found parasitizing *P. camtschaticus*, as well as the congeneric *P. platypus*. The second species, *Briarosaccus autatum* n. sp., was, however, only parasitizing the third investigated host, *Lithodes aequispinus.* The latter species is rather distantly related to *P. camtschaticus* within the Lithodinae (see paper I), and congeneric with the native North Atlantic *L. maja.* This finding is of high significance for the herein discussed questions, since it revealed that instead of one *Briarosaccus* species being parasitic on a wide range of king crabs, the single parasite *B. callosus*, as previously recognized, apparently consists of a cryptic species complex with each species having a higher host specificity. As *B. regalis* was only found parasitizing *P. camtschaticus* and its congeneric species *P. platypus*, but not the genus *Lithodes*, this study further indicated that this parasite might be considered as a “safe” control agent regarding the native North Atlantic *L. maja* if being introduced to the Northeast Atlantic.

In paper III, *Briarosaccus* specimens from a wider host range and geographical distribution were included in a molecular genetic analyses. The pattern indicated in paper II, of *B. callosus* consisting of a large complex of cryptic species, could be confirmed on a global scale. Most of these cryptic species showed a high host specificity, and only one species was found parasitizing hosts belonging to two genera of Lithodinae. The reconciliation analyses indicated a high level of cophylogeny between rhizocephalan parasites and their lithodid hosts, where the parasites have been passed down through the host’s lineage. However, also host switches between distant lithodid lineages happened in the coevolutionary history between the taxa. These host switches have likely been triggered by the complex global dispersal of king crabs via the deep-sea (Hall & Thatje, 2009). For the questions regarding the invasive red king crab population, this further implies that only *B. regalis* n. sp. might be able to parasitize *P. camtschaticus*, while rhizocephalan parasites of other king crab species, including parasites from adjacent Atlantic regions, do not represent a direct threat to the commercial important red king crab stocks. The cases of host switches, revealed in the reconciliation analyses, on the other hand, suggest, that while *B. regalis* n. sp. apparently does not parasitize the genus *Lithodes* in its natural range, it might eventually be able to include the native *L. maja* in its host range if being introduced to the Northeast Atlantic.

The second potential threat to the red king crab stocks, represented by rhizocephalan parasites of hermit crabs, appeared of even higher significance considering the phylogenetic relationships of hermit crabs and lithodid crabs that were found in paper I. Here a distinct clade of pagurid hermit crabs, the “PLS-clade”, was found to comprise the closest relatives to the lithodids within the Paguridae. Two *Peltogaster* species, parasitic on hermit crabs, had been recognized in the introduced range of the red king crab. One of these, *P. curvata*, only has been reported from hosts that are not included in the closest sister group to king crabs. The second one, *P. paguri*, was reported from hermit crabs that are found both included in the PLS-clade and more distantly related to the Lithodinae (Høeg & Lützen, 1985). This apparently broad host range of *P. paguri,* spanning hosts with a more distinct phylogenetic relationship to each other than some have to the king crabs, made it plausible that *P. paguri* might be able to utilize *P. camtschaticus* as an additional host. However, also the species identity of both *P. paguri* and *P. curvata* had not been investigated using modern species delimitation methods, and slight morphological differences of parasites from different hosts had been highlighted (Høeg & Lützen, 1985). Similarly to *B. callosus* (paper II), also these two *Peltogaster* species could, therefore, be consisting of a complex of cryptic species. Indeed, we found both recognized *Peltogaster* species to consist of multiple cryptic species with individual higher host specificities (paper III). Resultantly, host ranges of the individual cryptic species were not spanning species with a phylogenetic range that would include the Lithodinae. Further, the cophylogeny analyses showed, that the divergence of lithodid crabs from king crabs was accompanied by two cophylogeny events, each leading to one *Briarosaccus* and one *Peltogaster* lineage. Since this divergence, apparently no host switch of a rhizocephalan parasite between hermit crabs and lithodid crabs successfully occurred (paper III). Prior to this thesis, the potential danger of king crabs to become parasitized by rhizocephalan parasites of hermit crabs was uncertain. Our results however show, that these species are not capable of infecting king crabs, and therefore do not represent any danger for the commercial king crab fisheries.

