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University of Alberta

Evolution of the Family Lithodidae (Crustacea, Anomura, Paguroidea)

by

Stefanie D. Zaklan ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Doctor of Philosophy

in

Systematics and Evolution

Department of Biological Sciences

Fall 2001

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Our purpose here, however, is not to weigh the Crustacea,
but to be entertained by them; and if that has been realized, who could ask more –
even of a scientist, or a crustacean.

-Waldo Schmidt – 1965

University of Alberta

Faculty of Graduate Studies and Research

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled *Evolution of the Family Lithodidae (Crustacea, Anomura, Paguroidea)* submitted by Stefanie D. Zaklan in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Systematics and Evolution.

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Date: 2 Oct. 2001

This is dedicated to my parents,
George and Evelyn Zaklan,
for giving me the tools to build whatever I so desired.

Abstract

Members of the family Lithodidae (stone or king crabs) are among the world's largest arthropods; they are morphologically diverse, spectacularly ornate, and possess considerable economic importance (e.g., *Paralithodes camtschaticus*, the Alaskan king crab). How and why this group of crabs evolved has been debated since the mid 1800's. Early morphologists suspected close genealogical ties to hermit crabs (Paguridae, Anomura), and recent molecular evidence supports this hypothesis of hermit crab ancestry. However, several recent treatments disagree with this placement and suggest that the lithodids are derived hermit crabs. Herein, evolutionary relationships based on 170 morphological characters and partial DNA sequences (mtDNA COI, COII, 12S, 16S and nuclear DNA 28S) are analyzed separately and then combined into a total evidence tree. Each tree is then used to discuss hypotheses regarding relationships between the families Paguridae and Lithodidae and to propose genus level relationships.

Overall, these phylogenies suggest that the family Lithodidae is a monophyletic assemblage, with the hermit crab genus *Pagurus* basally paraphyletic. Presently, there are two subfamilies: 1) the physically large (carapace width ≥300 mm, up to 11 kg), social, global, anti-tropical, deep-sea (up to 4150 m) members of the subfamily Lithodinae, and 2) the small, intertidal inhabitants of the temperate north Pacific members of the subfamily Hapalogastrinae.

Molecular sequences obtained from 10 genera suggest that both subfamilies are monophyletic. Previous molecular data indicate that this large group (presently 105 species, representing 15 or 16 genera) arose between 13-25 mya. Character mapping on

the proposed molecular-based phylogeny suggests that the group originated in the northeast Pacific Ocean from a small, asymmetric, intertidal ancestor that may have evolved under the protection of the recently evolved (16-30 mya) canopy-producing kelp order Laminariales.

The morphological characters were scored for 15 genera and subsequently analyzed. A phylogeny inferred from these data suggests that the subfamily Hapalogastrinae is basally paraphyletic to the monophyletic Lithodinae and that at least two genera (*Paralithodes* and *Lithodes*) are not monophyletic. As there was considerable congruence between data sets, the phylogenies were combined to produce a total evidence tree. This tree was used to map the evolution of pleopod use and compared to a reanalysis of McLaughlin and Lemaitre's (1997) phylogenetic hypothesis, which states that pagurids are derived lithodids. Bootstrapping of their tree showed limited resolution, and thus did not provide robust evidence for their hypothesis.

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Poseidon's Treasure

Tick tock

          Tock tick

Time, time, time

I need time
                    Gone gone gone

I've been blown in by a heavy, unforgiving sea
          To search for homes this eternity

The promised land of folk and lore
          Does not exist on this rocky shore

The shells I've passed
          Trailered houses to me
          Are filled with other prospective registries

Quick Quick
          Time time,
                              it's glancing by and predators
          Take watch from the unprotective sky

The water crushes in again covering my roams
          And I still search in vain for that evasive solace of a home

The seafloor is dark, although sunny the day
          engulfed in arms of enlarged protists they sway

The predators above are confused, as I roam still looking
          still looking,
                    still looking for protection
          still looking for home

I cower with fright and like a dog I cringe,
          my tail abides and
          between my legs this Achilles' heel it hides

          I crawl to the call
          of the dark inviting cavity made by the tall

Tall inviting algae, her hair thrashing in the flays of the seas roar
          and I live,
          and I live, I live yet another day, a day in search on its floor

From within the normalized distribution
        emerges a selected genetic contribution

These kind spread into new niche's with speed
        ordained kings of the ocean, but not imperialistic in need

Problem and opportunity inextricably entwined
        through stress's bottleneck emerges a new species, a different kind

        Goldschmidt's hopeful monster procures
                a bathymetric array of species and ensures

a ride through Wright's landscapes
        powered by Kimura's random drifts and
                                natural selection by Darwin

        here come the species
                hip hop, step up, let's go
                                through time.
        here come
        Poseidon's hidden treasures
                in a comotion of speciation motion

        And the depths,
                the depths, the bathys, hides the species below,

        Then, like army ants stoically marching away
        venture taxonomists and systematics perhaps at work, but most likely at play

        they ponder, and argue, what are species,
        what are kinds,

        is it allopatric, sympatric or parapatric, oh the complications of minds

        studying Poseidon's potential treasures
        before they're

        gone gone gone.

        tock tick

        Tock tick

Time. time. time

they need time
                Gone gone

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CHAPTER 1

Thesis introduction

I am punished when I do not work on this poem
or when I try to invent something
I am one of the slaves …
- Leonard Cohen 1972

Phylogenetic systematics

A fundamental aspect of human nature is the need to categorize. For countless ages, natural historians have attempted to explain, understand, contain, and organize the diversity of the biological world – a discipline presently known as systematics. This need to quantify the surrounding zoological world was dramatically altered by the formalization of Linnaeus' Systema Naturae in 1758. In this book, he not only formalized species names using Latin based descriptions, but introduced a hierarchical nature to classification. This useful framework later lent itself well to the eventual implication of evolutionary-based relationships instead of separate divine creation for individual species (Hillis et al. 1996).

A more recent stage in the history of phylogenetic systematics was the advent of an objective methodology based on shared characteristics to propose phylogenetic hypotheses. Cladistics, also known as phylogenetic systematics, was first proposed by the botanist Walter Zimmermann (e.g. 1930) and the German entomologist Willi Hennig in (1950, 1965). In its present form, cladistic methodology uses only shared derived characteristics (synapomorphies) as sources of phylogenetic information, and suggests that shared ancestral characteristics (plesiomorphies) are uninformative.

Presently, there are three broad-based types of data used in producing hypothetical phylogenetic relationships: molecular, morphological (including traits as behaviour, physiology, ecological data etc.) and total evidence trees. With the discovery of the ground-breaking polymerase chain reaction sections of the genome could be amplified and large-scale molecular variation could be investigated (Mullis and Faloona 1987). One fortuitous consequence was the production of DNA-based phylogenies remarkably soon after. The second method to assess phylogenetic relationship is through morphological analysis, wherein each taxa is divided into separate characters and scored for specific character states.

A third approach used to investigate phylogenetic information is to combine both molecular and morphologically based data sets into a total evidence tree. Presently, there are three different views concerning the combination of discontinuous data sets: always combine data sets, always keep data sets separate then combine via consensus trees, or combine only non-contradictory data sets (reviewed in Swofford, 1991, de Queiroz et al., 1995, Miyamoto and Fitch, 1995, Huelsenbeck et al., 1996).

An introduction to the Evolution of the family Lithodidae

Although crustaceans are known for hardened exoskeletons that act as a protective measure against the surrounding world, not all crustaceans are fully protected by a scleritized armor. For example, many taxa within the infraorder Anomura bear soft abdomens, including the hermit crab families Pylochelidae, Diogenidae, Coenobitidae, Parapaguridae, Paguridae, and the lithodid subfamily Hapalogastrinae (Table 6-1). Of these taxa, lithodids are the only anomurans with soft abdomens and a concurrent crab-like form. The possession of an uncalcified abdomen proved to be a conundrum for morphologists such as Boas (1880a,b), Bouvier (1884a,b, 1895, 1897) and Borradaile (1916). They suggested that the possession of an uncalcified abdomen in pagurids was selectively advantageous as they are found living in protective mobile habitats such as gastropod shells, bivalve shells, or polychaete worm castings. However, the subfamily

Hapalogastrinae are free-living intertidal crustaceans that live independently of carried protection, and instead wrap their unprotected soft abdomen beneath them. The persistence of naked abdomens in non-shell-bearing crabs, coupled with asymmetries in their abdominal appendages, strongly suggested to these early natural historians that hapalogastrine crabs were derived from hermit crab ancestors and likely represent an early branch in the radiation of the lithodid crabs (Boas 1880a,b, Bouvier 1895, Makarov 1962). Compelling as this suggestion may seem, phylogenetic relationships among lithodid taxa remained poorly resolved for lack of data and a modern cladistic analysis.

The family Lithodidae (Crustacea: Decapoda: Anomura) contains approximately 105 species (Chapter 2) belonging to 15 (if *Acantholithus* belongs to *Paralomis* as per Sakai 1976) or 16 genera (Dawson, 1989). Presently, there are two subfamilies, Hapalogastrinae and Lithodinae. Members of subfamily Hapalogastrinae are small, bear soft abdomens, and are solitary, intertidal inhabitants found only in the north Pacific Ocean. In contrast, members of the subfamily Lithodinae, are large, fully calcified, social, deep-water inhabitants (up to about 4150 m) that are concentrated in the north Pacific Ocean but globally distributed (Tables 2-1 & 2-2). Although lithodids have been the subject of periodically intense interest from systematic and evolutionary biologists (Boas 1880a,b, Bouvier, 1894, 1895, 1897, Borradaile 1916, Martin and Abele 1986, Cunningham et al. 1992, Richter and Scholtz 1992, McLaughlin and Lemaitre 1997) and continual attention by fishery and developmental biologists (see Dawson 1989 for an exhaustive bibliography), very little phylogenetic information is available. This lack of knowledge occurs in spite of their existence as an important temperate water fishery resource, representing some of the most economically important species in the world. Fished taxa include the Alaskan king crab (*Paralithodes camtschaticus*), blue crab (*Paralithodes platypus*), the golden king crab (*Lithodes aequispinus*), in the north Pacific Ocean, and centolla (*Lithodes santolla*), and centollon (*Paralomis granulosa*) in the southeast Pacific Ocean and the southwest Atlantic Ocean.

In this thesis I use partial molecular sequences (mtDNA 12S, 16S, COI, COII and nuclear DNA 28S; Chapter 3), 170 morphological characters (Chapter 4), and combination of all data sets to produce a total evidence tree (Chapter 6) to address evolution of the family Lithodidae. I use recent technological advances such as DNA sequencing and computer based phylogentic programs (e.g. PAUP*, Swofford 2000 and MaClade, Maddison and Maddison 2000) in the framework of phylogenetic systematics to rigorously test hypothetical evolutionary relationships that were first hypothesized over 100 years ago.

Within this thesis three main objectives are addressed. First, I provide an overview of what is known about the biology of this diverse, and speciose family of decapods. This includes a synthesis of geographic and bathymetric ranges, access to taxonomic keys, information concerning maximum size, the outlining of closely related species, taxonomic authority names and dates, predators, prey, parasites, and a cursory overview of present day fisheries (Chapter 2). Second, I use original partial sequences from four mitochondrial genes (COI, COII, 16S and 12S), and one nuclear gene (28S; Chapter 3) to assess genus level relationships within the family Lithodidae and to investigate relationships between the family Lithodidae and the family Paguridae (hermit crabs). I then use 170 morphological characters (Chapter 4) as an independent confirmation of the DNA based findings. I then combine both data types to produce a total evidence tree to investigate the possibility of repeated evolution of carcinization, or production of the crab-like form (Borradaile 1916, Chapter 6). Third, as phylogenetic trees are the starting point of any historical ecological study (Brooks and McLennan 1991), each data set (molecular, morphological and total evidence) was used to examine specific character evolution within the Lithodidae. In particular, modifications in the abdomen, changes in body size, geographical origin, and bathymetric distribution were mapped onto the phylogenies in order to infer ancestral states and to suggest a logical progression of the evolutionary history of the family Lithodidae.

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CHAPTER 2

A review of the family Lithodidae (Crustacea: Anomura: Paguroidea): distribution, biology, and fisheries

I: ABSTRACT

The family Lithodidae is a diverse group of decapods on which investigative research is coming of age. Herein, published literature and original data are compiled and summarized. This overview includes distributions, life-history parameters, morphology, and names. Lithodids are a large family of approximately 105 species that are broad-scale omnivores with seasonal reproduction. They have a global distribution but reside mainly in anti-tropical waters from intertidal to 4152 m. They most likely arose in the northern Pacific Ocean between 13-25 million years ago. Much remains unknown about this economically important group, most likely due to their abyssal nature. Before more crab fisheries collapse or new fisheries are opened, increased research and enhanced communication among crab biologists should be initiated.

II: INTRODUCTION

Deep-sea inhabiting members of the family Lithodidae Samouelle, 1819 (Crustacea: Decapoda: Anomura) rank among the world's largest arthropods. The family Lithodidae is divided into two subfamilies (Hapalogastrinae and Lithodinae Ortmann, 1901), that collectively include 15 (Sakai 1976) or 16 genera (Dawson 1989) and approximately 105 species (Table 2-1) that reside mainly in the north Pacific Ocean (Table 2-2). Lithodid characteristics include a crab-like exoskeleton, rudimentary fifth walking legs, no uropods, asymmetric abdomenal tergite plates and pleopods 3-5 found only on the left. However, the majority of lithodid characters are based on their unusual abdomen. First, the sternal plate of the first abdominal segment is articulated with the last thoracic segment. Second, the female's abdomen is distinctly asymmetric, with the medial plane of symmetry right of center. Third, while males do not have pleopods, females possess between four and six asymmetrically placed pleopods, with the majority (four or five) associated with her larger left abdominal plates. Finally, there are varying degrees of abdominal tergal plate calcification, from none (*Oedignathus*) to complete (e.g. *Cryptolithodes*; e.g. Makarov 1962, Richter and Scholtz 1994). These unusual morphologies associated with asymmetry and variable calcification have puzzled evolutionary biologists for over one hundred years (Bouvier 1894a,b, 1895b,c, 1896, 1897, Boas 1880a, b, Borradaile 1916), and recently there has been a resurgence of interest in lithodid evolution (Cunningham et al. 1992, Richter and Scholtz 1994, McLaughlin and Lemaitre 1997, 2000, Chapter 3).

II A: Identity and relationships

Lithodid evolutionary relationships were first proposed by Boas (1880a,b) and Bouvier (1894a,b, 1897), who suggested that the asymmetrical soft abdomen of king crabs evolved from the asymmetrical soft abdomen of an ancestor that resembled hermit crabs and inhabited gastropod shells. Recent molecular (Cunningham et al. 1992, Chapter 3, Fig. 2-1) and some (Richter and Scholtz 1994) but not all (Martin and Abele

1986, McLaughlin and Lemaitre 1997, 2000) morphological reconstructions agree with this hypothesis. Broad scale lithodid genus-level relationships, based on morphology of the abdomen, were first hypothesized by Bouvier (1897) and recently confirmed by the molecular phylogeny found in Chapter 3 (Fig. 2-1).

Although there is no single identification manual that distinguishes all known lithodid species, the most inclusive keys are found in Dawson and Yaldwyn (1985a) and Macpherson (1988c). Other helpful keys are referred to in Table 2-3. Original taxonomic descriptions (Table 2-1) also may be used to differentiate potentially confusing species (Table 2-4). The web site http://geocities.com/Lithodidae is useful for viewing photographs and accessing reference information.

II B: Origin and distribution

Lithodids are distributed across a variety of aquatic zones from mid-intertidal to abyssal depths (up to 4152 m for *P. bouvier*, Macpherson 1988c). They typically inhabit anti-tropical waters, with high concentrations in the northern Pacific Ocean (Table 2-1). Lithodid radiation most likely began in the intertidal zone of the northeastern Pacific (Bouvier 1896, Makarov 1962) from a hermit-crab like ancestor (Bouvier 1894a, 1897, Boas 1880a,b, Cunningham et al. 1992, Richter and Scholtz 1994, Chapter 3, but see McLaughlin and Lemaitre 1997, 2000). The family is a fairly recent taxonomic addition, arising between 13-25 mya as suggested by molecular (Cunningham et al. 1992) and fossil (Feldmann 1998) evidence, and possibly evolving under the protection of the recently evolved (16-30 mya, Estes and Steinberg 1988, Saunders and Druehl 1992) canopy-producing kelp family Laminariales (Chapter 3).

Makarov (1962) provided several lines of biogeographic evidence that suggested a northeastern Pacific Ocean lithodid origin. Recent observations (Tables 2-1 & 2-2) concur with Makarov's north Pacific hypothesis. First, 68% of species and 100% of genera are reported from the Pacific, compared to only 28% of species and 19% of genera from the Atlantic Ocean. The remaining species are found in the Indian (11%) and Antarctic Oceans (3%; note: since species have broad distribution ranges, locality percentages do not add up to 100%). Second, 55% of living lithodid species occur in the northern hemisphere, as compared to only 42% in the south, the remaining taxa being abyssal inhabitants of the tropics (Tables 2-1 & 2-2). Third, the subfamily Hapalogastrinae is basal within the family Lithodidae (Bouvier 1894b, 1897 as morphological evidence; Konishi 1986 as larval evidence; Chapter 3 as molecular evidence; see Fig. 2-1). This basal subfamily is found only in the north Pacific Ocean, mainly in the northeastern Pacific (89% of species compared to only 45% in the northwestern Pacific, Tables 2-1 & 2-2). Finally, two basal clades (Fig. 2-1; according to Chapter 3) within the Lithodidae, Hapalogastrinae and genus *Cryptolithodes* of the Lithodinae, occur in the intertidal or shallow subtidal zone, suggesting an intertidal origin.

Although most intertidal lithodids inhabit the northeast Pacific, six intertidal species exist outside this region, five of which reside in the northwest Pacific. The sixth intertidal inhabitant is *Paralomis granulosa*, a shallow-water inhabitant, that apparently recently colonized southern South America's Beagle Channel, after the last deglaciation (8,200 years ago; Makarov 1962, Rabassa et al. 1986). This is the only member of the genus that inhabits shallow coastal waters (Macpherson 1988). This species also retains certain reproductive features associated with a varying or unpredictable food supplies such as few large eggs and a reproductive cycle in which zoeal eclosion is independent of food supply (Lovrich and Vinuesa 1993, 1999).

From the northeast Pacific's intertidal, lithodids are thought to have advanced west along the Aleutian range to the northwest Pacific shores of east Kamchatka and the Kurile Islands of Russia, followed by a range expansion to eastern Asia's Japan, Korea and China. Concurrently, northeast Pacific lithodids spread south along the eastern Pacific shores of North America. Due to cold-water abyssal upwelling, intertidal species are found farther south (Baja California) than their northwestern Pacific counterparts (Japan, Makarov 1962, Table 2-1). Deep sea lithodids probably crossed the tropics into the temperate, sub-antarctic, and antarctic regions of the southern hemisphere where a limited recolonization of South America's intertidal occurred (Makarov 1962, Lovrich and Vinuesa 1993, Table 2-1). Lithodids presumably passed through the Antarctic Ocean and spread upwards through to the Atlantic, across the southern tip of Africa into the Indian Ocean and finally into the southeast Pacific (Makarov 1962).

Along with the Pacific radiation of lithodids was a northern Atlantic radiation. Lithodids are thought to have passed north from the northeastern Pacific by way of the Bering Sea through the Arctic Ocean, spreading throughout the north Atlantic and southward around Africa into the Indian Ocean. Lithodids found in the Indian ocean are thought to have migrated by way of the Atlantic Ocean and not via the western Pacific Ocean due to the lack of observed lithodid inhabitants in the waters surrounding western Australia and Indonesia (p. 35, Fig. 12 in Makarov 1962; for an overview of their present distribution see Table 2-1).

Perhaps the abyssal nature of these animals (depth averaged from Table 2-1 minimum and maximum depths: *Neolithodes* = 1570m; *Lithodes* = 532m; *Paralomis* = 821m; Table 2-1), along with a large protective exoskeleton (CW ≤ 300 mm, Table 2-4), group social dynamics, migratory abilities, large broods (up to 280 000 eggs, Matsuura et al. 1972), expansive larval dispersal capabilities (Table 2-5) and opportunistic foraging strategies, allowed them to spread into extreme habitats that offer little environmental protection from overhead predators (Table 2-6).

II C: Sperm morphology

Only three lithodid species have been examined for spermatozoal morphology one hapalogastrinid: *Hapalogaster dentata* (Goshima et al. 1995), and two lithodinids: *Lithodes maja* (Retzius 1909, Tudge et al. 1998) and *Paralithodes camtschaticus* (Marukawa 1933). Overall, their spermatozoa are spherical, have globular nuclei and concentrically zoned acrosome vesicles. They are topped by a centrally perforated operculum, and are penetrated by a perforatorial chamber that is posteriorly embedded in the cytoplasm (Jamieson and Tudge 2000: 32). The spermatophores and sperm of *L. maja* share many synapomorphic features with the hermit crab genus *Pagurus*. These include accessory ampulae, homogenous granular spermatophore wall, concentric zonation of the acrosomal vesicle, operculum shape and differentiation, and an electron-dense plume basally in the perforatorial chamber (Tudge et al. 1998).

II D: Parasites

There are three major types of lithodid parasites: rhizocephalans (*Briarosaccus sp.*), liparid snailfish (*Careproctus* sp.), and microsporidans (Table 2-7). *Briarosaccus callosus* (Cirripedia: Peltogastridae) has four naupliar stages and one cyprid stage. It is the primary rhizocephalan barnacle parasite as it is hosted by several lithodids and has a nearly world-wide distribution (Boschma 1970; Table 2-7). *Briarosaccus tenellus* has five naupliar stages and has been found associated only with *H. mertensii* (Boschma 1970, Walossek et al. 1996). Larval morphology indicates that rhizocephalans hosted by *P. camtschaticus*, *P. platypus*, and *L. aequispinus* are conspecifics (Hawkes et al. 1985a), and hemolymph responses and electrophoresis lend additional support to this hypothesis (Shirley et al. 1986). Rhizocephalans cause feminization through castration and reduce growth in both sexes. Parasitized *P. platypus* and *L. aequispinus* are smaller than their unparasitized conspecifics (Sloan 1984, Hawkes et al. 1986a, Hawkes et al. 1987) and lithodids with multiple infections (up to five, observed in fjord dwelling northern B.C. *L. aequispinus*) have even slower growth rates (Sloan 1984). Parasitism can potentially affect reproductive stock as infection levels of *B. callosus* can range from 40.5%-66.7% of the total population (McMullen and Yoshiara 1970, Sloan 1984). However, occurrence is typically less than 1% in commercial landings of legal *P. camtschaticus* and *L. aequispinus* and up to 12% in *P. platypus* (Hawkes et al. 1986b).

The other major lithodid parasite is the liparid fish genus *Careproctus*. This snailfish oviposits its eggs into the protected cavity of aerated lithodid gill chambers. Although *Careproctus* eggs are found in relatively few species of king crabs (Table 2-7) they can exist in up to 43.6 % of the population (*L. aequispinus*; Jewett et al. 1985, Love and Shirley 1993, Somerton and Donaldson 1998). Negative effects of parasitism include egg mass induced gill compression (Anderson and Cailliet 1974, Melville-Smith and Louw 1987, Somerton and Donaldson 1998), gill bleeding (Love and Shirley 1993) and gill necrosis. In extreme cases gills are reduced to blackened stubs and up to 35% mortality is observed (Somerton and Donaldson 1998).

Nemertean brood symbionts such as *Carcinonemertes regicides* and *Alaxinus oclairi* also are thought to cause reductions in *P. camtschaticus* populations by eliminating recruitment of some year classes to the fishery through brood mortality

(Gibson et al. 1990, Kuris et al. 1991). *Alaxinus oclairi* can reduce broods by more than 50% (Gibson et al. 1990), and *C. regicides* were thought to be responsible for near complete consumption of all brooded eggs in some localities during the *P. camtschaticus* 1983-85 breeding season (Kuris et al. 1991). Other egg predators such as amphipods as well as viral infections and microsporidans may have an impact on brood success and population growth (Sparks and Morado 1985, Kuris et al. 1991; Table 2-7).

III: SUBFAMILIES

III A: Subfamily Hapalogastrinae

This taxonomically small subfamily of nine species (if *Placetron forcipatus* is recognized as a species; see Dawson 1989) and five genera is found only in the northern Pacific Ocean, mainly in the northeast (89% of species; Table 2-2). Species inhabit intertidal and shallow subtidal (down to 245 m for *Acantholithodes hispidus* [United States National Museum of Natural History (U.S.N.M.)] rocky shores and reside in a variety of protective habitats such as rocks, crevices and kelp (order Laminariales). They are generally opportunistic suspension feeders (Table 2-6). Relatively little natural history is known about this group, except that they are annual spawners that lack any seasonal- or size-dependent migration patterns (Goshima et al. 1995, Table 2-5). Although some members of genus *Hapalogaster* can be found in groups (Goshima et al. 1995), mass gatherings or *P. camtschaticus*-like "pods" (see below) have never been documented. Members of *Oedignathus inermis* are found only in pairs during the August mating season, and they remain solitary dwellers of crevices for the remainder of the year (Zaklan pers. obs.). All Hapalogastrinae have four zoeal stages and one glaucothoe stage, whereas species in the subfamily Lithodinae have two to four zoeal stages. Lithodinae larval stage abbreviation may suggest hapalogastrinids are a basal lineage within the family Lithodidae (Konishi 1986).

III B: Subfamily Lithodinae

This speciose subfamily (96 species representing 10 genera if *Acantholithus* is a true genus; see Sakai 1976 and Dawson 1989) is globally distributed but is concentrated in benthic north Pacific waters. Although they are generally found between 100-1000 m sub-tidally, they range in habitat from the low intertidal (*Cryptolithodes*; Hart 1965) to abyssal depths (*Paralomis* 4152 m; Macpherson 1988c). All genera have north Pacific Ocean representatives whereas only 30% of genera are represented in other oceans (e.g. Atlantic, Antarctic, Arctic and Indian; Table 2-1). Many species are recorded only by their holotype or a single sex (e.g.: *Lithodes richeri*, Macpherson 1990; *L. wiracocha*, Haig 1974; *Paralomis zealandica*, Balss 1911; *P. longidactyla*, Birstein and Vinogradov 1972; *P. microps*, Filhol 1884; *P. anamerae*, *P. erinacea*, *P. grossmani*, *P. pectinata*, *P. serrata*, Macpherson 1988c; *P. tuberipes*, Macpherson 1988b; *P. sp.*, Macpherson 1990; *P. jamsteci*, Takeda and Hashimoto 1990; Table 2-4). Thus, taxonomic, systematic and distributional understanding of lithodinids is still in its infancy.

Species in this subfamily are known to have seasonal- and size-dependent migrations, seasonal or aseasonal reproductive patterns, and omnivorous opportunist feeding habits (Table 2-6). Members of the subfamily Lithodinae generally have a greater and more abyssal geographic distribution, are more speciose (Table 2-1), larger (Table 2-4), carry more eggs, have fewer zoeal stages (Table 2-5), and live in larger social groups than members of the subfamily Hapalogastrinae.

III B (i): Subfamily Lithodinae life-cycle

The most notable characteristic of the Lithodinae is their migratory pattern, which is inextricably intertwined with mating rituals and with associated seasonal abiotic factors (Marukawa 1930, Bright 1967). Bathymetric location, movement patterns and mass gatherings (podding) are influenced by increased benthic production (Rodin 1970, Stinson 1975), thermocline (Somerton 1985), halocline, timing of larval release, thermohaline mixing, temperature, food sources and photoperiod in adults (Stone et al. 1992). Larval movement patterns are modified by temperature, light and salinity (Shirley and Shirley 1988, 1989b), as larvae are negatively geotactic and positively rheotactic

(Shirley and Shirley 1988). King crabs are capable of long-distance navigation using both chemosensory cues and home-range environmental features as guides (Dew 1990, Stone et al. 1992). Substantial migrations are a major part of their lives. They move from one area to another in discrete groups that are often segregated into sex and size-classes [Marukawa (1930), Powell and Nickerson (1965a), Bright (1967) for *Paralithodes camtschaticus*; Abello and Macpherson (1986) for *L. ferox*; Miquel et al. (1985) for *Lithodes murrayi*]. For example, female *P. camtschaticus* have a 3.6-11.9 km^2 range (Stone et al. 1992) and males can move 112 km in 113 days in Alaska (Simpson and Shippen 1968). In Japan they can migrate up to 10.4 (females) and 13.1 (males) km/day (Marukawa 1933). Tracking benthic crustaceans has become easier with the advent of internal tags that can be retained throughout ecdysis, such as coded wire tags and passive integrated transponder tags (Donaldson 1997). Laser line scans (Tracey et al. 1998), submersibles (Zhou and Shirley 1998) and ultrasonic biotelometry (Stone et al. 1992) also can be used for identification and tracking purposes.

Size at reproductive maturity is well-documented for economically important lithodinids compared to their unharvested conspecifics. Generally, maturity is defined as gonadal maturity unless otherwise stated, but several measures of reproductive maturity exist. For example, crabs of a given size class are considered functionally mature when they have been observed procreating. Males are gonadally mature when they possess spermatozoa in deferent ducts, while females are considered gonadally mature when they have embryos attached to their pleopods (Lovrich and Vinuesa 1999). Members of the family Lithodidae are morphometrically mature when the relative growth of the right chela's height changes with respect to carapace growth (Somerton and MacIntosh 1983). As size at female reproductive maturity is assumed to be the smallest ovigerous female documented or observed, carapace length at reproductive onset will decrease with future research and further published observations (Table 2-5).

The majority of studied Lithodinae have a distinct, annual life-history pattern associated with their reproductive cycle. Generally, females molt under the protection of a larger, recently molted male (in *P. camtschaticus* and *L. aequispinus*; but old-shell *L. santolla*, Lovrich and Vinuesa 1999). Molting is then followed by mating (Marukawa 1933, Powell and Nickerson 1965b, Somerton and MacIntosh 1983, Paul and Paul 1990, Vinuesa 1991, Goshima et al. 1995, Wada et at. 1997). They then carry eggs for approximately one year (Table 2-5), and if zoea are planktivorous, eclosion is concurrent with the spring diatom bloom (Kurata 1959, Paul and Paul 1980, Shirley and Shirley 1989a).

Migration occurs throughout this cycle for all developmental stages, from vertically migrating zoea (Shirley and Shirley 1987, 1989b) to horizontally migrating adults in genera such as *Lithodes*, *Paralithodes* and *Paralomis* (i.e. Miquel et al. 1985, Vinuesa 1991, Abe 1992, Stone et al. 1992, Hoggarth 1993). Large-scale migration is unknown but probable for the long-legged *Neolithodes*, and unlikely for the more robust *Phyllolithodes*, *Cryptolithodes*, *Rhinolithodes* and *Lopholithodes*. There are both inter- and intra-specific variations to this life-history pattern. For example, life-history patterns of *L. aequispinus* are locality dependent (Rodin 1970) so that they are aseasonal (have members of the population in varying stages of their life-cycle throughout the year) and migratory in fjords of British Columbia, Canada (Sloan 1985, Somerton and Otto 1986) whereas they are non-migratory and reproduce seasonally on Japan's continental shelf (Hiramoto and Sato 1970).

Bottom temperature has a great effect on growth (Stevens 1990), and thus on lithodid fecundity. For example, extreme cold-water inhabitants, such as *P. granulosa* (Lovrich 1997) and *P. camtschaticus* (McCaughran and Powell 1977; Zheng et al. 1995), take between five and ten years to reach gonadal maturity. Differences in water temperature is thought to cause the inverse correlation (Jewett et al. 1985) between size at maturity and latitude in *L. aequispinus* found in the eastern Bering Sea (Somerton and Otto 1986) and *P. camtschaticus*. For example, female *P. camtschaticus* reach maturity at an average carapace width (CW) of 89 mm in Bristol Bay, but at 71 mm CW in Norton Sound (Fishery Management plan for Bering Sea/Aleutians Islands King and Tanner Crabs 1998, North Pacific Fishery Management Council, Table E. 5).

III B (ii): Subfamily Lithodidae behaviors

All lithodids probably have anti-predator behavior, however, this is mainly documented in the economically important red king crab, *P. camtschaticus*. Following juvenile metamorphosis, these crabs are solitary and use crypsis and protected refuges afforded by complex habitats (e.g. rocks and kelp) in the intertidal and shallow subtidal as a sanctuary from benthic predators (Loher and Armstrong 2000). As they increase in size, they are often found in the protective crevices between starfish arms located on barnacle encrusted dock pilings (*Evasterias troschelii* and *Asterias amurensis* in Alaska: Powell and Nickerson 1965a, Dew 1990); and *Leptasterias* sp. in the Gulf of Shelekov, Russia: Vinogradov 1968). They are also found among *Metridium senile* anemone stalks, where they feed upon food particles dislodged by their commensal hosts (Powell and Nickerson 1965a). Juvenile king crabs leave their protective niches after sunset and move into the open to forage (Dew 1990). The most striking behavior pattern of lithodids is "podding," exemplified by both adult and juvenile *P. camtschaticus*. Podding describes a dense aggregation of hundreds to thousands or even to millions of similarly sized *P. camtschaticus*. Podding is thought to serve as a predatory-defense mechanism, and may also divide pre-mating adult populations into subgroups (Powell and Nickerson 1965a,b, Bright 1967, Dew 1990, Stone et al. 1993).

III B (iii): Subfamily Lithodinae adaptations

Lithodinids possess several adaptations that allow them to thrive in the vast open regions of the deep sea (Somerton 1981). First, some lithodids (*Paralithodes, Lithodes, Neolithodes, Glyptolithodes*, and some species of *Paralomis*) have long and slender pereopods. The associated reduced musculature is considered less costly to maintain, and long legs allow rapid and efficient movement by taking fewer, larger steps during long distance migrations (Somerton 1981). Second, *L. couesi*, the scarlet king crab, possesses red coloration that is found in many deepwater crustaceans and believed to represent cryptic coloration due to the rapid attenuation of red surface light (Marshall 1954). Third, deep water inhabitants possess enlarged exhalent openings and scaphognathites, allowing for greater water volume to be pumped over gills compared to shallow water conspecifics (Somerton 1981). These enlarged gills may be associated with inflated branchial chambers, as found in *P. camtschaticus*, *L. aequispinus* and *Paralomis verrilli* (Takeshita et al. 1978). Fourth, deep water crabs such as *L. couesi* and *L. aequispinus* have asynchronous or protracted spawning and breeding periods that are most likely a function of aseasonal productivity at great depths (Somerton 1981, Sloan 1985). Fifth, lecithotrophy and associated large eggs are adaptive for the variably productive habitats of *L. aequispinus* (Shirley and Zhou 1997) and *Lithodes santolla* (Lovrich 1999). Lecithotrophic development allows for successful hatching and recruitment, independently of phytoplankton blooms, thus allowing reproduction and subsequent larval release to be asynchronous (Comoglio and Vinuesa 1991, Shirley and Zhou 1997). Finally, *L. couesi* often live on remote seamounts on the continental slope that are isolated from the ocean surface, coastal areas, and possibly predators. These submarine islands can be inhabited by species that are able to tolerate vast ranges in depth and possess sufficient dispersal capabilities to migrate through the continental slope (Sakai 1971, Somerton 1981) or by species with larvae possessing adaptations that allow them to remain as seamount inhabitants. For example, lecithotrophic larvae of *L. aequispinus* remain near the bottom in laboratory cultures (Jewett et al. 1985, Shirley and Zhou 1997) and have never been collected in the plankton (Somerton and Otto 1986, Shirley and Shirley 1989a). These behavioral adaptations would limit their distribution and effectively confine lecithotrophic larvae within restricted habitats such as seamounts (T. Shirley in litt.)

III B (iv): Subfamily Lithodinae fishery

The north and south Pacific Ocean contains extensive and diverse coast lines and open shelf areas that support some of the most commercially significant crustacean stocks in the world, including four species of king crab (*P. camtschaticus, P. platypus, L. aequispinus* and *L. couesi*) in the north and two species in the south (*P. granulosa* and *L. santolla*). The Bering Sea, the Sea of Japan, the Kamchatka region and the Gulf of Alaska were part of a rapidly expanding king crab fishery from 1960-1980 (Fig. 2-2). Peak landings of 84 000 t occurred in this male-only fishery in 1980. At this stage *P. camtschaticus* was the most valuable single-species fishery in the United States (168.7 million; Alaska Department of Fish and Game 2001). Landings declined precipitously to 1362 t in 1982, and the Bristol Bay fishery was closed in 1983 (Alaska Department of Fish and Game 2001) and more recently in 1994. Overall, declines in stock are considered to be a function of both anthropogenic and environmental effects (Loher et al. 1998). Specific reasons for population declines include an assortment of factors such as overfishing due to serial depletion (Orensanz 1998), brood mortality due to parasites (Kuris et al. 1991), viral and microsporidan infections (Sparks and Morado 1985), climate change combined with overharvesting (Finney et al. 2000), temperature dependent growth, overharvesting based on incorrect population estimates (Stevens 1990), and changes in predator abundance (Anderson and Pait 1999). Fisheries are now open as populations have stabilized (Orensanz et al. 1998). However, rebuilding strategies have had little effect on stock recovery (Loher et al. 1998). Prompted by the collapse of the *P. camtschaticus* (red king crab) fishery, fisherman started to target *L. aequispinus* (golden king crab) in the Aleutians during the early 1980s and *P. platypus* (blue king crab). *Paralithodes platypus* occurs in a number of isolated pockets in southeast Alaska, specifically Prince William Sound and the Kodiak region. Landings are small and sporadic, and are generally associated with *P. camtschaticus* (Orensanz 1998).

Currently, *P. camtschaticus, P. platypus* and *L. aequispinus* remain among the most conservatively managed commercial fisheries in the world (T. Shirley in litt.). These fisheries are regulated under the American Fisheries Act (Kruse et al. 2000). Regulations include a pre-specified harvest cap based on estimates of the effective spawning biomass of lithodids, a newly instated (2000) observer program, immediate catch size updates, pot limits, and enforcement vessels. For example, in 2000, fishing in Bristol Bay was opened on October 16th at 4:00 pm and closed by emergency order when quotas were met at 9:00 pm on October 20th (Alaska Department of Fish and Game 2001). Studies analyzing alternative rebuilding strategies are constantly being published and updated, taking into account important behavioral and biological information (e.g. Zheng et al. 1997a,b,c, Kruse et al. 2000). Table 2-8 contains cursory fishery comparisons, but up-to date fishery information can be downloaded from the internet (e.g. Alaska Department of Fish and Game 2001).

In southern South America (Chile and Argentina) two sympatric species, *P. granulosa* (the false centolla) and *L. santolla* (centolla), have constituted a mixed fishery since the 1930s (Vinuesa et al. 1996, Lovrich 1996, Lovrich and Vinuesa 1999). Originally *L. santolla* was the primary fishery with landings peaking in 1974 at 320 t. However, after 1984 landings of *L. santolla* precipitously declined (260 t), and the fishery for *P. granulosa* began to develop. Landings of *P. granulosa* peaked in 1996 (360 t), with *L. santolla* maintaining only bycatch status (1.5 t in 1996; for summary statistics and refer to Fig. 1 of Lovrich and Vinuesa 1999). The continual violation of Argentine and Chilean fishery regulations is considered the main reason for the collapse. Transgressions, such as harvesting females and sublegal males, are frequent as effective controls are lacking (Vinuesa et al. 1995). The present reduction of *L. santolla* and *P. granulosa* landings, along with more restrictive regulations such as a shorter fishing season, has motivated the exploration and potential openings of new fisheries (G. Lovrich pers. com). These include other lithodids such as *Lithodes confundens* on the Atlantic coast of southern Argentina (49-53°S), and *Paralomis spinosissima* and *P. formosa* in South Georgia Islands (Otto and Macintosh 1996).

IV: CONCLUSION

This paper provides an overview of what is known about a diverse and speciose (approximately 105 species) family of decapods. The family Lithodidae is divided into subfamilies Hapalogastrinae and Lithodinae. Members of the subfamily Hapalogastrinae are small, soft-abdomen bearing, solitary, intertidal inhabitants found only in the north Pacific Ocean. Members of the subfamily Lithodinae, in comparison, are large, fully calcified, social, deep-water inhabitants that have a pan-global distribution, also concentrated in the north Pacific Ocean (Tables 2-1 & 2-2). Although there is no single key differentiating all lithodids, good keys emphasizing the differences between lithodid genera have been published (Table 2-3). Evolutionary relationships are just beginning to be understood at the generic level (Fig. 2-1), however species-level relationships are poorly understood, especially in some species of *Paralomis*, *Neolithodes* and *Lithodes*, where often only the type specimen is known (Table 2-4). Little is known about life-history traits, including age of first reproduction of non-harvested species (Table 2-5). Only a cursory view of lithodid predators and prey is currently available (Table 2-6). Lithodids are host to several parasites such as the liparid fish, *Careproctus spp.*, and the rhizocephalan *B. callosus*, as well as microsporidans and nemerteen brood parasites which may be a major mortality source (Table 2-7) of harvestable species (Table 2-8, Fig. 2-2).