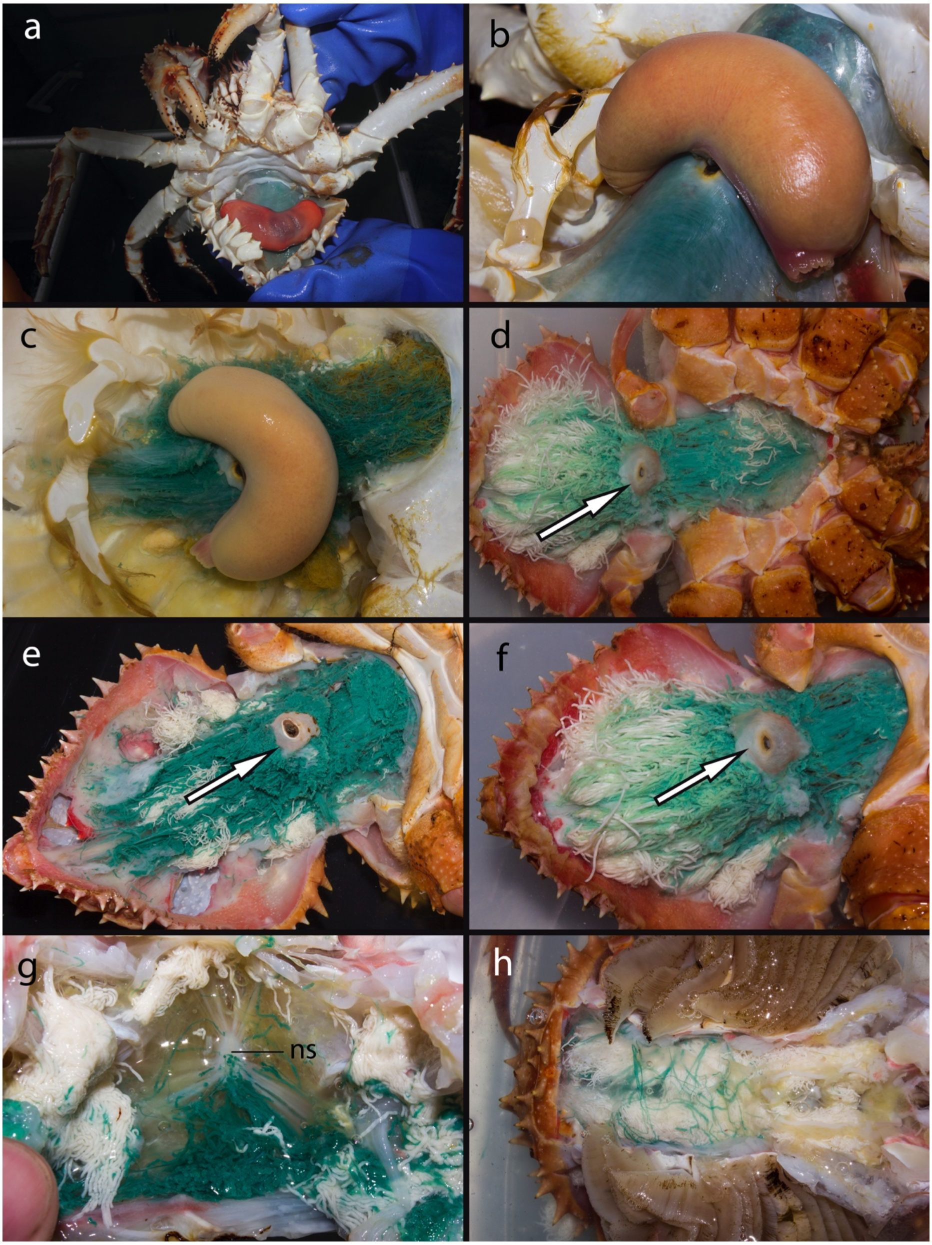

Figure 9: *Briarosaccus* infections of king crabs. a) The red king crab with a externa of *Briarosaccus regalis* located on the pleon. b) Externa of *B. regalis* on its host, c) Externa and interna of *B. regalis*. Soft, ventral cuticle of the hosts pleon removed, exposing the green coloured interna of the parasite. d-f) *Lithodes aequispinus* parasitized by *B. auratum*. Externa removed and ventral integument of the host removed, exposing the green interna inside the host. Arrow indicating scar from the attachment site of the externa. g, h) Green coloured rootles of the parasite interna inside the cephalothorax of *L. aequispinus*. ns: nervous system of the host.

Implications for the Northeast Atlantic red king crab populations:

Rhizocephalan parasites of hermit crabs do not represent a potential danger for the currently rhizocephalan-free red king crab stocks in the Northeast Atlantic. Also the risk of rhizocephalan parasites of other king crab species, e.g. from adjacent regions in the Atlantic, to parasitize *P. camtschaticus* in its introduced range is generally low, since host specificity is much higher than previously assumed.

Briarosaccus grows an extensive system of green rootlets inside the crab, making infested king crabs unusable for marketing (Fig. 9). In case of high prevalence, this implies a significant commercial loss. *Briarosaccus* further has strong negative effects on its hosts, including parasitic castration, which have led to concerns about the parasite's impact on the stocks of highly valuable king crabs (Isaeva, Dolganov, & Shukalyuk, 2005; Shields, 2012). The potential use of rhizocephalan parasites as biological control agent against introduced marine pests has been discussed (Lafferty & Kuris, 1996; Thresher *et al.*, 2000; Goddard *et al.*, 2005; Kuris *et al.*, 2007). The partial sterility of a king crab population might cause a decline in population size (Hawkes *et al.*,1986b; Shukalyuk *et al.*, 2005). However, the effectiveness of rhizocephalans as such agents has not been proven, as even crab populations with high levels of parasite infections appear to be stable (Innocenti & Galil, 2007).

A potential use of rhizocephalans as biological control agent against the red king crab in its introduced range appears inappropriate for various reasons. *P. camtschaticus* is an invasive species in Norwegian waters, and its fisheries management is highly controversial (Gederaas *et al.*, 2012). But in the native range of *P. camtschaticus*, its parasite *B. regalis* is regarded as unwanted organism, since it causes substantial economic loss for the king crab fisheries (Sparks & Morado, 1986; Hawkes *et al.*, 1986b). For the Norwegian king crab fishery, a rhizocephalan-free king crab stock is highly favourable. As rhizocephalans in general might not be as suitable to control the population size of their hosts, as initially presumed by Kuris (1997) (see Innocenti & Galil (2007)), also the effectiveness of *Briarosaccus* to control the invasive red king crab population is doubtful. Target fisheries must be considered to be much more efficient in reducing the population stocks of these large sized animals, since unrestricted fishing west of the North Cape has greatly reduced the spread southwards the Norwegian coast (Gederaas *et al.*, 2012; Sundet & Hoel, 2016). Further, a host switch to the native king crab species *L. maja* cannot be completely excluded, which would implement a further negative impact on the native fauna.

4. Main conclusions

- King crabs are found deeply nested within the hermit crab family Paguridae. Here, they have a sister relationship with a clade of predominantly North Pacific shallow water hermit crabs.
- Phylogenetic analyses revealed the two lithodid subfamilies to be polyphyletic. Small sized, shallow water taxa are found basal in the phylogenetic tree, while an increase in size and a following deep-sea distribution occurred later in the evolution of the group.
- The hermit crab genus *Pagurus* is highly polyphyletic, and spans a phylogenetic range that even includes the king crabs. Distinct phylogenetic linages, however, confirmed several previously established informal morpho-groups of this genus.
- What had been recognized as only a single parasite of king crabs, *B. callosus*, turned out representing a complex of cryptic species. Even parasites from the type's locality were found to represent two distinct species.
- Individual species of king crab rhizocephalans showed a much higher host specificity that previously assumed, usually restricted to a single species or genus.
- The rhizocephalan genus *Briarosaccus*, parasitic on lithodid crabs, is nested within the genus *Peltogaster*, parasitic on hermit crabs. Further, two independent linages of *Briarosaccus* originated within *Peltogaster*, rendering both genera polyphyletic.
- Reconciliation analyses showed significant correlation between host and parasite phylogenies, indicating that coevolution between the two taxa did occur. The co-phylogeny of Paguridae and Rhizocephala strongly corroborates the origin of king crabs from hermit crabs.
- MicroCT proofed to be a powerful method for morphological investigations of Rhizocephala. Both for visualizing the rhizocephalan root systems in situ inside of their crustacean hosts, as well as for the investigation of the parasite's interna, which generally is in focus of taxonomic studies.
- The overall organisation of the interna of *Peltogaster* and *Briarosaccus* is comparable, both regarding the location and main target organs. The loss of an

elongated main trunk in *Briarosaccus* must be seen as adaption of the parasite to the reduction of the hosts pleon in lithodid crabs, due to the process of carcinization.

- Rhizocephalan parasites of hermit crabs do not represent a potential danger for king crabs. Also the risk of rhizocephalan transfer from other king crab hosts to the introduced red king crab in the Northeast Atlantic is generally low.
- Rhizocephalans are unsuitable as biological control agents against invasive king crabs. The effectiveness of rhizocephalans to reduce the population size of a host is doubtful, and fisheries appears to be much more efficient in reducing king crab populations.

5. Future perspectives

5.1 Systematic of Paguridae

Internal relationships within the Paguridae are still far from being fully resolved. Such are phylogenetic placements of various hermit crab genera unknown, and especially the highly polyphyletic assemblage of the hermit crab genus *Pagurus* causes problems in nomenclature of the Paguridae. We showed, that previously established informal species complexes for this genus largely correspond to distinct clades resolved by molecular markers (paper I). An increased effort to sequence a larger range of species, e.g. via DNA “barcoding” of the mitochondrial COI (Hebert, Ratnasingham, & de Waard, 2003), will help to understand internal relationships and biogeographical pattern in the Paguridae. This will not only be of importance for the hermit crabs, but also for the king crabs. Internal relationships within the species rich deep-sea genera are largely unknown, and molecular sequences are only available from a fraction of species (see paper I). Detailed phylogenetic investigations of the deep-sea lineages *Paralomis, Lithodes, and Neolithodes* will eventually help to understand the complicated, global radiation of these taxa in detail.

5.2 Molecular work in Rhizocephala

The diversity of Rhizocephala appears to be highly underestimated. Not only are rhizocephalans, as parasites in general, overlooked in faunistic studies (Gómez & Nichols, 2013). Further, our studies (paper II, III) strongly indicate that rhizocephalans are often more host specific than assumed, and species records from various hosts represent complexes of cryptic species. The paucity of morphological characters in the adult parasite makes species delimitation of closely related species difficult, if not impossible, by morphology alone (see paper II, III). Future molecular investigations on rhizocephalans might therefore resolve further cryptic species groups, and provide information for further examples of coevolutionary scenarios between these parasites and their host taxa.

5.3 Morphological studies in Rhizocephala

We showed that MicroCT is a valuable tool for morphological analyses in Rhizocephala. Not only for the spatial analysis of the structural complex interna, which is hidden inside the body of the host, but also for the study of the parasites externa, which generally is in focus of taxonomy (paper IV). While the investigation of the externa usually requires thin sectioning, and thus a destruction of the specimen, MicroCT offers a method of non-destructive investigation, and, in addition, enables a complete overview of the structural organization of the organs.

We also showed, that classical dissection, in conjunction with Scanning Electron Microscopy, can provide a complete overview of both the structure and location of the receptacles (paper II). These organs are located embedded in the visceral mass of the parasites externa and are important characters for species descriptions of Rhizocephala.

6. References

Abelló P, Macpherson E. 1992. Epibiosis and rhizocephalan infestation patterns in relation to the reproductive biology of *Lithodes ferox* (Filhol, 1885) (Anomura: Lithodidae). *Journal of Crustacean Biology* 12: 561–570.

Agnew DJ, Daw TM, Pilling GM, Purves MG. 2001. Fishing for toothfish using pots: results of trials undertaken around South Georgia, March-May 2000. *CCAML Science* 8: 93–105.

Ahyong ST, Dawson EW. 2006. Lithodidae from the Ross Sea, Antarctica, with descriptions of two new species (Crustacea: Decapoda: Anomura). *Zootaxa* 1303: 45–68.

Ahyong ST, O'Meally D. 2004. Phylogeny of the Decapoda Reptantia: resolution using three molecular loci and morphology. *The Raffles Bulletin of Zoology* 52: 673–693.

Ahyong ST, Schnabel KE, Maas EW. 2009. Anomuran phylogeny: new insights from molecular data. In: Martin JW, Crandall KA, Felder DL, eds. *Decapod Crustacean Phylogenetics*. Taylor & Francis, CRC Press, Boca Raton, 399–414.

Anderson J. 1858. On the genus *Peltogaster* (Rathke); an animal form parasitic on the abdomen of crabs. *Proceedings of the Royal Physical Society of Edinburgh* 1: 412–414.

Anker A, Paulay G. 2013. A remarkable new crab-like hermit crab (Decapoda: Paguridae) from French Polynesia, with comments on carcinization in the Anomura. *Zootaxa* 3722: 283–300.

Anosov SE, Spiridonov VA., Neretina TV., Uryupova EF, Schepetov D. 2015. King crabs of the western Atlantic sector of Antarctic and adjacent areas: new records, molecular barcode data and distribution (Crustacea: Decapoda: Lithodidae). *Polar Biology* 38: 231–249.

Arnaud PM, Do-Chi T. 1977. Biological and biometrical data on the lithodid crab *Lithodes murrayi* (Crustacea, Decapoda, Anomura) of Crozet Islands (SW Indian Ocean). *Marine Biology* 39: 147–159.

van Bakel BWM, Fraaije RHB, Jagt JWM, Artal P. 2008. An unexpected diversity of Late Jurassic hermit crabs (Crustacea, Decapoda, Anomura) in Central Europe. *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen* 250: 137–156.

Balss H. 1924. Über Anpassungen und Symbiose der Paguriden. Eine zusammenfassende Übersicht. *Zeitschrift für Morphologie und Ökologie der Tiere* 1: 752–792.

Banks JC, Palma RL, Paterson AM. 2006. Cophylogenetic relationships between penguins and their chewing lice. *Journal of Evolutionary Biology* 19: 156–66.

Bickford D, Lohman DJ, Sodhi NS, Ng PKL, Meier R, Winker K, Ingram KK, Das I. 2007. Cryptic species as a window on diversity and conservation. *Trends in Ecology and Evolution* 22: 148–55.

Boas JE V. 1880a. Studier over decapodernes slægtskabsforhold. *Kongelige Danske Videnskabernes Selskabs Skrifter, Naturvidenskabelig of Mathematisk Afdeling* 5: 25–210.

Boas JE V. 1880b. *Lithodes* und *Pagurus*. *Zoologischer Anzeiger* 3: 349–352.

Boas JE V. 1924. Die Verwandtschaftliche Stellung der Gattung *Lithodes*. *Det Kgl. Danske Videnskabernes Selskab. Biologiske Meddelelser* 4: 1–34.

Borradaile LA. 1916. Crustacea. Part II. *Porcellanopagurus*: an instance of carcinization. British Antarctic (Terra Nova) Expedition, 1910. *British Antarctic ('Terra Nova') Expedition, 1910. Natural History Reports (Zoology)* 3: 111–126.