The family Lithodidae is a large and diverse group of poorly understood animals. They possess complex life-history patterns and live in environments that tend to be inhospitable and inaccessible to biologists. Behaviors such as podding (Powell and Nickerson 1965a, Dew 1990), female preference, sperm limitation (Powell and Nickerson 1965b, Powell et al. 1973a, Sapelkin and Fedoseev 1986, Paul and Paul 1997, Paul and Paul 2001) and slow growth rates (Paul 1992, Lovrich 1997) are important keys for fisheries management tools, as well as biodiversity estimates. Many species with high morphological similarity are known only from holotypes or a single sex, thus named species may represent natural intra-specific variation or may be indicative of the taxonomic infancy of this family, suggesting that there is a serious underestimation of oceanic biological diversity (Miya and Nishida 1997, Etter et al. 1999). However, due to their abyssal life-styles, discerning valid species from those variants that are merely natural morphological extremes is often a difficult task. In this age of molecular systematics and increased taxonomic interest, future genetic analysis may aid in the basic goals of understanding species numbers, diversity, distributions, and evolutionary history and trajectories of lithodids.

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Table 2-1. Location and distribution summaries of the family Lithodidae (update of Dawson 1989).

species	authority	location (Pacific, Atlantic, Indian, Antarctic, Arctic Oceans)	depth (m)*
sub-family Lithodinae	Ortmann 1901		
Acantholithus hystrix	de Haan 1849	west Pacific: Japan, New Zealand (Dawson 1989): species uncertain, see Table 2-4 for details	shallow and deep water (Dawson 1989)
Cryptolithodes expansus	Miers 1879	northwest Pacific: Japan (Miers 1879), Minyako, Rikuzen Province, Aomori near Hanaguri Cape between Aomori and Gutago Cape and between Benten Island and Cape Kurosaki (Yokoya, Makarov 1962); Korean coast on rocky bottoms in the sublittoral region (Kim and Hong 2000)	50-60 (Kim and Hong 2000)
C. sitchensis	Brandt 1853	northeast Pacific: Sitka, Alaska (Makarov 1962) south to San Diego, California, U.S.A. (Bowman 1972)	intertidal to 37 (U.S.N.M. collection)
C. typicus	Brandt 1848	northeast Pacific: Monterey, California (Schmitt 1921); to Amchitka Island, Alaska, U.S.A. on rock-rubble bottom (Barr 1973)	low intertidal to 45 (Hart 1965)
Glyptolithodes cristatipes	(Faxon 1893)	east Pacific: (7° 9' N, 80° 50'W), Iquique, Chile (25° 11' S, 70° 31' W; Bahamonde 1967); south of Banco de Mancora, Peru (del Solar 1972), 03° 51' S, 81° 18' W, del Solar 1981; to Peurto Chicama, Mexico (07° 42' S, 80° 26'), mud or rocky bottoms (Haig 1974); northern range of south California (Chapter 2)	245-580 (Bahamonde 1967), 245-800 (Haig 1974)
Lithodes aequispinus	Benedict 1894	north Pacific: Bering Sea, Pribilof Islands (Benedict 1894); Sea of Okhotsk, Japan, east of Siwoya Cape (Makarov 1962); to south B.C., Canada, in the upper continental slope (Butler and Hart 1962); west Sagami Bay (Hiramoto and Sato 1970); off Shioya-zaki, off Matsushima, off Enoshima (Sakai 1976); and Suruga Bay, Japan (Suzuki and Sawada 1978)	315-730 (Makarov 1962), 77-366 (Butler and Hart 1962), 400-900 (Hiramoto and Sato 1970), 500-600 (Sakai 1976), up to 742 (U.S.N.M. collection)
L. couesi	Benedict 1894	north Pacific: Bering Sea, north of Unalaska near the Shumagin Islands, Alaska (Benedict 1894); to San Diego, California (Makarov 1962); N. W. far off Midway Island (32° 03.8' N, 172° 50.2' E); Kushiro, Shioya-zaki (Takeda 1974); Hokkaido and off Onahama, Japan (Sakai 1976)	542-1125 (Makarov 1962), 695-820 (Takeda 1974), 258-1829 (Hart 1982)
L. confundens	Macpherson 1988	southwest Atlantic: south of Falkland Islands (54° 02' S, 58° 40 W), to Strait of Magellan (Punta Arenas), muddy bottoms (Macpherson 1988c)	50 - 119 (Macpherson 1988c)

L. ferox	Filhol 1885	Atlantic: coasts of Mauritania and Namibia, continental slope off west coast of Africa (22° 03'N to 28° 16'S), and South American coast of Saint Helena, Brazil (36° 29.6'S to 53° 46.7 W), on muddy bottoms (Macpherson 1988c)	160 and 1013 (Macpherson 1988c), continental shelf 300-350 (Abello and Macpherson 1991)
L. longispina	Sakai 1971	west Pacific: off Matsushima, Miyagi Prefecture; off Kominato, Chiba Prefecture (Sakai 1971); off Midway Island (32° 02.9' N, 172° 45.3' E; Takeda 1974); off Sendai, Boso Peninsula and Sagami Bay, Japan (Hiramoto 1974); south Pacific, Guam (Dawson 1989)	600 (Sakai 1971), 400-900 (Hiramoto 1974)
L. maja	(Linnaeus 1758)	north Atlantic: Shetland Islands, Scotland; Faroes Islands, England; Belgium, Holland; Norway; Murman Sea (as far as Teriberka), northernmost locality 74° 25' N, 17° 36' E, Iceland, Greenland; coast of North America from Newfoundland to 40° N (Hansen 1908)	95- 532 (Hansen 1908), 40-500 (Makarov 1962), 65-790 (Williams 1984), 4- 200 (Macpherson 1988c)
L. mamillifer	Macpherson 1988	west Indian Ocean: Mozambique Channel between Madagascar and Africa (Kensley 1977; as *L. murrayi*); La Reunion, Madagascar (22° 18.9 S-43° 01.1 E), and off Natal (28° 00'S-32° 46'E), South Africa, in mud (Macpherson 1988a)	550-800 (Macpherson 1988a)
L. manningi	Macpherson 1988	central Atlantic: Dominica, French Guiana (Macpherson 1988c)	640-777 (Macpherson 1988c)
L. murrayi	Henderson 1888	southwest Pacific, southeast Atlantic, south Indian: south New Zealand (Yaldwyn and Dawson 1970); Fondos de fango, Islas Posesion, Prince Edwards, Macquarie and Crozet Islands of South Africa and off Namibia (18° 11' S and 28° 16' S), south of Chile (Macpherson 1983)	coast of Namibia 360-800, Fondos de fango 120 - 810 (Macpherson 1983), 75-700 (Takeda and Hatanaka 1984), Indian Ocean 80-1015 (Miquel et al. 1985), 35-200 (Macpherson 1988c)
L. nintokuae	Sakai 1978	northwest Pacific: north of Nintoku Seamount, Emperor Seamount Chain, Japan (Sakai 1978); northwest of Midway/ Hawaiian Islands Ridge (21° 23' N, 158° 14' W; 32° 03.8' N, 172° 50.2' E; Dawson and Yaldwyn 1985b)	450-1070 (Dawson and Yaldwyn 1985b)

L. panamensis	Faxon 1893	east Pacific: Colombia (07° 31' N, 79° 14' W; Faxon 1895); to Peru (03° 48' S, 81° 22' W; 07° 59' S, 80° 22' W; 17° 34' S, 71° 55' W), on hard bottoms (del Solar 1972, Haig 1974); Gulf of Panama (Wicksten 1989); northern range Baja California, U.S.A. (Dawson 1989)	680-850 (del Solar 1972)
L. richeri	Macpherson 1990	southwest Pacific: New Caledonia, southeast Australia (Macpherson 1990)	trapped outside coral reef- depth unrecorded (Macpherson 1990)
L. santolla	(Molina 1782)	southeast Pacific and southwest Atlantic: south of South America, Strait of Magellan, north (Takeda and Hatanaka 1984); to Talcahuano, Chile (36° 41'S; Hernandez 1985); east coast of South America, Tierra del Fuego to Uruguay (34° S Vinuesa et al. 1996)	intertidal to 700 (Boschi et al. 1984), concentrate between 10 to 50 (Macpherson 1988c)
L. turkayi	Macpherson 1988	southeast Pacific and southwest Atlantic: Falkland islands, U.K. and coast of Chile from Tierra del Fuego north to 31° 56'S, 71° 38'W (Campodonico and Guzman 1972 (as *L. murrayi*), Revuelta and Andrade 1978, Macpherson 1988c)	70 (Campodonico and Guzman 1972), to 581 Revuelta and Andrade 1978)
L. turritus	Ortmann 1892	northwest Pacific: Sagami Bay, off Boso Peninsula, Chiba Prefecture to Tosa Bay, Japan (Sakai 1971); Philippines on soft sandy-mud bottoms (Macpherson 1990); east China Sea, Taiwan (Wu et al. 1998)	200 (Sakai 1971), to 812 (Macpherson 1990)
L. unicornis	Macpherson 1984	southeast Atlantic: off southwest Africa, Valdivia Bank (24° 43.7'S, 06° 24.3'E), on muddy bottoms (Macpherson 1984)	934-936 (Macpherson 1984)
L. wiracocha	Haig 1974	southeast Pacific: 03° 48'S, 81° 22'W; 07° 59' S, 80° 22' W (del Solar 1972); SW Banco de Mancora Peru, mud bottom (Haig 1974)	620-800 (del Solar 1972, Haig 1974)
Lopholithodes diomedeae	(Faxon 1893)	east Pacific: 07° 31'30" N, 79° 14' W; 07° 21' N, 79° 35' W (Faxon 1895); hard mud bottoms, Gulf of Panama to Peru (03° 48' S, 81° 22' W; 10° 01'S, 79° 10'W; del Solar 1972, Hart 1974)	680-935 (Faxon 1893, 1895, del Solar 1972)
L. foraminatus	(Stimpson 1859)	northeast Pacific: San Diego, California to Banks Island, Hecate strait, B.C., Canada (53° 40'N, 130° 30'W); on muddy bottoms (Hart 1982); north to Aleutian Islands and Bering Sea (Dawson 1989, Wicksten 1989)	intertidal to 547 (Hart 1982, U.S.N.M. collection)
L. mandtii	Brandt 1848	northeast Pacific: Sitka, Alaska to Monterey California, U.S.A. (Makarov 1962); rocky habitats with strong currents, juveniles found under rocks during extremely low tides (Hart 1982, Jensen 1995)	intertidal to 137 (Hart 1982)
L. odawarai	Sakai 1980	northwest Pacific: Sagami Bay, Japan (Sakai 1980)	240-280 (Sakai 1980)

Neolithodes agassizii	(Smith 1882)	northwest Atlantic: east coast of North America between 34° 39'N, 75° 14'W (Smith 1882); and 07° 22'N, muddy bottoms (Macpherson 1988c); Gulf of Mexico and off Suriname and French Guyana (Dawson 1989)	650-1900 (Macpherson 1988c)
N. asperrimus	Barnard 1946	southeast Atlantic: off Saldanha Bay and Cape Point, south South Africa (Barnard 1946); area del Cabo, Namibian coast (18° 11' S to 28° 16' S; Macpherson 1983); 13° 46 S, 47° 33 E; 13° 48 S, 47° 29'E (Macpherson 1988a); Ivory coast, West Africa on muddy bottoms (Macpherson 1988c)	870 and 1007 (Barnard 1946), 530 and 615 (Macpherson 1983), 600-2000 (Macpherson 1988c)
N. brodiei	Dawson and Yaldwyn 1970	southwest Pacific: New Zealand and southeast Australia, Campbell plateau (50° 58'S, 173° 57'E; Dawson and Yaldwyn 1970)	832 (Dawson and Yaldwyn 1970)
N. capensis	Stebbing 1905	southeast Atlantic, Indian Ocean: south South Africa, off Cape Point (Kensley 1968); on muddy bottoms (Macpherson 1988c)	1570-2745 (Kensley 1968), 1480-3200 (Macpherson 1988c)
N. diomedeae	Benedict 1894	east Pacific: south Chile (42° 36'S and 45° 35'S; Benedict 1894); Scotia Sea, Antarctica, north to Mexico and southern California, U.S.A. (Dawson 1989); Gulf of Panama (Wicksten 1989)	1382-2454 (Haig 1974), 1100- 2000 (Baez et al. 1986)
N. grimaldii	(A. Milne Edwards and Bouvier 1894)	north Atlantic: Iceland, off east coast of Canada and U.S.A. (Hansen 1908); north of 35° 23' N, Greenland and western Ireland, south to Bay of Biscay, Canary Islands, and Cape Verde, Spain on muddy bottoms (Macpherson 1988c)	1065 (Hansen 1908), 1267-3000 (Macpherson 1988c), to 3207 (U.S.N.M. collection)
N. martii	Birstein and Vinogradov 1972	southwest Atlantic: near South America (53-54° S, 34-36° W; Birstein and Vinogradov 1972)	305-650 (Birstein and Vinogradov 1972)
N. nipponensis	Sakai 1971	northwest Pacific: Mikawa Bay and Kii Peninsula, Japan (Sakai 1971,1976)	200-600 (Sakai 1971, 1976)
N. sp. nov.	Dawson and Yaldwyn MS	Indian Ocean: Bay of Bengel and Madagascar (Dawson 1989)	deep water (Dawson 1989)
N. vinogradovi	Macpherson 1988	southwest Pacific and southeast Indian Ocean: 31° 50'43" S, 87° 22' 27 "E (Macpherson 1988c); New Caledonia, Coral Sea (Macpherson 1990)	1600 (Macpherson 1988c), to 2100 (Macpherson 1990)
Paralithodes brevipes	(A. Milne Edwards and Lucas 1841)	north Pacific: Sea of Japan, south to Cape Povorotnyi, Sea of Okhotsk, east Kamchatka, Russia; south Bering Sea, Aleutian Islands, U.S.A. (Makarov 1962)	intertidal to 66 (Makarov 1962, U.S.N.M. collection)

P. californiensis	(Benedict 1894)	northeast Pacific: Monterey Bay to San Diego, California (Schmitt 1921, Anderson and Cailliet 1974)	148-306 (Schmitt 1921), to 349 (U.S.N.M. collection)
P. camtschaticus	(Tilesius 1815)	north Pacific: Bristol Bay, Alaska, U.S.A. (Benedict 1894); Bering Sea to Sea of Japan (Marukawa 1930); Hokkaido, Japan; Cape Gamova, Sea of Okhotsk, eastern Kamchatka to Cape Olyutorsk, Russia; Aleutian Islands and Norton Sound, U.S.A. to Queen Charlotte Islands, B.C., Canada (Makarov 1962); Korea (Kim 1970); sand or mud bottoms (Jensen 1995) age 0-1 located on complex bottoms (Loher and Armstrong 2000)	3-366 small juveniles found intertidally among rocks and algae (Marukawa 1930, Jensen 1995)
P. platypus	(Brandt 1850)	north Pacific: Sea of Japan; south to Cape Gamova, Sea of Okhotsk, east Kamchatka, Russia; Bering Strait (Makarov 1962); Alaska; Tartary Bay, Vladivostok; Sakhalin, Kurile Island, Kitami, Japan; Korea (Sakai 1976)	12-500 (Makarov 1962)
P. rathbuni	(Benedict 1894)	northeast Pacific: San Simeon Bay, California, U.S.A. (Benedict 1894); to Baja California, Mexico (Wicksten 1987)	367-402 (Schmitt 1921), 201 (Wicksten 1987)
Paralomis aculeata	Henderson 1888	southeast Atlantic, Indian Ocean: Prince Edward (Takeda 1974); and Crozet Islands, south of South Africa (Dawson 1989)	560 (Takeda 1974)
P. africana	Macpherson 1982	southeast Atlantic: Fondos de fango, Namibian coast (20° 31' S to 24° 42' S), mud habitat (Macpherson 1982, 1983)	570- 770 (Macpherson 1988c)
P. anamerae	Macpherson 1988	southwest Atlantic: north of Falkland Island (Malvinas), off Argentina (Macpherson 1988c)	132-135 (Macpherson 1988c)
P. aspera	Faxon 1893	east Pacific: 07° 06' N, 80° 34'W (Faxon 1895); Panama to Peru (03° 48' S, 81° 20' W; del Solar 1972, Haig 1974)	560-1271 (Faxon 1893, 1895, del Solar 1972)
P. birsteini	Macpherson 1988	Antarctic Ocean: 67° 29'S, 79° 55'W (Macpherson 1988b)	500-1080 (Macpherson 1988b)
P. bouvieri	Hansen 1908	northeast Atlantic: between Greenland and Iceland (65° 24'N, 29° 00W; Hansen 1908); northeast U.S.A. and off SW Ireland (Macpherson 1988c); Canadian Atlantic (43° N, 59° W; Pohle 1992b)	1345-1454 (Hansen 1908), 1460- 4152 (Macpherson 1988c), 889-1500 (Pohle 1992b)
P. ceres	Macpherson 1989	Indian: Arabian Sea (22° 22'12"N, 59° 57'30"E; Macpherson 1989)	1189-1354 (Macpherson 1989)
P. cristata	Takeda and Ohta 1979	northwest Pacific: Suruga Bay off Osaki (Takeda and Ohta 1979); abyssal valley off Gamoda-misaki, Japan (Sakai 1987)	750 (Takeda and Ohta 1979), to 1100 (Sakai 1987)

P. chilensis	Andrade 1980	southeast Pacific: central Chile to Peru (31° 56'S to 29° 50' S; Andrade 1980)	400-420 (Andrade 1980)
P. cristulata	Macpherson 1988	southeast Atlantic: west Africa, off Guinea Bissau and Senegal, on muddy bottoms (Macpherson 1988c)	261-650 (Macpherson 1988c)
P. cubensis	Chace 1939	central west Atlantic, West Indies: east of Havana, Cuba (Chace 1939); east of Florida, Gulf of Mexico and northern Brazil (Macpherson 1988c)	439-550 (Chace 1939), 329-730 (Macpherson 1988c)
P. debodeorum	Feldmann 1998	southwest Pacific: middle to late Miocene fossils (10 mya), of Motunau Beach, North Canterbury, New Zealand (Feldmann 1998)	200-300 (Feldmann 1998)
P. dofleini	Balss 1911	northeast Pacific: off Sendai Bay off Kominato, Sagami Bay, Japan (Takeda 1974, Sakai 1976)	470-780 (Takeda 1974)
P. erinacea	Macpherson 1988	east Atlantic: west Africa, off Guinea Bissau and Ivory Coast on muddy bottoms (Macpherson 1988c)	251-900 (Macpherson 1988c)
P. formosa	Henderson 1888	southwest Atlantic: off Rio Plata (Takeda 1974); off Argentina and Uruguay, South Georgia and South Orkney Islands (Macpherson 1988c)	400-1599 (Macpherson 1988c)
P. granulosa	(Jacquinot 1852)	southwest Atlantic and southeast Pacific: southern South America from Rio de Janeiro, Brazil through Falkland Islands, U.K. and Magellanic district, Argentina to the vicinity of Chiloe island, Chile (Takeda and Hatanaka 1984); juveniles found in kelp beds (Hoggarth 1993)	intertidal to 100 (Takeda and Hatanaka 1984)
P. grossmani	Macpherson 1988	central west Atlantic: coast of French Guiana (Macpherson 1988c)	770 (Macpherson 1988c)
P. haigae	Eldredge 1976	central west Pacific: Adelup point, Guam (Eldredge 1976); New Caledonia, Samoa Islands (Macpherson 1990)	400-730 (Eldredge 1976)
P. heterotuberculata	Yumao et al. 1984	northwest Pacific: east China Sea (30° 26' N, 128° 53' E; Yumao et al. 1984)	860-890 (Yumao et al. 1984)
P. hystrixoides	Sakai 1980	northwest Pacific: Sagami Bay off Daiozaki, Mie Prefecture (Sakai 1980); Abyssal valley off Gamoda-misaki, Tokushima, Japan (Sakai 1987)	750-1100 (Sakai 1987)
P. hystrix	de Haan 1846	northwest Pacific: Tokyo to Tosa Bay (Takeda 1974); Boso Peninsula, Chiba Prefecture, south to Nagasaki, Japan (Sakai 1976)	300-600 (Takeda 1974), 230-300 (Sakai 1980)
P. inca	Haig 1974	southeast Pacific: Peru (06° 31' S, 81° 01' W); mud and sand (Haig 1974)	620-800 (Haig 1974)
P. indica	Alcock and Anderson 1899	Indian: Travancore coast, India (Alcock and Anderson 1899)	786 (Alcock and Anderson 1899)

P. investigatoris	Alcock and Anderson 1899	Indian: Travancore coast, India (Alcock and Anderson 1899)	786 (Alcock and Anderson 1899)
P. japonica	Balss 1911	northwest Pacific: Sagami Bay, Japan (Balss 1911, Sakai 1971)	shallow water (Dawson 1989)
P. jamsteci	Takeda and Hashimoto 1990	northwest Pacific: Minami-Ensei Knoll (28° 23'N, 127° 38'E), in the mid-Okinawa trough, Japan (Takeda and Hashimoto 1990)	710 (Takeda and Hashimoto 1990)
P. kyushupalauensis	Takeda 1985	northwest Pacific: northern part of the Kyushu-Palau submarine ridge, Japan (26° 47'N, 135° 20' E to 26° 48' N, 135° 21' E; Takeda 1985)	340 - 460 (Takeda 1985)
P. longidactyla	Birstein and Vinogradov 1972	southwest Atlantic: near mouth of River Plate (35° 34'S, 52° 40' W), Uruguay (Birstein and Vinogradov 1972)	485-500 (Macpherson 1988c)
P. longipes	Faxon 1893	east Pacific: 05° 26' N, 86° 55' W (Faxon 1895); Peru (07° 59' S, 80° 22' W; 16° 29' S, 73° 33' W; del Solar 1972); off San Diego, California, U.S.A., hard bottom (Haig 1974)	760-1409 (Faxon 1893, 1895, del Solar 1972)
P. manningi	Austin et al. 2000	northeast Pacific: San Clemete Basin, southern California (Austin et al. 2000)	1922 (Austin et al. 2000)
P. medipacifica	Takeda 1974	northwest Pacific: off Midway, Japan (Takeda 1974)	695-820 (Takeda 1974)
P. microps	Filhol 1884	northeast Atlantic: Bay of Biscay, France and Spain (45° 59'N, 06° 29'W), coral bottom (Macpherson 1988c)	1480 (Macpherson 1988c)
P. multispina	(Benedict 1894)	north Pacific: Queen Charlotte Islands, B.C., Canada (Benedict 1894); Shumagin Islands, Alaska to San Diego, California, U.S.A.; west Bering Sea, Kamchatka, Russia (Makarov 1962); off Hokkaido, Miyagi Prefecture, Chiba Prefecture, off Manazuru and Enoshima, Sagami Bay, Japan (Sakai 1971)	1603 (Benedict 1894), 1143-1603 (Rathbun 1904), 1125-1577 (Makarov 1962), 600-830 (Sakai 1971), 830-1665 (Hart 1982)
P. ochthodes	Macpherson 1988	Indo-Pacific: Sulawesi (Celebes), Islands, Indonesia (04° 43 'S, 121° 23 'E; Macpherson 1988b)	1281 (Macpherson 1988b)
P. otsuae	Wilson 1990	southeast Pacific: off Mejillones del Sol, Chile (22° 55'S, 70° 46'W; Wilson 1990)	1740 (Wilson 1990)
P. pacifica	Sakai 1978	northwest Pacific: north of Nintoku Seamount, Japan (42° 20'N:170° 50'E; Sakai 1978)	800 (Sakai 1978)

P. papillata	(Benedict 1894)	east Pacific: southern California (Benedict 1894); to Peru (06° 31' S, 81° 01' W), in mud and sand (Haig 1974)	712-744 (Haig 1974)
P. pectinata	Macpherson 1988	west central Atlantic: Caribbean Sea, off Isla Margarita, Venezuela (Macpherson 1988c)	1409-1629 (McPherson 1988c)
P. phrixa	Macpherson 1992	southeast Pacific: coast of Peru (04° 10'S, 81° 27' W; Macpherson 1992)	1815-1860 (Macpherson 1992)
P. roeleveldae	Kensley 1981	southwest Indian Ocean: east coast of South Africa (30° 32'S, 30° 52 E'; Kensley 1981)	625-900 (Kensley 1981)
P. seagranti	Eldredge 1976	southwest Pacific: Double Reef area and Tanguisson Point, northwest coast of Guam (Eldredge 1976)	250-620 (Eldredge 1976) 750 (Macpherson 1990)
P. serrata	Macpherson 1988	west central Atlantic: Caribbean sea off Colombia (Macpherson 1988c)	1100 (Macpherson 1988c)
P. shinkaimaruae	Takeda 1984	southwest Atlantic: Bromley Plateau (31° 13'S, 34° 49'W; Takeda and Hatanaka 1984)	668 (Takeda and Hatanaka 1984)
P. sp. nov.	cf. Macpherson 1990, fide Webber and Dawson MS	southwest Pacific: Louisville Ridge, east of the North Island, New Zealand (Webber pers. comm.)	731- 1097 (Webber pers. comm.)
P. sp. nov.	Macpherson 1990	southwest Pacific: New Caledonia (Macpherson 1990)	depth unrecorded (Macpherson 1990)
P. spectabilis	Hansen 1908	northwest Atlantic and sub-Antarctic: Scott Island in Ross Sea, near Iceland and Greenland (64° 44'N, 32° 32'W; Hansen 1908)	1345-1786 (Hansen 1908), 1470-2075 (Macpherson 1988c)
P. spinosissima	Birstein and Vinogradov 1972	southwest Atlantic, Antarctic Ocean: South Georgia Island (53-54° S, 34-36° W; Birstein and Vinogradov 1972); between Burwood Bank and Falkland Islands (Macpherson 1988c)	215-650 (Birstein and Vinogradov 1972), 132-650 (Macpherson 1988c)
P. stella	Macpherson 1988	west Indian Ocean: Madagascar and La Reunion (19° 41 'S: 54° 08 'E; Macpherson 1988a)	350-750 (Macpherson 1988a)
P. truncatispinosa	Takeda and Miyake 1980	northwest Pacific: continental slope of East China Sea, stone and sandy mud (Takeda and Miyake 1980)	642-840 (Takeda and Miyake 1980)
P. tuberipes	Macpherson 1988	southeast Pacific: off Huichas Islands, Puerto Aguirre, Chile (45° 10'S, 73° 33'W; Macpherson 1988b)	depth unrecorded (Macpherson 1988b)

P. verrilli	(Benedict 1894)	north Pacific: Bering Sea, Pribilof Islands (Benedict 1894); south to Cortez Bank, California, U.S.A. (Makarov 1962); coast of Nemuro Hokkaido (Sakai 1976); Kumano-nada, off Daiozaki, Mie prefecture, Abyssal valley off Gamoda-misaki, Japan (Sakai 1987)	1238-1480 (Makarov 1962), 1238-2379 (Hart 1982), 850-1250 (Sakai 1987)
P. zealandica	Dawson and Yaldwyn 1971	southwest Pacific: Chatham Rise, New Zealand (44° 18'S, 174° 31'E), fine sandy mud (Dawson and Yaldwyn 1971)	640 (Dawson and Yaldwyn 1971)
Phyllolithodes papillosus	Brandt 1848	northeast Pacific: Unalaska, Alaska to Monterey, California, U.S.A. (Makarov 1962); rocky areas with currents (Jensen 1995)	sub-tidal to 183 (Hart 1982), some juveniles low intertidal (Jensen 1995)
Rhinolithodes wosnessenskii	Brandt 1848	northeast Pacific: Kodiak Island, Alaska to Crescent City, California, generally on rocky bottoms and on shells (Makarov 1962)	6-73 (Hart 1982), up to 102 (Chapter 2)
Sculptolithodes derjugini	Makarov 1934	northwest Pacific: Sea of Japan, near Silant'ev Bay and in the area of Nel'ma Bay, Andreev Bay (Ussuri Bay), and Rishiri Island, rocky bottoms (Makarov 1934, 1962); Hokkaido, Japan (Sakai 1976)	20-35 (Makarov 1962)
sub-family Hapalogastrinae	Ortmann 1901		
Acantholithodes hispidus	(Stimpson 1860)	northeast Pacific: off Moorovskoy Bay, Alaska to Monterey, California (Hart 1982)	intertidal to 245 (Benedict in litt. U.S.N.M. collection)
Dermaturus mandtii	Brandt 1850	north Pacific: Bering Sea to the Pribilof Islands, Alaska, U.S.A. along the Asiatic coasts north to Cape Olyutorsk, eastern shores of Kamchatka; Sea of Okhotsk, north Sea of Japan in rocky areas (Makarov 1962); among kelp holdfasts and shell rubble in cavities (Jensen 1995)	low intertidal to 72 (Makarov 1962)
Hapalogaster cavicauda	Stimpson 1859	northeast Pacific: Washington, California, U.S.A., and Mexico (Dawson 1989); clings tightly to the undersides of rocks (Jensen 1995)	intertidal to 15 (Dawson 1989)
H. dentata	(de Haan 1849)	northwest Pacific: south Japan, north to Aomori and Hakodate, Japan, Sea of Japan, north to Peter the Great Bay, Russia (Makarov 1962); Korean coasts (Kim 1970); intertidal and subtidal cobble rocky shores, in groups clinging to or hiding under cobbles (Goshima et al. 1995)	intertidal to 180 (Makarov 1962)

H. grebnitzkii	Schalfeew 1892	north Pacific: eastern shores of Kamchatka, Sea of Okhotsk, Russian shores of Sea of Japan, to Sibiryakov Island; Bering Sea, north to Bering Strait, west coast of North America from Aleutians, Alaska south to Humboldt Bay, California, U.S.A., on rocky bottoms (Makarov 1962)	intertidal to 90 (Makarov 1962)
H. mertensii	Brandt 1850	northeast Pacific: Atka, Alaska to Puget Sound, Washington, U.S.A. (Makarov 1962); found between algae-covered rocks (Jensen 1995)	low intertidal to 55 (Hart 1982)
Oedignathus inermis	(Stimpson 1860)	north Pacific: Japan, from the Tsushima Strait to Aomori (Tsugaru Strait); Patrocles Bay, Peter the Great Bay, Russia, west to Unalaska, Alaska south to Pacific Grove, California, U.S.A. (Makarov 1962); Korea (Kim 1970)	middle intertidal to 15 (Hart 1982)
Placetron wosnessenskii	Schalfeew 1892	northeast Pacific: Aleutian Islands, Alaska (Makarov 1962); south to Puget Sound, Washington, U.S.A. amongst anemones (*Metridium*; Hart 1982); on vertical rock faces and among boulders (Jensen 1995)	intertidal to 110 (Hart 1982)
P. forcipatus	(Benedict 1894)	northeast Pacific: Parry Passage, Graham Island, B.C. Canada (Benedict 1894): species uncertain, see Table 2-4 for details	shallow water (Dawson 1989)

* U.S.N.M. = Information was obtained from the United States Natural Museum of Natural History collections.

Table 2-2. A summary of global distribution of lithodid taxa.

Ocean	north / south / central	east / west	number of species*	% of species *
Pacific			71 (62 / 9) **	68 (65 / 100)**
	north		51 (42 / 9)	49 (44 / 100)
		east	33 (25 / 8)	31 (26 / 89)
		west	28 (24 / 4)	27 (25 / 45)
	south		25	24
		east	16	15
		west	12	11
	central		1	1
Atlantic			29	28
	north		7	7
		east	4	4
		west	3	3
	south		17	16
		east	8	8
		west	11	10
	central		7	7
Indian			11	11
Antarctic			3	3

* As species may reside in multiple areas the numbers do not total 105 species and the % does not total 100%. Localities are obtained from Table 1.

** Percentage of members of the family Lithodidae (sub-family Lithodinae / sub-family Hapalogastrinae) that inhabit each of the specified oceans.

** The subfamily Hapalogastrinae resides only in the north Pacific Ocean.

Table 2-3. A list of taxonomic keys to members of the family Lithodidae.

taxon	larvae or adult	comments	reference
Decapoda	L	keys to the families of decapod crustacean larvae	Hart 1971
Anomura	L	identification manual for larvae of commercially important crabs in Japan	Konishi and Shikatani 1998, 1999
Anomura	L	key for identification of Anomura and Brachyura zoea in the Beagle Channel, Argentina and Chile	Lovrich 1999
Paguridae and Lithodidae	L	morphological keys for zoea and glaucothoe and chromatophore key for zoea (*L. maja* only lithodid)	MacDonald et al. 1957
Lithodidae	A	keys to sub-families and genera of lithodids as well as species level keys of *Lithodes*, *Cryptolithodes* and *Paralomis*	Makarov 1962
Lithodidae	A	keys to lithodid species of B.C., Canada	Hart 1982
Lithodidae	A	keys to subfamilies, genera and species (*Lithodes*, *Neolithodes* and *Paralomis*) of Atlantic lithodids	Macpherson 1988c
Lithodidae	A	keys to the species of lithodids found in the Pacific northwest of America	Kozlov 1996
Lithodidae	L	key to species of lithodid zoea of north Pacific Ocean; characters used to distinguish lithodid and pagurid zoea and between stages I-IV of lithodid zoea	Haynes 1984
Lithodinae	L	two tables, one comparing larval characters of subfamily Lithodinae and one comparing zoea of *Paralomis granulosa*, *P. japonicus* and *P. hystrix*	Konishi and Taishaku 1994
Lithodidae	A	key to some lithodid species (*Lithodes*, *Neolithodes*, *Paralomis*, *Paralithodes*)	Sandberg and McLaughlin 1998

Hapalogaster	A	key to genus *Hapalogaster*	Schalfeew 1892
Lithodes and *Paralithodes*	L	distinguishing between larvae *L. aequispinus* from *L. maja, L. santolla* and *Paralithodes* larvae	Haynes 1982
Lithodes	A	features used for lithodid identification; key to lithodid genera; key to twelve *Lithodes* species and based on rostral and carapace characters they are divided into four groups: *aequispinus*, *antarcticus*, *maja* and *tropicalis*	Dawson and Yaldwyn 1985a
Paralithodes	A	differentiates between *P. camtschaticus*, *P. platypus* and *P. brevipes*	Abe 1992
Paralithodes	L	differentiates between *P. camtschaticus* and *P. platypus* zoea	Jensen et al. 1992
Paralomis and *Lithodes*	L	differentiates between *P. granulosa* and *L. santolla* larvae	Campodonico and Guzman 1981
Paralomis	A	key to Japanese *Paralomis*	Sakai 1971, 1976
Paralomis	A	key to eastern Pacific species of *Paralomis*	Macpherson 1992
Paralomis	A	modifications to key to species of *Paralomis* from Macpherson (1988c) to distinguish *P. manningi* from its congeners	Austin et al. 2000

Table 2-4. Photos, distributions, maximum sizes and general information concerning lithodids.

species and vernacular names*	locations of photos or drawings	distribution map **	previous generic names and comments	maximum size (mm) male/female ***	closely related species
sub-family Lithodinae					
Acantholithus hystrix			considered *Paralomis hystrix* (Sakai 1976)		
Cryptolithodes expansus Menko-gani	photo (Miyake 1982)			male: CL=42, CW=75 (Miyake 1982), female: CL=25.84, R=5.88, CW=35.82 (Zaklan pers. obs.)	other species of *Cryptolithodes*
C. sitchensis sitka crab, turtle crab, umbrella crab	drawings (Makarov 1962, Hart 1982, Macpherson 1988c), photos (Schmitt 1921, Barr 1973, Jensen 1995)			male: CL=65, CW= 90, female: CL=68, CW=87 (Hart 1982)	other species of *Cryptolithodes*
C. typicus butterfly crab, turtle crab	drawing (Makarov 1962, Hart 1982), photo (Schmitt 1921, Barr 1973, Jensen 1995)			male: CL=41, CW= 75, female: CL=49, CW=80 (Hart 1982)	other species of *Cryptolithodes*
Glyptolithodes cristatipes	drawing (Bahamonde 1967), dorsal, lateral and abdominal drawings (Haig 1974, Macpherson 1988c), photo (del Solar 1981)			male: CL =79.5, R= 6 , CW=98, female: CL=89.5 (Haig 1974)	*Paralomis cristata* (Takeda and Ohta 1979)
Lithodes		Sakai 1971, 1976 Macpherson 1988c	includes *Pseudolithodes* of Birstein and Vinogradov 1972 (Dawson 1989)		

L. aequispinus Ibaragani-modoki, golden king crab	drawing (Makarov 1962, Hart 1982), photo (Sakai 1971, 1976, Miyake 1982)	Sakai 1971, 1976		male: CW=220, female: CW=192 (Hiramoto and Sato 1970)	
L. confundens	drawings (Macpherson 1988c)	Macpherson 1988c	Latin "*confundo*" as it is similar to *L. santollo* thus confusion would arise (Macpherson 1988c)	male: CL= 100 CW= 85, female: CL=105 (Lovrich and Vinuesa 1999)	*L. santolla* (Macpherson 1988c)
L. couesi Kita-ibaragani, deep-sea or scarlet king crab	drawing (Makarov 1962, Hart 1982), photo (Schmitt 1921, Takeda 1974, Sakai 1971, 1976, Somerton 1981)	Sakai 1971, 1976		male: CL = 105, CW=103, female: CL= 115, CW= 113 (Takeda 1974)	
L. ferox	photo and drawings (Macpherson 1988c)	Macpherson 1988c	*Lithodes tropicalis* of A. Milne-Edwards 1883 (Macpherson 1988c)		
L. longispina Hari-ibaragani	drawing (Sakai 1971), photos (Takeda 1974, Sakai 1971, 1976, 1987, Hiramoto 1974, Macpherson 1990), drawing (Sakai 1987)	Sakai 1971, 1976, Hiramoto 1974		male: CL=145, R=62, CW=140 (Sakai 1987), female: CW=125 (Hiramoto 1974)	*Lithodes turritus* and *L. aequispinus* (Hiramoto 1974)
L. maja northern stone crab, prickly crab	drawing (Makarov 1962, Sandberg and McLaughlin 1998), drawings and photos (Macpherson 1988c)	Macpherson 1988c, Sandberg and McLaughlin 1998	a female with reversed abdominal asymmetry (Zaklan 2000)	male: CL=110, CW=113, female: CL=97, CW=95 (Macpherson 1988c)	
L. mamillifer	photo (Macpherson 1988a)		Latin "*mamilla*" referring to the carapace's rounded protrusion (Macpherson 1988a)	male: CL=37, CW=40, female: CL=145, CW=158 (Macpherson 1988a)	

L. manningi	photos and drawings (Macpherson 1988c)	Macpherson 1988c	named after Dr. R.B. Manning (Macpherson 1988c)	male: CL=94, CW=103, female:CL=106, CW=120 (Macpherson 1988c)	
L. murrayi	drawings (Perez 1934, Macpherson 1988c) photos (Campodonico and Guzman 1972, Macpherson 1988 b,c)	Campodonico and Guzman 1972, Macpherson 1988c		male: CL=132.5, 1500 g, female: CL= 93.5, 360 g (Miquel et al. 1985)	*L. turkayi*, *L. unicornis* and *L. ferox* (Macpherson 1988c)
L. nintokuae	photo and drawings (Sakai 1978), drawings (Dawson and Yaldwyn 1985b)	Dawson and Yaldwyn 1985b	a female with reversed abdominal asymmetry (Dawson and Yaldwyn 1985b)	male: CL=116, CW=123, R= 19 (Sakai 1978), female: CL=115 (Dawson and Yaldwyn 1985b)	
L. panamensis	photo (del Solar 1981)		male CL=970 between tips of extended pereopods (del Solar 1972)	male: CL =190 (del Solar 1972), female: CL=100, CW=108 (Haig 1974)	*L. murrayi* (Faxon 1893)
L. richeri	photo (Macpherson 1990)		only males found, dedicated to Dr. Bertrand Richer of Forges of Orstom (Macpherson 1990)	male: CL=102, CW=102 (Macpherson 1990)	*L. longispina* (Macpherson 1990)
L. santolla centolla	photo and drawings (Macpherson 1988c)	Macpherson 1988c	*L. antarcticus* of Jacquinot 1852 *Pseudolithodes zenkevitschi* of Birstein and Vinogradov 1972 (Dawson 1989)	male: CL=198, CW=250 (Boschi et al. 1984), female: CL=142, CW=140 (Macpherson 1988c),up to 8 kg (Vinuesa et al. 1996)	*Lithodes confundens* (Macpherson 1988c)

L. turkayi	photo and drawings (Macpherson 1988c)	Macpherson 1988c	named after Dr. M. Turkay of Senckenberg Museum in Frankfurt, Germany (Macpherson 1988c)	male: CL=109, CW= 110, female: CL=66, CW=65 (Campodonico and Guzman 1972)	*L. murrayi* (Campodonico and Guzman 1972)
L. turritus Ibaragani	photo (Sakai 1971, 1976, Wu et al. 1998), drawings (Sakai 1976)	Sakai 1976		male: CL=149.0, CW=155, female: CL=133.5, CW=132.1 (Wu et al. 1998)	*L. longispina* (Wu et al. 1998)
L. unicornis	photos (Macpherson 1984), drawings (Macpherson 1988c)	Macpherson 1988c		male: CL=129, CW=124, female: CL=118, CW=119 (Macpherson 1984)	*L. murrayi* (Macpherson 1988c)
L. wiracocha	drawings (Haig 1974)		females only and found on trawler "Wiracocha" (= creator God in Inca myth, Haig 1974)	female: CL =103.5, R =16, CW=97 (Haig 1974)	*L. murrayi* and *L. tropicalis* (Haig 1974)
Lopholithodes diomedeae	photo (del Solar 1981)		in *Paralomis*, fide Macpherson 1988c	male: CL =101, R= 9, CW=128 (Haig 1974)	
L. foraminatus box crab	drawings (Hart 1982, Macpherson 1988c), photo (Schmitt 1921, Jensen 1995)			male: CL=185, CW=165, female: CL=175, CW= 145 (Hart 1982)	
L. mandtii box crab, noduled crab	drawing (Makarov 1962, Hart 1982), photo (Schmitt 1921, Jensen 1995)		=*Echinocerus* White (Dawson 1989)	male: CL=200, CW=270 (Hart 1982), CW ≥ 300 (Jensen 1995)	

L. odawarai			named after Dr. T. Odawara, the director of the Odawara Carcinological Museum, Tokyo (Sakai 1980) in *Paralomis*, fide Macpherson 1988c	male: CL=41, CW=47 (Sakai 1980)	
Neolithodes		Macpherson 1988c			
Neolithodes agassizii	drawings (Smith 1882, Macpherson 1988c)	Macpherson 1988c	*Lithodes agassizii* (Smith 1882)	male: CL=167, CW=162, female: CL=154, CW=143 (Macpherson 1988c)	
N. alcocki			=*L. agassizii* of "Investigator" authors and *(?) N.* aff. *Asperrimus* Barnard of Macpherson 1988 (Dawson 1989)		
N. asperrimus	photo (Macpherson 1983, Macpherson 1988a), drawings and photos (Macpherson 1988c)	Macpherson 1988c		male: CL=195, CW=189, female: CL=180, CW=156 (Macpherson 1988c)	*N. agassizii* (Macpherson 1988c)
N. brodiei			named after J.W. Brodie, Director of the New Zealand Oceanographic Institute (Dawson and Yaldwyn 1970)	CL =130, R=18, CW=104 (Dawson and Yaldwyn 1970)	*N. agassizii*, *N. asperrimus* (Dawson and Yaldwyn 1970)

N. capensis	photo and drawings (Macpherson 1988c)	Macpherson 1988c		male: CL= 131, CW=130, female: CL=86, CW= 86 (Macpherson 1988c)	*N. vinogradovi* and *N. grimaldii* (Macpherson 1988c)
N. diomedeae centolla patache (Baez et al. 1986)	drawings (Baez et al. 1986, Macpherson 1988c)	Macpherson 1988c	*Neolithodes martii* Birstein and Vinogradov 1972 (Macpherson 1988c)	male: CL= 197, CW=166, female: CL=41.5, CW=35.0 (Baez et al. 1986)	
N. grimaldii Atlantic porcupine stone crab (Pohle 1992)	photo and drawings (Macpherson 1988c), drawing (Sandberg and McLaughlin 1998)	Macpherson 1988c, Sandberg and McLaughlin 1998	*Lithodes goodei* Benedict 1894 *Lithodes agassizii* Smith 1882 (Dawson 1989)	male: CL=152, CW=145, female: CL=153, CW=138 (Macpherson 1988c)	
N. nipponensis nihon-ibaragani	drawings (Sakai 1971, 1976), photo (Miyake 1982)			male: CL=168, CW=142 (Sakai 1976)	*N. agassizii*, *N. capensis*, *N. asperrimus* (Sakai 1976)
N. vinogradovi	photos (Macpherson 1988c, 1990)		named after Dr. L.G. Vinogradov (Macpherson 1988c)	male: CL=109, CW=113 (Macpherson 1988c), female: CL= 91, CW=105 (Macpherson 1990)	*N. grimaldii* (Macpherson 1988c)
Paralithodes		Sakai 1976			
P. brevipes Hanasaki-gani hanasaki crab (Abe 1992)	drawing (Makarov 1962, Sakai 1971, 1976), photo (Miyake 1982)	Sakai 1971, 1976, Abe 1992		male: CL= 95, CW= 102 (Sakai 1976), female: CL= 118 (Sato & Abe 1941)	
P. californiensis	photo (Schmitt 1921)				

P. camtschaticus Tarabagani, Alaskan, Russian, Japanese or red king crab	drawing (Makarov 1962, Sakai 1971, 1976, Hart 1982, Sandberg and McLaughlin 1998), photo (Miyake 1982, Bliss 1983, Stevens and Munk 1991, Jensen 1995), drawing (Macpherson 1988c)	Sakai 1976, Otto et al. 1980, Abe 1992, Sandberg and McLaughlin 1998	up to 11 kg body (Hart 1982), up to 21 years (Matsuura and Takeshita 1985), = *P. rostrofalcatus* of MacKay 1932 and *L. spinosissimus* of Brandt 1848 (Dawson 1989), gynandromorphistic individual (Stevens and Munk 1991)	male: CL=227, CW=283, female: CL=195, CW= 213 (Powell and Nickerson 1965b)	can hybridize with *P. platypus* (Nizyayev 1991)
P. platypus Aburagani, blue king crab	drawing (Makarov 1962, Sakai 1971, 1976, Sandberg and McLaughlin 1998), photo (Miyake 1982)	Sakai 1976, Otto et al. 1980, Abe 1992	up to 17 years (Jensen and Armstrong 1989)	CL=159, CW=170 (Sakai 1976)	can hybridize with *P. camtschaticus* (Nizyayev 1991)
P. rathubuni	photo (Schmitt 1921)				
Paralomis		Takeda 1974, Sakai 1971, Macpherson 1988c	synonomous with *Leptolithodes* and *Pristopus* in Benedict 1894 and (?) *Acantholithus* Stimpson 1858 (Dawson 1989)		
P. africana	photo and drawings (Macpherson 1982), drawings (Macpherson 1983, Macpherson 1988c)	Macpherson 1988c		male: CL=79, female: CL=68 (Macpherson 1988c)	*P. indica* (Macpherson 1982), *P. cristulata, P. anamerae* (Macpherson 1988c)

P. anamerae	photos and drawings (Macpherson 1988c)	Macpherson 1988c	named after the Asociacion Nacional de Armadores de Buques Congeladores de Pesca de Merluza (=ANAMER, Hake fishery freezer Trawlers owners National association; Macpherson 1988c)	male: CL=97, CW=102, female: CL=68, CW=68 (Macpherson 1988c)	*P. africana* (Macpherson 1988c)
P. aspera	photo (del Solar 1981)			CL=75, CW=75 (Hart 1974)	
P. birsteini	photo and drawings (Birstein and Vinogradov 1967, Macpherson 1988b)	Birstein and Vinogradov 1967	=*P. spectabilis* of Birstein and Vinogradov 1967, not of Hansen 1908 (Dawson 1989); named after Dr. Y.A. Birstein from State University of Moscow (Macpherson 1988b)	male: CL = 78, CW = 74, female: CL=55, CW=53 (Macpherson 1988b)	*P. spectabilis* (Macpherson 1988b)
P. bouvieri	drawings (Hansen 1908, Macpherson 1988c, Sandberg and McLaughlin 1998), photos (Pohle 1992)	Macpherson 1988c, Sandberg and McLaughlin 1998		male: CL=23, CW=21, female: CL=34.8, CW=34 (Hansen 1908)	
P. ceres				male: CL=52, CW=57 (Macpherson 1989)	*P. investigatoris* (Macpherson 1989)

P. cristata Hiraashi-ezoibaragani (Takeda and Ohta 1979)	photos (Takeda and Ohta 1979)			male: CL=89, R=11, CW = 96 (Takeda and Ohta 1979), CL=108 (Sakai 1987)	*Glyptolithodes* (Takeda and Ohta 1979)
P. chilensis	drawings (Andrade 1980)			male: CL=47.2, CW=47.6, female: CL=55.4, CW=56.4 (Andrade 1980)	*P. aspera* (Andrade 1980)
P. cristulata	drawings (Macpherson 1988c)	Macpherson 1988c	Latin "*cristula*" small crest, referring to crests on walking legs and lateral carapace edges (Macpherson 1988c)	female: CL=55, CW=57 (Macpherson 1988c)	
P. cubensis	photos and drawings (Macpherson 1988c)	Macpherson 1988c		female: CL= 61.2, CW=53.0 (Chace 1939)	*P. investigatoris* (Chace 1939)
P. debodeorum	photo and drawing (Feldmann 1998)		fossil only, named after John and Anne Debode (Feldmann 1998)	CL=63.6, CW=53.2 (Feldmann 1998)	*P. zealandica* (Feldmann 1998)
P. dofleini Tsubu-ezoibaragani	drawing (Balss 1911), photo (Sakai 1971, 1976)	Sakai 1971, 1976		CL=94, CW=99 (Sakai 1976)	
P. erinacea	photo and drawings (Macpherson 1988c)	Macpherson 1988c	Latin "*ericius*" urchin or hedgehog, due to the spiny carapace, only female specimens found (Macpherson 1988c)	female: CL=78, CW=76 (Macpherson 1988c)	

P. formosa	photo (Macpherson 1988c)	Macpherson 1988c		male: CL=95, CW=96, female: CL=89, CW=87 (Macpherson 1988c)	*P. spectabilis* (Macpherson 1988c)
P. granulosa false king crab, centollon	photo (Campodonico 1978, Ingle and Garrod 1987), photos and drawings (Macpherson 1988c)	Macpherson 1988c	only species of this genus that inhabits shallow coastal waters (Macpherson 1988c)	CW= 95 (Takeda and Hatanaka 1984), CL=120 1.5 kg max (Vinuesa et al. 1996)	*P. dofleini* (Macpherson 1988c)
P. grossmani		Macpherson 1988c	only females known, named after G.D. Grossman (Macpherson 1988c)	female: CL=94, CW=106 (Macpherson 1988c)	*P. longidactyla* and *P. papillata* (Macpherson 1988c)
P. haigae	photo (Eldredge 1976, Macpherson 1990)			male: CL=95, CW= 95, female: CL=97, CW=93.5 (Eldredge 1976)	*P. dofleini*, *P. aspera* and *P. papillata* and *P. inca* (Eldredge 1976)
P. heterotuberculata				CL=50, CW=55 (Yumao et al. 1984)	*P. hystrix* (Yumao et al. 1984)
P. hystrixoides	photo (Sakai 1987)			male: CL=81, CW= 78 (Sakai 1980), CL=70-95 (Sakai 1987)	*P. hystrix* (Sakai 1980)
P. hystrix Igagurigani	photo (Sakai 1971, 1976, Miyake 1982)	Sakai 1976		CL=106, R=20, CW=114 (Sakai 1976)	*P. multispina* (Sakai 1976)
P. inca	photos (Haig 1974, del Solar 1981)			male: CL=80, R=10.5, CW=93, female: CL=108, R= 13, CW=123 (Haig 1974)	
P. indica				CL=39.5, CW= 37 (Alcock and Anderson 1899)	*P. verrucosa* (Alcock and Anderson 1899)
P. investigatoris				CL= 33, CW=29.5 (Alcock and Anderson 1899)	*P. aspera* (Alcock and Anderson 1899)

P. japonica Kofuki-ezoibaragani	drawings (Balss 1911, Sakai 1971, 1976), photo (Miyake 1982)	Sakai 1971, 1976		Cl=39, CW=36 (Sakai 1971)	
P. jamsteci Ensei-ezo-ibaragani (Takeda and Hashimoto 1990)	photos (Takeda and Hashimoto 1990)		named after Japan Marine Science technology center (JAMSTEC; Takeda and Hashimoto 1990)	male: CL=64.7, CW= 67.8, female: CL=70.5, CW=68.8 (Takeda and Hashimoto 1990)	*P. africana* (Takeda and Hashimoto 1990)
P. kyushupalauensis	photo (Takeda 1985)		named after the Kyushu-Palau submarine ridge (Takeda 1985)	CL = 66.2, CW=61.9 (Takeda 1985)	
P. longidactyla	drawings (Birstein and Vinogradov 1972), photo and drawings (Macpherson 1988c)	Macpherson 1988c	only one male specimen (Birstein and Vinogradov 1972)	male: CL= 99, CW=105 (Macpherson 1988c)	*P. grossmani* (Macpherson 1988c)
P. longipes	drawings (Haig 1974), photo (del Solar 1981)			CL=106, R= 14, CW=117 (Haig 1974)	
P. manningi	drawings (Austin et al. 2000)		only males known, named after R.B. Manning (Austin et al. 2000)	male: CL= 146, CW= 133 (Austin et al. 2000)	*P. pentinata*, *P. serrata*, *P. cristulata*, *P. africana* (Austin et al. 2000)
P. medipacifica	photos (Takeda 1974)			CL = 70, CW= 58 (Takeda 1974)	
P. microps	dorsal and drawings (Macpherson 1988c)	Macpherson 1988c	only one specimen female (Macpherson 1988c)	female: CL=15, CW=15 (Macpherson 1988c)	
P. multispina Ezo-ibaragani	drawing (Makarov 1962, Hart 1982), photo (Schmitt 1921, Sakai 1971, 1976)	Sakai 1971, 1976		CL=80, CW=78 (Benedict 1894), male: CL=76, CW=82 (Sakai 1971)	
P. ochthodes	dorsal and photos (Macpherson 1988b)		from greek "ochthos" hilly elevation (Macpherson 1988b)	male: CL =72 , CW =78 (Macpherson 1988b)	

P. otsuae	drawings (Wilson 1990)			male: CL=84.6, CW= 83.5, female: CL=98.3, CW=96.0 (Wilson 1990)	
P. pacifica	photo and drawings (Sakai 1978)		only one male known (Sakai 1978)	male: CL=74, R= 8, CW=77 (Sakai 1978)	*P. zealandica* (Sakai 1978)
P. papillata	drawings (Haig 1974), photo (del Solar 1981)			male: CL=118, R=10, CW=130 (Haig 1974)	
P. pectinata	photos (Macpherson 1988c)	Macpherson 1988c	Latin "*pectinata*" comb, refering to pereopod spinulation; only one female (Macpherson 1988c)	female: CL=96, CW=96 (Macpherson 1988c)	*P. serrata* (Macpherson 1988c)
P. phrixa	photos (Macpherson 1992)		Greek "phrixos" bristled (Macpherson 1992)		*P. spinossima* (Macpherson 1992)
P. roeleveldae	photo and drawings (Kensley 1981)		named after Martina Roeleveld (Kensley 1981)	female: CL=50, CW=45 (Kensley 1981)	*P. investigatoris* and *P. seagranti* (Kensley 1981)
P. seagranti	photos (Eldredge 1976)		named after the office of Sea Grant Programs (Eldredge 1976)	male: CL=80.5, CW=81, female: CL=62, CW=57 (Eldredge 1976)	*P. aspera*, *P. verrilli*, *P. longipes*, *P. investigatoris*, *P. medipacifica*, and juvenile *P. inca* (Eldredge 1976)

P. serrata	photos and drawings (Macpherson 1988c)	Macpherson 1988c	Latin "*serra*" saw, due to pereopod spines; only one male (Macpherson 1988c)	male: CL=106, CW=112 (Macpherson 1988c)	*P. pectinata* and *P. verrilli* (Macpherson 1988c)
P. shinkaimaruae	photo and drawings (Takeda and Hatanaka 1984, Macpherson 1988c)	Macpherson 1988c		female: CL=75, CW= 78 (Takeda and Hatanaka 1984)	*P. hystrix*, *P. hystrixoides P. bouvieri*, and *P. spinosissimus*. (Takeda and Hatanaka 1984), and *P. erinacea* (Macpherson 1988c)
P. sp.	photo and drawings (Macpherson 1990)		being studied by Webber and Dawson at the National Museum of New Zealand, no males (Macpherson 1990)	female: CL=71, CW=72 (Macpherson 1990)	*P. granulosa* (Macpherson 1990)
P. spectabilis	drawings (Hansen 1908, Sandberg and McLaughlin 1998), photos and drawings (Macpherson 1988c)	Macpherson 1988c, Sandberg and McLaughlin 1998		male: CL=90, CW=78 (Birstein and Vinogradov 1967), female: CL= 45.5, CW=46 (Hansen 1908)	*P. birsteini*, *P. formosa* (Macpherson 1988c)
P. spinosissima	drawings (Birstein and Vinogradov 1972), photo and drawings (Macpherson !988c)	Macpherson 1988c		male: CL=125 (Otto and MacIntosh 1996), female: CL=100, CW=103 (Macpherson 1988c)	*P. erinacea*, *P. shinkaimaruae* (Macpherson 1988c)
P. stella	photo and drawings (Macpherson 1988a)			male: CL= 71, CW=72, female: CL=49, CW=50 (Macpherson 1988a)	*P. indica* (Macpherson 1988a)

P. truncatispinosa Ibo-ezoibaragani (Takeda and Miyake 1980)	photo (Takeda and Miyake 1980)			male: CL= 45, CW=40, female: CL= 45, CW= 39 (Takeda and Miyake 1980)	
P. tuberipes	photo and drawings (Macpherson 1988b)		Latin "*tuber*" tubercle, and "*pes*" foot (Macpherson 1988b)	CL = 41, CW = 47 (Macpherson 1988b)	*P. granulosa* (Macpherson 1988b)
P. verrilli Gokaku-ezoibaragani	drawing (Makarov 1962, Hart 1982), photo (Schmitt 1921, Sakai 1971, 1976, 1987, Miyake 1982)	Sakai 1971, 1976		CL=102, R=10, CW=113 (Sakai 1971), male: CL=112, CW=102 (Hart 1982)	
P. zealandica	photos (Dawson and Yaldwyn 1971)		named after New Zealand (Dawson and Yaldwyn 1971)	male: CL=111, CW= 101 (Dawson and Yaldwyn 1971)	
Phyllolithodes papillosus	drawing (Makarov 1962, Hart 1982, Macpherson 1988c), photos (Schmitt 1921, Jensen 1995)			male: CL=90, CW=90, female: CL=50, CW=60 (Hart 1982)	
Rhinolithodes wosnessenskii rhinoceros crab	drawing (Makarov 1962, Hart 1982, Macpherson 1988c), photos (Schmitt 1921, Jensen 1995)			male: CL=59, CW=64, female: CL=50, CW=57 (Hart 1982)	
Sculptolithodes derjugini Eri-tarabagani	photo (Makarov 1934), drawing (Makarov 1962, Sakai 1971, 1976, Macpherson 1988c)			male: CL=38, CW=36, female: CL=32, CW=31 (Makarov 1934)	
sub-family Hapalogastrinae					
Acantholithodes hispidus	drawing (Hart 1982), photo (Schmitt 1921, Jensen 1995)			male: CL= 62, CW= 64, female: CL= 49, CW=50 (Hart 1982)	

Dermaturus mandtii hairy crab	drawing (Schalfeew 1892, Makarov 1962), photo (Miyake 1982, Jensen 1995)			CL=23.0, CW=23.0 (Makarov 1962), male: CL=25.0, CW=21.0, female: CL=11.20, CW=9.78 (Zaklan pers.obs.)	
Hapalogaster cavicauda furry crab	photo (Schmitt 1921, Jensen 1995)			CL=20 (Jensen 1995), female: Cl=12.62, CW=14.71 (Zaklan pers. obs.)	
Hapalogaster dentata	drawing (Makarov 1962), photo (Miyake 1982)			male: CL=21.5, female: CL=15.6 (Goshima et al. 1995)	
H. grebnitzkii Syojo-gani	drawing (Schalfeew 1892, Makarov 1962, Hart 1982), photo (Schmitt 1921, Miyake 1982)			CL=20.5, CW=22 (Miyake 1982), male: CL=23, CW=24 (Hart 1982)	
H. mertensii	drawing (Schalfeew 1892, Hart 1982), photo (Jensen 1995)			male: CL=25, CW=25, female: CL=22, CW=24 (Hart 1982), CL= 35 (Jensen 1995)	
Oedignathus inermis Ibo-gani	drawing (Schalfeew 1892, Makarov 1962, Hart 1982), photo (Schmitt 1921, Miyake 1982, Jensen 1995)		*Hapalogaster inermis* of Stimpson 1860, *H. brandtii* of Schalfeew 1892, *O. gilli* of Benedict 1894 (Dawson 1989)	male: CL=25, CW=30, female: CL=22, CW= 20 (Hart 1982)	
Placetron wosnessenskii Urokogani	drawing (Schalfeew 1892, Makarov 1962, Hart 1982), photo (Sakai 1971, 1976, Jensen 1995)		includes *Lepeopus* Benedict 1894 (Dawson 1989)	male: CL=61.5, CW=73.3 (Schalfeew 1892), female: CL=50, CW=53 (Hart 1982)	

Placetron forcipatus			probably synonymous with *P. wosnessenskii* (Dawson 1989)		

* for an exhaustive list see Dawson 1989, all uncited common Japanese names are obtained from Sakai 1976, other common names from Dawson 1989

** Macpherson 1988c maps are for Atlantic Ocean distributions only

***CL= carapace length (includes rostral length unless otherwise noted), CW= carapace width, R=rostrum

Table 2-5 Life history traits of the family Lithodidae

species	age (years) & size (mm) at reproductive maturity - males	age (years) & size (mm) at reproductive maturity - females	reproductive cycle	brood size (eggs/clutch)	egg diameter (mm)	eclosion date	number of zoeal (Z) & glaucothoe (G) stages	size of zoea (Z) & glaucothoe (G) (mm) *	duration of zoeal & glaucothoe stages (days)	size of first settling juvenile, C1 (mm)*	zoeal (Z), glaucothoe (G), or juvenile (C) drawings
sub-family Lithodinae											
Cryptolithodes expansus		CL=25.84, R=5.88, CW=35.82 (Zaklan pers. obs.)					4 Z 1 G (Kim and Hong 2000)	Z1= 1.6 Z2= 2.2 Z3= 2.6 Z4= 3.2 G= 2.5 (Kim & Hong 2000)	Z1= 4.8 Z2= 8.9 Z3= 8.2 Z4= 14.8 G= 10.5 (Kim & Hong 2000)		Z 1-4 & G (Kim & Hong 2000)
C. sitchensis		CL=35.97, CW=49.84 (Zaklan pers. obs.)	uneyed embryos in August (Zaklan pers. obs.)	471 (Zaklan pers. obs.)	1.01-1.06 (Zaklan pers. obs.)						
C. typicus		CL=24.5, CW= 36; possibly CL=18.5, CW=26.5 (Hart 1965)	uneyed eggs in August with developmental signs in December (Hart 1965)		0.75-0.92 and just before hatching 0.8-1.1 (Hart 1965)	March-April (Hart 1965)	PZ, 4 Z, 1 G (Hart 1965)	Z1= 3 TL Z2= 3.25 TL Z3= 3.4 TL Z4= 3.6 TL G= 2.8 TL G= 1.9 G= 1.6 CW (Hart 1965)	Z1-Z4 = 14-16 (Hart 1965)	C1=2.25 CL C1= 2.0 CW (Hart 1965)	Z 1-4 & G & C1 (Hart 1965)
Lithodes aequispinus	CL= 114 based on chelae allometry (N B.C. Jewett et al. 1985), CL=92-130 (latitude dependent; Somerton and Otto 1986), functional CL=107 (Paul and Paul 2001)	CL= 105 (Japan, Hiramoto & Sato 1970, B.C., Canada, Jewett et al. 1985), CL= 98-111 (latitude dependent; Somerton and Otto 1986)	spawn July – Oct. (Hiramoto and Sato 1970), aseasonal reproduction (Sloan 1985, Somerton & Otto 1986)	9 500-30 100 (Hiramoto and Sato 1970)	2.1 (Hiramoto & Sato 1970), 2.4 (Jewett et al. 1985), 2.07 - 2.52 (Zaklan pers. obs.)	Feb.-July (Hiramoto and Sato 1970), March (Haynes 1982), April-August (Shirley & Zhou 1997)	4 Z & G (Haynes 1982), 3 Z skips Z3 or Z4 (Shirley & Zhou 1997), 3 Z (Paul & Paul 1999, Adams & Paul 1999)	Z1= 7.3 TL Z2= 7.5 TL Z3= 7.6 TL Z4= 6.8 TL G= 5.9 TL (Haynes 1982)	Z1= 6.6 Z2= 7-8.8 Z3= 12 Z4= 9.3 G= 41.3 Z1-4 &G = 67 (Shirley & Zhou 1997), Z1-4 &G = 75-148 (T° dependent, Paul & Paul 1999)		Z 1-4 & G (Haynes 1982)
L. couesi	CL=91.4 (Somerton 1981)	CL=80.2 (Somerton 1981)	asynchronous or protracted spawning (Somerton 1981)	2600-5500 (Somerton 1981)	2.3 (Somerton 1981)						
L. ferox	CL=108 (Abello & Macpherson 1992)	CL= 69 (Macpherson 1988c)	aseasonal (Abello & Macpherson 1992)	8000 (Abello & Macpherson 1992)	1.97 (Abello & Macpherson 1992)						
L. longispina		CL= 98 (Hiramoto 1974)	spawning August-October (Hiramoto 1974)	3900-11200 (Hiramoto 1974)							

L. maja		CL=59, CW=57 (Macpherson 1988c), CL=61.16, R=21.53, CW=56.92 (Zaklan pers. obs.)	spawning Sept- Nov., zoeal eclosion in April/May (Pike & Williamson 1959) aseasonal hatching of zoea (Anger 1996)		2.0 x 1.8 (Macdonald et al 1957)		2 Z 1 G (Macdonald et al 1957) 3 Z 1 G (Anger 1996)	Z1= 6.7-8.5 TL (CL= 4.2-5.1) Z2= 6.7-9.0 TL (CL=4.2-5.4), G= 4.6-4.3 TL (CL=2.7-2.4) (Macdonald et al. 1957)	Z1=4 Z2=5 Z3=8 G=29 C1=31 (Anger 1996)	C1= 2759 ug (Anger 1996)	Z 1-2 & G (Macdonald et al. 1957)
L. mamillifer		CL= 123, CW=118 (Macpherson 1988a)									
L. manningi		CW=120 CL=106 (Macpherson 1988c)									
L. murrayi	chela allometry CL= 69.5-71.0 (Miquel et al. 1985)	CL= 60-66 (Arnaud & Do-Chi 1977), chela allometry CL=64.5-65.5 (Miquel et al. 1985)		380 - 3582 (Arnaud & Do-Chi 1977)	1.92 - 2.88 (Arnaud & Do-Chi 1977)						
L. nintokuae		CL= 62 (Dawson & Yaldwyn 1985b)									
L. panamensis		CL-R =100CW=108 (Haig 1974)									
L. santolla	morphometric maturity CL=90-99 (Boschi et al. 1984), gonadal maturity CL= 60-75 (Vinuesa 1984), age 5 (Vinuesa 1991)	CL=77.5 (Guzman & Campodonico 1972), gonadal maturity CL= 66-87 (Vinuesa 1984), age 4, oogenesis 24 months (Vinuesa et al 1991)	December to mid-January molt/mate/ egg release (Hernandez 1985), annual (Vinuesa 1991, Lovrich & Vinuesa 1999), embryogenesis 9-11 months (Hernandez 1985, Vinuesa 1987)	4111 (Guzman & Campodonico 1972), to 60 000 (Vinuesa 1982)	1.40- 2.47 (Guzman & Campodonico 1972), 2.1 (Vinuesa 1987)	mid-September-October (Lovrich & Vinuesa 1999)	3 Z 1G (Campodonico 1971)	Z1=1.88-3.75 Z2=2.06-3.75 Z3=2.06-3.83 G=1.8-2.16 (Campodonico 1971)	Z1=4-12 Z2=4-16 Z3=14-26 Z & G= 33-55 (T° and salinity dependent Campodonico 1971, Vinuesa et al. 1985)	C1= 1.5 (Oyarzun 1992)	Z1-3 and G drawings (Campodonico 1971)
L. turkayi		CL=58, CW=55 (Macpherson 1988c)			1.7 (Lovrich & Vinuesa 1999)						
L. turritus		CL=123.7, CW=127.7 (Wu et al. 1998)									
L. unicornis		CL=118, CW= 115 (Macpherson 1988c)			1.5 (Macpherson 1984)						

Lopholithodes mandtii						April (Haynes 1993), March (Barkley Sound, B C , Canada, Zaklan pers obs.)	4 -5 Z 1 G (Crain & McLaughlin 2000a)	Z1=1.1-1.5, Z1=5.1-6.0 TL (Haynes 1993) Z1= 2.6 Z2= 3.0 Z3= 3.3 Z4= 3.5 Z5= 3.4 G= 2.2 (Crain & McLaughlin 2000a)	Prezoea (brief) Z1= 6-8 Z2= 5-10 Z3= 5-9 Z4= 6-14 Z5= unknown G= 24-29 (Crain & McLaughlin 2000a)	C1= 2.4 C2= 2.8 C1= 32-40 days C2= unknown duration (Crain & McLaughlin 2000a)	Z1 drawings (Haynes 1993), Z1-4, G, C1 & C2 (Crain & McLaughlin 2000a)
Neolithodes agassizii		CL=113 (Macpherson 1988c)									
N. asperrimus		CL= 133 (Macpherson 1988c)									
N. brodiei		CL=130, CW=104 (Dawson & Yaldwyn 1970)									
N. grimaldii		CL=118 (Macpherson 1988c)									
Paralithodes brevipes	CL= 96.4, age 6 (Abe & Koike 1982), CL=70 (Abe 1992)	CL=94 5, age 6 (Abe & Koike 1982)	molt, mate and egg release in June and July (Sato & Abe 1941), larvae settle in June (Sasaki & Yoshida 1999b)	8000-79000 (Sato & Abe 1941)		March/April (Kurata 1956)	PZ 3Z 1G (Kurata 1956)	Z1= 1.41 Z2= 1.49 Z3= 1.68 G= 1.60 (Kurata 1956) Z1= 1.36 Z2= 1.69 Z3= 1.77 G= 1.69 (Nakanishi 1981)	Z1-G= 35-70 (T° dependent; Nakanishi 1981)	C1=1.78 (Kurata 1956) C2=2.28 (Sasaki & Yoshida 1999)	Z1 & G (Kurata 1956), C2 (Sasaki & Yoshida 1999), mouthparts and foregut (Ambrunhosa & Kittaka 1997)
P. californiensis				3833 (Rypien pers obs)	1.62-1.96 (Rypien pers. obs)						
P. camtschaticus	area dependent. age 5 (McCaughran and Powell 1977), chelae allometry CL=103 (Somerton 1980), CL=120, presence of spermatophores at CL= 70-99 (Alaska, Paul et al. 1991)	area dependent: CW= 85-100 (Marukawa 1930), CL=83- 95 (Powell & Nickerson 1965b), 86-119 (Powell et al. 1973b), age 5 (McCaughran and Powell 1977), chelae allometry CL=102 (Somerton 1980), CL= 76-105 (Otto et al. 1980), CL=76-88 (Paul 1992)	11-13 month cycle, annual spring migration and synchronized spawn (Makukawa 1933), mate February to April shallow water (Powell et al. 1973b), brood for 300 days (Nakanishi 1987)	70 000 - 270 000 (Marukawa 1930), 15, 330 - 214, 410 (Sato 1958)	0.71- 0.82 (Marukawa 1930), 0.88-1.03 (Matsuura & Takeshita 1985)	March to May (Marukawa 1930)	4Z 1G (Marukawa 1930)	Z1= 1.18 Z2= 1.38 Z3= 1.45 Z4= 1.53 G= 1.8 G= 1.5 CW (Sato & Tanaka 1949), G= 2.0 G= 1.7 CW (Marukawa 1930)	Z1= 14 Z2= 8 (Marukawa 1930), Z1-4= 47-84 (Sato 1958) Z1= 14 Z2= 14 (Shirley & Shirley 1988)	C1 CL=2.5, C1 CW=2.0 (Marukawa 1930) C1 CL = 2.50, C1 CW= 1.33 (Sato & Tanaka 1949), T° dependent, (Stevens 1990) C1 CL= 2.18 (Donaldson et al. 1992)	egg, Z1-4 & G (Marukawa 1930, Sato & Tanaka 1949, Kurata 1964), egg (Nakanishi 1987), mouth and foregut (Abrunhosa & Kittaka 1997)

P. platypus	area dependent. sperm CL > 70 (Sasakawa 1971), CL=77-108 (Alaska, Somerton & MacIntosh 1983), spermatophores in CL=50-69 (Alaska, Paul et al. 1991)	area dependent. CL=80 6-96 3 (Alaska-Somerton & MacIntosh 1983), CL=101-105 (Otto et al. 1980)	19 month cycle (Sasakawa 1975a), biennial mating & broods for 14-15 months (Somerton & MacIntosh 1985), 12 months (Jensen & Armstrong 1989)	3000-160 000 (Sasakawa 1975b)	1 18 x 0 98 Asia (Sasakawa 1975b), 1 2 x 1.0 Alaska (Somerton & MacIntosh 1985)	March to May (Jensen & Armstrong 1989)	4 Z 1 G (Sato 1958)	Z1= 1 2, 3.2 Z2= 1 3, 3.4 Z3= 1.6, 3 5 Z4= 2 0, 4 5 (CL, TL) G= 1.8 CL (Hoffman 1968)	Z1= 12 4 Z2= 12 3 Z3= 12 5 Z4= 14 3 G= 12 8 (Hoffman 1968)	2 6 (Hoffman 1968)	Z1 (Marukawa 1930, Kurata 1964), Z 1-4 & G (Hoffman 1968), mouth and foregut (Ambrunhosa & Kittaka 1997)
Paralomis africana		CL=38 (Macpherson 1988c)									
P. anamerae		CL=68, CW=68 (Macpherson 1988c)									
P. bouvieri	CL= 38.5, CW=35.0 (Pohle 1992b)	CL= 33.0, CW= 32 0 (Pohle 1992b)									
P. cristulata		CL= 48, CW=51 (Macpherson 1988c)									
P. erinacea		CL= 58, CW=57 (Macpherson 1988c)									
P. formosa		CL= 64 (Macpherson 1988c)									
P. granulosa	gonadal maturity CL=50.2 or age 10, morphometric maturity CL=57 (Lovrich & Vinuesa 1993, 1995, 1999), functional maturity CL=52 (Hoggarth 1993)	gonadal maturity CL= 60.6, morphometric maturity CL= 66.5 (Lovrich & Vinuesa 1993), functional maturity CL=46 (Hoggarth 1993)	biennial, mate and molt Oct- Jan. asynchronous development, eggs extruded Oct-Nov, embryogenesis 18-22 months with a 10 month diapause (Lovrich & Vinuesa 1993, 1996)	50% of adults do not carry eggs (Hoggarth 1993), 800-10 000 (Lovrich & Vinuesa 1993)	2 3 (Vinuesa 1987), 1.9 (Lovrich & Vinuesa 1993)	June – August (2 years after mating), (Lovrich & Vinuesa 1993)	Z1-2 1G (Campodonico & Guzman 1981)	Z1= 2.1 Z1= 5.9-6 0 TL G= 2.0 G= 2.0 CW G= 4.5 TL (Campodonico & Guzman 1981)	Z1= 5 1-5.7 Z2= 4.2-4 8 (Campodonico & Guzman 1981)	C1=3 CL (Lovrich and Vinuesa 1996)	Z1-2 & G (Campodonico & Guzman 1981)
P. grossmani		CL= 98, CW= 98 (Macpherson 1988c)									
P. haigae		CL=49, CW=48 (Macpherson 1990)									
P. hystrix						April (Konishi & Taishaku 1994)	2Z & 1 G (Konishi & Taishaku 1994)	Z1= 3.4 Z2= 3.6 G= 2.5 (Konishi & Taishaku 1994)	Z1 & Z2= 17 (Konishi & Taishaku 1994)		Z1 & ZII & G (Konishi & Taishaku 1994)
P. inca		CL = 93, R= 10, CW= 109 (Haig 1974)									
P. japonica							2Z & G (Hayashi & Yanagisawa 1985)	Z1=2.5-2.9 (Hayashi & Yanagisawa 1985)			PZ & Z1 (Hayashi & Yanagisawa 1985)
P. jamsteci		CL+R= 56 8, CW=55.5 (Takeda & Hashimoto 1990)									
P. longipes					2 (Faxon 1893)						
P. medipacifica		CL+R=63, CW=55 (Takeda 1974)									

P. otsuae		CL= 89.5, CW= 88.3 (Wilson 1990)									
P. pectinata		CL=96, CW=96 (Macpherson 1988c)									
P. phrixa		CL= 59, CW= 63 (Macpherson 1992)									
P. seagranti		CL= 62, CW = 57 (Eldredge 1976)			2.5 (Eldredge 1976)						
P. sp		CL=71, CW=72 (Macpherson 1990)									
P. spectabilis		CL= 47, CW=45 (Macpherson 1988c)									
P. spinosissima	CL=74.8 South Georgia, CL= 66.4 Shag Rocks Antarctic (Otto & MacIntosh 1996)	CL= 61.7 (Otto & MacIntosh 1996)	asynchronous release date (Otto & Macintosh 1996)	2000-14000 (Otto 1993)	2.0 (Otto 1993)						
P. stella		CL=49, CW=50 (Macpherson 1988a)									
P. tuberipes		CL=41, CW=47 (Macpherson 1988b)									
P. verrilli		CL= 99 (Sakai 1987)									
Rhinolithodes wosnessenskii		CL= 44.87, R= 6.35, CW=39.18 (Zaklan pers. obs.)		1959-8705 (Rypien pers. obs.)	1.07-1.18 (Zaklan pers. obs.)	March (Haynes 1984)		Z1=1.29 CL (Haynes 1984)			drawing of Z1 & Z2 (Haynes 1984)
Sculptolithodes derjugini		CL= 24 (Macpherson 1988c)									
sub-family Hapalogastrinae											
Acantholithodes hispidus		CL= 24.01, R=5.9, CW=32.81 (Zaklan pers. obs.)									
Dermaturus mandtii		CL=24.01, CW=5.52 (Zaklan pers. obs.)					4Z 1G (Kurata 1964)				Z1-4 & G (Kurata 1964)
Hapalogaster cavicauda		CL=14.71, CW=12.62 (Zaklan pers. obs.)		1162-2265 (Zaklan pers. obs.)	0.71-0.84 (Zaklan pers obs.)						
H. dentata	morph maturity CL=5.2, gonadal maturity CL=5.3 or age 1, functional maturity CL=9.5 (Goshima et al. 1995, 2000)	CL= 6.5 - 8 age 2 (Goshima et al 1995)	180 day brooding period, (Takahashi et al. 1985), seasonal, spawn from Oct. to Nov. 110 day brooding period (Goshima et al. 1995)	73-3051 (Goshima et al. 1995)	0.9-1.04 (Goshima et al. 1995), 1.14-1.19 (Zaklan pers. obs.)	Feb-March release (Goshima et al 1995)	4Z 1G (Konishi 1986)	Z1= 1.73-1.89 Z2= 1.74-1.93 Z3= 1.98-2.13 Z4= 2.09-2.37 G= 1.53-1.64 (Konishi 1986)	Z1-4 =19-23 Z1-C1>30 (Konishi 1986)	C1=1.71 CL C1=1.21 CW (Konishi 1986)	Z1-4 & G (Konishi 1986)
H. mertensii		CL=18, CW=16 (Miller & Coffin 1961)		900-1800 (Miller & Coffin 1961)		February - March (Zaklan pers. obs.)	PZ 4 Z 1 G (Miller & Coffin 1961)	PZ= 3.30 TL Z1= 3.65 TL Z2= 4.35 TL Z3= 4.6 TL Z4= 5.5 TL G= 1.98 CL G= 1.3, CW G= 3.25 TL (Miller & Coffin 1961)	PZ-5-6 hours Z1= 8.5 Z2= 11 Z3= 12 Z4= 12 G= 16 (Miller & Coffin 1961)	C1=2.0 CL C2=2.05 CL (Miller & Coffin 1961)	Z1-4, G and C1 (Miller & Coffin 1961)