Boschma H. 1930. *Briarosaccus callosus*, a new genus and new species of a rhizocephalan parasite of *Lithodes agassizii* Smith. *Proceedings U.S. National Museum* 76: 1–8.

Boschma H. 1962. Rhizocephala. *Discovery Reports* 33: 55–92.

Boschma H. 1970. Notes on rhizocephala of the genus *Briarosaccus*, with the description of a new species. *Preceedings. Koninklijke Nederlandse Akademie van Wetenschappen, Series C* 73: 233–242.

Bouvier EL. 1894. Sur la transformation des Paguriens en crabes anomoures de la sous-familie des Lithodinés. *C. r. hebd. Séanc. Acad. Sci., Paris* 119: 350–352.

Bouvier EL. 1897. La transformation des Bernards l'Ermite en *Lithodes*. *Naturaliste* (2)19: 41–43.

Boyko CB, Moss J, Williams JD, Shields JD. 2013. A molecular phylogeny of Bopyroidea and Cryptoniscoidea (Crustacea: Isopoda). *Systematics and Biodiversity* 11: 495–506.

Boyko CB, Williams JD. 2009. Crustacean parasites as phylogenetic indicators in decapod evolution. In: Martin JW, Crandall KA, Felder DL, eds. *Crustacean Issues 18. Decapod Crustacean Phylogenetics*. CRC Press, Boca Raton, FL, 197–220.

Bracken-Grissom HD, Cannon ME, Cabezas P, Feldmann RM, Schweitzer CE, Ahyong ST, Felder DL, Lemaitre R, Crandall KA. 2013. A comprehensive and integrative reconstruction of evolutionary history for Anomura (Crustacea: Decapoda). *BMC Evolutionary Biology* 13: 1–28.

Bracken HD, Toon A, Felder DL, Martin JW, Finley M, Rasmussen J, Palero F, Crandall KA. 2009. The decapod tree of life: compiling the data and moving toward a consensus of decapod evolution. *Arthropod Systematics & Phylogeny* 67(1): 99–116.

Bresciani J, Høeg JT. 2001. Comparative ultrastructure of the root system in rhizocephalan barnacles (Crustacea: Cirripedia: Rhizocephala). *Journal of Morphology* 249: 9–42.

Brooks DR. 1988. Macroevolutionary comparisons of host and parasite phylogenies. *Annual Review of Ecology and Systematics* 19: 235–259.

Cadien DB, Martin JW. 1999. *Myzotarsa anaxiphilius*, new genus, new species, an atylopsine amphipod (Gammaridea: Pleustidae) commensal with lithodid crabs in California. *Journal of Crustacean Biology* 19: 593–611.

Caira JN, Jensen K. 2001. An investigation of the co-evolutionary relationships between onchobothriid tapeworms and their elasmobranch hosts. *International Journal for Parasitology* 31: 960–975.

Cárdenas CA, Cañete JI, Oyarzún S, Mansilla A. 2007. Podding of juvenile king crabs *Lithodes santolla* (Molina, 1782) (Crustacea) in association with holdfasts of *Macrocystis pyrifera* (Linnaeus) C. Agardh, 1980. *Investigaciones Marinas* 35: 105–110.

Chu KH, Tsang LM, Ma KY, Chan TY, Ng PKL. 2009. Decapod phylogeny: what can protein-coding genes tell us? In: Martin JW, Crandall KA, Felder D., eds. *Decapod Crustacean Phylogenetics*. Taylor & Francis, CRC Press, Boca Raton, 89–99.

Conow C, Fielder D, Ovadia Y, Libeskind-Hadas R. 2010. Jane: a new tool for the cophylogeny reconstruction problem. *Algorithms for Molecular Biology* 5: 16.

Cunningham CW, Blackstone NW, Buss LW. 1992. Evolution of king crabs from hermit crab ancestors. *Nature* 355: 539–542.

Demastes JW, Spradling TA, Hafner MS, Spies GR, Hafner DJ, Light JE. 2012. Cophylogeny on a fine scale: *Geomydoecus* chewing lice and their pocket gopher hosts, *Pappogeomys bulleri*. *Journal of Parasitology* 98: 262–270.

Desdevises Y. 2007. Cophylogeny: insights from fish-parasite systems. *Parassitologia* 49: 125–8.

Desdevises Y, Morand S, Jousson O, Legendre P. 2002. Coevolution between Lamellodiscus (Monogenea: Diplectanidae) and Sparidae (Teleostei): the study of a complex host-parasite system. *Evolution* 56: 2459–71.

Dixon CJ, Ahyong ST, Schram FR. 2003. A new hypothesis of decapod phylogeny. *Crustaceana* 76: 935–975.

Duguid WDP. 2010. The enigma of reversed asymmetry in lithodid crabs: absence of evidence for heritability or induction of morphological handedness in *Lopholithodes foraminatus*. *Evolution & Development* 12: 74–83.

Feldmann RM. 1998. *Paralomis debodeorum*, a new species of decapod crustacean from the Miocene of New Zealand : first notice of the Lithodidae in the fossil record. *New Zealand Journal of Geology and Geophysics* 41: 35–38.

Fraaije RHB. 2003. The oldest in situ hermit crab from the Lower Cretaceous of Speeton, UK. *Palaeontology* 46: 53–57.

Fraaije RHB. 2014. Diverse Late Jurassic anomuran assemblages from the Swabian Alb and evolutionary history of paguroids based on carapace morphology. *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen* 273: 121–145.

Fraaije RHB, van Bakel BWM, Jagt JWM, Machalski M. 2015. A new hermit crab (Anomura, Paguroidea) from the upper Albian (Cretaceous) of Annopol, Poland. *Zootaxa* 3955: 588.

Fraaije RHB, Krzemiński W, van Bakel BWM, Krzemińska E, Jagt JWM. 2012a. The earliest record of a diogenid hermit crab from the Late Jurassic of the Southern Polish Uplands, with notes on paguroid carapace terminology. *Acta Palaeontologica Polonica* 57: 655–660.

Fraaije RHB, Krzemiński W, Van Bakel BWM, Krzemińsk E, Jagt JWM. 2012b. New Late Jurassic symmetrical hermit crabs from the southern Polish Uplands and early paguroid diversification. *Acta Palaeontologica Polonica* 59: 681–688.

Fraaije RHB, Schweigert G, Nützel A, Havlik P. 2013. New Early Jurassic hermit crabs from Germany and France. *Journal of Crustacean Biology* 33: 802–817.