Oedignathus inermis		CL=10.2, CW=10.3 (Zaklan pers obs)	annual, spawn in August (Zaklan pers obs)	208-2421 (Zaklan pers obs)	1.16-1 19 (Zaklan pers obs)	Feb – March (Zaklan pers obs)			Z1-4= 30 (Zaklan pers. obs.)		
Placetron wosnessenskii						March (Haynes 1984)	PZ 4Z 1G (Crain & McLaughlin 2000b)	Z1=2.12 (Haynes 1984) Z1= 3.1 Z2= 3.7 Z3= 4.5 Z4= 4.8 G= 3.1 (Crain & McLaughlin 2000b)	PZ= 2 min. Z1= 8-12 Z2= 10-15 Z3= 10-13 Z4= 12-15 G= 10-15 (Crain & McLaughlin 2000b)	C1= 2.6 CL (Crain & McLaughlin 2000b)	Z1 (Haynes 1984) Z1-4 & G (Crain & McLaughlin 2000b)

- ✦ R= rostrum; CL=carapace length; CW=carapace width; TL=total length, G=glaucothoe, Z=zoea; PZ=pre-zoea, C1=first juvenile instar (=crab one), C2=second juvenile instar (=crab two)
- ✦✦ McLaughlin and Lemaitre (2000) report the possession of glaucothoeal and first crab stages of *Phyllolithodes papillosus*, *Cryptolithodes sitchensis*, *Acantholithodes hispidus*, *Hapalogaster dentata* (courtesy of Greig Jensen, C. Nyblade and Hokkaido University) and *Oedignathus inermis*.
- • measurement of carapacae length (CL) unless otherwise noted

Table 2-6. Predator and prey relationships of the family Lithodidae.

species	adult diet	larval diet	predators
sub-family Lithodinae			
Cryptolithodes sitchensis	calcareous algae, *Corallina*, *Calliarthron* and *Bossiella* (Hart 1982) and other sessile organisms (Jensen 1995)		
C. typicus	opportunistic grazer on bryozoans, coralline algae and other encrusting or sessile organisms (Hart 1982, Jensen 1995)		
Lithodes aequispinus		lecithotrophic (Shirley and Zhou 1997)	
L. maja		lecithotrophic (Anger 1996)	
L. murrayi	benthic opportunist omnivore includes polychaetes, echinoderms, sponges, gastropods, small crustaceans (Arnaud and Do-Chi 1977)		
L. panamensis			sperm whales (*Physeter catodon*, Haig 1974)
L. santolla	broad opportunists consisting of molluscs (mainly gastropods), crustaceans and bryozoa; prey was size class and season dependent; consumption greatest in wintering large crabs; autumn diet of *Pseudechinus magellanicus* (66.7%); winter diet of Bryozoa (*Membranipora isabellean*); spring diet of Crustacea e.g. *Isopoda* and *Munida* spp; summer diet of algae, *Macrocystis pirifera*, feed on more mobile organisms than *P. granulosa* (Comoglio et al. 1990, Comoglio and Amin 1996)	consume plankton in zoea stage I, non-feeding in zoea stage II, and glaucothoe, thus faculatatively lecithotrophic (Comoglio and Vinuesa 1991), lecithotrophic (Oyarzun 1992)	
Lopholithodes foraminatus	a deposit feeder, a filterer of chelae-dredged sediment and an opportunist consumer of buried prey such as clams (Jensen 1995)		
L. mandtii	opportunist feeder, e.g. echinoderms and sea anemones (Hart 1982) muscles in the lab (Zaklan pers. obs.)		
Neolithodes diomedeae			sperm whales (Baez et al. 1986)
Paralithodes brevipes	*Laminaria longissima* and *Corallina pilulifera* (Sasaki and Kuwahara 1999)	glaucothoe a non-feeding stage (Abrunhosa and Kittaka 1997)	

P. camtschaticus	Adults are opportunist omnivores (see Takeuchi 1959, 1967, Feder et al. 1980, Jewett and Feder 1982 for overviews) feeding on molluscs (bivalve families Tellinidae and Cardiidae, gastropods family Trochidae), Crustacea (mainly barnacles), fish, annelids, Polychaeta, Echinoderms and algae (Takeuchi 1959, 1967, Tarverdieva 1976, Jewett and Feder 1982), kelp (*Laminaria* sp.), *Ulva* sp., molt exuvia, sea stars (*Evasterias troschellii* and *Pycnopodia helianthoides*; Dew 1990). Young juveniles forage through sediment eating crustaceans, polychaetes, diatoms, tintinnids, foraminiferans, algae and bryozoans (Feder et al. 1980).	see Paul et al. 1989 for overview, diel feeding patterns exist (Shirley and Shirley 1987) newly hatched zoeae are herbivorous and carnivory increases with age (Shirley and Shirley 1989b) zoea feed and glaucothoe are non-feeding (Abrunhosa and Kittaka 1997) phytoplankton prey include diatoms, barnacle and crab larvae (Bright 1967) zooplankton such as *Artemia*, *Thalassiosira* spp., *Skeletonema costatum*, *Chaetoceros* spp., copepod nauplii, canabalism (Kurata 1959, Paul et al. 1989)	egg predator, *Carcinonemertes regicides* (Nemertea; Shields et al. 1989, Kuris et al. 1991): for overview see Loher et al. 1998, predators include Pacific halibut (*Hippoglossus stenolepis*), Pacific cod (*Gadus macrocephalus*), sablefish (*Anoplopoma fimbria*), various flatfish, flounders (*Atheresthes spp.*), sole, herring, salmon and sculpins yellow irish lords (*Hemilepidotus*), snailfish (*Liparis* sp.), eelpout (*Lycodes*), skates (*Raja* spp.) and arrowtooth
P. platypus	use chelae for crushing molluscs and urchin testes, feed on hard and soft bottoms where they excavate large pits (Somerton 1985)	as glaucothoe mouth parts atrophy (Sato and Tanaka 1949) they are a non-feeding stage (Abrunhosa and Kittaka 1997)	
Paralomis bouvieri			northern wolffish *Anarhichas denticulatus* (Pohle 1992b)
P. formosa			toothfish *Dissostichus eliginoides* (Konforkin and Kozlov 1992)
P. granulosa	algae, Foraminifera, Bryozoa, bivalves, gastropods, barnacles, ascidians and Polychaeta (Comoglio et al. 1990)	lecithotrophic (Campodonico and Guzman 1981, Campodonico and Vinuesa 1991)	
P. spinosissima			toothfish (Konforkin and Kozlov 1992)
Phyllolithodes papillosus	in captivity they eat small sea urchins (Jensen 1995) and muscles (Zaklan pers. obs.) and sponges in the wild (Jensen 1995)		

sub-family Hapalogastrinae			
Acantholithodes hispidus	found foraging in prawn-traps, most likely unable to catch shrimp under natural conditions (Jensen 1995)		
Dermaturus mandtii	consumer of algae or algal detritus (Jensen 1995)		
Hapalogaster cavicauda	filter feeds and is a broad opportunist omnivore (Jensen 1995)		
H. mertensii	filter feeds and is a broad opportunist omnivore (Jensen 1995)	glaucothoe are non-feeding (Miller and Coffin 1961)	
Oedignathus inermis	omnivorous and a filter feeder, captive specimens consume worms and crustaceans and crushed mussels (Jensen 1995)		
Placetron wosnessenskii	a fast lithodid predator, pincher-like chelae are used to obtain crevice-dwelling prey such as brittle stars, shrimp, amphipods, crabs and brachiopods (Jensen 1995)	planktonic omnivore (Crain 1999)	

Table 2-7. Parasites and commensals of the family Lithodidae.

species	*Briarosaccus callosus*	*Careproctus sp.*	other parasites etc.	commensals and unknowns
sub-family Lithodinae				
Lithodes aequispinus	Boschma 1970, McMullen and Yoshihara 1970, Sloan 1984, Bower and Sloan 1985, Sparks and Morado 1985, Hawkes et al. 1985a, 1986	pink snailfish *C. furcellus*, red snailfish *C. sp.* (Love and Shirley 1993, Somerton and Donaldson 1998)	trematode metacercariae, larval acanthocephans, parasitic dinoflagellates, viral infection, microsporidan of Nosematidae family producing "cottage cheese disease" (Sparks and Morado 1985)	
L. couesi	Boschma 1970, Somerton 1981			
L. ferox	Abello and Macpherson 1992	*C. griseldea* infects males only (as *L. tropicalis*, Melville-Smith and Louw 1987)		epibionts: cirripede *Poecilasma kaempferi* and Hydroid - *Stegopoma plicatile* (Abello and Macpherson 1992)
L. murrayi	Arnaud and Do-Chi 1977			isopods, hydroids and polychaetes (spirorbs; Arnaud and Do-Chi 1977)
L. santolla	Boschma 1970	*C. sp.* (Campodonico and Guzman 1977), *C. falklandica* (Balbontin et al. 1979)	eggs exposed to cadmium and lead resulted in early eclosion and larval hatching decrease (Amin et al. 1998)	
Lopholithodes foraminatus		*C. melanurus* (Parrish 1972), *C. sp.* (Peden and Corbett 1973)		
Neolithodes agassizii	Boschma 1930, 1970			
N. grimaldii	Pohle 1992a			cryptoniscinid isopod hyperparasite (Pohle 1992a)
Paralithodes californiensis	this study, collected by Donald Cadien, Redondo Submarine Canyon, Los Angeles, U.S.A. at 305 m: 33°49.23/118°27.09: August 6, 1997	*C. sp.* (Anderson and Cailliet 1974)		*Myzotarsa anaxiphilius* (Gammaridea: Amphipoda, Cadien and Martin 1999)

P. camtschaticus	Faxon 1895, Boschma, and Haynes 1969, Boschma 1970, McMullen and Yoshihara 1970, Sparks and Morado 1985, Hawkes et al. 1986b, Jansen et al. 1998	*C. sp.* (Nakazawa 1915, Hunter 1969), *C. sinensis* (Rass 1950, Vinogradov 1950)	parasitic dinoflagellates, viral infection, trematode metacercariae, microsporidan infection (*Thelohania*, Sparks and Morado 1985), carcinoma-like growth in hind-gut (Sparks and Morado 1987), Acanthocephalans (Sparks 1987), Nemertea (e.g. *Carcinonemertes regicides*, Shields et al. 1989, Kuris et al. 1991; *Alaxinus oclairi*, Gibson et al. 1990), Protozoa, gill ciliates, flagellates, Turbelarians (Promesostomidae?), Nemertea, Hirudinea (*Johanssonia arctica*), Acanthocephala (*Profilicollis botulus*, Jansen et al. 1998)	amphipods (*Ischyrocerus commensalis*), copepods and *Mytilus edulis* larvae (Jansen et al. 1998)
P. platypus	Hawkes et al. 1985a,b, 1986a, 1987, *Thompsonia* sp., Johnson et al. 1986		trematode metacercariae, larval acanthocephans, viral infection, parasitic dinoflagellates, microsporidan (*Thelohania sp.*, Sparks and Morado 1985) Herpesviridae (Sparks and Morado 1985, 1986), Rickettsiae (Johnson 1984)	
P. rathbuni	this study, collected by D. Cadien, Redondo Submarine Canyon (see *P. californiensis* above)			*Myzotarsa anaxiphilius* (Gammaridea: Amphipoda, Cadien and Martin 1999)
Paralomis aspera	Faxon 1895, Lutzen 1987			
Paralomis bouvieri	only males infected - Pohle 1992b		cryptoniscinid isopod hyperparasite (Pohle 1992b)	
Paralomis cristata			infested by a sacculinid parasite (Takeda and Ohta 1979, Sakai 1987)	
P. cubensis	Chace 1939			
P. granulosa	Boschma 1970	*C. sp.* (Balbontin et al. 1979)	*Pseudione tuberculata* (Isopoda: Bopyridae; Roccatagliata and Lovrich 1999)	

P. spinosissima	Otto and MacIntosh 1996		microsporidian infection (possibly family Nosematidae) isopod hyperparasite on *B. callosus* (Otto and MacIntosh 1996)	
P. sp.	Lutzen 1985			
P.truncatispinosa			sacculinid parasite (Takeda and Miyake 1980)	
Phyllolithodes papillosus	Zaklan pers.obs. (Barkley Sound, B.C., 20 m)			
sub-family Hapalogastrinae				
Hapalogaster mertensii	*Briarosaccus tenellus* (Boschma 1970, Walossek et al. 1996)			

Table 2-8. Summary information concerning fisheries of the family Lithodidae.

species	area harvested	minimum size of males *	fishing method	comments	suggested references*
Lithodes aequispinus (brown or golden king)	central Japan, along Aleutian Islands and continental slope of southeastern Bering Sea, Alaska, U.S.A. to southern B.C., Canada	area and year dependent, 5.0 to 7.0 inches	Mesh covered pots are set on longlines in Aleutians, Bristol Bay and Bering Sea, Alaska, U.S.A. Pot limits vary with area, and depend on guideline harvest levels, vessel size and biomass estimates. In southeast Alaska, pot limits vary between 20-250 pots (T. Shirley pers. com.).	age of recruitment into the fishery is unknown	Hiramoto 1985, Otto et al. 1990, Jewett et al. 1985, Orensanz 1998
L. couesi (deep sea or scarlet king crab)		5.5 inches (140 mm)	Both rectangular sablefish (*Anoplopoma finbria*) traps of 0.8 m x 0.8 x 2.5 m that are covered with 8.9 cm webbing, or rectangular *P. camtschaticus* traps (see below) arranged at 91.5 m intervals with surface floats connected to both ends are used.	a small fishery, due to deep water habitat (592-850 m), generally as bycatch to *L. aequispinus*, *P. camtschaticus* and *P. brevipes*	Somerton 1981
L. confundens				morphology similar to *L. santolla* and overlaps in distribution thus likely to be landed as *L. santolla* in places, fishery opening soon in Argentina	Macpherson 1988c, Vinuesa et al. 1996
L. murrayi	Crozet Islands (S.W. Indian Ocean)		Caught using beam trawl and two kinds of PVC pots ("Alaskan" king crab ots and regular lobster pots.	exploratory fishery	Arnaud et al. 1976

L. santolla (centolla, formerly *L. antarcticus*)	Argentina (Beagle Channel and Golfo San Jorge at 46°S near the city of Comodoro Rivadavia) and strait of Magellan (Chile)	CL= 120	Caught legally with spherical (Chilean design) or the more efficient conical traps (Japanese design), or illegally with tangle nets. Often a bycatch of the Argentinean hake (*Merluccius hubsii*) in the Atlantic. Pots are truncated cones (1.3 m high) of three iron hoops united by eight crossbars of thinner iron rods covered with mesh. Pots have a base diameter of 1.5 -1.8 m and opening entrance of 0.6-0.8 m with a circular plastic escape guard. Ten pots are long-lined and each separated by twenty meters.	one of the largest fisheries in the southern hemisphere until the collapse in 1993. Now open periodically. In the Golfo San Jorge it is a trawling fishery with high population impact as there is no sex or size selectivity nor returns of sublegal crabs.	Campodonico 1983, Boschi et al. 1984, Bertuche 1985, Lovrich and Vinuesa 1996, 1999, Vinuesa et al. 1996, Wyngaard and Iorio 1996, Lovrich 1997
Neolithodes diomedeae	Peurto Mont Argentina			very small fishery	Baez et al. 1986, Lovrich and Vinuesa 1999
Paralithodes brevipes (Hanasaki crab)	mostly a Japanese fishery, in the Sea of Japan			increasing in size with the decline of *P. camtschaticus*	Abe 1992
P. camtschaticus (Alaskan, Russian, Japanese, red king crab)	northern B.C. Canada, U.S.A., Japan, and Russia, beginning in Norway	CW=5.5 - 8 inches (varies with harvest district in Alaska, U.S.A.), 8-9 years of age	In Alaska, crab pots are the only legal commercial fishing gear and measure 1.8 x 1.8 x 0.9 covered by polypropylene mesh with two side tunnel openings of 18.5 by 89 cm.	The fishery occurs in the fall months until quotos (based on population estimates) are attained (between 7-10 days). There is no fishing during spring, molting and mating periods.	Marukawa 1930, 1933, Otto 1990, Abe 1992, Zheng et al. 1997a, Orensanz et al. 1998, Loher et al. 1998, Kruse et al. 2000, Zheng and Kruse 2000

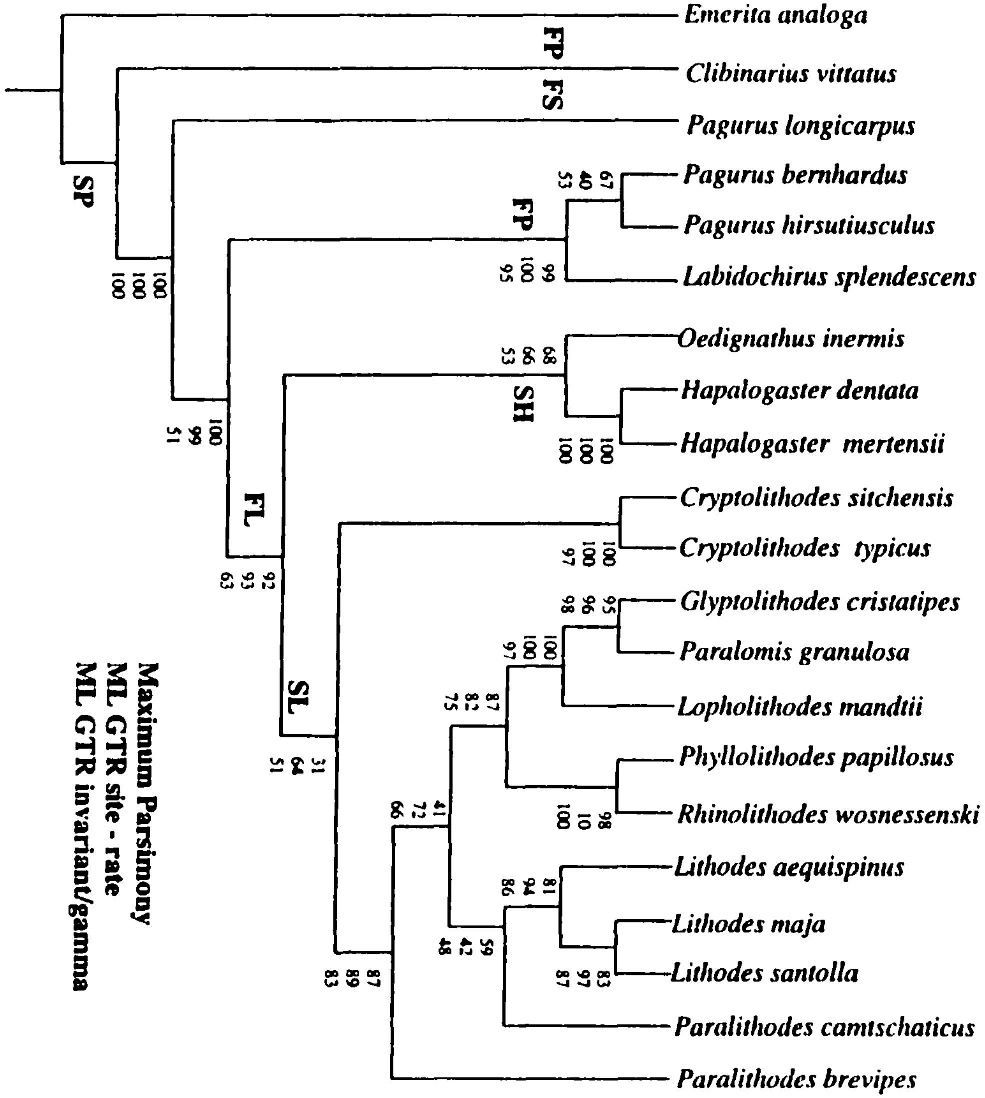
P. platypus (blue king crab)	Pribiloff and St. Matthew Islands in Aleutians (Chukchi Sea to SE Alaska)	CW= 165 mm (6.5 inches) Pribiloff Islands; CW=140 mm (5.5 inches) St. Matthew Island		age of recruitment into the fishery is unknown	Otto 1990, Zheng et al. 1997b, 1998, Orensanz et al. 1998
Paralomis formosa	South Georgia area Antarctic Ocean			exploratory fishery, July-November; fishery opening soon in Argentina	Otto and MacIntosh 1996
P. granulosa (false centolla)	Argentina (Beagle Channel) and strait of Magellan (Chile)	CW= 90 mm CL= 82 mm	caught using similar nets and traps as *L. santolla*	A co-fishery with *L. santolla*, and since the early 1990s landings of *P. granulosa* are higher than those of *L. santolla*. Annual catch of 3000 t.	Campodonico 1983, Vinuesa et al. 1996, Lovrich 1997, Lovrich and Vinuesa 1993,1995, 1999
P. spinosissima	Chile/ south Georgia area of the Southern Ocean	CW= 94 mm at South Georgia CW= 84 mm at Shag Rocks		exploratory fishery, January and November; fishery opening soon in Argentina	Otto and MacIntosh 1996

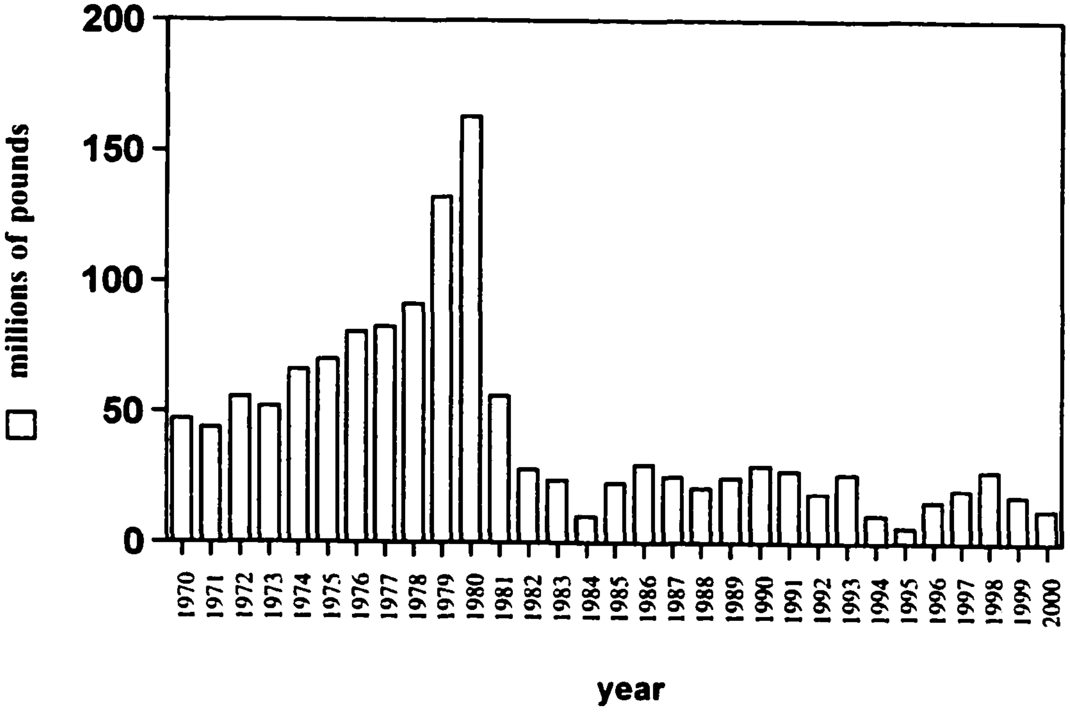
* As harvest guidelines are modified year to year to reflect changes in the population, please refer to fishery internet sites including Alaska Department of Fish and Games Commerical Shell-fish regulations for up-to-date information including opening dates, minimum harvest sizes, and catch limits.

FIGURE LEGENDS

Figure 2-1: Most parsimonious tree based on combined analysis of partial sequences from four mitochondrial (12S, 16S COI, COII) and one nuclear (28S) data sets. Numbers at nodes represent bootstrap values for each of three analyses. First, maximum parsimony a method which assumes the least changes over time. Second, maximum likelihood based on general times reversal model and site rate analysis, a method that accomodates rate heterogeneity across sites of each gene. Third, maximum likelihood invariant/gamma that takes accomodates invariant sites. Letters at nodes represent the following: FL= family Lithodidae, SH= subfamily Hapalogastrinae, SL= subfamily Lithodinae, FP= family Paguridae, FD= family Diogenidae, SP=superfamily Paguroidea. Outgroup taxa are *Emerita analoga* (superfamily Hippoidea) and *Clibinarius vittatus* (superfamily Paguroidea, family Diogenidae).

Figure 2-2: Harvest size, in millions of pounds, of king crabs (*Paralithodes camtschaticus, Paralithodes platypus*, and *Lithodes aequispinus*) landed in Alaska (Bristol Bay, Pribilof Islands, St. Mathews, Aleutian Islands, Southeast Alaska and Norton Sound) between the years 1970-2000 (Alaska Department of Fish and Game 2001).


Emerita analoga
Clibinarius vittatus
Pagurus longicarpus
Pagurus bernhardus
Pagurus hirsutiusculus
Labidochirus splendescens
Oedignathus inermis
Hapalogaster dentata
Hapalogaster mertensii
Cryptolithodes sitchensis
Cryptolithodes typicus
Glyptolithodes cristatipes
Paralomis granulosa
Lopholithodes mandtii
Phyllolithodes papillosus
Rhinolithodes wosnessenski
Lithodes aequispinus
Lithodes maja
Lithodes santolla
Paralithodes camtschaticus
Paralithodes brevipes
FP
FS
SP
FP
SH
FL
SL
67 40 53
99 100 95
100 100 100
68 66 53
100 100 100
100 99 51
100 100 97
92 93 63
95 96 98
100 100 97
87 82 75
98 10 100
31 64 51
41 72 66
81 94 86
83 97 87
59 42 48
87 89 83
Maximum Parsimony
ML GTR site - rate
ML GTR invariant/gamma


200
150
100
50
0
☐ millions of pounds
1970
1971
1972
1973
1974
1975
1976
1977
1978
1979
1980
1981
1982
1983
1984
1985
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1987
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1990
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year

CHAPTER 3

Molecular phylogeny, circumstances, and consequences of the transition from hermit crabs to king crabs (Crustacea: Anomura: Paguroidea: Lithodidae)

ABSTRACT

The repeated appearance of the crab-like form (carcinization) is a phenomenon that has long been recognized but little understood. An extreme example of carcinization is represented by the family Lithodidae, which includes the giant Alaskan king crabs, from hermit crab ancestors. We used sequence data from four mitochondrial (12S, 16S, COI and COII) and one nuclear (28S) gene to construct a phylogeny based on parsimony and maximum likelihood. This phylogeny allowed us to support Bouvier's hypothesis that the evolution of the Lithodidae proceeded gradually from taxa with soft, asymmetric abdomens to taxa with fully symmetrical abdomens with fully articulated abdominal plates. Further reconstructions allowed us to hypothesize that the Lithodidae arose in the North Pacific intertidal between 13-25 mya, with subsequent and dramatic increases in size that accompanied invasions of deeper waters. We found that there was a large concordance between morphological and molecular hypotheses concerning relationships within the Lithodidae, including a monophyletic Lithodidae and two monophyletic subfamilies, Lithodinae and Hapalogastrinae.

Keywords: king crabs, hermit crabs, molecular systematics, Paguridae, Lithodidae

1. INTRODUCTION

The evolution of the giant Alaskan king crabs (family Lithodidae) from hermit crab ancestors is a striking combination of evolutionary divergence and convergence (Boas 1880a, b; Bouvier 1894; 1897; Cunningham *et al.* 1992; Richter & Scholtz 1994 but see McLaughlin & Lemaitre 1997). Hermit crabs are small animals characterized by soft abdomens and the use of gastropod shells for protection. Many hermit crab lineages have reduced or lost dependence on gastropod shells. In most cases, escape from the confining shells results not only in a body size increase but in carcinization — the assumption of a crab-like form (Borradaile 1916). The crab-like form is defined as a broadened, fully calcified carapace and a reduced abdomen tucked forward under the thorax. In their striking divergence from their hermit crab ancestors, lithodid crabs converged on this crab-like form, which has arisen not only in the distantly related true crabs (infraorder Brachyura), but at least four other times in the infraorder Anomura (e.g. families Lomidae, Porcellanidae and the genera *Probeebei*, *Birgus*; Harms 1932; Wolff 1961; Reese 1968; Martin & Abele 1986; but see McLaughlin & Lemaitre 1997).

In the accompanying paper by Morrison *et al.* (submitted), we use molecular phylogenetics and ancestral reconstruction to document the multiple origins of the crab-like form in the Brachyura and Anomura. In this paper, we investigate the circumstances leading to one of these origins, the evolution of king crabs from hermit crab ancestors, estimated by molecular data to have taken place within the last 25 million years (Cunningham *et al.* 1992). This recent origin leaves open the possibility that phylogenetic approaches might help to reconstruct the circumstances that accompanied the origin of the first lithodid crabs.

In this paper, we carry out a phylogenetic analysis of the family Lithodidae, including representatives of both the soft-abdomened subfamily Hapalogastrinae and the fully armored subfamily Lithodinae. We use ancestral state reconstruction to investigate the circumstances of the transition to the crab-like form, and test Bouvier's hypothesis that existing variation in the degree of hardening of the exoskeleton in lithodids may reflect a gradual transition from hermit crab ancestors (Fig. 3-1).

2. MATERIALS AND METHODS

(a) *Taxon Sampling*

All taxa included in our analysis are members of the Crustacean infraorder Anomura. The ingroup consisted of nineteen members of the superfamily Paguroidea. These included four hermit crabs of the family Paguridae, with representatives of major clades of pagurid hermit crabs identified by Cunningham *et al.* (1992). The remaining members of the ingroup included fifteen members of the king crab family, Lithodidae, with three members of the subfamily Hapalogastrinae and twelve members of the subfamily Lithodinae (Table 1). The family Lithodidae is represented by ten of fifteen described genera (with *Acantholithus* included in the genus *Paralomis*, as per Sakai 1976): the subfamily Hapalogastrinae is represented by two of five described genera, and the subfamily Lithodinae is represented by eight of ten described genera (Dawson 1989). The outgroups were chosen based on a higher level phylogeny of the Anomura (McLaughlin 1983; see Morrison *et al.* submitted), and represent the two most closely related families in that analysis, including the left-handed hermit crab *Clibanarius vittatus* Bosc, 1802 (superfamily Paguroidea, family Diogenidae) and the mole crab *Emerita analoga* Stimpson, 1857 (superfamily Hippoidea, family Hippidae).

(b) *DNA Extraction, Amplification and Sequencing*

Taxa were obtained either by diving, intertidal exploration, or through donations (see Table 3-1 for source material). In most cases it was the second pereopod (the first walking leg) that was removed, from either living, newly preserved (in 95% ETOH), or frozen crabs. The exoskeleton was then sliced, and muscle tissue was placed immediately in 95% ethanol (ETOH).

DNA was isolated from fresh, frozen or ethanol-preserved specimens by grinding small fragments of muscle tissue in a buffer (0.1M EDTA, 0.01M Tris, 1%SDS, ph7.5, ddH20, Palumbi *et al.* 1991), with extraction using phenol-chloroform-isoamyl alcohol mix and precipitation with 7.5M ammonium acetate and cold isopropanol, as described by

Palumbi *et al.* (1991). We obtained partial sequences from five genes, including one nuclear (28S rDNA) and four mitochondrial (16S rDNA, 12S rDNA, COI and COII). These genes span a range of mutation rates, from the slow evolving 28S gene to the rapidly evolving 3rd codon positions of the COI and COII genes.

Primers used in the polymerase chain reaction (PCR) amplification were: 28S rDNA 0I (GCGGAG GAAAAGAAACTAAC) and DIB (TAGCTTTAGAAGGAGTTTACC, both designed by R. DeSalle, pers. comm.). Most of the remaining mitochondrial primers were obtained from Simon *et al.* (1994) and are given with their official designations and aliases as in that paper: mitochondrial 12S rDNA (SR-N-14588, alias 12Sai and SR-J-14612, alias 12Sair); mitochondrial 16S rDNA (LR-N-13398, alias 16 Sar, LR-J-12887, alias 16 Sbr); mitochondrial COII (C2-N-2661, alias Barbara, C2-N-3138, alias Pierre mt 3138); mitochondrial COI (9H= GCAGGTAAAATSARAATATAAACTTC, modified from C1-N-2191, alias Nancy, and TRPLF= TAAACTAATAGCCTTCAAAGCT, designed de novo for this study). Amplification involved 40 seconds at 94 degrees, 1.5 minutes at 50 degrees, and 2.5 minutes at 72 degrees for 35 cycles. Cycle sequencing was performed using ABI Prism sequencing kits following the manufacturers instructions. Sequencing fragments were run on an ABI 377 DNA sequencer.

Sequences are deposited in Genbank under Accession numbers as found in Table 3-2.

(c) *Sequence Alignment and Phylogenetic Analysis*

Sequences were aligned using Clustal X (Thompson *et al.* 1997) with gap insertion and extension costs 10 and 5, respectively. The only length variation was observed in the 12S and 16S fragments, and regions of ambiguous homology were removed from the alignment.

Both parsimony and maximum likelihood analyses were applied to the aligned sequences using PAUP* (4.0b2, D.L. Swofford 1999). Parsimony analyses included equally weighted and unequally weighted parsimony. For maximum likelihood, we used the general time reversible models (determined to be the best-fit model using ModelTest, Posada & Crandall 1998), together with each of two methods for accommodating among-site rate variation: first using the site-rate approach (Swofford *et al.* 1996) by estimating different rates for each of five *a priori* partitions [28S, 12S, 16S, and two partitions from the combined COI and COII fragments (1st and 2nd codon positions, and 3rd codon positions)]; second by estimating the proportion of invariant sites and the alpha parameter of the gamma distribution from the data (the best-fit model according to ModelTest). Bootstrapping (Felsenstein 1985) was replicated 1000 times. This involved sampling with replacement, and was performed to ascertain the confidence for each hypothesized clade. Parsimony reconstructions were carried out using MacClade 4.0 (Maddison & Maddison 2000). Maximum likelihood reconstructions were not carried out because all of our characters had more than two character states.

3. RESULTS

(a) *Phylogenetic analysis*

The aligned sequences (Appendix 3-1, p 272) from the five genes were analyzed using heuristic searches with TBR branch swapping with the following criteria: (1) equally weighted parsimony; (2) maximum likelihood approaches to accommodate among-site variation (described above). All three analyses support the monophyly of the family Lithodidae (63-94% bootstrap support) and suggest that the Lithodidae are the sister-group of one lineage of hermit crabs (Fig. 3-1, label A). All analyses found a monophyletic subfamily Hapalogastrinae (53-70% support, label B), thereby uniting the two genera with soft abdomens and the lowest degree of carcinization (Fig. 3-1). The maximum likelihood analyses supported a monophyletic Lithodinae (51-64% bootstrap support), whereas parsimony marginally preferred a sister group relationship between *Cryptolithodes* and the Hapalogastrinae (36% vs. 31% for a monophyletic Lithodinae; label C). The most parsimonious solution for this relationships found virtually no support in either ML analysis (< 5% support). The remaining Lithodinae are strongly monophyletic (83-97% support, Figure 1, label D).

Within the monophyletic Lithodidae, several other clades were observed. All three analyses supported the monophyly of a clade defined by the presence of fully-articulated abdominal plates: *Rhinolithodes*. *Phyllolithodes*, *Lopholithodes*, *Glyptolithodes* and *Paralomis* (75-87% support, label D). All three analyses agreed on the monophyly of the genera *Hapalogaster*, *Cryptolithodes*, and *Lithodes*. However, evidence that *Paralithodes* is not monophyletic ranges (41%-72%) over two nodes.

To summarize, our phylogeny is for the most part well supported, with the exception of the placement of the genus *Cryptolithodes*. For the purposes of the character analyses to follow, we will use the placement preferred by both ML analyses (Figure 1), because support for the two alternative placements by parsimony was poorly supported (36% vs. 31% bootstrap).

(b) *Analysis of Character Evolution*: *Character analysis of the transition from hermit to lithodid*

Our analyses of character evolution were carried out only for the ingroup taxa. This was due to inadequate sampling of the extremely diverse sister group, Paguridae, which includes many members of the paraphyletic genus *Pagurus* as well as several unsampled genera (including *Elassochirus*, *Phymochirus* and *Discorsopagurus*, *Orthopagurus*, *Parapagoroides*). An enormous sampling effort will be necessary to fully comprehend pagurid relationships. In two of the four analyses (degree of carcinization and maximum size), hermit crabs in general are homogeneous enough to confirm our reconstructions based on lithodids alone.

(i) **Degree of carcinization**

Like Bouvier (1894, 1897) — whose work pioneered the study of the evolution of the crab-like form — we use the condition of the abdomen as a proxy for overall carcinization. Our ordered parsimony reconstruction supports a soft, asymmetric abdomen as the ancestral condition for the Lithodidae (Figure 2A), as Bouvier predicted. This is true even without using character information about the hermit crab outgroups, almost all of which also have soft, asymmetric abdomens. The ancestor is still asymmetric even if *Cryptolithodes* is placed as the sister group to the Hapalogastrinae as marginally preferred by parsimony. This phylogeny, according to ordered parsimony reconstruction methods, supports two independent origins of symmetric abdomens with fully articulated abdominal plates (Figure 2a). We chose ordered parsimony as we felt that the transition series, as proposed by Bouvier, was the most biologically plausible method of interpreting the data.

(ii) Maximum size

Representatives of all three basal genera within the Lithodidae are small-bodied (Figure 2b), supporting a hypothesis of a small ancestral lithodid. This conclusion, using ordered parsimony reconstruction, is greatly strengthened by inclusion of outgroup information, since hermit crabs in the Paguroidea are generally under 65 mm in width (Wolff 1961), and on average are much smaller. We chose ordered parsimony as we felt that a transition series, from small to large, was the most biologically plausible method of interpreting the data.

(iii) Minimal depth

Using ordered parsimony, all three basal genera within the Lithodidae are intertidal (Figure 2c), supporting an intertidal origin for the lithodids. The depth distribution for species within the hermit crab sister group is widely variable, requiring much greater sampling to assess its ancestral state. We chose ordered parsimony as we felt that a transition series, from shallow to deep waters was the most biologically plausible method of interpreting the data.

(iv) Geographical origin

A great majority of lithodids including all three basal genera (Figure 2d) are confined to the North Pacific, supporting a North Pacific origin for the Lithodidae. The

North Atlantic has been colonized by *Lithodes maja*, whose sister taxon *L. santolla* has colonized the Southern Hemisphere. The Southern Hemisphere was apparently colonized a second time by *Glyptolithodes* and *Paralomis*, which are nested within a North Pacific clade (Figure 2d). As with depth, much broader sampling is necessary in the hermit crab sister group to assess the site of origin. We used unordered parsimony reconstruction as no one plausible transition series was envisioned.

4. CONCLUSIONS

Our molecular analyses strongly support a monophyletic Lithodidae, suggesting that the transition from gastropod-shell dwelling hermit crabs to king crab happened only once within the Paguroidea. The monophyly of the Lithodidae is in agreement with morphological evidence uniting the group, including the lack of uropods as adults, which sets them apart from all other anomuran taxa (Bouvier 1894, Makarov 1962). We have investigated the circumstances of the transition from hermit to king crab both with ancestral reconstruction.

(a) *The transition from hermit crab to king crab*

The Lithodidae are only one of several groups of hermit crabs that have reduced or lost dependence on gastropod shells. Each of these lineages has shown varying degrees of carcinization, including a broad carapace and a relatively smaller abdomen than most hermit crabs (Borradaile 1916; Harms 1932; Wolff 1961; Reese 1968). Of these hermit crab descendants, the Lithodidae are by far the most crab-like, with complete carcinization— characterized by symmetric abdomens and fully articulated abdominal plates—having originated at least twice in the group (Fig. 3-2a).

Our phylogenetic analysis suggests that Bouvier (1894, 1897) was correct in arguing that the range in carcinization of extant lithodids reflects a gradual transition from the soft, asymmetrical abdomens of the hermit crabs to the symmetrical abdomens with fully articulated abdominal plates (Fig. 3-2a). This observed progression— in addition to the phylogenetic placement of the Lithodidae within several groups of hermit crabs

—strongly supports Bouvier's theory that the lithodids are descended from hermit crab ancestors.