Fuhrmann MM, Pedersen T, Ramasco V, Nilssen EM. 2015. Macrobenthic biomass and production in a heterogenic subarctic fjord after invasion by the red king crab. *Journal of Sea Research* 106: 1–13.

Garassino A, Angeli A De, Pasini G. 2009. In situ hermit crab (Crustacea, Anomura, Paguroidea) from the Early Eocene (Ypresian) of NE Italy. *Atti Soc. it. Sci. nat. Museo civ. Stor. nat. Milano* 150: 229–238.

García-Gómez J. 1994. The systematics of the genus *Anapagurus* Henderson, 1886, and a new genus for *Anapagurus drachi* Forest, 1966 (Crustacea: Decapoda: Paguridae). *Zool. Verh. Leiden* 295: 1–131.

Gederaas L, Moen TL, Skjelseth S, Larsen LK (Eds.). 2012. *Alien species in Norway – with the Norwegian Black List 2012*. The Norwegian Biodiversity Information Centre, Norway.

Glenner H. 2001. Cypris metamorphosis, injection and earliest internal development of the Rhizocephalan *Loxothylacus panopaei* (Gissler). Crustacea: Cirripedia: Rhizocephala: Sacculinidae. *Journal of Morphology* 249: 43–75.

Glenner H, Hebsgaard MB. 2006. Phylogeny and evolution of life history strategies of the parasitic barnacles (Crustacea, Cirripedia, Rhizocephala). *Molecular Phylogenetics and Evolution* 41: 528–38.

Glenner H, Høeg JT. 1994. Metamorphosis in the Cirripedia Rhizocephala and the homology of the kentrogon and trichogon. *Zoologica Scripta* 23: 161–173.

Glenner H, Høeg JT. 1995. A new motile, multicellular stage involved in host invasion by parasitic barnacles (Rhizocephala). *Nature* 377: 147–149.

Glenner H, Høeg JT, O'Brien JJ, Sherman TD. 2000. Invasive vermigon stage in the parasitic barnacles *Loxothylacus texanus* and *L. panopaei* (Sacculinidae): closing of the rhizocephalan life-cycle. *Marine Biology* 136: 249–257.

Glenner H, Høeg JT, Stenderup J, Rybakov A V. 2010. The monophyletic origin of a remarkable sexual system in akentrogonid rhizocephalan parasites: a molecular and larval structural study. *Experimental Parasitology* 125: 3–12.

Glenner H, Lützen J, Takahashi T. 2003. Molecular and morphological evidence for a monophyletic clade of asexually reproducing rhizocephala: *Polyascus*, new genus (Cirripedia). *Journal of Crustacean Biology* 23: 548–557.

Goddard JHR, Torchin ME, Kuris AM, Lafferty KD. 2005. Host specificity of *Sacculina carcini*, a potential biological control agent of the introduced European green crab *Carcinus maenas* in California. *Biological Invasions* 7: 895–912.

Gómez A, Nichols E. 2013. Neglected wild life: parasitic biodiversity as a conservation target. *International Journal for Parasitology: Parasites and Wildlife* 2: 222–227.

Gurney RH, Grewe PM, Thresher RE. 2006. Mitochondrial DNA haplotype variation in the parasitic cirripede *Sacculina carcini* observed in the cytochrome oxidase gene (COI). *Journal of Crustacean Biology* 26: 326–330.

Guzman GL, Moreno RA, Moyano HI. 2002. New hosts to *Briarosaccus callosus* Boschma, 1930. (Crustacea, Rhizocephala). *Bol. Soc. Biol. Concepcion, Chile* 73: 83–86.

Hafner MS, Nadler SA. 1988. Phylogenetic trees support the coevolution of parasites and their hosts. *Nature* 332: 258–259.

Hafner MS, Sudman PD, Villablanca FX, Spradling TA, Demastes JW, Nadler SA. 1994. Disparate rates of molecular evolution in cospeciating hosts and parasites. *Science* 265: 1087–90.

Hall S, Thatje S. 2009. Global bottlenecks in the distribution of marine Crustacea: temperature constraints in the family Lithodidae. *Journal of Biogeography* 36: 2125–2135.

Hawkes CR, Meyers TR, Shirley TC. 1985. Parasitism of the blue king crab, *Paralithodes platypus*, by the rhizocephalan, *Briarosaccus callosus*. *Journal of Invertebrate Pathology* 45: 252–253.

Hawkes CR, Meyers TR, Shirley TC. 1986a. Length-weight relationships of blue, *Paralithodes platypus*, and golden, *Lithodes aequispina*, king crabs parasitized by the rhizocephalan, *Briarosaccus callosus* Boschma. *Fishery Bulletin* 84: 327–332.

Hawkes CR, Meyers TR, Shirley TC, Koeneman TM. 1986b. Prevalence of the parasitic barnacle *Briarosaccus callosus* on king crabs of Southeastern Alaska. *Transactions of the American Fisheries Society* 115: 252–257.

Haynes E, Boschma H. 1969. Occurrence of the rhizocephalan *Briarosaccus callosus* Boschma in the king crab *Paralithodes camtschatica* (Tilesius) in the Northeast Pacific Ocean. *Crustaceana* 16: 97–98.

Hebert PDN, Ratnasingham S, de Waard JR. 2003. Barcoding animal life: cytochrome c oxidase subunit 1 divergences among closely related species. *Proceedings of the Royal Society B: Biological Sciences* 270: S96–S99.

Hendricks SA, Flannery ME, Spicer GS. 2013. Cophylogeny of quill mites from the genus Syringophilopsis (Acari: Syringophilidae) and their North American passerine hosts. *The Journal of Parasitology* 99: 827–34.

Hirose M, Hirose E, Yoshida R. 2014. Hermit crab host prevalence by species of Peltogastridae (Cirripedia: Rhizocephala): hosts vary with locations on the Pacific coast in mainland Japan. *Journal of Crustacean Biology* 34: 467–480.

Hjelset AM, Sundet JH, Nilssen EM. 2009. Size at sexual maturity in the female red king crab (*Paralithodes camtschaticus*) in a newly settled population in the Barents Sea, Norway. *Journal of Northwest Atlantic Fishery Science* 41: 173–182.

Hoberg EP, Klassen GJ. 2002. Revealing the faunal tapestry: co-evolution and historical biogeography of hosts and parasites in marine systems. *Parasitology* 124: 3–22.

Høeg JT. 1987. Male cypris metamorphosis and a new male larval form, the trichogon, in the parasitic barnacle *Sacculina carcini* (Crustacea: Cirripedia: Rhizocephala). *Philosophical Transactions of the Royal Society B: Biological Sciences* 317: 47–63.

Høeg JT. 1990. 'Akentrogonid' host invasion and an entirely new type of life cycle in the rhizocephalan parasite *Clistosaccus paguri* (Thecostraca: Cirripedia). *Journal of Crustacean Biology* 10: 37–52.

Høeg JT. 1995. The biology and life cycle of the Rhizocephala (Cirripedia). *Journal of the Marine Biological Association of the United Kingdom* 75: 517–550.

Høeg JT, Lützen J. 1985. *Crustacea Rhizocephala. Marine Invertebrates of*

Scandinavia Number 6. Oslo, Norway: Norwegian University Press.

Høeg JT, Lützen J. 1995. Life cycle and reproduction in the Cirripedia Rhizocephala. *Oceanography and Marine Biology: an Annual Review* 33: 427–485.

Høeg JT, Rybakov A V. 1992. Revision of the Rhizocephala Akentrogonida (Cirripedia), with a list of a the species and a key to the identification of families. *Journal of Crustacean Biology* 12: 600–609.

Hoggarth DD. 1990. The effects of parasitism by the rhizocephalan, *Briarosaccus callosus* Boschma on the lithodid crab, *Paralomis granulosa* (Jacquinot) in the Falkland Islands. *Crustaceana* 59: 156–170.

Ingle RW. 1985. Northeastern Atlantic and Mediterranean hermit crabs (Crustacea: Anomura: Paguroidea: Paguridae). I. The genus *Pagurus* Fabricius, 1775. *Journal of Natural History* 19: 745–769.

Innocenti G, Galil BS. 2007. Modus vivendi: invasive host/parasite relations– *Charybdis longicollis* Leene, 1938 (Brachyura: Portunidae) and *Heterosaccus dollfusi* Boschma, 1960 (Rhizocephala: Sacculinidae). *Hydrobiologia* 590: 95–101.

Innocenti G, Galil BS, Yokes MB, Diamant A, Goren M. 2009. Here and there: a preliminary note on the prevalence of an alien rhizocephalan parasite at the southern and northern limits of its introduced range. *The Journal of Parasitology* 95: 1387–90.

Isaeva VV., Akhmadieva AV., Shukalyuk AI. 2012. The hidden coloniality at the parasitic stage in *Peltogaster reticulatus* (Crustacea: Rhizocephala). *Journal of the Marine Biological Association of the United Kingdom* 92: 457–462.

Isaeva VV., Dolganov SM, Shukalyuk AI. 2005. Rhizocephalan barnacles-parasites of commercially important crabs and other decapods. *Russian Journal of Marine Biology* 31: 215–220.

Jagt JWM, Bakel BWM Van, Fraaije RHB, Neumann C. 2006. In situ fossil hermit crabs (Paguroidea) from northwest Europe and Russia. Preliminary data on new records. *Revista Mexicana de Ciencias Geológicas* 23: 364–369.

Jaszkowiak K, Keiler J, Wirkner CS, Richter S. 2015. The mouth apparatus of *Lithodes maja* (Crustacea: Decapoda)-form, function and biological role. *Acta Zoologica* 96: 401–417.

Jensen GC. 1995. *Pacific coast crabs and shrimps*. Monterey, California: Sea Challengers.

Jørgensen LL, Primicerio R. 2007. Impact scenario for the invasive red king crab *Paralithodes camtschaticus* (Tilesius, 1815) (Reptantia, Lithodidae) on Norwegian, native, epibenthic prey. *Hydrobiologia* 590: 47–54.

Keiler J, Richter S. 2011. Morphological diversity of setae on the grooming legs in

Anomala (Decapoda: Reptantia) revealed by scanning electron microscopy. *Zoologischer Anzeiger* 250: 343–366.

Keiler J, Richter S, Wirkner CS. 2013. Evolutionary morphology of the hemolymph vascular system in hermit and king crabs (Crustacea: Decapoda: Anomala). *Journal of Morphology* 274: 759–78.

Keiler J, Richter S, Wirkner CS. 2015. The anatomy of the king crab *Hapalogaster mertensii* Brandt, 1850 (Anomura: Paguroidea: Hapalogastridae)–new insights into the evolutionary transformation of hermit crabs into king crabs. *Constributions to Zoology* 84: 149–165.

Klassen GJ. 1992. Coevolution: a history of the macroevolutionary approach to studying host-parasite associations. *The Journal of Parasitology* 78: 573.

Kruse I, Hare MP, Hines AH. 2012. Genetic relationships of the marine invasive crab parasite *Loxothylacus panopaei*: an analysis of DNA sequence variation, host specificity, and distributional range. *Biological Invasions* 14: 701–715.

Kuris AM. 1997. Conceptual framework for biocontrol of introduced marine pests. In: Thresher RE, ed. *Proceedings of the First International Workshop on the demography, impacts and management of introduced populations of the European crab, Carcinus maenas*. Centre for Research on Introduced Marine Pests Technical Report (11), 66–68.

Kuris AM, Goddard JHR, Torchin ME, Murphy N, Gurney R, Lafferty KD. 2007. An experimental evaluation of host specificity: the role of encounter and compatibility filters for a rhizocephalan parasite of crabs. *International Journal for Parasitology* 37: 539–45.

Lafferty KD, Kuris AM. 1996. Biological Control of Marine Pests. *Ecology* 77: 1989–2000.

Lanterbecq D, Rouse GW, Eeckhaut I. 2010. Evidence for cospeciation events in the host–symbiont system involving crinoids (Echinodermata) and their obligate associates, the myzostomids (Myzostomida, Annelida). *Molecular Phylogenetics and Evolution* 54: 357–371.

Lemaitre R, McLaughlin PA. 2009. Recent advances and conflicts in concepts of anomuran phylogeny (Crustacea: Malacostraca). *Arthropod Systematics & Phylogeny* 67: 119–135.

Lovrich GA, Roccatagliata D, Peresan L. 2004. Hyperparasitism of the cryptoniscid isopod *Liriopsis pygmaea* on the lithodid *Paralomis granulosa* from the Beagle Channel, Argentina. *Diseases Of Aquatic Organisms* 58: 71–77.

Lützen J. 1981. Observations on the rhizocephalan barnacle *Sylon hippolytes* M. Sars parasitic on the prawn *Spirontocaris lilljeborgi* (Danielssen). *Journal of Experimental*

Marine Biology and Ecology 50: 231–254.

Lützen J, Glenner H, Lörz A. 2009. Parasitic barnacles (Cirripedia: Rhizocephala) from New Zealand off-shore waters. *New Zealand Journal of Marine and Freshwater Research* 43: 613–621.