The three basal genera within the Lithodidae (here, *Oedignathus*, *Hapalogaster* and *Cryptolithodes*) share characteristics that help to reconstruct the circumstances of the loss of dependence on gastropod shells in the ancestral lithodid. Representatives of all three genera are small, intertidal, and currently restricted to the North Pacific Ocean (Figure 2b-d).

The origin of the Lithodidae most likely occurred in the North Pacific between 13-25 MYA as suggested by molecular (Cunningham *et al.* 1992) and fossil evidence (Feldmann 1998). Climatic changes and geographic rearrangements during the last 20 MY allowed their radiation through to the Atlantic, Arctic and Pacific Oceans (Vermeij 1991). Interestingly, the radiation of the Lithodidae took place in the context of the radiation of kelp (Laminariales) in the North Pacific 16-30 MYA (Saunders & Druehl 1992). *Oedignathus inermis*— which belongs to one of the two most basal lithodid genera and is certainly the least carcinized lithodid — is usually found in the canopy cover and under hold-fasts of the kelp *Hedophyllum sessile* (Zaklan pers. obs.). This is consistent with the hypothesis that kelp cover may have helped the ancestral lithodid compensate for the lack of protection afforded by the gastropod shell. The dramatic increase in size found within the genera *Paralithodes* and *Lithodes* was associated with movement to deeper water, beyond the protection of the kelp canopy cover.

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Table 3-1. Anomuran taxa, collector, location, depth and maximum size

species	collector	location: depth (m)	general distribution & depth (m)	maximum size (mm)*
family Lithodidae	*sub-family Hapalogastrinae*			
Hapalogaster dentata, (de Haan 1849)	Seiji Goshima	Hakodate Bay, Hokkaido, Japan (41°44'N, 140°36'E): intertidal	northwest Pacific Ocean – Japan, Russia (Makarov 1962) and Korea (Kim 1970); intertidal to subtidal (Goshima *et al.* 1995)	male CL=21.5, female CL=15.6 (Goshima *et al.* 1995)
H. mertensii, Brandt 1850	Stefanie Zaklan	Seapool Rocks, Trevor Channel, Barkley Sound, B.C., Canada (43°53'N, 125°20' W): 11	northeast Pacific Ocean - Atka, Alaska to Puget Sound, Washington, U.S.A. (Makarov 1962); intertidal to 55 (Hart 1982)	male CL=25, CW=25; female CL=22, CW=24 (Hart 1982)
Oedignathus inermis, (Stimpson 1860)	Stefanie Zaklan	Seppings Island, Deer Group, Barkley Sound, B.C., Canada (43°53'N, 125°20' W): intertidal	north Pacific Ocean – Japan, Korea, Russia; west to Unalaska, Alaska south to California, U.S.A. (Makarov 1962; Kim 1970); intertidal to 15 (Hart 1982)	male CL=30, CW=25; female CL= 22, CW= 20 (Hart 1982)
	sub-family Lithodinae			
Cryptolithodes sitchensis, Brandt 1853	Stefanie Zaklan	Trevor Channel, Barkley Sound, B.C., Canada (43°53'N, 125°20' W): 6.8	northeast Pacific Ocean - Sitka, Alaska to Point Loma California, U.S.A.; intertidal to 17 (Hart 1982)	male CL=65, CW= 90; female CL=68, CW=87 (Hart 1982)
C. typicus, Brandt 1848	Stefanie Zaklan	Seapool Rocks, Trevor Channel, Barkley Sound, B.C., Canada (43°53'N, 125°20' W): 12	northeast Pacific Ocean – Alaska to Monterey, California, U.S.A. (Makarov 1962); intertidal to 45 (Hart 1965)	male CL=41, CW= 75; female CL=49, CW=80 (Hart 1982)

Glyptolithodes cristatipes, (Faxon 1893)	Donald Cadien	Redondo Submarine Canyon, L.A., California, U.S.A. (33°49' N, 118°27' W): 305	east Pacific Ocean - Iquique, Chile (Bahamonde 1967) north to California (this study); 245-800 (Bahamonde 1967; Hart 1974)	male CL =85.5, CW=98; female CL =89.5 (Haig 1974)
Lithodes aequispinus, Benedict 1894	Jun Sasaki	Kitamiyamato Bank, (Abashiri) Japan (44°15' N, 144°05' E): 150-214	north Pacific Ocean –Japan, Bering Sea to Alaska, U.S.A. (Makarov 1962) to central B.C., Canada (Hart 1982); 77-900 (Hart 1982; Jewett *et al.* 1985)	male CL=220; female CL=192 (Hiramoto & Sato 1970)
L. maja, (Linnaeus 1758)	Michael Eagles and Alan Reeves	southwest Nova Scotia, Canada (43°41'N, 64° 20'E): 175	north Atlantic – west Atlantic, North Sea, Barents Sea, Iceland and Greenland; east Atlantic, Nova Scotia, Canada to Gulf of Maine, U.S.A. (Makarov 1962); 4-790 (Williams 1984; Macpherson 1988)	male CL=110, CW=113; female CL=97, CW=95 (Macpherson 1988)
L. santolla, (Molina 1782)	Gustavo Lovrich	Beagle Channel, Argentina (55°S, 67°W): 12	southeast Pacific and southwest Atlantic Oceans - Magellan Straight, Chile north to 42°S (Takeda & Hatanaka 1984); Tierra del Fuego, Argentina north to Uruguay (34°S; Vinuesa *et al.* 1996); subtidal to 700 (Boschi *et al.* 1984)	male CL=198, CW=250 (Boschi *et al.* 1984); female CL=142, CW=140 (Macpherson 1988)
Lopholithodes mandtii, Brandt 1848	Stefanie Zaklan	Execution Rocks, Barkley Sound, B.C., Canada (43°53'N, 125°20' W): 10	northeast Pacific Ocean - Sitka, Alaska to Montery, California, U.S.A. (Makarov 1962); subtidal to 137 (Hart 1982)	male CL=200, CW=270 (Hart 1982); CW $\geq$ 300 (Jensen 1995)
Paralithodes brevipes, (A. Milne Edwards & Lucas 1841)	Jun Sasaki	Habomai, Nemura, Japan (43°20' N, 145°45' E): 1	north Pacific Ocean - Sea of Japan, southern Bering Sea and Aleutian Islands; intertidal to 50 (Makarov 1962)	male CL= 95, CW= 102 (Sakai 1976); female CL=118 (Sato & Abe 1941)

P. camtschaticus, (Tilesius 1815)	Jun Sasaki	Kitamiyamato Bank, (Abashiri) Japan (44°15' N, 144°05' E): 150-214	north Pacific Ocean – Korea; Sea of Japan; Bering Sea; Aleutian Islands, Alaska; central B.C., Canada (Kim 1970; Makarov 1962); 3-366 (Marukawa 1930, Jensen 1995)	male CL=227, CW=283; female CL=195, CW= 213 (Powell & Nickerson 1965)
Paralomis granulosa, (Jacquinot 1852)	Gustavo Lovrich	Beagle Channel, Argentina (55°S, 67°W): 20	southeast Pacific and southwest Atlantic Oceans - Rio de Janeiro, Brazil to Falkland Islands, U.K. through the Magellanic district to Chiloe Island, Chile; intertidal to 100 (Takeda & Hatanaka 1984)	CL=120 (Vinuesa *et al.* 1996); CW= 95 (Takeda & Hatanaka 1984)
Phyllolithodes papillosus, Brandt 1848	Stefanie Zaklan	Ohiat Island, Deer Group, Barkley Sound, B.C., Canada (43°53'N, 125°20' W): 10	northeast Pacific Ocean - Dutch Harbor, Alaska to Montery, California, U.S.A. (Makarov 1962); subtidal to 183 (Hart 1982)	male CL=90, CW=90; female CL=50, CW=60 (Hart 1982)
Rhinolithodes wosnessenskii, Brandt 1848	James Orr and Mark Wilkins	Alaska, U.S.A. R/V Vesteraalen (52.00° N, 176.76° E): 102	northeast Pacific Ocean - Kodiak, Alaska to California, U.S.A. (Makarov 1962); 6-73 (Hart 1982) to 102 (this study)	male CL=59, CW=64; female CL=50, CW=57 (Hart 1982)
family Paguridae				
Labidochirus splendescens, Owen 1839	Cliff Cunningham	Bering Sea, Alaska: 50	north Pacific Ocean – Japan; Alaska to Puget Sound, Washington, U.S.A.; 3-412 (Jensen 1995)	CL≤ 28 (Jensen 1995)
Pagurus bernhardus, Benedict 1892	John Wares	Roscoff, France: intertidal	northeast Atlantic Ocean - intertidal (Hayward & Ryland 1995)	CL=35 (Hayward & Ryland 1995)
P. hirsutiusculus, Dana 1851	Stefanie Zaklan	Scott's Bay, Trevor Channel, Barkley Sound, B.C., Canada (43°53'N, 125°20' W): intertidal	northeast Pacific Ocean - Pribilof Islands, Alaska to Monterey, California; upper intertidal rarely to 110 (Jensen 1995)	CL=19 (Jensen 1995)

P. longicarpus, Say 1817	Cliff Cunningham	Beaufort, N.C. U.S.A.: intertidal	northwest Atlantic Ocean – Nova Scotia, Canada to Florida and Gulf of Mexico, U.S.A.; intertidal to 45 (Gosner 1978)	CL=9 (Gosner 1978)
outgroup				
Clibanarius vittatus, Bosc 1802	Cliff Cunningham	Wilmington Beach, N.C., U.S.A.: intertidal	northwest Atlantic Ocean – Virginia to North Carolina, U.S.A.; shallow water (Gosner 1978)	CL=31 (Gosner 1978)
Emerita analoga, Stimpson 1857	Cliff Cunningham	Beaufort, N.C. U.S.A.: intertidal	east Pacific Ocean - Kodiak Island, Alaska to Baja California, U.S.A.; Peru, Chile and Argentia; intertidal (Morris *et.al.* 1980)	CL=12 (Zaklan pers. obs.)

*CL=carapace length; CW=carapace width; R=rostrum

Table 3 - 2. Accession numbers from GenBank.

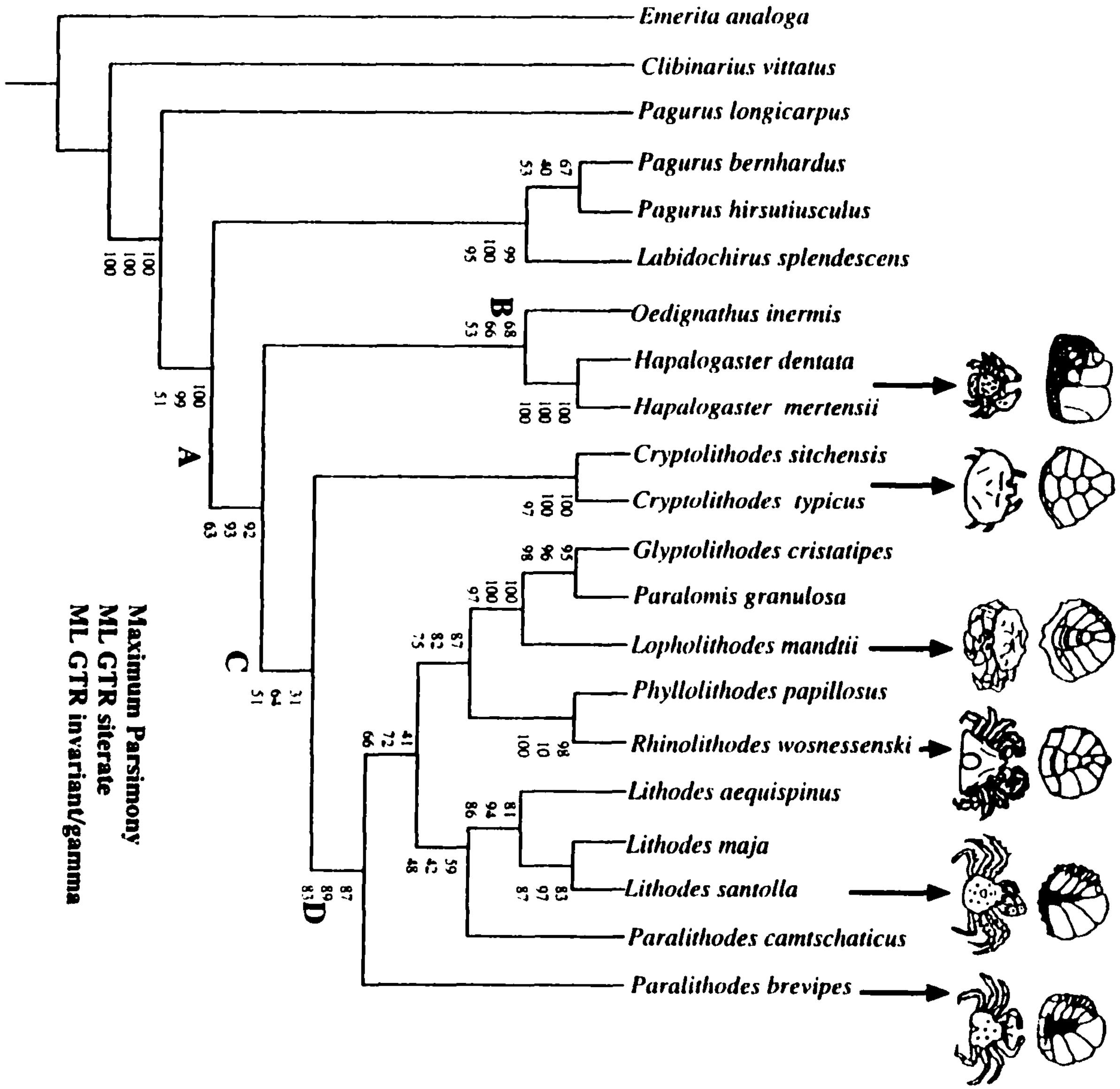
Species	12S	16S	COI	COII	28S
Emerita analoga	AF425341	AF425322	AF425361		AF425302
Clibanarius vittatus	AF425321	AF425323	AF425362	AF425362	
Pagurus bernhardus	AF425314	AF425335	AF425314	AF425374	AF425354
Pagurus hirsuticusulus	AF425315	AF425336	AF425315		AF425355
Pagurus longicarpus					AF425343
Labidochirus splendescens	AF425311	AF425332	AF425371	AF425371	AF425351
Cryptolithodes sitchensis	AF425303	AF425324	AF425363	AF425363	AF425344
Cryptolithodes typicus	AF425304	AF425325	AF425364	AF425364	AF425345
Glyptolithodes cristatipes	AF425305	AF425326	AF425365	AF425365	AF425346
Hapalogaster dentata	AF425306	AF425327	AF425366	AF425366	AF425347
Hapalogaster mertensii	AF425307	AF425328	AF425367	AF425367	AF425348
Lithodes aequispinus	AF425308	AF425329	AF425368	AF425368	AF425349
Lithodes maja	AF425309	AF425330	AF425369	AF425369	AF425350
Lithodes santolla	AF425310	AF425331	AF425370	AF425370	
Lopholithodes mandtii	AF425312	AF425333	AF425372	AF425372	AF425352
Oedignathus inermis	AF425313	AF425334	AF425373	AF425373	AF425353

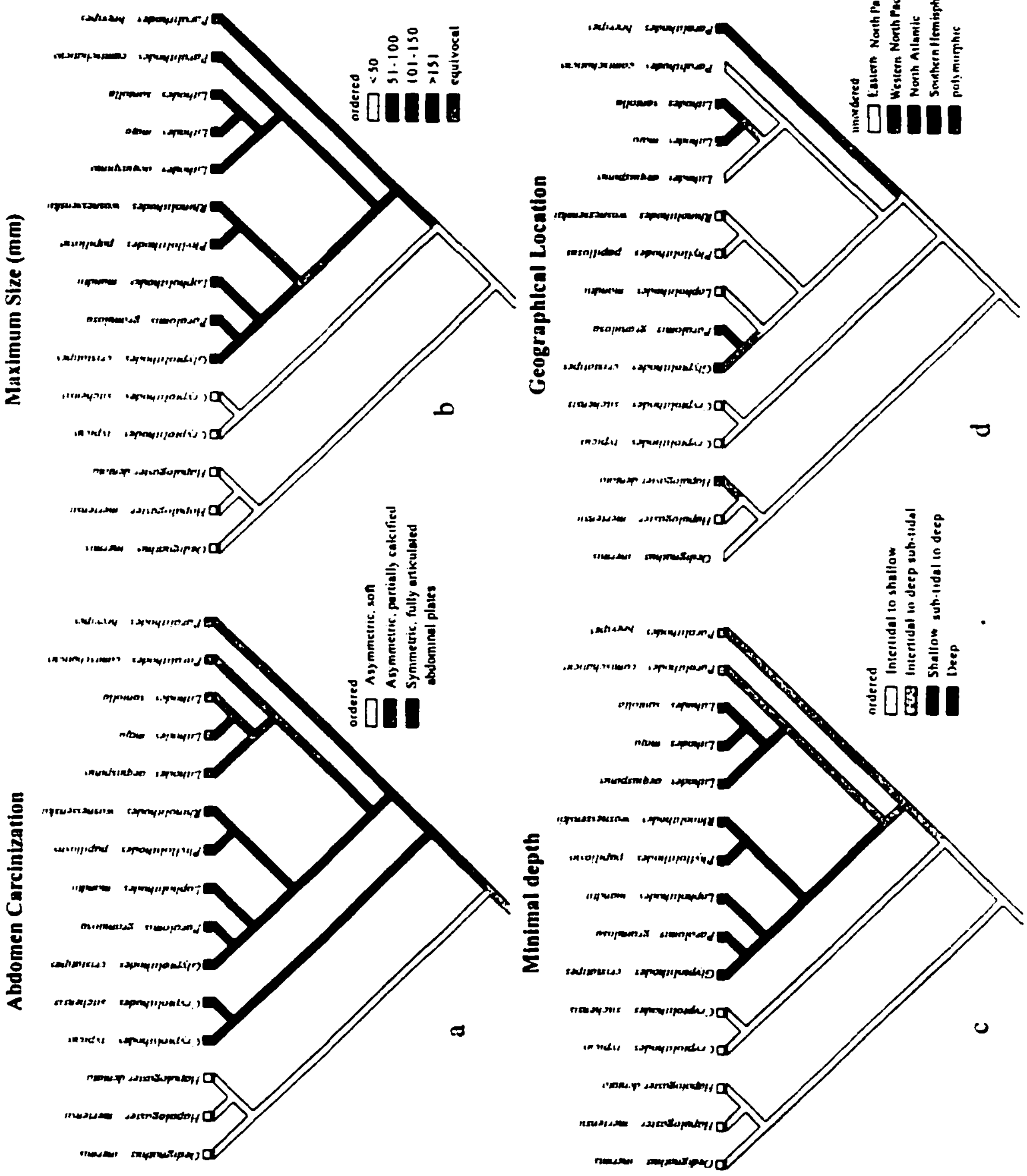
Paralithodes brevipes	AF425316	AF425337	AF425375	AF425375	AF425356
Paralithodes camtschaticus	AF425317	AF425338	AF425376	AF425376	AF425357
Paralomis granulosa	AF425318	AF425339	AF425377	AF425377	AF425358
Rhinolithodes wosnessenskii	AF425320		AF425379	AF425379	AF42536
Phyllolithodes papillosa	AF425319	AF425340	AF425378	AF425378	AF425359

FIGURE LEGENDS

Figure 3-1: The most parsimonious phylogeny based on the combined analysis of partial sequences from four mitochondrial (12S, 16S COI, COII) and one nuclear (28S) data sets. Numbers at nodes are listed vertically and represent bootstrap values for each of the three analyses: maximum parsimony, maximum likelihood siterate and maximum likelihood invariant gamma. Letters at nodes represent the following: A= family Lithodidae, B= subfamily Hapalogastrinae, C= subfamily Lithodinae, D= subfamily Lithodinae without *Cryptolithodes*. Original drawings of abdominal tergites (top) and dorsal carapaces (bottom) by SDZ or modified from Sakai 1976; Morris *et al.* 1980; or Dawson & Yaldwyn 1985.

Figure 3-2: Parsimony reconstructions using MacClade 4.0. All analyses were ordered with the exception of geographical location. All data from Table 3-1: A= degree of carcinization as reflected by calcification and asymmetry of the abdomen; B= maximum size across carapace; C= depth range; D= geographical location.


Emerita analoga
Clibinarius vittatus
Pagurus longicarpus
Pagurus bernhardus
Pagurus hirsutiusculus
Labidochirus splendescens
Oedignathus inermis
Hapalogaster dentata
Hapalogaster mertensii
Cryptolithodes sitchensis
Cryptolithodes typicus
Glyptolithodes cristatipes
Paralomis granulosa
Lopholithodes mandtii
Phyllolithodes papillosus
Rhinolithodes wosnessenski
Lithodes aequispinus
Lithodes maja
Lithodes santolla
Paralithodes camtschaticus
Paralithodes brevipes
A
B
C
D
100 100 100
67 40 53
99 100 95
68 66 53
100 100 100
100 99 51
92 93 63
100 100 97
95 96 98
100 100 97
87 82 75
98 10 100
31 64 51
41 72 66
81 94 86
59 42 48
83 97 87
87 89 83
Maximum Parsimony
ML GTR siterate
ML GTR invariant/gamma


Abdomen Carcinization
ordered
Asymmetric, soft
Asymmetric, partially calcified
Symmetric, fully articulated abdominal plates
a
Maximum Size (mm)
ordered
< 50
51-100
101-150
>151
equivocal
b
Minimal depth
ordered
Intertidal to shallow
Intertidal to deep sub-tidal
Shallow sub-tidal to deep
Deep
c
Geographical Location
unordered
Eastern North Pacific
Western North Pacific
North Atlantic
Southern Hemisphere
polymorphic
d
Paralithodes brevipes
Paralithodes camtschaticus
Lithodes santolla
Lithodes maja
Lithodes aequispinus
Rhinolithodes wosnessenskii
Phyllolithodes papillosus
Lopholithodes mandtii
Paralomis granulosa
Glyptolithodes cristatipes
Cryptolithodes sitchensis
Cryptolithodes typicus
Hapalogaster dentata
Hapalogaster mertensii
Oedignathus inermis

Appendix 3-1a: Mitochondrial gene 12S aligned

```
[                                     10        20        30        40        50        60        70        80        90       100       110       120]
[                                      .         .         .         .         .         .         .         .         .         .         .         .]

Emerita_analoga               AAAATTAATAACATTAT-ACAATCTGACTACACGAT--TAATTTT-TTATTAA--A---GTTAACTATAA---CCAATTTTTTATT-ACTATCTCTTAAAGTATAACCGCGGCGGCTGG
Clibanarius_vittatus          AAATTTAATATTATTGTTTATATTCTGAAAAAAATAACCTAATTAACTACTTAACCCA----AAACTAAAC--ACCAAAACCTATTTTACTTCACCTCTAAGTATAACCGCGTCTGCTGG
Pagurus_longicarpus           AAATTT-TTATTATTCCC-AAAATATTATAAGGATAA--TAAAAAT-CAATAAATCAAATTTATACTACAC--ACTAATTTATATTT-ACTCACCCTTTAAGTTTAACCGCGACTGCTGG
Pagurus_bernhardus            AAAATCATTACTATTATT-AAATTCTGAAAAAAATAA--TAAATTT-TAGTTAACAAATAACTTACTATAC-TACCAAATTATATTT-ATTTACCCCCTAAGTATAACCGCGACTGCTGG
Pagurus_hirsuticusulous       AAAATTATTATTATTATT-AAATTCTGAAAAAAATAA--TAAATTT-TAATTAATAAGTAATTTACTATATA-ACCAAATCATATTT-ATTTACCCTCTAAGTATAACCGCGACTGCTGG
Labidochirus_splendescens     AAAATTATTATTATTATT-AAATTCTGAAAAAAATAA--TAAATTT-TAATTAACAAATAATTTACTATAGA-ACCAAATTATATTT-ATTCACCCCCTAAGTATAACCGCGACTGCTGG
Oedignathus_inermins          AAAATTATTATTATTATT-AAATTCTGAAAAAAATAA--TAAGTTT-TAATTAACTAATAATTTACTATAAATACCAAATTATATTT-ATTTACCCTCTAAGTATAACCGCGACTGCTGG
Hapalogaster_dentata          AAAATTATTATTATTATT-AAATTCTGAAAAAAATAA--TAAATTT-TAATTAACTTATAATTTACTATAAACACCAAATTATATTT-ATTTACCCTTTAAGTATAACCGCGACTGCTGG
Hapalogaster_mertensii        AAAATTATTATTATTATT-AAATTCTGAAAAAAATAA--TAAATTT-TTATTAACCAATAATTTACTATAAATACCAAATTATATTT-ATTTACCCTTTAAGTATAACCGCGACTGCTGG
Cryptolithodes_sitchensis     AAATT-ATTATTATGATT-AAATTCTATAAAAAATAA--TAAATTT-TAGTTAACTAACAGTCTACTATAAT-ACCAAATTGTATTT-ATTTACCCCCTAAGTATAACCGCGACTGCTGG
Cryptolithodes_typicus        AAAATTATTATTATAATT-AAATCCTGAAAAAAATAA--TAAGTTT-TAGTTAACTAATAATCTACTATAAC-ACCAAACTGTGTTT-ATTCACCCCCTAAGTATAACCGCGACTGCTGG
Glyptolithodes_cristatipes    AAATTTATTATTATAATT-AAATTCTGAAAAAAATAA--TAATTTT-TATTTAACTAATAATTTACTATAAATACCAAATTGTATTT-ATTTACCCCTTAAGTATAACCGCGACTGCTGG
Paralomis_granulosa           AAATTTATTATTATAATT-AAATTCTATAAAAAATAA--TAAATTT-TATTTAACTAATAATTTACTATGAA-ACCAAATTGTATTT-ATTTACCCTCTAAGTATAACCGCGACTGCTGG
Phyllolithodes_papillosus     AAACTTATTATTATAATT-AAATTCCGAAAAAAATAA--TAAGTTT-TATTTAACTAATAATTTACTATAAT-ACCAAATTGTATTT-ATTTACCCCCTAAGTATAACCGCGACTGCTGG
Lopholithodes_mandtii         AAAATTATTATTATAATT-AAACTCCGAAAAAAATAA--TAAATTT-TATTTAACTAATAATTTACTATAA-TACCAAATTGTATTT-ATTTACCCCTTAAGTATAACCGCGACTGCTGG
Paralithodes_brevipes         AAATTTATTATTATAATT-AAATACCGAAAAAAATAA--TAAATTT-TATTTAACTAATAATTTACTATAAC-ACCAAATTATATTT-ATTTACCCTCTAAGTATAACCGCGACTGCTGG
Paralithodes_camtscahticus    AAATT-ATTATTATAATT-AAATCCCGAAAAAAATAA--TAATATA-TATTTTACTAATAATTTACTATAAATACCAAATTATATTT-ATTTACCCTCTAAGTATAACCGCGACTGCTGG
Lithodes_maja                 AAAATTATTATTATAATT-AAATTCTGAAAAAAATAA--TAATTTT-TATTTAACTAATAATTTACTACAA-TACCAAATTGTATTT-ATTTACCCTTTAAGTATAACCGCGACTGCTGG
Lithodes_santolla             AAAATTATTATTATAATT-AAATTCCGTAAAAAATAA--TAAATTT-TATTTAACTAATAATTTACTATAAATACCAAATTGTATTT-ATTTACCCTTTAAGTATAACCGCGACTGCTGG
Lithodes_aequispinus          AAAATTATTATTATAATT-AAATTCCGAAAAAAATAA--TAAATTT-TATTTAACTAATAATTTACTATAAT-ACCAAATTGTATTT-ATTTACCCTTTAAGTATAACCGCGACTGCTGG
Rhinolithodes_wosnessenskii   ----------------------------AAAAAATAA--TAAGTTT-TATTTAACTAATAATTTACTATAA-CACCAAATTGTATTT-ATTTACCCTTTAAGTATAACCGCGACTGCTGG
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[                                                        130        140        150        160        170        180        190        200        210        220        230        240]
[                                                          .          .          .          .          .          .          .          .          .          .          .          .]

Emerita_analoga                CACAAGATTTTGCCAGAGAAATTATGATA-ACCAGATCTAGCTATAACTAATAATATTATATATTGAAAATTTTATTTTTAAATTT------AATTAA-ACTGAAGTTTCCATATACATT
Clibanarius_vittatus           CACAAATTTTGGACAGATGTTTCTTAATTTACTCTGTCTTACCTTAATAAGTAATATYATACACTGAGAAAAYCCCAATTTAATCTTTAAGCCTAGATCATTAAAATTTTCATATGCTAT
Pagurus_longicarpus            CACAAATTTTAGCCAGGATTTAAATAGTT-ACCAATTCTAATTTTAATTAATAAAATTAAATACTGAGATTTATTTTTTTAAATTTATATA-AAGGAGCACAATTATTTTCATGTATTTA
Pagurus_bernhardus             CACAAAATTTAGTCAGAATTAAAATGATTCACCAATTCTAATTTTAATTAATAAAATTAAATACTGAGATTTATTCCTTTTAATTTATATA-AAGGAACACTAAAATTTTCATGTATTTT
Pagurus_hirsuticusulous        CACAAATTTTAGTCAGAATTAAAATGATT-ACCAATTCTAATTTTAATTAATAAAATTAAATACTGAGATTTAATTTTTTTAATTATAATA-AAGGAACACTA-AATTTTCATGTATTTT
Labidochirus_splendescens      CACAAATTTTAGTCAGAATTAAAATGATA-GCCAATTCTAATTTTAATTAATAAAATTAAATACTGAGATTTATTATTTTTTAATTTAATA-AAGGAACACTAAAATTTTCATGTATTAT
Oedignathus_inermins           CACAAATTTTGGTCAGGATTTAAATGATT-ACCAATTCTAATGTTAATTAATAATACTGAATACTGAGATTTA-ATTTTTAAATTTATATA-AGGGAACACTATAATTTTCATGTATTTT
Hapalogaster_dentata           CACAAATTTTGGTCAGGATTAAAATGATT-ACCAATTCTAATTTTAATTAATAAAATTAAATACTGAGATTTACATTTTTTAATTTATATA-AAGGAACACTATAATTTTCATGTATTTT
Hapalogaster_mertensii         CACAAATTTTGGTCAGGATTAAAATGATT-ACCAATTCTAATTTTAATTAATAAAATTAAATACTGAGATTTATATTTTTTAATTTATATA-AAGGAACACTATAATTTTCATGTATTTT
Cryptolithodes_sitchensis      CACAAATTTTAGTCAGGATTAAAATGATT-ACCAACTCTAATTTTAATTAATAAAACTAAATACTGAGATTAATGTTTTTTAATTTAAATA-AAAGAACACTATAATTTTCATGTATTTT
Cryptolithodes_typicus         CACAAATTTTAGTCAGGATTAAAATGACC-ACCAATTCTAATTTTAATTAATAAAATTAAATACTGAGACTAAAGTTTTTTAATTTATATA-AAAGAACACTATAATTTTCATGTATTTT
Glyptolithodes_cristatipes     CACAAATTTTAGTCAGGATTAAAATGATT-ACCAATTCTAATTTTAATTAATAAAATTAAATACTGAGATTTATATTTTTTAATTTTAA---AAGGAACACTATAATTTTCATGTATTTT
Paralomis_granulosa            CACAAATTTTAGTCAGGATTAAAATGACT-ACCAATTCTAATTTTAATTAATAAAATTAAACACTGAGATTTATATTTTTTAATTTTGA---AAGGAACACTATAATTTTCATGTATTTT
Phyllolithodes_papillosus      CACAAATTTTAGTCAGGATTAAAATGATT-ACCAATTCTAATTTGAATTAATAAAACTAAATACTGAGATTTATATTTTTTAATTTTTATA-AAGGAACACTATAATTTTCATGTATTTT
Lopholithodes_mandtii          CACAAATTTTAGTCAGGATTAAAATGATT-ACCAATTCTAATTTTAATTAATAAAATTAAATACTGAGACTTATATTTTTTAATTTTTATA-AAGGAACACTATAATTTTCATGTATTTT
Paralithodes_brevipes          CACAAATTTTAGTCAGGATTAAAATGATT-ACCAATTCTAATTTTAATTAATAAAATTAAATACTGAGATTTATATTTTTTAATTTTTATA-AAGGAACACTATAATTTTCATGTATTTT
Paralithodes_camtscahticus     CACAAATTTTAGTCAGGATTAAAATGATT-ACCAATTCTAATTTTAATTAATAAAATTAAATACTGAGACTTATATTTTTTAATTTTTATA-AAGGAACACTATAATTTTCATGTATTTT
Lithodes_maja                  CACAAATTTTAGTCAGGATTAAAATGATT-ACCAATTCTAATTTTAATTAATAAAATTAAATACTGAGATTTATACTTTTTAATTTTTATA-AAGGAACACTATAATTTTCATGTATTTT
Lithodes_santolla              CACAAATTTTAGTCAGGATTAAAATGATT-ACCAATTCTAATTTTAATTAATAAAATTAAATACTGAGATTTATATTTTTTAATTTT-AT--AAGGAACACTATAATTTTCATGTATTTT
Lithodes_aequispinus           CACAAATTTTAGTCAGGATTAAAATGATT-ACCAATTCTAATTTTAATTAATAAAATTAAATACTGAGACTTATATTTTTTAATTTTTATA-AAGGAACACTATAATTTTCATGTATTTT
Rhinolithodes_wosnessenskii    CACAAATTTTAGTCAGGATTAAAATGATT-ACCAATTCTAATTTTAATTAATAAAATTAAATACTGAGACTTATATTTTTTAATTT-TATA-AAGGAACACTATAATTTTCATGTATTTT
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[                                       250       260       270       280       290       300       310       320       330       340       350       360]
[                                        .         .         .         .         .         .         .         .         .         .         .        .]

Emerita_analoga                 TTTAACATAAAGCAATAA-TTTTAAGCAAGAATCAAACTTTACTAAAATATAGTAGTATAAATATTTTAAATAAGATTTTAGGTTAATTTAAACCCTCAGCCTTCAAAGCT---GAAATT
Clibanarius_vittatus            T-AACTAAAAAGCAAACA-TTACAAGCAAGAATCAAACTTAACCCTATTACACTYT-A-AATCAAAAAAGTTAAGACTAATACTTT-TATTAA--AA--GCTTTGAAGGCTTTCGGTTTA
Pagurus_longicarpus             T-AACTATATTATAAAAA-TCATAAGCAAGAA-CAAACTTTATGTTTTTATATAC--A-AAATATACCTTTAGAGATTTTAAGTTA-TATAAACTAATAGCCTTCAAAGCTATAAAAATA
Pagurus_bernhardus              TCAATCATAATATAAAAA-CTACA-AGCAGAATCAAACTTCAAGCTATTCAATAATTA-AAATACAGATTATGAGATTTTAAGTTA-TATAAACTAATGGCCTTCAAAGCCATAAAAATA
Pagurus_hirsuticusulous         TCAATCATAGTATAAAAACTTCAA-GCAAGAATCAAACTTCAAGCTATTAAACAAT-A-ATCTATAATTTATGAGATTTTAAGTTA-TAT------------------------------
Labidochirus_splendescens       TCAATCATAATATAAAAA-TTACA-ACAAGAATCAAACTTCAAGCTATTAGATAAT-A-AAACATAACTAATGAGATTTTAAGTTA-TATAAACTAATGGCCTTCAAAGCCATAAAAATA
Oedignathus_inermins            TTAATCATAATATAAAAA-ATATA-ACAAGAATCAAACTTTAAGCTGTTATGTAA--A-AAACATAACTAATGAGATTTTAAGTTA-TAAAAACTAATGGCCTTCAAAGCCATAAAAATA
Hapalogaster_dentata            TTAATCATAATATAAAAA-TTATA-ACAAGAATCAAACTTTAAACTGTTATACAA--G-AAT-GTAACTAATGAGATTTTAAGTTA-TATAAACTAATGGCCTTCAAAGCCATAAAAATA
Hapalogaster_mertensii          TTAATCATAATATAAAAA-TTATA-GCAAGAATCAAACTTTAAGCTGTTGTACAA---AAACGTAACTAATGAGATTTTAAGTTA-TATAAACTAATGGCCTTCAAAGCCATAAAAATA
Cryptolithodes_sitchensis       TCAATCATAATATAAACA-CCAAA-GCAAGAATCAAACTTTAAGCTATTGTACAA--A-ACAC--AACAAATGAGATTTTAAGTTA-TAAAAACTAGTAGCCTTCAAAGCCACAAAAATA
Cryptolithodes_typicus          TTAGCCATAATATAAAAA-CTATA-ACAAGAATCAAACTTTAAAATATTATGCAAA-A-AAACACAACTAATGAGATTTTAAGTTA-TATAAACTAATGGCCTTCAAAGCCATAAAAATA
Glyptolithodes_cristatipes      TTAATCATAATATAAAAA-ATATA-ACAAGAATCAAACTTAAAACTATTATACAA--A-GAATGTAACTAATGAGATTTTAAGTTA-TATAAACTAATGGCCTTCAAAGCCATAAAAATA
Paralomis_granulosa             TTAGCCATAATATAAAAA-TTATA-GCAAGAATCAAACTTAAAGCTATTATACAA--A-AAACGTAACTAATGAGATTTTAAGTTA-CATAAACTAATGGCCTTCAAAGCCGTAAAAATA
Phyllolithodes_papillosus       TTAATCATAATATAAAAA-TTATA-GCAAGAATCAAACTTAAAGCTATTATCCAA--A-AAACGTAACTAATGAGATTTTAAGTTA-TATAAACTAATAGCCTTCAAAGCCATAAAAATA
Lopholithodes_mandtii           TTAATCATAATATAAAAA-TTATA-AGCAGAATCAAACTTAAAGCTATTATACAA--A-AAACGTAACTAATGAGATTTTAAGTTA-TACAAACTAATGGCCTTCAAAGCCATAAAAATA
Paralithodes_brevipes           TTAATCATAATATAAAAA-TCATA-GCAAGAATCAAACTTAAAGCTATTATACAA--A-AATATTACT-AATGAGATTTTAAGTTA-TAAAAACTAATAGCCTTCAAAGCTATAAAAATA
Paralithodes_camtscahticus      TTAATCATAGTATAAAAA-TTATA-GCAAGAATCAAACTTAAAGCTATTATACAA--A-AAACGTAATTAATGAGATTTTAAGTTA-TATAAACTAATGGCCTTCAAAGCCATAAAAATA
Lithodes_maja                   TTAATCATAATATAAAAA-TTATA-ACAAGAATCAAACTTAAAACTATTATACAA--A-AAACGTAATTAATGAGATTTTAAGTTA-TATAAACTAATGGCCTTCAAAGCCATAAAAATA
Lithodes_santolla               TTAATCATAATATAAAAA-TTATA-GCAAGAATCAAACTTAAAAATATTATACAA--A-AAACGTAACTAATGAGATTTTAAGTTA-TATAAACTAATGGCCTTCAAAGCCATAAAAATA
Lithodes_aequispinus            TTAATCATAATATAAAAA-TTATA-GCAAGAATCAAACTTAAAGCTATTATACAAA-A-AA-CGTAACTAATGAGATTTTAAGTTA-TATAAACTAATGGCCTTCAAAGCCATAAAAATA
Rhinolithodes_wosnessenskii     TTAATCATAATATAAAAA-TTATA-ACAAGAATCAAACTTAAAGCTATTATACAA--A-AAACGTANCTAATGAGATTTTCAGTTA-TATAAACTAATGGCCTTCAAAGCCATAANNATA
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[                                              370       380       390       400       410       420       430       440       450       460       470       480]
[                                                .         .         .         .         .         .         .         .         .         .         .        .]

Emerita_analoga                 AGAAATAGATTCTAAATCTTA---TATGTACTGGGATCCCACCAGAAACCTAAAAGATCAAAACTTTTTATGC-TCT-ACACCAACATATATTAAGCTGTAGTGCTTC----------A
Clibanarius_vittatus            ATTAA---CCTAAAACCTTA----TATGGAAGGGAATTTCACCT-TATCCTAGAAGATCAAAACTTCTTGTGCTTTT-ACACCATCATATAACACCCCCCAGTAAATCTCAGTGAGTAC
Pagurus_longicarpus             AGTAAACTCTTTTAAATCTTA-TTATATGTAAAGGATTCTCACCA-AAACCTAGAAGGTCAAAGCTTCTTATGCATTT-ACACTAACATATATTAAGCCTCAGTAATTT----------A
Pagurus_bernhardus              AGTAAATTCTTTTAAATCTTATTTATATGTAAGGGATTTTCACCA-AAACCTAAAAGATCAAAACTTTTTATGCATTTAACACTAACATATAATAAGCTTTAGCGACTT---------AA
Pagurus_hirsuticusulous         ---------TTTTAAATCTTATTTATATGTAAAGGACTTTCACCA-AAACTTAAAAGATCAAAACTTTTTGTGCATTTAACACTAACATATAT-AAGCTTTAGCGATTC---------AA
Labidochirus_splendescens       AGTAAATTCTTTTAAATCTTATTTACATGTAAGGGACTTTCACCA-AAACCTAAAAGATCAAAACTTTTTATGCACTTAACACTAACATGTAT-AAGCTTTAGCGATTT---------AA
Oedignathus_inermins            AGTAAATTCTTTTAAATCTTATTTATATGTAAAGGACTTTCACCA-AAACCTAAAAGATCAAAACTTTTTGTGCATTTAACACTAACATATAT-AAGCTTTAGCAATTTT-------TAA
Hapalogaster_dentata            AGTAAATTCTTTTAAATCTTATTTATATGTAAAGGACTTTCACCA-AAACCTAAAAGATCAAAACTTTTTGTGCATTTAACACTAACATATATAAAGCTTTAGCAATTTT-------TAA
Hapalogaster_mertensii          AGTAAATTCTTTTAAATCTTATTTATATGTAAAGGACTTTCACCA-AAACCTAAAAGATCAAAACTTTTTGTGCGTTTAACACTAACATATA-AAAGCTTTAGCAATTTT-------TAA
Cryptolithodes_sitchensis       AGTAAATTCTTCTAAATCTTGTTTATACGTAAAGGACTTCCACCA-AAACCTAAAAGATCAAAACTTTTTGTGCATTTGACACTAACATATATAAAGCTTTAGCAATTTT--------AA
Cryptolithodes_typicus          AGTAAATTCTTTTAAATCTTATTTATATGTAAAGGACTTTCACCA-AAACCTAAAAGATCAAAACTTTTTGTGCATTTAACACTAACATATA-AAAGCTTTAGCAATTTT-------TAA
Glyptolithodes_cristatipes      AGTAAATTCTTTTAAATCTTACTTATACGTAAAGGACTTTCACCA-AAACTTAAAAGATCAAAACTTTTTATGCATTTTACATTAACATATAT-AAGCTTTAGCAATTTT-------TAA
Paralomis_granulosa             AGTGAATTCTTTTAAATCTTATTTATATGTAAAGGACTTTCACCA-AAACTTAAAAGATCAAAACTTTTTATGCATTT-ACATTAACATATAT-AAGCTTTAGCAATTTT-------TAA
Phyllolithodes_papillosus       AGTAA-TTCTTTTAAATCTTATTTATATGTAAAGGACTTTCACCA-AAACTTAAAAGATCAAAACTTTTTGTGCATTTAACACTAACATATAT-AAGCTTTAGCAATTTT-------TAA
Lopholithodes_mandtii           AGTAAATTCTTTTAAATCTTATTTATATGTAAAGGACTTTCACCA-AAACTTAAAAGATCAAAACTTTTTGTGCATTTAACACTAACATATATAAAGCTTTAGCAATTTT-------TAA
Paralithodes_brevipes           AGTAAATTCTTTTAAATCTTATTTATATGTAAAGGACTTTCACCA-AAACTTAAAAGATCAAAACTTTTTGTGCATTTAACACTAACATATA-AAAGCTTTAGCAATTTT-------TAA
Paralithodes_camtscahticus      AGTAAATTCTTTTAAATCTTATTTATATGTAAAGGACTTTCACCG-AAACTTAAAAGATCAAAACTTTTTGTGCATTTAACACTAACATATA-AAAGCTTTAGCAATTTT-------TAA
Lithodes_maja                   AGTAAATTCTTTTAAATCTTATTTATATGTAAAGGACTTTCACCA-AAACTTAAAAGATCAAAACTTTTTGTGCGTTTAACACTAACATATATAAAGCTTTAGCAATTTT-------TAA
Lithodes_santolla               AGTAAATTCTTTTAAATCTTATTTATATGTAAAGGACTTTCACCA-AAACTTAAAAGATCAAAACTTTTTGTGCATTTAACACTAACATATAA-AAGCTTTAGCAATTTT-------TAA
Lithodes_aequispinus            AGTAAATTCTTTTAAATCTTATTTATATGTAAAGGACTTTCACCA-AAACTTAAAAGATCAAAACTTTTTGTGCATTTAACACTAACATATA-AAAGCTTTAGCAATTTT-------TAA
Rhinolithodes_wosnessenskii     AGTAAATTCTTTTAAATCTTATTTATATGTAAAGGACTTTCNCCGGNAACTTAAAAGATCAAAACTTTNTGTGCATTTAACACTAACATATA-AAAGCTTTAGCAATTTT-------TAA
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[                                          490       500       510       520       ]
[                                            .         .         .         .       ]

Emerita_analoga                 GCACATCTTCAGATTTGCAATCCGACGTTTTA-ATTTATACTATAAAGC
Clibanarius_vittatus            TCACATTTTTAGATTTGCAATCTAACGTCTTACAATTCCACTATGAGAT
Pagurus_longicarpus             CTACATTTTCAGATTTGCAATCTAACGTCTTATATT-CCACTATAAGGC
Pagurus_bernhardus              TCACATTTTTAGATTTGCAGTCTAACGTCTTATATTTCCACTATAAAGC
Pagurus_hirsuticusulous         TCACATTTTTAGATTTGCAGTCTAACGTCTTATATTTCCACTATNAAGC
Labidochirus_splendescens       TCACATTTTCAGATTTGCAATCTAACGTCTTATATTTCCACTATAAAGC
Oedignathus_inermins            TTACATTTTTAGATTTGCAATCTAACGTCTTATATTTCCACTATAAAGC
Hapalogaster_dentata            TTACATTTTCAGATTTGCAATCTAACGTCTTATATTTCCACTATAAAGC
Hapalogaster_mertensii          TTACATTTTCAGATTTGCAATCTAACGTCTTATATTTCCACTATAAAGC
Cryptolithodes_sitchensis       TTACATTTTCAGATTTGCAAGCTGACGTCTTATATTTCCACTATAAAGC
Cryptolithodes_typicus          TTACATTTTCAGATTTGCAATCTAACGTCTTATATTTCCACTATAAAGC
Glyptolithodes_cristatipes      TTACATTTTTAGATTTGCAATCTAACGTCTTACATTTCCACTATAAAGC
Paralomis_granulosa             TTACATTTTCAGATTTGCAATCTAACGTCTTGTATTTCCACTATAAAGC
Phyllolithodes_papillosus       TTACATTTTCAGATTTGCAATCTAACGTCTTGTATTTCCACTATAAAGC
Lopholithodes_mandtii           TTACATTTTCAGATTTGCAATCTAACGTCTTATATTTCCACTATAAAGC
Paralithodes_brevipes           TTACATTTTCAGATTTGCAATCTAACGTCTTGTATTTCCACTATAAAGC
Paralithodes_camtscahticus      TTACATTTTCAGATTTGCAATCTAACGTCTTATATTTCCACTATAAAGC
Lithodes_maja                   TTACATTTTTAGATTTGCAATCTAACGTCTTATATTTCCACTATAAAGC
Lithodes_santolla               TTACATTTTTAGATTTGCAATCTAACGTCTTATATTTCCACTATAAAGC
Lithodes_aequispinus            TTACATTTTCAGATTTGCAATCTAACGTCTTATATTTCCACTATAAAGC
Rhinolithodes_wosnessenskii     TTACATTTTCAGATTTGCAATCTAACGTCTTATATTTCCNCTATAAAGC
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Appendix 3-1b: Mitochondrial gene 16S aligned

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[                                           10        20        30        40        50        60        70        80        90       100       110       120]
[                                            .         .         .         .         .         .         .         .         .         .         .         .]

Emerita_analoga                    TGCCCACTGGTATAAAATCTAAAGGGCCGCAGTATCT-TGACTGTGCAAAGGTA-GCATAATCATTAGTCTTTTAATTGAAGACTCGTATGAATGGTTGGACGAGAAATAAACTGTTTCT
Clibanarius_vittatus               TGCCCACTG--ATTAATT-TAAGG-GCCGCGGTATTCCTAACCGTGCTAAGGTATGCATAATCATTAGTCTCTTAATTGGAGGCTTGTATGAAAGGTTGGACGAGAAATATACTGTTTCA
Pagurus_longicarpus                TGCTCACTG--ATTTAAT-TAAAGAGCCGCAGTATTT-TGACTGTGCGAAGGTA-GCATAATAGATTGTCTTTTAAATGGAGGCTGGAATGAATGGTTGGACAAAGTATCATCTGTTTCT
Pagurus_bernhardus                 TGCTCACTG--ATTATAT-TAAAGAGCCGCAGTATTC-TGACTGTGCGAAGGTA-GCATAATAAATTGTCTTTTAAATGGAGGCTTGAATGAAAGGTTGGACAAAGTATCATCTGTTTCT
Pagurus_hirsutiusculus             TGCTCACTG--ATTAAAT-TAAAGAGCCGCAGTATTC-TGACTGTGCGAAGGTA-GCATAATAAATTGTCTTTTAAATGGAGGCTTGAATGAAAGGTTGGACAAAGTATCATCTGTTTCT
Labidochirus_splendescens          ----CACTG--ATTATAT-TAAAGAGCCGCAGTATTT-TGACTGTGCGAAGGTA-GCATAATAAATTGTCTTTTAAATGAAGGCTTGAATGAAAGGTTGGACAAAGAATCATCTGTTTCT
Oedignathus_inermis                TGCTCACTG--ATTAAAT-TAAAGAGCCGCAGTATTT-TGACTGTGCGAAGGTA-GCATAATAAATTGTCTTTTAAATAAAGGCTTGAATGAAAGGTTGGACAAAGTATCATCTGTTTCT
Hapalogaster_dentata               TGCTCACTG--ATAAAAT-TAAAGAGCCGCAGTATTC-TGACTGTGCGAAGGTA-GCATAATAAATTGTCTTTTAAATAAAGGCTTGAATGAAAGGTTGGACAAAGTATCATCTGTTTCT
Hapalogaster_mertensii             TGCTCACTG--ATAAAAT-TAAAGAGCCGCAGTATTC-TGACTGTGCGAAGGTA-GCATAATAAATTGTCTTTTAAATAAAGGCTTGAATGAAAGGTTGGACAAAGTATCATCTGTTTCT
Cryptolithodes_sitchensis          TGCTCACTG--ATTAAAT-TAAAGAGCCGCAGTATCT-TGACTGTGCGAAGGTA-GCATAATAAATTGTCTTTTAAATAAAGGCTTGAATGAAAGGTTGGACAAAGTATCATCTGTTTCT
Cryptolithodes_typicus             TGCTCACTG--ATCAAAT-TAAAGAGCCGCAGTATTT-TGACTGTGCGAAGGTA-GCATAATAAATTGTCTTTTAAATAAAGGCTTGAATGAAAGGTTGGACAAAGTATCATCTGTTTCT
Glyptolithodes_cristatipes         ----------------------------------------------------------------------------------GCTTGAATGAAAGGTTGGACAAAGTATCATCTGTTTCT
Paralomis_granulosa                TGCTCACTG--ATTAAAT-TAAAGAGCCGCAGTATTT-TGACTGTGCGAAGGTA-GCATAATAAATTGTCTTTTAAATAAAGGCTTGAATGAAAGGTTGGACAAAGTATCATCTGTTTCT
Phyllolithodes_papillosus          -----------------T-CAAAGAGCCGCAGTATTT-TGACTGTGCGAAGGTG-GCATAATAAATTGTCTTTTAAATAAAGGCTTGAATGAAAGGTTGGACAAAGTGTCATCTGTTTCT
Lopholithodes_mandtii              TGCTCACTG--ATTAAAT-TAAAGAGCCGCAGTATTT-TGACTGTGCGAAGGTA-GCATAATAAATTGTCTTTTAAATAAAGGCTTGAATGAAAGGTTGGACAAAGTATCATCTGTTTCT
Paralithodes_brevipes              TGCTCACTG--ATTAAAT-TAAAGAGCCGCAGTATTT-TGACTGTGCGAAGGTA-GCATAATAAATTGTCTTTTAAATAAAGGCTTGAATGAAAGGTTGGACAAAGTATCATCTGTTTCT
Paralithodes_camtschaticus         TGCTCACTG--ATTAAAT-TAAAGAGCCGCAGTATTT-TGACTGTGCGAAGGTA-GCATAATAAATTGTCTTTTAAATAAAGGCTTGAATGAAAGGTTGGACAAAGTATCATCTGTTTCT
Lithodes_maja                      TGCTCACTG--ATTAAAT-TAAAGAGCCGCAGTATTT-TGACTGTGCGAAGGTA-GCATAATAAATTGTCTTTTAAATAAAGGCTTGAATGAAAGGTTGGACAAAGTATCATCTGTTTCT
Lithodes_santolla                  TGCTCACTG--ATTAAAT-TAAAGAGCCGCAGTATTT-TGACTGTGCGAAGGTA-GCATAATAAATTGTCTTTTAAATAAAGGCTTGAATGAAAGGTTGGACAAAGTATCATCTGTTTCT
Lithodes_aequispinus               TGCTCACTG--ATTAAAT-TAAAGAGCCGCAGTATTT-TGACTGTGCGAAGGTA-GCATAATAAATTGTCTTTTAAATAAAGGCTTGAATGAAAGGTTGGACAAAGTATCATCTGTTTCT
Rhinolithodes_wosnessenskii        ????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????
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(                                         130       140       150       160       170       180       190       200       210       220       230       240)
(                                           .         .         .         .         .         .         .         .         .         .         .        .)

Emerita_analoga                    TTTATACATTTTGAATTTAACTTTTAAGTGAAAAGGCTTAAATACTTTAGAGGGACGATAAGACCCTATAAATCTTAATATTTTAT-TATTAGAGATACTAT-TTATAACGTC-TATGTA
Clibanarius_vittatus               AATAAAAAATTTGAATTTAACTTTTAAGTGAAAAGGCTTAAATAAATTAAAAAGACGATAAGACCCTATAAATCTTAACGGTAAAGTTAATGTTT--TTTGATTTATTA-GTA-TAAA-A
Pagurus_longicarpus                TAAATAAATATTGAATTTGACTTTTAAGTTAAAAGGCTTAAATAAAATAAAAAGACGATAAGACCCTATAAATCTTTACATAAATTATATTTTAAATTTTAATTTATAA-TTT-TATAAA
Pagurus_bernhardus                 TAAATATTTATTGAATTTGACTTTCAAGTGAAAAGGCTTGAATAAATTAAAAAGACGATAAGACCCTATAAATCTTTACAATAAACATGTTCTATATTTTAATTTATAA-GTA-TATAAA
Pagurus_hirsutiusculus             TAAATATTTATTGAACTTGACTTTCAAGTGAAAAGGCTTGAATAAATTAAAAAGACGATAAGACCCTATAAATCTTTACAATAAATATATTTTATATTTTAATTTATAA-GTG-TAAAAA
Labidochirus_splendescens          TAAATATTTATTGAATTTGACTTTTAAGTGAAAAGGCTTAAATAAATTAAAAAGACGATAAGACCCTATAAATCTTAACAATAAATAGACTTTATATTTTAATTTATAA-GTG-TGTAAG
Oedignathus_inermis                TAAATATTTATTGAATTTGACTTTTAAGTGAAAAGGCTTAAATAATACAAAAAGACGATAAGACCCTATAAATCTTTACAATAAATATATTTTATATTTTAGTTTATAA-GTA-AATA-A
Hapalogaster_dentata               TAAATATTTATTGAATTTGACTTTTAAGTGAAAAGGCTTAAATAATCCAAAAAGACGATAAGACCCTATAAATCTTTACAATAAATATATTTTATATTTAAGTTTATAA-GTA-TATAAA
Hapalogaster_mertensii             TAAATATTTATTGAATTTGACTTTTAAGTGAAAAGGCTTAAATAATCCAAAAAGACGATAAGACCCTATAAATCTTTACAATAAATATGTTTTATATTTAAGTTTATAA-GTA-AATAAA
Cryptolithodes_sitchensis          TAAATATTTATTGAATTTGACTTTTAAGTGAAAAGGCTTAAATACCTCAAAAAGACGATAAGACCCTATAAATCTTTACAATAATTATATTTTATATTTTAGTTTATTAAGTG-TATA-A
Cryptolithodes_typicus             TAAATATTTATTGAATTTGACTTTTAAGTGAAAAGGCTTAAATAACTCAAAAAGACGATAAGACCCTATAAATCTTTACAATAGTTATATTTTATATTTTAGCTTATAA-GTA-TATAAA
Glyptolithodes_cristatipes         TAAATATTTATTGAATTTGACCTTTAAGTGAAAAGGCTTAAATAAACCAAAAAGACGATAAGACCCTATAAATCTTTACAAGAAATATATTTTATATTTTAACTTATAA-GTG-TATAAG
Paralomis_granulosa                TAAATATTTATTGAATTTGACTTTTAAGTGAAAAGGCTTAAATAAATCAAAAAGACGATAAGACCCTATAAATCTTTACAAGAAATATATTTTATGTTTTAGCTTATAA-GTAATATAAG
Phyllolithodes_papillosus          TAAATATTTATTGAATTTGACTTTTAAGTGAAAAGGCTTAAATAAACCAAAAAGACGATAAGACCCTATAAATCTTTACAATAAATATATTTTATATTTTAATTTATAA-GTG-TATAAG
Lopholithodes_mandtii              TAAATATTTATTGAATTTGACCTTTAAGTGAAAAGGCTTAAATAAATCAAAAAGACGATGAGACCCTATAAATCTTTACAATAAATATATTTTATATTTTAGCTTATAA-GTA-TATAAA
Paralithodes_brevipes              TAAATATTTATTGAATTTGACTTTTAAGTGAAAAGGCTTAAATAAATCAAAAAGACGATAAGACCCTATAAATCTTTACAATAAATATATTTTATATTTTATATTATAA-GTG-TATA-A
Paralithodes_camtschaticus         TAAATATTTATTGAATTTGACTTTTAAGTGAAAAGGCTTAAATAAATCAAAAAGACGATAAGACCCTATAAATCTTTACAATAAATATATTTTATATTTTAGTTTATAA-GTG-AATG-A
Lithodes_maja                      TAAATATTTATTGAATTTGACTTTTAAGTGAAAAGGCTTAAATAAATCAAAAAGACGATAAGACCCTATAAATCTTTACAATAAATATATTTTATATTTTAGCTTAT-AAGTG-TATA-A
Lithodes_santolla                  TAAATATTTATTGAATTTGACTTTTAAGTGAAAAGGCTTAAATAAATCAAAAAGACGATAAGACCCTATAAATCTTTACAATAAATATATTTTATATTTTAACTTATAA-GTG-TATA-A
Lithodes_aequispinus               TAAATATTTATTGAATTTGACTTTTAAGTGAAAAGGCTTAAATAAATCAAAAAGACGATAAGACCCTATAAATCTTTACAATAAATATATTTTATATTTTAGCTTATAA-GTG-TATAAG
Rhinolithodes_wosnessenskii        ????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????
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[                                     250       260       270       280       290       300       310       320       330       340       350       360]
[                                      .         .         .         .         .         .         .         .         .         .         .         .]

Emerita_analoga               TCTTTA---ATATTCTA---CTGGGCGGTATAAATAAAATT---AGTAACTGTTTA---ATATAAATTCAGAAGTGCCTGATAATT-GATCCT--TATATAAAGATCAAAAGGTTAAGTT
Clibanarius_vittatus          -AAATACTTAAATTGG----TTGGGGCGACATAAATATAAAATAATTAACTGTTTGAATATTTAAACA-----ATTATTGTTGAAG-GATCCTGCTATAGA--GATTAAAAGACCAAGTT
Pagurus_longicarpus           A-TATA---AAATTGTTGTGCTGGGGCGGCGTAGATATATAA--ATGAACTGTCTATGAAATTAAAT-CAATAATAGTTGATTATTTGATCCT--TTAATA--GATTAAAAGATTAAGAT
Pagurus_bernhardus            A-TATT---AAATTGTTTCGCTGGGGCGGCGTGGATATATTA--ATAAACTGTCTATGTG-TTAAATCCAATAATTATTGATTAGTTGATCCT--TAAATA--GATTAAAAGATTAAGAT
Pagurus_hirsutiusculus        ATATTA---AATTTGTTTCGCTGGGGCGGCGTAGATATATAA--ATAAACTGTCTATATT-TTAAATACAGTAGTTGTTGATTAATTGATCCT--TAAAAA--GATTAAAAGATTAAGAT
Labidochirus_splendescens     G-TATA---AATTTGTTTCGCTGGGGCGGCGTAGATATATTA--ATAAACTGTCTAT-ATATTATATCCAATAATTGTTGATTAATTGATCCT--TAAATA--GATTAAAAGATTAAGAT
Oedignathus_inermis           TATAAA---AAATTGTTACGCTGGGGCGGCGTAGATATATAA--ATAAACTGTCTATA-ATTTAAATACAATAGTCGTTGTTTACCTGATCCT--TAAATA--GATTAAAAGATTAAGAT
Hapalogaster_dentata          A-CATA---AAATTGTTGCGCTGGGGCGGCGTAGATATATAA--ATAAACTGTCTATAAT-TTAAATACAATAATCATTGCTTAATTGATCCT--TAAATA--GATTAAAAGATTAAGAT
Hapalogaster_mertensii        A-CATA---AAATTGTTGCGCTGGGGCGGCGTAGATATATAA--ATTAACTGTCTAT-AGTTTAAATACAATAATCATTGCTTAATTGATCCT--TAAATA--GATTAAAAGATTAAGAT
Cryptolithodes_sitchensis     AAGGTA---AAATTGTTTCGCTGGGGCGGCGCAGATATATAA--ATAAACTGTCTGTG-GTTTAAATACAATAGTTATTGCTTAGTTGATCCT--TAGATA--GATTGAAAGATTAAGAT
Cryptolithodes_typicus        A-GATA---AAATTGTTTCGCTGGGGCGGCGTAGATATATAA--ATAAACTGTCTAT-GGTTTAAATACAGTAGTCACTGTTTAGTTGATCCT--TAAATA--GATTAAAAGATTAAGAT
Glyptolithodes_cristatipes    A-AATA---AAATTGTTGCGCTGGGGCGGCGTAGATATATAA--ATAAACTGTCTGT-GTTTTAAATACAATAATTATTGTTTAGTTGATCCT--TAAATA--GATTAAAAGATTAAGAT
Paralomis_granulosa           A-AATA---AAATTGTTGCGCTGGGGCGGCGTAGATATATAA--ATAAACTGTCTATGAT-TTAAATACAGTAATTATTGCTTAATTGATCCT--TAAATA--GATTAAAAGATTAAGAT
Phyllolithodes_papillosus     A-GATA---AAATTGTTGCGCTGGGGCGGCGTAGATATATAA--ATAAACTGTCTATAAT-TTAAATACAGTAATCATTGCTTAACTGATCCT--TAAATA--GATTAAAAGAGTAAGAT
Lopholithodes_mandtii         A-AATA---AAATTGTTGCGCTGGGGCGGCGTAGATATATAA--ATAAACTGTCTATAGT-TTAAATACAATAATCATTGCTTAATTGATCCT--TAAATA--GATTAAAAGATTAAGAT
Paralithodes_brevipes         TAAATA---AAATTGTTGCGCTGGGGCGGCGTAGATATATAA--ATAAACTGTCTATA-ATTTAAATACAATAATCATTGTTTAGTTGATCCT--TAAATA--GATTAAAAGATTAAGAT
Paralithodes_camtschaticus    GATATA---AAATTGTTGCGCTGGGGCGGCGTAGATATATAA--ATAAACTGTCTATA-GTTTAAATACAATAATCATTGCTTAATTGATCCT--TAAATA--GATTAAAAGATTAAGAT
Lithodes_maja                 AAAATA---AAATTGTTGCGCTGGGGCGGCGTAGATATATAA--ATAAACTGTCTATA-ATTTAAATACAATAATCATTGTTTAATTGATCCT--TAAATA--GATTAAAAGATTAAGAT
Lithodes_santolla             GAAATA---AAATTGTTTCGCTGGGGCGGCGTAGATATATAA--ATAAACTGTCTATA-ATTTAAATACAGTAATTATTGCTTAATTGATCCT--TAAATA--GATTAAAAGATTAAGAT
Lithodes_aequispinus          A-AATA---AAATTGTTGCGCTGGGGCGGCGTAGATATATAA--ATAAACTGTCTATAAT-TTAAATACAATAATCATTGCTTAATTGATCCT--TAAATA--GATTAAAAGATTAAGAT
Rhinolithodes_wosnessenskii   ????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????
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[                                        370        380        390        400        410        420        430        440        450        460        470        480]
[                                                     .          .          .          .          .          .          .          .          .          .          .|

Emerita_analoga                ACTTTAGGGATAACAGCGTTATTTCTTTTAAGAGTTCATATCTAAAAAGAAGTTTGCGACCTCGATGTTGAATTAAAATTTCTTTGTGGTTGCAGCAGCTACAAAAGAAAGTCTGTTCGA
Clibanarius_vittatus           ACTTTAGGGATAACAGCGTTATTCTTTTTGAGAGTTCTTATTAAAAAAAGAGTTTGCGACCTCGATGTTGAATTAAAAATTCTTTATGGT-GCAGCAGCTATGAAAGAAAGTCTGTTCGA
Pagurus_longicarpus            ACTTTAGGGATAACAGCGTTATTTTTTCTGAGAGTTCTTATCGAAGAAAAAGTTTGCGACCTCGATGTTGAATTAAAGTTTCTTTATGGT-GTAGCAGCTATAAAAGAGAGTCTGTTCGA
Pagurus_bernhardus             ACTTTAGGGATAACAGCGTTATTTTTTTTGAGAGTTCTTATCGAAGAAAAAGTTTGCGACCTCGATGTTGAATTAAAGTATCTTTATGGT-GCAGCCGCTATAAGAGAGAGTCTGTTCGA
Pagurus_hirsutiusculus         ACTTTAGGGATAACAGCGTTATTTTTTCTGAGAGTTCTTATCGAAGAAAAAGTTTGCGACCTCGATGTTGAATTAAAGTATCTTTATGGT-GTAGTCGCTATAAGAGAGAGTCTGTTCGA
Labidochirus_splendescens      ACTTTAGGGATAACAGCGTTATTTTTTTTGAGAGTTCTTATCGAAGAAAAAGTTTGCGACCTCGATGTTGAATTAAAGTATCTCTATGGT-GTAGCCGCTATAAGAGAGAGTCTGTTCGA
Oedignathus_inermis            ACTTTAGGGATAACAGCGTTATTTTTTCTGAGAGTTCTTATCGAAGAAAAAGTTTGCGACCTCGATGTTGAATTAAAGTTTCTCTATGGT-GCAGCCGCTATAAGAGAGAGTCTGTTCGA
Hapalogaster_dentata           ACTTTAGGGATAACAGCGTTATTTTTTCTGAGAGTTCTTATCGAAGAAAAAGTTTGCGACCTCGATGTTGAATTAAAGTATCTCTATGGT-GCAGCCGCTATAAGAGAGAGTCTGTTCGA
Hapalogaster_mertensii         ACTTTAGGGATAACAGCGTTATTTTTTTTGAGAGTTCTTATCGAAGAAAAAGTTTGCGACCTCGATGTTGAATTAAAGTATCTCTATGGT-GCAGCCGCTATAAGAGAGAGTCTGTTCGA
Cryptolithodes_sitchensis      ACTTTAGGGATAACAGCGTTATTTTTTCTGAGAGTTCYTATCGAAGAGAAAGTTTGCGACCTCGATGTTGAATTAAAGTATCTCTATGGT-GCAGCCGCTATAAGAGAGAGTCTGTTCGA
Cryptolithodes_typicus         ACTTTAGGGATAACAGCGTTATTTTTTCTGAGAGTTCTTATCGAAGAGAGAGTTTGCGACCTCGATGTTGAATTAAAGTATCTTTATGGT-GTAGCCGCTATAAGAGAGAGTCTGTTCGA
Glyptolithodes_cristatipes     ACTTTAGGGATAACAGCGTTATTTTTTCTGAGAGTTCTTATCGAAGAAAAAGTTTGCGACCTCGATGTTGAATTAAAGTTTCTTTGTGGT-GCAGCCGCTATAAAAGAAAGTCTGTTCGA
Paralomis_granulosa            ACTTTAGGGATAACAGCGTTATTTTTTTTGAGAGTTCTTATCGAAGAAAAAGTTTGCGACCTCGATGTTGAATTAAAGTTTCTTTGTGGT-GTAGCCGCTATAAGAGAGAGTCTGTTCGA
Phyllolithodes_papillosus      ACTTTAGGGATAACAGCGTTATTTTTTTTGAGAGTTCTTATCGAAGAAAAAGTTTGCGACCTCGATGTTGAATTAAAGTATCTCTGTGGT-GTAGCCGCTACAAGAGAGAGTCTGTTCGA
Lopholithodes_mandtii          ACTTTAGGGATAACAGCGTTATTTTTTTTGAGAGTTCTTATCGAAGAAAAAGTTTGCGACCTCGATGTTGAATTAAAGTTTCTTTGTGGT-GTAGCCGCTATAAGAGAGAGTCTGTTCGA
Paralithodes_brevipes          ACTTTAGGGATAACAGCGTTATTTTTTTTGAGAGTTCCTATCGAAGAAAAAGTTTGCGACCTCGATGTTGAATTAAAGTATCTTTATGGT-GTAGCCGCTATAAGAGAGAGTCTGTTCGA
Paralithodes_camtschaticus     ACTTTAGGGATAACAGCGTTATTTTTTTTGAGAGTTCTTATCGAAGAAAAAGTTTGCGACCTCGATGTTGAATTAAAGTTTCTCTGTGGT-GTAGCCGCTATAAGAGAGAGTCTGTTCGA
Lithodes_maja                  ACTTTAGGGATAACAGCGTTATTTTTTTTGAGAGTTCTTATCGAAGAAAAAGTTTGCGACCTCGATGTTGAATTAAAGTATCTCTATGGT-GTAGCCGCTATAAGAGAGAGTCTGTTCGA
Lithodes_santolla              ACTTTAGGGATAACAGCGTTATTTTTTTTGAGAGTTCTTATCGAAGAAAAAGTTTGCGACCTCGATGTTGAATTAAAGTATCTCTATGGT-GCAGCCGCTATAAGAGAGAGTCTGTTCGA
Lithodes_aequispinus           ACTTTAGGGATAACAGCGTTATTTTTTTTGAGAGTTCTTATCGAAGAAAAAGTTTGCGACCTCGATGTTGAATTAAAGTATCTCTATGGT-GTAGCCGCTATAAGAGAGAGTCTGTTCGA
Rhinolithodes_wosnessenskii    ????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????
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[                                            490        500        510        520      ]
[                                              .          .          .          .      ]

Emerita_analoga                   CTTTT-AAAATTTTACATGATTTGAGTTCAGACCGGCGTGAGCCAGGTT
Clibanarius_vittatus              CTTTT-AAATTTTTACATGATTTGAGTTCAGACCGGTGTGAGCCAGGTC
Pagurus_longicarpus               CTTTT-AATACTTTACATGATTTGAGTTCAGACCGGCGTGAGCCAGGTT
Pagurus_bernhardus                CTTTT-AATACTTTACATGATTTGAGTTCAGACCGGCGTGAGCCAGGTT
Pagurus_hirsutiusculus            CTTTT-AATACTTTACATGATTTGAGTTCAGACCGGCGTGAGCCAGGTT
Labidochirus_splendescens         CTTTT-AATACTTTACATGATTTGAGTTCAGACCGGCGTGAGCCAGGTT
Oedignathus_inermis               CTTTT-AATACTTTACATGATTTGAGTTCAGACCGGCGTGAGCCAGGTT
Hapalogaster_dentata              CTTTT-AATACTTTACATGATTTGAGTTCAGACCGGCGTGAGCCAGGTT
Hapalogaster_mertensii            CTTTT-AATACTTTACATGATTTGAGTTCAGACCGGCGTGAGCCAGGTT
Cryptolithodes_sitchensis         CTTTT-AATACTTTACATGATTTGAGTTCAGACCGGCGTGAGCCAGGTT
Cryptolithodes_typicus            CTTTTTAATACTTTACATGATTTGAGTTCAGACCGGCGTGAGCCAGGTT
Glyptolithodes_cristatipes        CTTTT-AATACTTTACATGATTTGAGTTCAGACCGGCGTGAGCCAGGTT
Paralomis_granulosa               CTTTT-AATACTTTACATGATTTGAGTTCAGACCGGCGTGAGCCAGGTT
Phyllolithodes_papillosus         CTTTT-AATACTTTACATGATTTGAGTTCAGACCGGCGTGAGCCAGGTT
Lopholithodes_mandtii             CTTTT-AATACTTTACATGATTTGAGTTCAGACCGGCGTGAGCCAGGTT
Paralithodes_brevipes             CTTTT-AATACTTTACATGATTTGAGTTCAGACCGGCGTGAGCCAGGTT
Paralithodes_camtschaticus        CTTTT-AATACTTTACATGATTTGAGTTCAGACCGGCGTGAGCCAGGTT
Lithodes_maja                     CTTTT-AATACTTTACATGATTTGAGTTCAGACCGGCGTGAGCCAGGTT
Lithodes_santolla                 CTTTT-AATACTTTACATGATTTGAGTTCAGACCGGCGTGAGCCAGGTT
Lithodes_aequispinus              CTTTT-AATACTTTACATGATTTGAGTTCAGACCGGCGTGAGCCAGGTT
Rhinolithodes_wosnessenskii       ?????????????????????????????????????????????????
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Appendix 3-1c- Mitochondrial gene COI aligned.

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[                                      10         20         30         40         50         60         70         80         90        100        110        120]
[                                       .          .          .          .          .          .          .          .          .          .          .          .]

Emerita_analoga                 CCGTATAAATAATATAAGATTTTGACTCTTACCTCCGTCTTTGACTTTATTACTTATAAGAGGGATAGTGGAAAGAGGAGTTGGGACAGGATGAACAGTCTATCCTCCCTTATCAGCAGC
Pagurus_longicarpus             TCGAATAAACAATATAAGGTTTTGACTTCTACCACCCTCATTAACACTTCTACTAACAAGAGGAATAGTAGAAAGAGGTGTTGGAACAGGATGAACTGTCTACCCTCCATTATCTGCTGC
Pagurus_hirsutiusculus          ???????????????????TTTTGATTATTACCACCATCACT?ACTCTGCTTTTAACTAGAGGTATAGTTGAAAGAGGAGTTGGAACAGGATGAACTGTATATCCCCCCCTATCAGCTGC
Oedignathus_inermis             ACGTATAAATAATATAAGATTTTGACTTCTTCCACCCTCTTTAACTCTTTTACTAACCAGTGGTATAGTAGAAAGAGGAGTTGGAACAGGATGAACTGTTTACCCACCACTATCTGCAGC
Hapalogaster_mertensii          ACGAATAAATAATATAAGATTTTGATTATTACCCCCCTCTTTAACTCTTTTACTAACTAGTGGTATAGTAGAAAGAGGTGTTGGAACAGGATGAACCGTTTATCCGCCTTTGTCTGCAGC
Cryptolithodes_typicus          TCGTATAAATAATATAAGTTTTTGACTTTTACCTCCATCCTTAACTCTTCTCCTAACCAGAGGGATAGTAGAAAGAGGCGTTGGGACAGGGTGAACTGTTTACCCTCCTTTATCCGCAGC
Paralomis_granulosa             ACGAATAAATAACATAAGTTTTTGGCTTCTGCCCCCGTCTTTAACTCTTTTATTGACTAGTGGTATAGTAGAAAGAGGTGTAGGAACAGGATGAACTGTCTATCCGCCGCTATCCGCAGC
Lopholithodes_mandtii           ACGAATAAATAATATAAGTTTTTGACTTTTACCCCCGTCTTTGACTCTTTTATTAACCAGTGGTATAGTAGAAAGAGGCGTTGGAACAGGGTGAACTGTATACCCGCCGCTGTCTGCAGC
Paralithodes_camtschaticus      ?CGAATTAATAATATAAGTTTTTGACTTTTACCCCC?TCTTTAACTCTTTTATTAACTAGAGGTATAGTAGAAAGAGGAGTAGG?ACAGGATGAACTGTTTACCCACCA?TATC?GCGGC
Lithodes_santolla               ACGAATAAATAATATAAGTTTTTGACTTTTACCTCCATCATTAACTCTTTTATTAACTAGGGGGATAGTAGAAAGAGGTGTAGGTACAGGATGAACTGTTTACCCACCGTTGTCTGCGGC
Rhinolithodes_wosnessenskii     ACGAATAAATAATATAAGTTTTTGACTTTTACCCCCATCTCTAACTCTTTTATTAACCAGTGGTATAGTAGAAAGAGGGGTAGGTACAGGATGAACTGTTTACCCTCCCCTATCTGCAGC

[                                     130        140        150        160        170        180        190        200        210        220        230        240]