Lützen J, Itani G, Jespersen Å, Hong JS, Rees D, Glenner H. 2016. On a new species of parasitic barnacle (Crustacea: Rhizocephala), *Sacculina shiinoi* sp. nov., parasitizing Japanese mud shrimps *Upogebia* spp. (Decapoda: Thalassinidea: Upogebiidae), including a description of a novel morphological structure in the Rhizocephala. *Zoological Science* 33: 204–212.

Lützen J, Takahashi T. 1996. Morphology and biology of *Polysaccus japonicus* (Crustacea, Rhizocephala, Akentrogonida, Polysaccidae, fam. n.), a parasite of the ghost-shrimp *Callianassa japonica*. *Zoologica Scripta* 25: 171–181.

McDermott JJ, Williams JD, Boyko CB. 2010. The unwanted guests of hermits: a global review of the diversity and natural history of hermit crab parasites. *Journal of Experimental Marine Biology and Ecology* 394: 2–44.

McLaughlin PA. 2003. Illustrated keys to families and genera of the superfamily Paguroidea (Crustacea: Decapoda: Anomura), with diagnoses of genera of Paguridae. *Memoirs of Museum Victoria* 60: 111–144.

McLaughlin PA, Holthuis LB. 1985. Anomura versus Anomala. *Crustaceana* 49: 204–209.

Mclaughlin PA, Lemaitre R. 1997. Carcinization in the Anomura – fact or fiction ? I. Evidence from adult morphology. *Contributions to Zoology* 67: 79–123.

McLaughlin PA, Lemaitre R. 2000. Aspects of evolution in the anomuran superfamily Paguroidea: one larval prospective. *Invertebrate Reproduction & Development* 38: 159–169.

McLaughlin PA, Lemaitre R, Sorhannus U. 2007. Hermit crab phylogeny: a reappraisal and its 'fall-out'. *Journal of Crustacean Biology* 27: 97–115.

Mclaughlin PA, Lemaitre R, Tudge CC. 2004. Carcinization in the Anomura – fact or fiction? II. Evidence from larval, megalopal, and early juvenile morphology. *Contributions to Zoology* 73: 165–205.

Morrison CL, Harvey AW, Lavery S, Tieu K, Huang Y, Cunningham CW. 2002. Mitochondrial gene rearrangements confirm the parallel evolution of the crab-like form. *Proceedings: Biological sciences / The Royal Society* 269: 345–50.

Nygren A. 2014. Cryptic polychaete diversity: a review. *Zoologica Scripta* 43: 172–183.

Øksnebjerg B. 2000. The Rhizocephala (Crustacea: Cirripedia) of the Mediterranean and Black seas: taxonomy, biogeography, and ecology. *Israel Journal of Zoology* 46: 1–102.

Olson PD, Caira JN, Jensen K, Overstreet RM, Palm HW, Beveridge I. 2010. Evolution of the trypanorhynch tapeworms: parasite phylogeny supports independent lineages of sharks and rays. *International Journal for Parasitology* 40: 223–42.

Orlov YI, Ivanov BG. 1978. On the introduction of the Kamchatka king crab *Paralithodes camtschatica* (Decapoda: Anomura: Lithodidae) into the Barents Sea. *Marine Biology* 48: 373–375.

Oug E, Cochrane SKJ, Sundet JH, Norling K, Nilsson HC. 2011. Effects of the invasive red king crab (*Paralithodes camtschaticus*) on soft-bottom fauna in Varangerfjorden, northern Norway. *Marine Biodiversity* 41: 467–479.

Page RDM. 1994. Maps between trees and cladistic analysis of historical associations among genes, organisms, and areas. *Systematic Biology* 43: 58–77.

Palmer AR. 2004. Symmetry breaking and the evolution of development. *Science* 306: 828–33.

Paterson AM, Banks J. 2001. Analytical approaches to measuring cospeciation of host and parasites: through a glass, darkly. *International Journal for Parasitology* 31: 1012–1022.

Paterson AM, Poulin R. 1999. Have chondracanthid copepods co-speciated with their teleost hosts? *Systematic Parasitology* 44: 79–85.

Paterson M, Wallis GP, Lise A. 2000. Seabird and louse coevolution: complex histories revealed by 12S rRNA sequences and reconciliation analyses. *Systematic Biology* 49: 383–399.

Pérez C. 1931. Sur les racines des rhizocéphales parasites de pagures. *Comptes Rendus de l'Académie des Sciences*: 769–772.

Pérez C. 1937. Sur les racines des Rhizocéphales. *C R Int Congr Zool 12 Lisboa* 3: 1555–1563.

Pino J, Larriviere P, Shiga B, Argüelles J. 2010. Histology of the pedicle of the 'externa' of *Briarosaccus callosus* (Cirripedia, Peltogastridae) parasite of *Paralomis longipes* (Crustacea, Decapoda). *The Biologist (Lima)* 8: 73–78.

Pohle W. 1992a. First Canadian record of *Paralomis bouvieri* Hansen, 1908 (Decapoda: Anomura: Lithodidae), infected by the rhizocephalan *Briarosaccus callosus* (Cirripedia: Peltogastridae) and carrying a hyperparasitic cryptoniscinid isopod (Epicaridea). *Canadian Journal of Zoology* 70: 1625–1629.

Pohle GW. 1992b. First record of the rhizocephalan *Briarosaccus callosus* (Cirripedia, Peltogastridae) infecting the Atlantic porcupine stone crab *Neolithodes* *grimaldii* (Decapoda, Anomura, Lithodidae). *Crustaceana* 62: 133–136.

Rasmussen E. 1959. Behaviour of sacculinized shore crabs (*Carcinus maenas* Pennant). *Nature* 183: 479–480.

Rathke H. 1842. Beiträge zur vergleichenden Anatomie und Physiologie: Reisebemerkungen aus Skandinavien, nebst einem Anhange über die rückschreitende Metamorphose der Thiere. VI. *Peltogaster paguri*. *N. Schrift Naturf. Gesselch. Danzig* 3: 105–111.

Reimann A, Richter S, Scholtz G. 2011. Phylogeny of the Anomala (Crustacea, Decapoda, Reptantia) based on the ossicles of the foregut. *Zoologischer Anzeiger* 250: 316–342.

Richter S, Scholtz G. 1994. Morphological evidence for a hermit crab ancestry of lithodids (Crustacea, Decapoda, Anomala, Paguroidea). *Zoologischer Anzeiger* 233: 187–210.