[                                       .          .          .          .          .          .          .          .          .          .          .          .]

Emerita_analoga                 TATTGCACATGCGGGAGCTTCAGTAGATTTAGGAATTTTCAGATTACACTTAGCTGGGGTTTCTTCTATTTTAGGTGCAGTTAATTTCATAACTACAGTTATTAATATACGTCCTCATGG
Pagurus_longicarpus             AATTGCCCATGCAGGTGCTTCAGTAGATTTAGGTATTTTTTCCCTTCACTTAGCAGGAGTTTCTTCTATTCTAGGAGCAGTTAATTTTATAACTACAGTTATTAATATACGTCCACAAGG
Pagurus_hirsutiusculus          CATTGCTCACGCCGGAGCCTCAGTAGATTTAGGAATTTTCTCTTTACATTTAGCGGGTGTCTCCTCAATCTTAGGAGCTGTAAATTTTATAACTACTGTTATTAACATACGACCACAAGG
Oedignathus_inermis             AATCGCCCACGCGGGAGCATCAGTAGATTTAGGTATTTTTTCTTTACATTTAGCAGGTGTCTCTTCTATTTTAGGAGCTGTAAATTTTATAACTACAGTTATTAATATACGTCCCCAAGG
Hapalogaster_mertensii          TATCGCTCATGCGGGAGCATCAGTAGATTTGGGTATTTTCTCTTTACATTTAGCTGGGGTGTCTTCTATTTTAGGGGCTGTTAATTTTATAACTACGGTTATTAATATACGCCC?CAAGG
Cryptolithodes_typicus          GATTGCTCACGCAGGAGCATCAGTAGACCTGGGTATTTTTTCTTTACATTTAGCGGGAGTTTCTTCTATTTTAGGAGCTGTAAATTTTATAACCACAGTTATTAACATGCGACCGCAAGG
Paralomis_granulosa             GATTGCTCATGCAGGGGCGTCAGTAGATTTGGGAATTTTCTCTTTGCACTTAGCAGGGGTGTCTTCTATTTTAGGAGCTGTCAATTTTATAACCACAGTTATCAATATGCGACCCCAGGG
Lopholithodes_mandtii           AATTGCACACGCAGGAGCATCAGTAGACCTGGGTATTTTTTCTTTACACTTGGCCGGAATTTCTTCTATTTTAGGAGCCGTAAATTTTATAACTACAGTTATTAACATGCGGCCCCAGGG
Paralithodes_camtschaticus      AATTGCACATGCAGGAGCATCAGTGGATTTAGGTATTTTTTCTTTGCATTTAGCTGGAGTATCTTCTATTTTAGG?GCTGTAAATTTTATAACTACAGTTATTAATATACGTCC?CAAGG
Lithodes_santolla               AATCGCACATGCAGGAGCATCAGTAGATTTAGGAATTTTTTCTTTGCATTTAGCTGGTGTATCTTCTATTTTAGGAGCTGTAAATTTTATAACTACAGTTATTAATATACGACCTCAAGG
Rhinolithodes_wosnessenskii     AATCGCACATGCCGGAGCATCAGTAGATTTAGGTATTTTTTCTTTACATTTAGCCGGAGTGTCTTCCATTTTAGGGGCTGTAAATTTTATAACCACAGTTATTAATATACGGCCCCAAGG

[                                     250        260        270        280        290        300        310        320        330        340        350        360]
[                                       .          .          .          .          .          .          .          .          .          .          .          .]

Emerita_analoga                 GATAACTATAGATCGAATACCTCTTTTTGTTTGGTCAGTATTTATTACTGCAATCTTACTTCTACTTTCTCTTCCCGTTTTAGCAGGAGCTATTACCATATTATTAACAGATCGGAATTT
Pagurus_longicarpus             TATAACAATGGATCGTATACCTTTATTTGTATGAGCTGTTTTTATTACAGCAGTTCTTCTACTTCTGTCCCTACCTGTTCTTGCAGGTGCAATTACAATACTTCTTACAGATCGTAATTT
Pagurus_hirsutiusculus          TATAACAATGGACCGTATACCTTTATTTGTTTGAGCAGTGTTTATTACTGCTATTTTACTTTTACTTTCGCTACCAGTATTAGCAGGTGCTATCACCATGTTATTAACAGATCGAAATTT
Oedignathus_inermis             TATAACTCTGGATCGTATACCTTTATTTGTGTGAGCGGTTTTTATTACTGCTATTTTACTTTTATTATCCCTTCCTGTTTTAGCTGGAGCTATTACCATATTGCTAACAGATCGAAACTT
Hapalogaster_mertensii          TATAACTTTAGACCGAATACCTTTATTTGT?TGAGC?GTATTTATTACTGCTATCCTACTTTTATTATCTTTACCAGTTTTAGCGGGAGCCATTACCATATTATTAACAGATCGTAATTT
Cryptolithodes_typicus          AATAACTTTGGACCGCATGCCTTTATTTGTGTGATCAGTTTTTATTACTGCAATTTTGCTTTTATTATCATTACCCGTCTTAGCAGGGGCTATTACAATATTATTAACAGATCGAAACCT
Paralomis_granulosa             AATAACCTTAGATCGCATACCTTTATTTGTGTGGTCAGTATTTATTACTGCGATTCTACTTTTATTATCATTGCCAGTTTTAGCCGGCGCAATTACTATATTACTCACAGATCGAAATTT
Lopholithodes_mandtii           AATAACCTTAGACCGCATACCTTTATTTGTATGGTCAGTATTTATTACTGCTATTCTACTTTTATTATCATTACCAGTTTTAGCCGGAGCAATTACTATGTTACTCACAGATCGAAATTT
Paralithodes_camtschaticus      AATAACCTTAGACCGTATACCTTTATTTGTGTGATC?GTATTTATTACTGCAATTCT?CTTTTATTATCACT?CCAGTTTTAGCAGG?GCTATTACTATATTACTTACAGATCGAAATTT
Lithodes_santolla               AATAACCCTAGACCGTATACCTTTATTTGTATGATCAGTATTTATTACTGCAATTTTACTTTTATTATCACTACCAGTTTTAGCAGGGGCCATTACTATATTACTTACAGATCGAAATTT
Rhinolithodes_wosnessenskii     AATAACTCTAGATCGAATGCCCCTGTTTGTATGATCAGTATTTATTACTGCAATTCTACTTTTATTATCACTGCCAGTTTTAGCAGGAGCAATTACTATGTTACTCACAGATCGAAATTT
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[                                    370       380       390       400       410       420       430       440       450       460       470       480]
[                                      .         .         .         .         .                   .         .         .         .         .         .]

Emerita_analoga               AAATACTTCTTTTTTTGATCCAGCAGGAGGGGGAGATCCAGTTCTTC???ANA???CCGCATAAACAACATAAGATTCTGATTATTACCCCCCTCTCTCACTTTGCTTTTAATAAGAGGA
Pagurus_longicarpus           AAACACATCATTCTTTGATCCAGCAGGAGGTGGTGATCCAGTTTTA?????N?A??CCGTATAAATAATATAAGATTTTGACTTTTACCCCCCTCATTAACTCTTCTTCTTACCAGAGGT
Pagurus_hirsutiusculus        AAATACTTCTTTTTTTGATCCAGCAGGGGGTGGAGATCCGGTACTA?A????????--------------------------------------------------------CYAGGGGT
Oedignathus_inermis           AAATACTTCTTTCTTTGATCCTGCTGGAGGGGGAGACCCAGTTTTA?A????NTATACGAATAAATAATATAAGATTTTGACTTTTACCACCCTCCCTAACTCTCCTACTAACTAGTGGA
Hapalogaster_mertensii        AAATACTTCATTTTTTGATCCGGCGGGGGGTGGAGATCCTGTATTAC?Y?T???TCCGTATAAATAATATGAGTTTCTGACTTTTACCCCCCTCTTTAACCCTTCTACTGACTAGTGGTA
Cryptolithodes_typicus        AAATACTTCTTTTTTTGATCCGGCCGGAGGAGGAGATCCAATTTTAG?Y?T???T?GCGAATAAATAATATAAGTTTTTGACTTTTACCTCCATCTTTAACTCTTTTGTTGACCAGAGGT
Paralomis_granulosa           AAACACCTCTTTTTTTGACCCTGCCGGAGGAGGGGATCCCGTTCTA???A??????GCGAATAAATAATATAAGTTTTTGACTTCTTCCCCCATCTTTAACTCTTTTACTAACCAGAGGA
Lopholithodes_mandtii         AAATACTTCTTTTTTCGATCCTGCAGGAGGAGGAGATCCAGTTTTA?A?A?????ACGAATAAATAATATAAGATTTTGACTTTTACCCCCATCTTTAACTCTTTTATTAACTAGTGGTA
Paralithodes_camtschaticus    AAACACCTCTTTTTTTGA?CCTGCAGGAGGAGGAGATCCAGTTTTA??T???A?ACGAATAAATAATATAAGTTTTTGACTTTTACCCCCCTCACTAACTCTTTTATTAACTAGGGGAAT
Lithodes_santolla             AAATACCTCTTTTTTCGACCCCGCAGGAGGAGGAGATCCTGTTTTA??T??A??ACGAATAAATAATATAAGTTTTTGACTTTTACCCCCATCTTTAACTCTTTTATTAACTAGGGGGAT
Rhinolithodes_wosnessenskii   AAACACCTCTTTTTTTCGACCCTGCCGGAGGGGGAGACCCCGTCTTG?????????????????????????????????????????????????????????????????????????

[                                    490       500       510       520       ]
[                                      .         .         .         .       ]

Emerita_analoga               ATAGTTGAAAGAGGTGTAGGAACAGGATGAACTGTTTACCCACCCCTAT
Pagurus_longicarpus           ATAGTTGAAAGAGGTGTTGGAACCGGATGAACTGTGTATCCACCACTGT
Pagurus_hirsutiusculus        ATAGTTGAAAGAGGTGTTGGNACYGGATNAACTGT?TATCCACCTCTNT
Oedignathus_inermis           ATAGTAGAAAGAGGTGTAGGAACAGGATGAACTGTCTATCCCCCATTAT
Hapalogaster_mertensii        TAGTAGAAAGAGGCGTTGGTACGGGATGAACTGTTTACCCTCCGCTGTC
Cryptolithodes_typicus        ATAGTCGAAAGAGGTGTGGGAACAGGATGAACTGTCTACCCACCACTGT
Paralomis_granulosa           ATGGTAGAAAGGGGCGTGGGCACAGGATGAACTGTTTACCCTCCCCTAT
Lopholithodes_mandtii         TAGTAGAAAGAGGTGTAGGTACAGGATGAACTGTGTATCCCCCACTTTC
Paralithodes_camtschaticus    AGTAGAAAGAGGTGTAGGTACAGGATGAACTGTTTACCCACCATTATCT
Lithodes_santolla             AGTAGAAAGAGGTGTAGGTACAGGATGAACTGTTTACCCACCATTATCC
Rhinolithodes_wosnessenskii   ?????????????????????????????????????????????????
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Appendix 3-1d- Mitochondrial gene COII aligned.

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[                                     10        20        30        40        50        60        70        80        90       100       110       120]
[                                      .         .         .         .         .         .         .         .         .         .         .         .]

Emerita_analoga                TGACCATGCCATAGTTGTACTAATTCTTATTACTACTTTAGTAGGTTATATAATAGTTTCATTATTTTGAAATACCCTTATTAATCGAGTTTTACTAGAAAATCAAACTATCGAAATTAT
Pagurus_longicarpus            CGATCATACAATAGTTGTTTTAATTCTTATTACAACATTTGTAGGTTATATAATAATATCATTGTTTTTAATTCTTATATCAACCGTTTCCTACTAGAGAATCAAACTATCGAAATTAT
Pagurus_hirsuticusulus         ????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????
Oedignathus_inermis            CGATCATGCTATAATTGTTTTAATTTTAATTACAACACTTGTAGGATATATAATAGCATCTTTATTTGCTAATTCTTATATTAACCGGTTTCTTCTAGAACACCAAACAATTGAAATTAT
Hapalogaster_mertensii         CGATCACGCTATAATTATTTTAATTTTAATTACAACACTTGTTGGGTATATAATAGCGTCTTTATTTGCTAACTCTTACATTAATCGATTTCTTTTAGAAAATCAAACAATTGAAATCAT
Cryptolithodes_typicus         --------------------------------CAACCCTCGTAGGATACATAATAGCATCTTTATTCGCAAATTCTTATATTAACCGATTTCTTTTGGAAAATCAAACAATCGAAATTAT
Paralomis_granulosa            CGACCATGCAATAATTGTTTTGATTTTAATTACAACACTTGTCGGCTATATAATAGCATCTTTATTTACTAATTCCTATATTAACCGATTTCTTCTAGAAAATCAAACAATTGAAATTAT
Lopholithodes_mandtii          CGATCACGCAATAATTGTTCTGATTTTAATTACAACACTTGTGGGTTATATAATAGCATCTTTATTTGCTAATTCTTATATTAACCGATTTCTTTTAGAAAATCAAACAATTGAAATTAT
Paralithodes_camtschaticus     CGATCA?GCAATAATTGT?TTAATTTTAATTAC?ACACTTGTAGGATATATAATAGC?TCTTTATT?GCTAATTCTTATATTAATCGATTTCTTCTAGAGAATCAA?CAATTGAAATTAT
Lithodes_santolla              CGATCACACAATAATTGTTTTAATTCTAATTACAACACTTGTAGGTTATATAATAGCATCTTTATTTTCTAACTCTTATATTAACCGATTTCTTCTAGAAAATCAAACAATTGAAATTAT
Rhinolithodes_wosnessenskii    CGACCATGCAATAATTGTTTTGATTTTAATTACAACGCTTGTAGGATACATAATAGCATCTTTATTTGCTAATTCTTATATTAATCGGTTTCTTCTAGAAAATCAAACAATTGAAATTAT

[                                    130       140       150       160       170       180       190       200       210       220       230       240]
[                                      .         .         .         .         .         .         .         .         .         .         .         .]

Emerita_analoga                TTGAACCATCCTTCCAGCTTTTATTCTTGTTTTCATTGCTCTTCCCTCTATTCGGCTTCTTTATCTTTTAGATGAAATTAACAACCCTAGAGTTACCTTAAAAACAATCGGACATCAGTG
Pagurus_longicarpus            TTGAACAATCCTACCAGCTGTTATTTTAATTTTTATTGCACTCCCATCTTTACGTTTACTTTATCTACTAGATGAAGTTAATAACCCAAGAGTTACCCTTAAAACCATTGGACATCAATG
Pagurus_hirsuticusulus         ????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????
Oedignathus_inermis            TTGAACTATTTTACCCGCATTTATTTTAATTTTTATTGCGCTCCCGTCTTTGCGACTTCTTTATTTATTAGATGAAGTTAATAACCCAAGTGTAACTCTTAAAACCATYGGCCATCAATG
Hapalogaster_mertensii         TTGAACTATTTTACCTGCGTTTATTTTAATTTTTATTGCACTACCTTCTTTACGACTTCTTTATTTACTAGATGAGATTAATAGTCCCAGTGTTACTCTTAAGACCATTGGACATCAATG
Cryptolithodes_typicus         TTGAACTGTTTTACCTGCTTTTATTTTAATTTTTATTGCGYTACCTTCTTTACGGCTTCTTTATTTACTAGACGAGGTAAATAGTCCAAGTGTAACCCTTAAAACTATTGGCCATCAATG
Paralomis_granulosa            TTGAACCGTACTGCCTGCGTTTATTTTAATTTTTATTGCGCTGCCTTCTTTACGACTTCTTTATTTATTAGATGAGGTAAATAGCCCTAGCGTAACCCTTAAAACCATCGGCCATCAGTG
Lopholithodes_mandtii          CTGAACCATCTTACCAGCATTTATTTTAATTTTTATTGCGTTACCCTCTTTACGACTTCTTTATTTATTAGATGAAGTAAATAACCCTAGCGTAACTCTTAAAGCTATCGGTCATCAATG
Paralithodes_camtschaticus     TTGAACTGTTTTACCTGCATTTATTTTAATTTTTATTGCATTACCTTCTTT?CGACTTCTTTATTTATTAGATGAAGTAAATAATCCTAGAGTAACTCTTAAAACCATTGGTCATCAGTG
Lithodes_santolla              TTGAACTATTTTACCTGCATTTATTTTAATTTTTATTGCACTACCTTCTTTACGACTTCTTTATTTATTAGATGAAGTAAATAACCCCAGAGTAACTCTTAAAACCATTGGTCACCAATG
Rhinolithodes_wosnessenskii    TTGAACTGTTTTACCTGCGTTTATTTTAATTTTTATTGCGCTACCTTCCCTGCGACTTCTTTATTTATTAGACGAAGTAAATAACCCCAGTGTAACCCTTAAAACTATTGGACACCAATG

[                                    250       260       270       280       290       300       310       320       330       340       350       360]
[                                      .         .         .         .         .         .         .         .         .         .         .         .]

Emerita_analoga                ATACTGAAGATATGAATATTCAGATTTTATACAATTAGAATTTGACTCTTATATACTTCCAATTAATGATTTAGAATTATCTGGATTCCGACTGTTAGAAGTAGATAATCGAACTGTTTT
Pagurus_longicarpus            ATACTGAAGATACGAATATTCTGATTTTTTCCAATTAGAATTTGATTCTTATATAATCCCATCTAATGAAATAGAAAATTCAATATTCC?ACTCTTAGAAGTAGATAACCGAACTGTACT
Pagurus_hirsuticusulus         ????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????
Oedignathus_inermis            GTACTGAAGATATGAATATTCTGATTTTCTTCAATTAGAGTTTGACTCATATATAATTCCTCTTAATGAGATAGATTCYTCTGG?TTTCGACTATTAGACGTTGATAACCGAACCGTTTT
Hapalogaster_mertensii         ATACTGAAGTTATGAGTATTCTGACTTCCTTCAATTAGAATTTGATTCTTATATAATTCCTCTCAATGAAATAGATTCTTCGAATTTCCGTTTATTAGATGTTGATAACCGAACAGTCTT
Cryptolithodes_typicus         ATATTGAAGTTATGAATACTCTGATTTTCTTCAATTAGAATTTGATTCTTATATAATTCCCCTTAATGAGATAGAACTATCTAGTTTCCGTCTTCTAGACGTTGACAACCGAACAGTTTT
Paralomis_granulosa            ATATTGAAGTTATGAGTATTCTGATTTTCTGCAGTTGGAATTTGATTCTTATATAATCCCCATTAGTGAAATAGATTCTTCAAGATTCCGGCTCTTAGATGTTGATAACCGAACAGTCCT
Lopholithodes_mandtii          ATATTGAAGTTATGAGTATTCTGATTTTCTGCAGTTAGAGTTTGATTCTTATATAACTCCCCTTAATGAAATAAACTCTTCAAGATTCCGACTCTTAGATGTTGATAATCGAACAGTTCT
Paralithodes_camtschaticus     ATA?TGAAGTTATGAATATTCTGACTTTCTTCAATTAGA?TTTGATTCTTATATAATTCCCCTCAATGAGATAGAATCTTCAAACTTTCGATTATTAGA?GTTGATAATCGAACAGTTTT
Lithodes_santolla              ATATTGAAGTTATGAATATTCTGATTTTCTTCAATTAGAGTTTGATTCTTATATAATTCCCATTAATGAAATAAATTCTTCAAGATTTCGATTATTAGATGTAGACAATCGAACAGTTTT
Rhinolithodes_wosnessenskii    GTATTGAAGTTACGAGTATTCTGATTTTCTTCAATTAGAGTTTGATTCTTATATAATTCCCCTTAATGAAATAGACTCTTCAAACTTCCGACTATTAGATGTTGATAATCGAACAGTTTT
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[                                    370       380       390       400       410       420       430       440       450       460       470       480]
[                                      .         .         .         .         .         .         .         .         .         .         .         .]

Emerita_analoga               ACCTATAAATACCCAGGTACGACTTTTAGTTACAGCTGCAGATGTTATTCACTCCTGAC???ANA???CGATCACGCTATAATTGTACTAATCCTAATTACCACACTAGTAGGATATATA
Pagurus_longicarpus           ACCAATAAATACACAAATTCGAGTACTTATTAGAGCCGCAGATGTTATTCACTCATGA????N?A??CGACCACACTATAATCGTTTTAATTTTAATTACAACATTAGTGGGTTATATA
Pagurus_hirsuticusulus        ???????????????????????????????????????????????????????????A????????CGACCACACTATAATTGTTTTAATTTTAATTACAACAATAGTAGGTTATATT
Oedignathus_inermis           ACCAATAAATACACAAATTCGAGTTCTTATTAGAGCTGCGGATGTAATCCACTCTTGA?A????NTATCGACCACGCTATAATTATTTTAATTTTAATTACAACACTTGTTGGATATATA
Hapalogaster_mertensii        GCCAATAAATACTCAAATTCGAGTTCTTATTAGAGCAGCGGATGTAATTCACTCCTGAC?Y?T???T----------------------------------------GTAGGATATATAA
Cryptolithodes_typicus        ACCAATAAACACACAAATTCGAGTTCTTATTAGCGCAGCCGATGTTATTCATTCTTGAG?Y?T???T?TGATCACGCAATAATTGTTTTGATTTTAATTACAACACTTGTAGGGTATATA
Paralomis_granulosa           GCCCATAAACACTCAAATTCGAGTTCTAATCAGTGCAGCAGATGTTATTCACTCTTGA???A??????CGATCATGCAATAATTGTTTTGATTTTAATTACAACACTTGTAGGATATATA
Lopholithodes_mandtii         ACCCATAAATACTCAAATTCGAGTTCTAGTTAGGGC?GCAGATGTTA?TCACTCTTGA?A?A?????CGATCACGCAATAATTGTTTTAATTTTAATTACAACACTTGTAGGATATATAA
Paralithodes_camtschaticus    ACCCATAAATACTCAAATTCGAGTTCTTATTAGAGCAGCAGATGTTATTCACTCTTGA??T???A?TGATCACACAATAATTATTTTAATTTTAATTACAACACTTGTGGGTTATATAAT
Lithodes_santolla             ACCGATAAATACTCAAATTCGAGTTCTTATTAGAGCAGCAGATGTTATTCACTCTTGA??T??A??CGATCACACAATAATTGTTTTAATTTTAATTACAACACTTGTAGGTTATATAAT
Rhinolithodes_wosnessenskii   ACCCATAAACACTCAAATTCGAGTTCTTATTAGAGCAGCAGATGTTATTCACTCTTGA??????????????????????????????????????????????????????????????


[                                    490       500       510       520       ]
[                                      .         .         .         .       ]

Emerita_analoga               ATATCTAGATTATTATTCAATAAATATATTAACCGATTCTTACTAGAAA
Pagurus_longicarpus           ATAGCATCTTTATTTGCTAATTCTTATATTAACCGATTTTTACTAGAAA
Pagurus_hirsuticusulus        ATAGCATCTTTATTTGCTAATTCTTATATTAATCGATTTTTATTAGAAA
Oedignathus_inermis           ATAGCATCTTTATTTGCTAATTCCTATATTAACCGATTTCTTTTAGAAA
Hapalogaster_mertensii        TAGCATCTTTATTCGCAAATTCTTATATTAACCGGTTTCTCTTGGAAAA
Cryptolithodes_typicus        ATAACATCTTTATTTGCTAATTCTTATATTAACCGGTTTCTTCTAGAAA
Paralomis_granulosa           ATAGC?TCTTTATTTGCTAACTCTTATATTAACCGATTTCTTCTAGA?A
Lopholithodes_mandtii         TAGCATCTTTATTTGCTAATTCTTATATTAACCGATTTCTTCTAGAAAA
Paralithodes_camtschaticus    AGCATCTTTATTTGCTAATTCTTATATTAACCGATTTCTTTTAGAAAAT
Lithodes_santolla             AGCATCTTTATTTGCTAATTCTTATATTAACCGATTTCTTCTAGAAAAT
Rhinolithodes_wosnessenskii   ?????????????????????????????????????????????????
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Appendix 3-1e- Nuclear gene 28S aligned.

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[                                            10        20        30        40        50        60        70        80        90        100       110       120]
[                                            .         .         .         .         .         .         .         .         .         .         .         .]

Emerita_analoga                   GGAGGAAAAGAAACTAACAGGGATTCCCCTAGTAAGGGCGACTGAACCGGGAAGAGCCCAGCGCATAACCTCGCGT--CCC--CACCGGGGCG----CGAGGGGTGTTGCGTTCCGGAGG   [112]
Clibanarius_vittatus              CGAGGAAAAGAAACTAACAGGGATTCCCTTAGTAAGGGCGACTGAAACGGGAAGAGCCCAGCGCATAACCTCGAA---CCCT-CACCGAGGCGTCTTCGAGGGGTGTTGCGTTTCAGAGG   [116]
Pagurus_longicarpus               GGAGGAAAAGAAACTAACAGGGATTCCCTGAGTAAGGGCGACTGAAATGGGAAGAGCCCAGCGCATAAGCTCGCTTTGCCCTTAACCGGG-CG----CGAGCGGTGTTGCGTTTCGGAGG   [115]
Pagurus_bernhardus                GGAGGAAAAGAAACTAACAGGGATTCCCTCAGTAAGGGCGACTGAAATGGGAAGAGCCCAGCGCATAAGCTCGCTTTGCCTTTTACCGGG-CG----CGAGCGGTGTTGCGTTTCGGAGG   [115]
Pagurus_hirsutiusculus            GGAGGAAAAGAAACTAACAGGGATTCCCTCAGTAAGGGCGACTGAAATGGGAAGAGCCCAGCGCATAAGCTCGCTTTGCCTTTTACCGGG-CG----CGAGCGGTGTTGCGTTTCGGAGG   [115]
Labidochirus_splendescens         GGAGGAAAAGAAACTAACAGGGATTCCCTCAGTAAGGGCGACTGAAATGGGAAGAGCCCAGCGCATAAGCTCGCTTTGCCTTTTACCGGG-CG----CGAGCGGTGTTGCGTTTCGGAGG   [115]
Oedignathus_inermis               GGAGGAAAAGAAACTAACAGGGATTCCCTCAGTAAGGGCGACTGAAATGGGAAAAGCCCAGCGCATAAGCTCGCTTTGCTCTTTACCGGG-CG----CGAGCGGTGTTGCGTTTCGGAGG   [115]
Hapalogaster_dentata              GGAGGAAAAGAAACTAACAGGGATTCCCTCAGTAAGGGCGACTGAAATGGGAAAAGCCCAGCGCATAAGCTCGCTTTGCCCTTCACCGGG-CG----CGAGCGGTGTTGCGTTTCGGAGG   [115]
Hapalogaster_mertensii            GGAGGAAAAGAAACTAACAGGGATTCCCTCAGTAAGGGCGACTGAAATGGGAAAAGCCCAGCGCATAAGCTCGCTTTGCCCTTCACCGGG-CG----CGAGCGGTGTTGCGTTTCGGAGG   [115]
Cryptolithodes_sitchensis         GGAGGAAAAGAAACTAACAGGGATTCCCTCAGTAAGGGCGACTGAAATGGGAAAAGCCCAGCGCATAAGCTCGCTTTGCCCTTCACCGGG-CG----CGAGCGGTGTTGCGTTTCGGAGG   [115]
Cryptolithodes_typicus            GGAGGAAAAGAAACTAACAGGGATTCCCTCAGTAAGGGCGACTGAAATGGGAAAAGCCCAGCGCATAAGCTCGCTTTGCCCTTCACCGGG-CG----CGAGCGGTGTTGCGTTTCGGAGG   [115]
Glyptolithodes_cristatipes        GGAGGAAAAGAAACTAACAGGGATTCCCTCAGTAAGGGCGACTGAAATGGGAAAAGCCCAGCGCATAAGCTCGCTTTGCCCTTCACCGGG-CG----CGAGCGGTGTTGCGTTTCGGAGG   [115]
Paralomis_granulosa               GGAGGAAAAGAAACTAACACGGATTCCCTCAGTAAGGGCGACTGAAATGGGAAAAGCCCAGCGCATAAGCTCGCTTTGCCCTTCACCGGG-CG----CGAGCGGTGTTGCGTTTCGGAGG   [115]
Phyllolithodes_papillosus         GGAGGAAAAGAAACTAACAGGGATTCCCTCAGTAAGGGCGACTGAAATGGGAAAAGCCCAGCGCATAAGCTCGCTTTGCCCTTCACCGGG-CG----CGAGCGGTGTTGCGTTTCGGAGG   [115]
Lopholithodes_mandtii             GGAGGAAAAGAAACTAACAGGGATTCCCTCAGTAAGGGCGACTGAAATGGGAAAAGCCCAGCGCATAAGCTCGCTTTGCCCTTCACCGGG-CG----CGAGCGGTGTTGCGTTTCGGAGG   [115]
Paralithodes_brevipes             GGAGGAAAAGAAACTAACAGGGATTCCCTCAGTAAGGGCGACTGAAATGGGAAAAGCCCAGCGCATAAGCTCGCTTTGCCCTTCACCGGG-CG----CGAGCGGTGTTGCGTTTCGGAGG   [115]
Paralithodes_camtschaticus        GGAGGAAAAGAAACTAACAGGGATTCCCTCAGTAAGGGCGACTGAAATGGGAAAAGCCCAGCGCATAAGCTCGCTTTGCCCTTCACCGGG-CG----CGAGCGGTGTTGCGTTTCGGAGG   [115]
Lithodes_maja                     GGAGGAAAAGAAACTAACAGGGATTCCCTCAGTAAGGGCGACTGAAATGGGAAAAGCCCAGCGCATAAGCTCGCTTTGCCCTTCACCGGG-CG----CGAGCGGTGTTGCGTTTCGGAGG   [115]
Lithodes_santolla                 ????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????   [120]
Lithodes_aequispinus              GAAGGAAAAGAAACTAACAGGGATTCCCTCAGTAAGGGCGACTGAAATGGGAAAAGCCCAGCGCATAAGCTCGCTTTGCCCTTCACCGGG-CG----CGAGCGGTGTTGCGTTTCGGAGG   [115]
Rhinolithodes_wosnessenskii       GGAGGAAAAGAAACTAACAGGGATTCCCTCAGTAAGGGCGACTGAAATGGGAAAAGCCCAGCGCATAAGCTCGCTTTGCCCTTCACCGGG-CG----CGAGCGGTGTTGCGTTTCGGAGG   [115]
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[                                   130       140       150       160       170       180       190       200       210       220       230       240]
[                                     .         .         .         .         .         .         .         .         .         .         .        .]

Emerita_analoga                GTCCGGCACGCCGCCCCACACCGCCTAAGTCATGCTTGAAAGCGGC-CACTACCCAGGGAGGGTGATAGGCCCGTGTGGCGGAGC--CCGCGAGGGCATACGTGGGGCGGTCGGAAAGGG   [229]
Clibanarius_vittatus           GTCTAGCACGCCGGCCATTCTCGCCTAAGTCTCGTTTGAAAGCGGCTCATTACCCATGGAGGGTGATAGGCCCGTATGGCGACTCACCCGTGAGGG-ATACCTTGGCCGG-CGGAAAGGA   [234]
Pagurus_longicarpus            GTCCGGCACGCCGCCTTACGACGCCTAAGTCATGCTTGAAAGCGGC-CACTACCCATGGAGGGTGAAAGGCCCGTCTGGCGGAGC--CCGTGAGGGCATAAGTGAGGCGGTCGGAAAGGA   [232]
Pagurus_bernhardus             GTCCGGCACGCCGCCTTACGACGCCTAAGTCATGTTTGAAAGCGGC-CACTACCCATTGAGGGTGAAAGGCCCGTCTGGCGGAGC--CCGTGAGGGCAGAAGTGAGGCGGTCGGAAAGGA   [232]
Pagurus_hirsutiusculus         GTCCGGCACGCCGCCTTACGACGCCTAAGTCATGTTTGAAAGCGGC-CACTACCCATTGAGGGTGAAAGGCCCGTCTGGCGGAGC--CCGTGAGGGCAGAAGTGAGGCGGTCGGAAAGGA   [232]
Labidochirus_splendescens      GTCCGGCACGCCGCCTTACGACGCCTAAGTCATGTTTGAAAGCGGC-CACTACCCATTGAGGGTGAAAGGCCCGTCTGGCGGAGC--CCGTGAGGGCAGAAGTGAGGCGGTCGGAAAGGA   [232]
Oedignathus_inermis            GTCCGGCACGCCGCCTCACGACGCCTAAGTCATGCTTGAAAGCGGC-CACTACCCATTGAGGGTGAAAGGCCCGTCTGGCGGAGC--CCGTGAGGGCATAAGTGAGGCGGTCGGAAAGGA   [232]
Hapalogaster_dentata           GTCCGGCACGCCGCCTTACGACGCCTAAGTCATGCTTGAAAGCGGC-CACTACCCATTGAGGGTGAAAGGCCCGTCTGGCGGAGC--CCGTGAGGGCATAAGTGAGGCGGTCGGAAAGGA   [232]
Hapalogaster_mertensii         GTCCGGCACGCCGCCTTACGACGCCTAAGTCATGCTTGAAAGCGGC-CACTACCCATTGAGGGTGAAAGGCCCGTCTGGCGGAGC--CCGTGAGGGCATAAGTGAGGCGGTCGGAAAGGA   [232]
Cryptolithodes_sitchensis      GTCCGGCACGCCGCCTTACGACGCCTAAGTCATGCTTGAAAGCGGC-CACTACCCACTGAGGGTGAAAGGCCCGTCTGGCGGAGC--CCGTGAGGGCATAAGTGAGGCGGTCGGAAAGGA   [232]
Cryptolithodes_typicus         GTCCGGCACGCCGCCTTACGACGCCTAAGTCATGCTTGAAAGCGGC-CACTACCCACTGAGGGTGAAAGGCCCGTCTGGCGGAGC--CCGTGAGGGCATAAGTGAGGCGGTCGGAAAGGA   [232]
Glyptolithodes_cristatipes     GTCCGGCACGCCGCCTTACGACGCCTAAGTCATGCTTGAAAGCGGC-CACTACCCATTGAGGGTGAAAGGCCCGTCTGGCGGAGC--CCGTGAGGGCATAAGTGAGGCGGTCGGAAAGGA   [232]
Paralomis_granulosa            GTCCGGCACGCCGCCTTACGACGCCTAAGTCATGCTTGAAAGCGGC-CACTACCCATTGAGGGTGAAAGGCCCGTCTGGCGGAGC--CCGTGAGGGCATAAGTGAGGCGGTCGGAAAGGA   [232]
Phyllolithodes_papillosus      GTCCGGCACGCCGCCTTACGACGCCTAAGTCATGCTTGAAAGCGGC-CACTACCCATTGAGGGTGAAAGGCCCGTCTGGCGGAGC--CCGTGAGGGCATAAGTGAGGCGGTCGGAAAGGA   [232]
Lopholithodes_mandtii          GTCCGGCACGCCGCCTTACGACGCCTAAGTCATGCTTGAAAGCGGC-CACTACCCATTGAGGGTGAAAGGCCCGTCTGGCGGAGC--CCGTGAGGGCATAAGTGAGGCGGTCGGAAAGGA   [232]
Paralithodes_brevipes          GTCCGGCACGCCGCCTTACGACGCCTAAGTCATGCTTGAAAGCGGC-CACTACCCATTGAGGGTGAAAGGCCCGTCTGGCGGAGC--CCGTGAGGGCATAAGTGAGGCGGTCGGAAAGGA   [232]
Paralithodes_camtschaticus     GTCCGGCACGCCGCCTTACGACGCCTAAGTCATGCTTGAAAGCGGC-CACTACCCATTGAGGGTGAAAGGCCCGTCTGGCGGAGC--CCGTGAGGGCATAAGTGAGGCGGTCGGAAAGGA   [232]
Lithodes_maja                  GTCCGGCACGCCGCCTTACGACGCCTAAGTCATGCTTGAAAGCGGC-CACTACCCATTGAGGGTGAAAGGCCCGTCTGGCGGAGC--CCGTGAGGGCATAAGTGAGGCGGTCGGAAAGGA   [232]
Lithodes_santolla              ????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????   [240]
Lithodes_aequispinus           GTCCGGCACGCCGCCTTACGACGCCTAAGTCATGCTTGAAAGCGGC-CACTACCCATTGAGGGTGAAAGGCCCGTCTGGCGGAGC--CCGTGAGGGCATAAGTGAGGCGGTCGGAAAGGA   [232]
Rhinolithodes_wosnessenskii    GTCCGGCACGCCGCCTTACGACGCCTAAGTCATGCTTGAAAGCGGC-CACTACCCATTGAGGGTGAAAGGCCCGTCTGGCGGAGC--CCGTGAGGGCATAAGTGAGGCGGTCGGAAAGGA   [232]
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[                                          250       260       270       280       290       300]
[                                            .         .         .                           ]

Emerita_analoga                  CCTCTCCGTAGAGTCGGGTTGCTTGAGAGTGCAGCCCAAAGTAGG---------------   [274]
Clibanarius_vittatus             CTTTTCTGTAGAGTCAGGTTGCTTGAAACTGCAGCCTAAAGTAGGTGGTAAACTCCTTCT   [294]
Pagurus_longicarpus              CCTTTCCGTAGAGTCGGGTTGCTTGAGAGTGCAGCCCAAAGCAGGTGGTAAACTCCTTCT   [292]
Pagurus_bernhardus               CCTATCCGTAGAGTCGGGTTGCTTGAAAGTGCAGCCCAAAGCAGGTGGTAAACTCCTTCT   [292]
Pagurus_hirsutiusculus           CCTATCCGTAGAGTCGGGTTGCTTGAAAGTGCAGCCCAAAGCAGGTGGTAAACTCCTTCT   [292]
Labidochirus_splendescens        CCTATCCGTAGAGTCGGGTTGCTTGAAAGTGCAGCCCAAAGCAGGTGGTAAACTCCTTCT   [292]
Oedignathus_inermis              CCTTTCCGTAGAGTCGGGTTGCTTGAAAGTGCAGCCCAAAGCAGGTGGTAAACTCCTTCT   [292]
Hapalogaster_dentata             CCTTTCCGTAGAGTCGGGTTGCTTGAAAGTGCAGCCCAAAGCAGGTGGTAAACTCCTTCT   [292]
Hapalogaster_mertensii           CCTTTCCGTAGAGTCGGGTTGCTTGAAAGTGCAGCCCAAAGCAGGTGGTAAACTCCTTCT   [292]
Cryptolithodes_sitchensis        CCTTTCCGTAGAGTCGGGTTGCTTGAAAGTGCAGCCCAAAGCAGGTGGTAAACTCCTTCT   [292]
Cryptolithodes_typicus           CCTTTCCGTAGAGTCGGGTTGCTTGAAAGTGCAGCCCAAAGCAGGTGGTAAACTCCTTCT   [292]
Glyptolithodes_cristatipes       CCTTTCCGTAGAGTCGGGTTGCTTGAAAGTGCAGCCCAAAGCAGGTGGTAAACTCCTTCT   [292]
Paralomis_granulosa              CCTTTCCGTAGAGTCGGGTTGCTTGAAAGTGCAGCCCAAAGCAGGTGGTAAACTCCTTCT   [292]
Phyllolithodes_papillosus        CCTTTCCGTAGAGTCGGGTTGCTTGAAAGTGCAGCCCAAAGCAGGTGGTAAACTCCTTCT   [292]
Lopholithodes_mandtii            CCTTTCCGTAGAGTCGGGTTGCTTGAAAGTGCAGCCCAAAGCAGGTGGTAAACTCCTTCT   [292]
Paralithodes_brevipes            CCTTTCCGTAGAGTCGGGTTGCTTGAAAGTGCAGCCCAAAGCAGGTGGTAAACTCCTTCT   [292]
Paralithodes_camtschaticus       CCTTTCCGTAGAGTCGGGTTGCTTGAAAGTGCAGCCCAAAGCAGGTGGTAAACTCCTTCT   [292]
Lithodes_maja                    CCTTTCCGTAGAGTCGGGTTGCTTGAAAGTGCAGCCCAAAGCAGGTGGTAAACTCCTTCT   [292]
Lithodes_santolla                ????????????????????????????????????????????????????????????   [300]
Lithodes_aequispinus             CCTTTCCGTAGAGTCGGGTTGCTTGAAAGTGCAGCCCAAAGCAGGTGGTAAACTCCTTCT   [292]
Rhinolithodes_wosnessenskii      CCTTTCCGTAGAGTCGGGTTGCTTGAAAGTGCAGCCCAAAGCAGGTGGTAAACTCCTTCT   [292]
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CHAPTER 4

Morphology-based phylogeny of the family Lithodidae (Crustacea: Anomura: Paguroidea: Lithodidae)

ABSTRACT

Cladistic analysis of morphological characters was used to examine the evolutionary history of the family Lithodidae (king crabs or stone crabs). The hermit-crab families Paguridae and Diogenidae (all superfamily Paguroidea) and the mole crab *Emerita analoga* (superfamily Hippoidea) were used as outgroups. Of the 105 known lithodid species, 29 taxa representing 15 genera were scored for 170 morphological characters embodying 12 regions of the exoskeleton. The cladistic analysis shows that the family Lithodidae is monophyletic, with the subfamily Hapalogastrinae paraphyletic with respect to the monophyletic subfamily Lithodinae. It further suggests reassignment of the hapalogastrine genera *Placetron* and *Acantholithodes* to the subfamily Lithodinae. As the cladistic analysis did not resolve the subfamilial position of *Dermaturus*, I have kept it within the subfamily Hapalogastrinae. Of lithodid genera with more than one representative sampled, three were found to be monophyletic at the current level of sampling (*Cryptolithodes*, *Hapalogaster*, and *Lopholithodes*), while the remaining genera were either paraphyletic (*Lithodes*), polyphyletic (*Paralithodes*), or produced unresolved polytomies (*Paralomis*). This tree topology suggests reassigning *Paralithodes californiensis* and *Paralithodes rathbuni* to their original genus *Lithodes*, preserving the monophyly of both *Lithodes* and *Paralithodes*. Production of phylogenetically robust topologies allowed morphological and distributional hypotheses to be investigated. Bouvier's (1897) transitional hypothesis concerning abdominal modifications was partially supported by the reconstructed phylogeny, in that the subfamily Hapalogastrinae can be considered a transitional group between outgroup genera *Pagurus* and *Labidochirus*, all of which have soft abdomens, and the subfamily Lithodinae, which is characterized by a hard abdomen. Bouvier's (1896) and Makarov's (1962) radiation hypotheses concerning lithodid origin and biogeographic distribution were supported by the analysis.

Key words: king crabs, hermit crabs, morphological systematics, Paguridae, Lithodidae

INTRODUCTION

Members of the family Lithodidae (Crustacea: Decapoda: Anomura) originated between 13 and 25 million years ago (Cunningham 1992) and radiated explosively to presently occupy oceans throughout the anti-tropical world (Fig. 4-1). This family includes approximately 105 described species (Table 2-1) belonging to 15 (if *Acantholithus hystrix* is a member of the genus *Paralomis*, Sakai 1976) or 16 (Dawson 1989) genera. There are two subfamilies, the small, solitary, Hapalogastrinae, which have soft abdomens, and the large, generally social Lithodinae, which possess calcified abdomens. These anomurans are distributed from the mid-intertidal region (the subfamily Hapalogastrinae, Makarov 1962) to abyssal depths (the subfamily Lithodinae, Macpherson 1988b, Dawson 1989), typically in temperate waters and concentrated in the north Pacific Ocean.

Previous theories concerning lithodid evolution suggest that the partially carcinized (crab-like appearance including a wide calcified carapace and abdomen, Borradaile 1916) subfamily Hapalogastrinae is a transitional group between the fully carcinized family Lithodidae and the family Paguridae, the latter being characterized by soft abdomens (Bouvier 1894 a,b, 1897). Although lithodids have been the subject of periodic interest from systematic, developmental, and evolutionary biologists (Milne-Edwards 1837, Boas 1880a, b, Bouvier 1894a, b, 1895, 1896, 1897, Borradaile 1916, Martin and Abele 1986, Macpherson 1988b, Cunningham et al. 1992, Richter and Scholtz 1994, McLaughlin and Lemaitre 1997), and consistent interest by fishery biologists (see Dawson 1989 for an exhaustive bibliography, and Chapter 2 for a recent review), agreement has not been reached concerning generic and specific relationships.

Brandt (1848, 1850) was the first to classify the species and genera of lithodids. Brandt's classification was extended by Benedict (1894), Bouvier (1895, 1896), Makarov (1962), Sakai (1971, 1976, 1980) and Takeda (1974), although it was not until fairly recently that a world-wide revision and taxonomic understanding of lithodids was attempted (Dawson and Yaldwyn 1985). However, additional taxonomic investigations into this family would be valuable for increasing our understanding of taxonomic affinities and improving our ability to identify taxa.

Presently, the most complete morphological and taxonomic treatment of lithodids is that of Macpherson (1988b), who provided morphological definitions, proposed new species, provided species locations, keys and annotated descriptive plates of Atlantic Lithodinae (*Neolithodes*, *Lithodes*, and *Paralomis*); equally comprehensive is the review of Japanese lithodids by Sakai (1971, 1976). Dawson (1989) contributed to lithodid knowledge, and communication among scientists by presenting an exhaustive annotated bibliography. Updates concerning species descriptions, life-history traits, distribution, predators, prey, taxonomic keys and fisheries are found in Chapter 2 of this thesis. The morphological data base presented here for cladistic analysis is intended to provide a clearer understanding of lithodid phylogeny, so that it may in turn provide better insight into the origin, radiation, distribution, and morphological adaptations of the family Lithodidae.

In this paper, a phylogeny for all 15 genera and 29 of 105 species of the family Lithodidae is proposed using morphological characters. The paper has two main objectives. First, the morphological matrix is used to assess inter-generic and subfamilial relationships within the family Lithodidae. Second, this proposed morphological phylogeny is used to examine lithodid abdominal evolution and biogeographical radiation and compare them to previous hypothetical reconstructions.

MATERIALS AND METHODS

Material for this study comes largely from examination of specimens at the United States Museum of Natural History, in Washington D.C., U.S.A. (U.S.N.M.), and the private collection of the author (P.C.). Specimens were also obtained via loans from U.S.N.M., The Royal British Columbia Provincial Museum, Canada, (R.B.C.P.M.) and The Victoria Museum, Australia (V.M.; Table 4-1).

Taxa Chosen:

All taxa included in the analysis are extant members of the Crustacean infraorder Anomura (Table 4-1), including 33 members of the superfamily Paguroidea and one member of the superfamily Hippoidea (*Emerita analoga*). Ingroup members include representatives of all 15 (if *Acantholithus* is included in the genus *Paralomis* as per Sakai 1976) genera of the king crab family Lithodidae. This includes 8 species, representing all five genera of the subfamily Hapalogastrinae (8 or 9 member species depending on whether *Placetron forcipatus* Benedict, 1894 is equivalent to *Placetron wosnessenskii*; as per Dawson 1989) and 21 species representing 10 genera of the diverse (94 species, Table 2-1) subfamily Lithodinae. All members of the following genera are represented: *Oedignathus*, *Hapalogaster*, *Dermaturus*, *Acantholithodes*, *Rhinolithodes*, *Phyllolithodes*, *Lopholithodes*, *Glyptolithodes*, *Sculptolithodes*, and *Placetron* (if it is monospecific as per Dawson 1989). Speciose genera with diverse forms, such as *Neolithodes* (10 species), *Lithodes* (17 species), and *Paralomis* (51 species; Table 2-1), were sampled sparsely.

The outgroup taxa were chosen based on published hypotheses of taxonomic relationships of the family Lithodidae to other members of infraorder Anomura (McLaughlin 1983, Martin and Abele 1988, Cunningham et al. 1992, McLaughlin and Lemaitre 1997). The outgroup consisted of three hermit crabs of the family Paguridae (*Pagurus bernhardus*, *Pagurus longicarpus*, and *Labidochirus splendescens*), one member of the hermit crab family Diogenidae (*Clibanarius vittatus*), and one mole crab, *Emerita analoga* (superfamily Hippoidea). *Emerita analoga* was removed from the second of two analyses, as many missing character states ("?" in Table 4-2), were required due to the absence of grasping chelae and abdominal sternites. Missing character states may influence tree topology (Nixon and Davis 1991, Maddison and Maddison 2000), and therefore both trees were produced and subsequently compared.

Character analysis