Ritchie LE, Høeg JT. 1981. The life history of *Lernaodiscus porcellanae* (Cirripedia: Rhizocephala) and co-evolution with its porcellanid hosts. *Journal of Crustacean Biology* 1: 334–347.

Rybakov A V., Høeg JT. 2013. The taxonomic position of rhizocephalan crustaceans of the genus *Parthenopea* Kossmann, 1874 (Cirripedia: Rhizocephala) with validation of a new family, Parthenopeidae fam. nov. *Russian Journal of Marine Biology* 39: 357–362.

Schnabel KE, Ahyong ST, Maas EW. 2011. Galatheoidea are not monophyletic-molecular and morphological phylogeny of the squat lobsters (Decapoda: Anomura) with recognition of a new superfamily. *Molecular Phylogenetics and Evolution* 58: 157–168.

Scholtz G. 2014. Evolution of crabs – history and deconstruction of a prime example of convergence. *Contributions to Zoology* 83: 87–105.

Shields JD. 2012. The impact of pathogens on exploited populations of decapod crustaceans. *Journal of Invertebrate Pathology* 110: 211–24.

Shukalyuk AI. 2002. Organization of interna in *Sacculina polygenea* (Crustacea: Rhizocephala). *Russian Journal of Marine Biology* 28: 329–335.

Shukalyuk AI, Baiborodin SI, Isaeva V V. 2001. Organization of the interna of the rhizocephalan barnacle *Peltogasterella gracilis*. *Russian Journal of Marine Biology* 27: 113–115.

Shukalyuk AI, Isaeva V V, Pushchin II, Dolganov SM. 2005. Effects of the *Briarosaccus callosus* infestation on the commercial golden king crab *Lithodes aequispina*. *Journal of Parasitology* 91: 1502–1504.

Sloan NA. 1984a. Observations on Portland Inlet system golden king crabs (*Lithodes aequispina*) and their infestation by a rhizocephalan barnacle parasite *(Briarosaccus callosus*). *Can. MS Rep. Fish. Aquat. Sci.* 1779:61 p.

Sloan NA. 1984b. Incidence and effects of parasitism by the rhizocephalan barnacle, *Briarosaccus callosus* Boschma, in the golden king crab, *Lithodes aequispina* Benedict, from deep fjords in northern British Columbia, Canada. *Journal of Experimental Marine Biology and Ecology* 84: 111–131.

Sparks AK, Morado JF. 1986. Histopathology and host response in lithodid crabs parasitized by *Briarosaccus callosus*. *Diseases of Aquatic Organisms* 2: 31–38.

Štefka J, Hoeck PEA, Keller LF, Smith VS. 2011. A hitchhikers guide to the Galápagos: co-phylogeography of Galápagos mockingbirds and their parasites. *BMC Evolutionary Biology* 11: 284.

Stevens BG, Lovrich GA. 2014. King crabs of the world: species and distributions. In: Stevens BG, ed. *King crabs of the world, biology and fisheries management*. CRC Press, Boca Raton, FL, 1–30.

Strong DR, Pemberton RW. 2000. Biological control of invading species-risk and reform. *Science* 288: 1969–1970.

Summers MM, Rouse GW. 2014. Phylogeny of Myzostomida (Annelida) and their relationships with echinoderm hosts. *BMC Evolutionary Biology* 14: 170.

Sundet JH, Hoel AH. 2016. The Norwegian management of an introduced species: the Arctic red king crab fishery. *Marine Policy* 72: 278–284.

Thomas M., Willis A. 1998. Biocontrol—risky but necessary? *Trends in Ecology & Evolution* 13: 325–329.

Thompson J V. 1836. Natural history and metamorphosis of an anomalous crustaceous parasite of *Carcinus maenas*, the *Sacculina carcini*. *The Entomological Magazine* 3: 452–456.

Thresher R, Werner M, Høeg J, Svane I, Glenner H, Murphy NE, Wittwer C. 2000. Developing the options for managing marine pests: specificity trials on the parasitic castrator, *Sacculina carcini*, against the European crab, *Carcinus maenas*, and related species. *Journal of Experimental Marine Biology and Ecology* 254: 37–51.

Tsang LM, Chan TY, Ahyong ST, Chu KH. 2011. Hermit to king, or hermit to all: multiple transitions to crab-like forms from hermit crab ancestors. *Systematic Biology* 60: 616–629.

Tsang LM, Ma KY, Ahyong ST, Chan TY, Chu KH. 2008. Phylogeny of Decapoda using two nuclear protein-coding genes: origin and evolution of the Reptantia. *Molecular Phylogenetics and Evolution* 48: 359–68.

Tsang LM, Schubart CD, Ahyong ST, Lai JCY, Au EYC, Chan TY, Ng PKL, Chu KH. 2014. Evolutionary history of true crabs (Crustacea: Decapoda: Brachyura) and the origin of freshwater crabs. *Molecular Biology and Evolution* 31: 1173–1187.

Walker G. 2001. Introduction to the Rhizocephala (Crustacea: Cirripedia). *Journal of Morphology* 249: 1–8.

Watabe H. 2007. Metabiology of decapods: construction of axiomaic system of the autopoiesis theory. *Ocean Policy Studies* 5: 31–125.

Weckstein JD. 2004. Biogeography explains cophylogenetic patterns in toucan chewing lice. *Systematic Biology* 53: 154–164.

Yoshida R, Hirose M, Hirose E. 2015. *Peltogasterella sensuru* n. sp. (Crustacea: Cirripedia: Rhizocephala) from off Okinawa Island (Ryukyu Archipelago, Japan) with remarks on its single brood externae. *Systematic Parasitology* 92: 31–44.

Yoshida R, Hirose M, Mok H kiu, Hirose E. 2012. The first records of peltogastrid rhizocephalans (Crustacea: Cirripedia: Rhizocephala) on hermit crabs (Paguroidea) in Taiwan and differences in prevalences among collection sites. *Zoological Studies* 51: 1027–1039.

Zaklan SD. 2002. Review of the family Lithodidae (Crustacea: Anomura: Paguroidea): Distribution, biology, and fisheries. In: Paul AJ, Dawe EG, Elner R, Jamieson GS, Kruse GH, Otto RS, Sainte-Marie B, Shirley TC, Woodby D, eds. *Crabs in cold water regions: biology, management, and economics*. Alaska Sea Grant, University of Alaska Fairbanks, 751–845.

Zelenina DA, Mugue NS, Volkov AA, Sokolov VI. 2008. Red king crab (*Paralithodes camtschaticus*) in the Barents Sea: A comparative study of introduced and native populations. *Russian Journal of Genetics* 44: 859–866.