Morphological variation was described using 170 characters for 29 species of lithodids (Appendix I). Characters were chosen by systematically comparing and describing notable traits from at least one male and female specimen. When collections permitted, 2-10 representatives of each gender were viewed (Table 4-1). In total, 12 morphological regions were established and characters were defined as follows: carapace (34 characters of 170 characters; 20.0% of characters), rostrum (9; 5.3%), branchiostegites (11; 6.5%), sternites (19; 11.1%), abdomen including telson (42; 24.7%), pleopods (2; 1.2%), chelae (33; 19.4%), pereopods (13; 7.6%), and ascicle, ocular peduncle and antenna region (7; 4.1%). Figures 4-2 and 4-3 and Appendix 4-1 provide figures and descriptions of each character and state. Previous treatises such as McLaughlin (1974), Sakai (1976), Macpherson (1988b), and Sandberg and McLaughlin (1998) provide most anatomical definitions. The states of each character are symbolized by numbers (Appendix 1, Table 4-2) Generally, but not always, the (0) state represents absence of a character. As plesiomorphic states are often unknown or controversial (e.g. McLaughlin and Lemaitre 1997), plesiomorphic states were not identified *a priori*. Multi-state characters are not listed in a transformation series (0, 1, 2, etc.) as the evolutionary history was either controversial (e.g. McLaughlin and Lemaitre 1997), or was investigated a posteriori (e.g. Bouvier 1897 transition theory). Unweighted characters were subjected to parsimony analysis with unordered character states as no hypothetical transformation series were inferred a priori.

Phylogenetic analysis

Phylogenetic analysis was performed using unweighted maximum parsimony on the morphological data (Table 4-2). All analyses were performed using PAUP* 4.08b (Swofford 2001), and characters associated with abdominal evolution (Bouvier 1897, Fig. 4-8) were mapped onto the phylogeny using MacClade 4.0 (Maddison and Maddison 2000). Gaps were treated as 'missing,' and starting trees were obtained via stepwise addition. Heuristic searches were carried out with ten random-taxon-addition iterations. Only one tree was held at each step during stepwise addition, and tree-bisection and reconnection (TBR) was used as the branch-swapping algorithm. Branches were collapsed (creating polytomies) if maximum branch length was zero. Clade stability was estimated using two different parameters, either multiple bootstrap replicates or decay indices (= Bremer support, Bremer 1994). Bootstrap values were generated in PAUP from 1000 replicates, each with ten random addition sequences. Branch support values were also calculated in PAUP* by finding the length of the best tree that did not include each of clades. Decay values were calculated by subtracting the length of the best overall tree from the length of the tree that disallowed the clade in question.

RESULTS

Parsimony analysis of the full morphological character matrix (including *E. analoga*) used 170 informative characters and yielded 48 most parsimonious trees of length 630. One tree was randomly chosen to display phylogenetic relationships including bootstrap and decay indices (Fig. 4-4). The associated phylogram (Fig. 4-5) shows inferred amounts of change. The matrix was reanalyzed after removal of *E. analoga*. This resulted in 168 parsimony informative characters yielding 144 most parsimonious trees of length 602 (Figs. 4-6, 4-7).

All strongly supported clades (bootstrap ≥ 70%) were observed in all final tree topologies, irrespective of *E. analoga* inclusion (Figs. 4-4 and 4-6), suggesting that *E. emerita's* missing character states did not seriously affect the reconstruction of phylogenetic relationships. All further discussion, including the reporting of bootstrap and decay indexes, is restricted to the phylogeny that includes *E. analoga* (Fig. 4-4).

Equally weighted parsimony analysis of the morphological data set strongly supports a monophyletic Lithodidae (87% bootstrap value, 7 decay index; label 'A', Fig. 4-4). The subfamily Hapalogastrinae was paraphyletic with respect to the well supported monophyletic subfamily Lithodinae (84%, 7; label 'B', Fig. 4-4). Within the subfamily Hapalogastrinae the only clades included *Oedignathus* and *Hapalogaster* (78%, 3; label 'C', Fig. 4-4). The remaining hapalogastrinid taxa were not strongly supported (57%, 0; label 'D', Fig. 4-4; *Dermaturus*) or were paraphyletic to the subfamily Lithodinae (label 'E', Fig. 4-5; *Acantholithodes*, and *Placetron*). Within the monophyletic subfamily Lithodinae are two major and strongly supported clades. First are taxa defined by the presence of fully articulated and calcified abdominal plates (*Rhinolithodes, Phyllolithodes, Cryptolithodes, Sculptolithodes, Lopholithodes, Glyptolithodes*, and *Paralomis*; 80%, 5; label 'F', Fig. 4-4). Second are taxa defined by the presence of medial abdominal nodules and lateral plates (*Paralithodes* and *Lithodes*; 83%, 3; label 'G', Fig.5). Of the genera with more than one representative species, three were found to be monophyletic (*Hapalogaster, Cryptolithodes*, and *Lopholithodes*), one paraphyletic

(*Lithodes*), one polyphyletic (*Paralithodes*), and one was an unresolved polytomy (*Paralomis*).

DISCUSSION

Understanding relationships among species as well as character evolution ultimately depends on the availability of robust phylogenetic trees. In this study 29 species of the globally distributed family Lithodidae (Fig. 4-1) and five outgroup taxa from superfamilies Paguroidea and Hippoidea (Table 4-1) were scored (Table 4-2) for 170 morphological characters (Figs. 4-2 and 4-3. Appendix 4-1). Using cladistic analysis and phylogenetic inference, a genus-level phylogenetic relationship of lithodids is proposed (Figs. 4-4 to 4-7). This phylogeny is used to investigate Bouvier's abdominal evolution hypothesis (Figs. 4-3 to 4-8) as well as Bouvier's (1896) and Makarov's (1962) biogeographic hypotheses.

Phylogeny of the family Lithodidae

The outgroup taxon *E. analoga* had many missing character states (Table 4-2). a deficiency that may affect final tree topologies (Nixon and Davis 1991). Although removing *E. analoga* increased basal support values it did not produce any strongly supported clades ($\geq$70%) that were not observed in the original analysis. Thus the presence of *E. analoga* was deemed to be inconsequential to final topologies (tree statistics in Table 4-3), and all further discussion of clade support will reflect the phylogeny inclusive of *E. analoga*. Although only one of 48 most parsimonious trees were chosen at random and displayed in Fig. 4-4, all well supported (bootstrap $\geq$70%) clades displayed are found in all most parsimonious trees.

Parsimony analysis strongly supported a monophyletic Lithodidae (87%. 7: label 'A' in Fig. 4-4. Fig. 4-5). This is in agreement with a morphologically based hypothesis of monophyly proposed by Samouelle in 1819 and previous cladistic analyses (Martin and Abele 1986. Cunningham et al. 1992, Richter and Scholtz 1994, McLaughlin and Lemaitre 1997). Monophyly is considered to be supported by the lack of uropods in the adults, calcified and asymmetrically divided abdominal tergites, males completely lacking pleopods 3-5, and females lacking right pleopods 3-5 (Bouvier 1894b, Makarov 1962, Richter and Scholtz 1994).

The family Lithodidae was divided into two subfamilies, the Hapalogastrinae and the Lithodinae, by Ortmann (1901) based on such characters as the presence (Hapalogastrinae) or absence (Lithodinae) of membranous tissue on the dorsal surface of the last three abdominal segments. However, parsimony analyses revealed that the subfamily Hapalogastrinae is a paraphyletic assemblage, suggesting that several members of this subfamily should be taxonomically reassigned. Within the Hapalogastrinae the only monophyletic grouping is the clade including the genera *Hapalogaster* and *Oedignathus* (78%, 3; label 'C', Fig. 4-4). The remaining hapalogastrinid taxa have either poorly supported affinities to either subfamily (*Dermaturus mandtii*; 57%, 0; label 'D', Fig. 4-4 or 65%, 0, Fig. 4-6) or are well-supported as basal to the subfamily Lithodinae (*Acantholithodes hispidus* and *Placetron wosnessenskii*; 82%, 7; label 'E', Fig. 4-4 or 98%, 8, Fig. 4-6).

This phylogenetic analysis of the subfamily Hapalogastrinae suggests that the genera *Acantholithodes* and *Placetron* should be reassigned to the subfamily Lithodinae. Pending more conclusive evidence on its relationships, *Dermaturus* should remain in the subfamily Hapalogastrinae along with *Hapalogaster* and *Oedignathus*. Although Bouvier (1895) suggested that the unusual morphology of *Dermaturus* supported creation of a new subfamily, the Ostracogastriques, my analysis does not emphatically support this taxonomic rank. Overall, these suggested taxonomic relocations are supported by both behavioral and morphological characters. The latter three hapalogastrine genera have smaller maximum sizes (CW= 20-35; Jensen 1995) compared to *Acantholithodes* (CW = 64; Hart 1982) and *Placetron* (CW= 73; Makarov 1962), they are found in the intertidal as adults, their sternite braces are round instead of triangular, they possess multiple branchiostegite plates, they lack a lateral invagination of abdominal tergite 2, and they have an abdominal tergite 2 perpendicular to abdominal tergite 3 (Appendix 4-1; Table 4-2). Although McLaughlin and Lemaitre (p. 116, 1997) do not suggest modification of the subfamily Hapalogastrinae, and do not support their phylogeny with bootstrap values (Chapter 6), they produce a consensus tree with *Placetron* paraphyletic to the remaining hapalogastrine genera, *Hapalogaster* and *Oedignathus*. Additional molecular analysis may be helpful in confirming the taxonomic subfamily placement of *Dermaturus*, *Placetron*, and *Acantholithodes*.

Phylogenetic analysis produced several well supported relationships among species and genera within the subfamily Lithodinae. Both *Lopholithodes* (96%, 6) and *Cryptolithodes* (100%, 23) are strongly supported clades (Fig. 4-4). However, the genus *Paralomis* was an unresolved polytomy (Fig. 4-4, 15 > bootstrap > 31, decay = 0). Short branches lengths (Fig. 4-5, 4-7) suggest a relatively rapid radiation of this speciose genus. As molecular evidence suggests lithodids originated between 13-25 mya, an old and rapid radiation hypothesis is supported by the 10 my apomorphic fossil *Paralomis debodeorum* (Feldmann 1998; Fig. 4-4). However, the morphological matrix was not produced with the intent of investigating species-level relationships of genus *Paralomis*, and only four of the 51 known species were characterized (Table 2-1).

One interesting aspect of my analysis is the close genealogical ties between the genera *Paralomis* and *Glyptolithodes* (decay=1, label 'H', Fig. 4). This close relationship has been proposed previously, and the generic status of *Glyptolithodes* has been questioned (Takeda and Ohta 1979). The genus *Paralomis* is a speciose taxon (51 members) that includes a large array of morphological variation, within which the genus *Glyptolithodes* could easily fit. Another interesting aspect of this analysis is the weak clade containing the genera *Lopholithodes* and *Glyptolithodes* (57%, 1; label 'H', Fig. 4-4). These share synapomorphies such as fusion of the lateral and marginal plates and formation of intercalary rods (=elongate sections, Fig. 4-3) between the fully fused medial plates.

The genera *Paralithodes* and *Lithodes* together exist in a single well supported (83%, 3; label 'G', Fig. 4-4) clade. This is not a surprising finding as these two genera are differentiated morphologically by the presence of 3 (*Lithodes*) or 5 (*Paralithodes*) plates on their 2nd abdominal segment, a character that is not always easy to discern and thus has the potential to produce misleading taxonomic assignments. This clade suggests either that these genera should be defined as one genus, *Lithodes*, as used in the early 1800's, or that a sub-sample of *Paralithodes* (i.e., *P. californiensis* and *P. rathbuni*) should be combined with *Lithodes*, as first proposed by Benedict (1894). However, only four of 17 *Lithodes* and four of five *Paralithodes* (Table 2-1) were observed. As for other genera, this character matrix was not created to investigate species level relationships, nor to specifically investigate the taxonomic affinities of *Lithodes* and *Paralithodes*. Although, I would suggest reassigning *Paralithodes rathbuni* and *Paralithodes californiensis* to *Lithodes*; further morphological and molecular investigation is desirable. Due to the important commercial nature of some species in these genera (e.g. *P. camtschaticus*, *P. platypus*, *L. aequispinus*, *L. couesi* (Alaska, Japan and Russia; e.g. Orensanz et al. 1998), and *L. santolla* (Chile and Argentina; e.g. Lovrich and Vinuesa 1999)), and the potential for commercial expansion to closely related species, a clearer understanding of phylogenetic relationships, species distinctions, and the ability to hybridize (e.g. *P. platypus* and *P. camtschaticus*; Nizyayev 1991) may have considerable practical implications for management of these fisheries.

The monotypic *Rhinolithodes* and *Phyllolithodes* consistently form a strong clade (96%, 3; Fig. 4-4), a relationship supported by their distinctive carapace relief and fusion of their lateral and marginal abdominal plates (but see Makarov 1962, pp. 28-29) and suggested by previous morphological studies (McLaughlin and Lemaitre 1997, p. 116). In this analysis *Cryptolithodes* and *Sculptolithodes* form a clade, the members of which share small rounded chelae, small adult body and extensive calcification. This is a clade that has not been previously suggested, perhaps because, although distinctive, these crabs are relatively scarce, and poorly studied. Because these lithodids have extreme morphologies with possible convergent characteristics, molecular analysis may further understanding of their relationships.

Relationship between the Lithodidae and the Paguridae

The families Paguridae and Lithodidae are considered sister taxa within the monophyletic superfamily Paguroidea (McLaughlin 1983). They share morphological synapomorphies such as sperm morphology (Jamieson and Tudge 2000), asymmetrical chelae, an asymmetrical abdomen and a full complement of pleopods on only the left side of the abdomen (as discussed in Richter and Scholtz 1994). Morphologists have long suspected close genealogical ties between these two families because the abdomen of hermit crabs is modified to coil within a gastropod shell and the asymmetric abdomen possessed by king crabs appears to be a remnant of their hermit crab ancestry (Milne-Edwards 1837, Boas 1880 a,b, Bouvier 1894 a,b, 1897). Recent morphological observations (Richter and Scholtz 1994) and analysis of DNA data (Cunningham et al. 1992) support this conclusion. However, modern morphologists, using current cladistic analysis and larval observations disagree with this proposal and instead argue that lithodids are a basal lineage (McLaughlin and Lemaitre 1997, 2000), or are a sister taxon to the remaining members of the superfamily Paguroidea (Martin and Abele 1986). However, if pagurids are derived lithodids, a scenario must be proposed wherein a free-living lithodid, unconstrained by the evolutionary history of dextral coiling and gastropod shell asymmetry, could evolve substantially larger left than right lateral abdominal plates, and bare pleopods only on the left side. If theories of Martin and Abele (1986) and McLaughlin and Lemaitre (1997, 2000) are correct, the Bouvier transition (see below) should be viewed in reverse, and the subfamily Lithodinae should be considered a basal clade to the subfamily Hapalogastrinae which has soft abdomens.

Bouvier's transition hypothesis

Not only are the cladistic relationships proposed here on the basis of morphological data consistent with previous morphological observations, but transitions between crabs from basal lineages to terminal taxa are consistent with the hypothetical topology suggested by morphologists over a century ago (Fig. 4-8). As early as 1837, morphologists speculated on the transformation of a typical shell-dwelling, membranous-abdomen-bearing hermit crab into a crab-like animal that was no longer dependent upon a gastropod shell for protection of the abdomen. Originating with a hermit crab (perhaps similar to *Nematopagurus* or *Pylopagurus*), a sequence was described where tergites (tissue or plates found dorsally) of the second abdominal segments were gradually replaced by small calcified circular pieces (called nodules) which eventually fused creating medial and lateral plates, while segments 3-5 remained membranous as observed in *Hapalogaster* (see Fig. 4-3 for pictorial definitions of morphological characters and

Fig. 4-8 for Bouvier's transition). This initial calcification was followed by a calcareous nodule covering of the entire dorsal surfaces of segments 3-5 and the onset of plate formation. Next, fusion calcareous nodules on abdominal segments 3-5 produced large adjoining lateral and smaller contiguous marginal plates as well as a series of small medial calcareous but unfused nodules (as in *Paralithodes*). This was followed by a reduction in the number of calcified plates in the second abdominal segment from five to three (as in *Lithodes*). Next, medial nodules of segments 3-5 fused to form medial plates contiguous with lateral plates (as in *Lopholithodes*). Subsequently, marginal plates are fused to their respective lateral plates (left side only for females; as in *Phyllolithodes*, *Paralomis* and *Glyptolithodes*). Finally, complete lateral and marginal plate fusion occurs from segments 3-5 and segment two becomes fully fused into one plate (as in *Cryptolithodes*; Boas 1880 a,b, Bouvier 1894 a, 1897, Makarov 1962, see McLaughlin and Lemaitre 1997 for a more detailed description).

The morphological analysis in the present study suggests that Bouvier's (1895 a,b, 1897) hypothesis of a progression from hermit to king crab was at least partially correct. First, the subfamily Hapalogastrinae, characterized by extreme asymmetry and limited calcification, forms a paraphyletic group sister to the fully calcified Lithodinae (Fig. 4-4, label 'B'). Genera with uncalcified abdomens such as *Hapalogaster* and *Oedignathus* (Fig. 4-4, label 'C') are basal to the genera with partially calcified abdomens (*Placetron* and *Acantholithodes*). Second, at the basal node of the subfamily Lithodinae, onset of full abdominal calcification is observed with *Neolithodes*. However, instead of a gradual and successive evolution towards the lithodid possessing a fully calcified and symmetrical abdomen, *Cryptolithodes*, two independent instances of carcinization are hypothesized to occur. First, is the clade with fused contiguous medial abdominal plates that includes *Rhinolithodes / Phyllolithodes / Cryptolithodes / Sculptolithodes / Lopholithodes / Glyptolithodes / Paralomis* – (85%, 5, label 'F', Fig. 4-4). In this clade abdomens possess the least number or, in accordance to my phylogenetic hypothesis, the greatest reduction in plate number, and thus it is the most symmetric of all lithodids. Second, is a clade that possesses unfused medial nodules, and distinct abdominal and chela asymmetry, *Lithodes / Paralithodes* clade (83% (3), label 'G', Fig. 4-4). Overall, Bouvier's (1897) hypothesis concerning abdominal evolution is partially supported by this new analysis. Furthermore, Bouvier's (1894a) ideas concerning *Hapalogaster*'s basal position between the Lithodinae, which have hard, calcified abdomens and genus *Pagurus*, which have soft abdomens are supported.

Origin and distribution of Lithodidae

In 1896 Bouvier discussed lithodid radiation and proposed that their distribution was a key to their evolutionary history. In 1938, Makarov (1962) expanded Bouvier's ideas and suggested that lithodid radiation most likely began in the northeastern Pacific. He used several lines of evidence concerning localities and preponderance of species throughout the world. This work was recently updated as new species have been described, and known distributions have expanded (Chapter 2). Four lines of evidence suggest that lithodids have a north Pacific Ocean origin, most likely in the northeastern Pacific intertidal or shallow subtidal zone. First, 68% of species and 100% of genera are reported from the Pacific, compared to only 28% of species and 19% of genera from the Atlantic Ocean; the remaining species are found in the Indian and Antarctic Oceans (14%; note: as species have broad distribution ranges, locality percentages do not add up to 100%). Second, 55% of living lithodid species occur in the northern hemisphere, compared to 42% in the south (the remainder being deep living tropical inhabitants). Third, basal members of the subfamily Hapalogastrinae are found only in the northern Pacific, mainly from northeastern Pacific Ocean (89%) compared to only 45% in the northwestern Pacific. Finally, the basal clade Hapalogastrinae occurs in the intertidal or shallow subtidal zone (Table 2-1). New molecular and fossil data correspond with Bouvier's and Makarov's suggestion of a recent radiation from a hermit-crab ancestor. Molecular clocks suggest a lithodid origin between 13-25 mya (Cunningham et al. 1992) and fossil evidence reveals a relatively young (10 mya) *Paralomis debodeorum* (Feldmann 1998).

Makarov (1962) suggested that lithodids originated in the northern Pacific and then advanced along the Aleutian range to the east coast of Kamchatka and the Kurile Islands. Concurrently they crossed the Arctic into the northern Atlantic. As they are cold-water adapted, they are thought to have entered the Indian Ocean through the cold-deep waters of the southern Atlantic around South Africa's Cape and not through the warm waters of the southwestern Pacific Ocean (Makarov 1962, Fig. 4-1). Generally, lithodids found outside of the northeastern Pacific zone are deep water inhabitants. However, several species such as *P. granulosa* inhabit shallow waters (intertidal-100m) and are thought to have colonized the Beagle Channel, Southern Argentina after the last deglaciation (8,500 years ago, Rabassa et al. 1986, Lovrich and Vinuesa 1993). Perhaps the abyssal nature of the subfamily Lithodinae (*Neolithodes* average depth = 1570m; *Lithodes* = 532m; *Paralomis* = 821m; Table 2-1), along with a large protective exoskeleton (CW ≤ 300 mm, Jensen 1995), group social dynamics, migratory abilities, large broods (up to 280 000 eggs, Matsuura et al. 1972), and opportunistic foraging strategies (Makarov 1962, Hart 1982, Jensen 1995), allowed them to spread into extreme habitats that afford little environmental protection from overhead predators (Table 2-6).

CONCLUSIONS

Cladistic analysis of this data set using PAUP* 4.08b (Swofford 2001) and MacClade 4.0 to map the Bouvier transition (Maddison and Maddison 2000) has added rigorous support to the generally accepted views of morphological evolution within Lithodidae. Using *Emerita analoga* (superfamily Hippoidea), along with hermit-crab families Paguridae and Diogenidae, the family Lithodidae sensu Ortmann 1901 was found to be monophyletic, and the subfamily Hapalogastrinae sensu Ortmann 1901 was found to be paraphyletic to the subfamily Lithodinae. This phylogeny supports the reassignment of *Placetron wosnessenskii* and *Acantholithodes hispidus* to the subfamily Lithodinae. The precise placement of *Dermaturus mandtii* remains unclear, thus should remain in the subfamily Hapalogastrinae until more evidence becomes available. The genera *Cryptolithodes*, *Hapalogaster*, and *Lopholithodes* were monophyletic, whereas the more speciose, but sparsely sampled genera were either paraphyletic (*Lithodes*), polyphyletic (*Paralithodes*), or had relationships that remained unresolved (*Paralomis*). By reassigning *Paralithodes rathbuni* and *Paralithodes californiensis* to the genus *Lithodes*, both genera would remain monophyletic. However, only four of the possible 17 member genus *Lithodes* were characterized, and further morphological and molecular investigation into the taxonomic affiliations of these species as well as the subfamily position of *Placetron* and *Acantholithodes* should be conducted.

Production of phylogenetically robust topologies allows morphological and distributional hypotheses to be proposed and investigated. Bouvier's transitional hypothesis concerning abdominal modifications was found to be partially supported by morphological topology. The subfamily Hapalogastrinae, which have soft abdomens, can be considered as a transitional group between the genera *Pagurus* and *Labidochirus*, whose species have soft abdomens, and the subfamily Lithodinae, in which crabs have hard abdomens. Bouvier's (1896) and Makarov's (1962) radiation hypothesis concerning a northeast Pacific intertidal origin and diversification were supported by the proposed morphological phylogeny.

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Table 4-1. Collectors and location of specimens

species	donator or museum collection	origin and number of specimens, males (M),and females (F),observed *	origin of studied specimens (Pacific or Atlantic Oceans), distribution and depth (m) *	global distribution (Pacific or Atlantic Oceans),and depth (m) ***
sub-family Lithodinae, Ortmann 1901				
Cryptolithodes sitchensis Brandt 1853	Stefanie Zaklan	PC: (5 M & 5 F)	northeast Pacific: Barkley Sound, B.C., Canada (43°53'N, 125°20' W): 8-11	northeast Pacific: Sitka, Alaska to Pacific Grove California, U.S.A. (Makarov 1962): intertidal to 37 (Smithsonian collection)
C. typicus Brandt 1848	Stefanie Zaklan	PC: (5 M & 5 F)	northeast Pacific: Barkley Sound, B.C. Canada: 9-12	northeast Pacific: Monterey, California to Alaska, U.S.A. (Schmitt 1921): intertidal to 45 (Hart 1982)
Glyptolithodes cristatipes (Faxon 1893)	Donald Cadien & Smithsonian	PC: USNM 259216 & 259217: (3 M & 3 F)	northeast and south Pacific: Los Angeles, California, U.S.A. (33°49' N, 118°27' W); south Pacific (07°49' S, 080° 38' W): 305	east Pacific: Iquique, Chile (Haig 1974), to southern California (this study): 245-800 (Haig 1974)
Lithodes aequispinus Benedict 1894	Ted Spencer & Smithsonian	PC: USNM 259209: (5 M & 5 F)	northeast Pacific: Pribilof Islands, Bering Sea, Petrel Banks Area, Alaska, U.S.A.: 481	north Pacific: Bering Sea (Benedict 1894), Sea of Okhotsk, Japan (Makarov 1962), to B.C., Canada: 77 (Hart 1982),to 742 (Smithsonian collection)
L. couesi Benedict 1894	James Orr & Smithsonian Collection	PC (Cruise 9711, R/V Miller Freeman): USNM 52752; 267722: (1 M & 1 F)	northeast Pacific: Aleutian Islands, Bering Sea, Alaska, U.S.A.	north Pacific: Bering Sea, Alaska (Benedict 1894), to San Diego, California (Makarov 1962), Hokkaido, Japan (Sakai 1976): 258-1829 (Hart 1982)

L. longispina Sakai 1971	American Museum of Natural History & Museum of Victoria	MV Lot 3: J 44009: AMNH: (1 M & 1 F)	northwest Pacific: Sagami Bay, Japan	northwest Pacific: Japan (Takeda 1974), south Pacific, Guam (Dawson 1989): 600 (Sakai 1971), to 865 (Takeda 1974)
L. maja (Linnaeus 1758)	Smithsonian Collection	USNM 14493 & 44710, 3793: (3 M & 3 F)	north Atlantic: Bergan, Norway; New England coast, U.S.A.; La Hare Bank, Nova Scotia, Canada: 64	north Atlantic: North and Berents Seas to Newfoundland, Canada (Makarov 1962): 4 (Macpherson 1988b), to 790 (Williams 1984)
Lopholithodes foraminatus (Stimpson 1859)	Smithsonian Collection	USNM: (1 M & 1F)	northeast Pacific: Juan de Fuca Straight, Washington; Santa Cruz, Monterey Bay, California, U.S.A: 114-265	northeast Pacific: Aleutian Islands and Bering Sea (Dawson 1989), to California: intertidal to 547 (Smithsonian collection, Hart 1982)
L. mandtii Brandt 1848	Stefanie Zaklan	PC: (5 M & 5 F)	northeast Pacific: Barkley Sound, B.C., Canada: 8-11	northeast Pacific: Sitka, Alaska to Monterey California, U.S.A. (Makarov 1962): intertidal to 137 (Hart 1982)
Neolithodes grimaldii (A. Milne Edwards & Bouvier 1894)	Smithsonian Collection	USNM 228844; 228844; 12250; 228852; 228852; 228846; 228854; 228848; 8046 (MSC); 11942 (MSC); 228844: (5 M & 5 F)	north Atlantic: North American Basin, Cape Henry (36° 46' N, 073° 45' W to 37° 05' N, 074° 12' W): South of Martha's Vineyard, Mass., U.S.A.: 2250-2825	north Atlantic: east coast of Canada to North Sea, south to Bay of Biscay, Canary Islands: 1267 (Macpherson 1988b), to 3207 (Smithsonian collection)
Paralithodes brevipes (A. Milne Edwards & Lucas 1841)	Smithsonian Collection	USNM 18580 acc 28626; 204288 (MSC); 18580; 18597; 69425: no label cruise 791 station 191 ref # 161 on Paragon II: (4 F & 4 M)	north Pacific: Bering Sea, Alaska, U.S.A. (57° 40'N, 169° 01'W); Commander Islands, Siberia, Russia; Ishurup Island, Kurils, Japan: 66	north Pacific: Sea of Japan, Japan; Kamchatka, Russia; Alaska, U.S.A.: intertidal to 66 (Makarov 1962, Smithsonian collection)

P. californiensis (Benedict 1894)	Donald Cadien & James Orr	PC: (1 M & 1 F)	northeast Pacific: R/V Miller Freeman cruise 9711, Los Angeles, California, U.S.A. (33° 49' N, 118° 27' W): 305	north Pacific: Monterey Bay to San Diego, California: 148 (Schmitt 1921), to 349 (Smithsonian collection)
P. camtschaticus (Tilesius 1815)	Ted Spencer, Alaska Fish and Game & Smithsonian Collection	USNM 204290; 204294 (MSC); 204287 (MSC); 204290 (MSC): (4 F & 4 M)	northeast Pacific: Bering Sea and Petrel Banks, Alaska: 13-481	north Pacific: Bering Sea, Alaska, U.S.A. (Benedict 1894), Hokkaido, Japan; Kamchatka, Russia (Makarov 1962), Korea (Kim 1970): 3-481 (Jensen 1995, Smithsonian collection)
P. rathbuni (Benedict 1894)	Donald Cadien & James Orr & Smithsonian collection	PC: USNM 17040: (1 M & 1 F)	north Pacific: R/V Miller Freeman cruise 9711, Los Angeles, California, U.S.A. (33°49' N, 118°27' W); San Simeon Bay, California, U.S.A.: 305-386	northeast Pacific: San Simeon Bay, California (Benedict 1894): 165-500 (Schmitt 1921, Wicksten 1989)
Paralomis birsteini Macpherson 1988	Museum of Victoria	MV Lot 5. J44017; Lot 2 J39632: (1 M & 1 F)	south Pacific: 94.5 km SSE of SE Cape, "V" seamount, Stranks, TN, et al, CSIRO, Tasmania, Australia	Antarctic Ocean: 67° 29'S, 79° 55'W: 500-1080 (Macpherson 1988a)
P. granulosa (Jacquinot 1852)	Smithsonian	USNM 154628: (2 F & 2 M),	southwest Atlantic and southeast Pacific: Tierra Del Fuego, Atlantic Ocean (53° 39' S, 070° 55' W and 54° 48' S, 065° 15' W): intertidal-115	southwest Atlantic and southeast Pacific: Brazil to southern South America, north to Chiloe islands, Chile: intertidal to 100 (Takeda & Hatanaka 1984)
P. multispina (Benedict 1894)	Donald Cadien, James Orr & Smithsonian	PC: USNM 18589; 90452: (2 M &1 F)	north Pacific: Los Angeles and San Diego, California; Shinnagin Banks, Alaska: 977-1504	north Pacific: Alaska to California, U.S.A.; Kamchatka, Russia (Makarov 1962), Sagami Bay, Japan: 600 (Sakai 1971), to 1665 (Hart 1982)

P. verrilli (Benedict 1894)	Donald Cadien, James Orr & Smithsonian	PC: USNM 267732: (1 M & 1 F)	north Pacific: off Cortez Bank and Monterey Bay, California, U.S.A.: 1594-1800	north Pacific: Bering Sea south to California, U.S.A. (Makarov 1962), Hokkaido, Japan (Sakai 1976): 850 (Sakai 1987), to 2379 (Hart 1982),
Phyllolithodes papillosus (Brandt 1848)	Stefanie Zaklan & B.C. Provincial Museum	PC: (5 M & 5 F)	northeast Pacific: Barkley Sound, B.C., Canada: 6-12	northeast Pacific: Unalaska, Alaska to Monterey, California, U.S.A. (Makarov 1962): sub-tidal to 183 (Hart 1982)
Rhinolithodes wosnessenskii (Brandt 1848)	B.C. Provincial Museum & Smithsonian	USNM 26733; 267734; 55478 Acc # 41840; 55478 Acc # 41840: BCPM 974-00226-009; 974-00186-006; 973-00007-031; 983-00023-001; 983-00024-001: (6 M & 6 F)	northeast Pacific: Canoe Cove, Potlock Bank, Sumner Strait, Yes Bay, Alaska, U.S.A; Admiralty Inlet Port Townsend, Washington, U.S.A.: 22-331	northeast Pacific: Alaska to Crescent City, California (Makarov 1962): 6 (Hart 1982), to 102 (Chapter 2)
Sculptolithodes derjugini (Makarov 1934)	Jan Sasaki & Smithsonian	PC: USNM 72386 Acc # 137749: (1M & 1 F)	northwest Pacific: off Rishiri Island, Japanese Sea, Japan	northwest Pacific: Sea of Japan, Japan; Russia: 20-35 (Makarov 1962)
sub-family Hapalogastrinae, Ortmann 1901				
Acantholithodes hispidus (Stimpson 1860)	Smithsonian	USNM 65676; 77421; 22824; Acc # 34872; 6607; 23-18-4-184-0: (2 M & 2 F)	northeast Pacific: Spacious Bay, Naha Bay, Alaska, U.S.A.; Monterey Bay, California, U.S.A.; Graham Island, B.C. Canada: 30-244	northeast Pacific: Alaska to Monterey, California, U.S.A. (Hart 1982): intertidal to 244 (Smithsonian collection)
Dermaturus mandtii Brandt 1850	Smithsonian	USNM 47910 Acc # 57607; 18608; 267705; 18605: (5 M & 5 F)	northeast Pacific: St. Paul Island, Kyska Harbor, Alaska, U.S.A.: 10-22	north Pacific: Alaska, U.S.A.; Kamchatka, Russia; Sea of Japan, Japan: intertidal to 72 (Makarov 1962)
Hapalogaster cavicauda Stimpson 1878	Smithsonian	26129 ac # 39485: (3 M & 3 F)	northeast Pacific: Monterey, Pacific Grove, Long Beach, San Nicolas Island, California, U.S.A. (33°16' 43" N, 119° 34' 41" W); Kodiak, Alaska: intertidal	northeast Pacific: Washington, U.S.A. to Mexico: intertidal to 15 (Dawson 1989)

H. dentata de Haan 1850	Donated by Seiji Goshima & Smithsonian	PC: (2 M & 2F)	northwest Pacific: Hokodate Bay, Hokkaido, Japan (41° 44'N, 140° 36'E and 38° 18' 00" N, 141° 31" E)	northwest Pacific: Sea of Japan, Japan; Russia (Makarov 1962), Korea (Kim 1970): intertidal to 180 (Makarov 1962)
H. grebnitzkii Schalfeew 1892	Smithsonian	PC: USNM 23846 Acc# 36870; cat # 19456 (1 M & 1F)	northeast Pacific: Bering Sea, Kodiak and Port Etches, Alaska: subtidal to 18	north Pacific: Kamchatka, Russia; Alaska to California, U.S.A.: intertidal to 90 (Makarov 1962)
H. mertensii Brandt 1850	Stefanie Zaklan & Smithsonian & B.C. Provincial Museum	PC: USNM 267738 & 36890; 180084: BCPM 976-1153-07 (5M &5 F)	northeast Pacific: Barkley Sound, and Seymour Inlet, B.C., Canada: 11	northeast Pacific: Atka, Alaska to Puget Sound, Washington, U.S.A. (Makarov 1962): intertidal to 55 (Hart 1982)
Oedignathus inermis (Stimpson 1860)	Stefanie Zaklan	PC (5 M & 5 F)	northeast Pacific: Barkley Sound, B.C. Canada: intertidal	north Pacific: Japan; Russia; Unalaska, Alaska, to California, U.S.A. (Makarov 1962), Korea (Kim 1970): intertidal to 15 (Hart 1982)
Placetron wosnessenskii Schalfeew 1892	Smithsonian & B.C. Provincial Museum	USNM 291242, Acc # 157371; 259214; 291243, Acc # 161385; 276166, Acc # 204947: BCPM 975 00226-001; 982-00195 -001; 982-00256-001; 975-00703–002: (5 M & 5 F)	north pacific: Atka, Canoe Bay, Bering Sea, Pleasant Island, Unimak Island, Gulf of Alaska, Alaska, U.S.A. (51° 55' N, 16° 52' W to 51° 54'N, 176° 52'W): 54-201	northeast Pacific: Aleutian Islands, Alaska (Makarov 1962), to Puget Sound, Washington, U.S.A.: intertidal to 110 (Hart 1982)
Outgroup				
Labidochirus splendescens Owen 1839	Smithsonian & B.C. Provincial Museum	USNM (no #): BCPM 987-383-08: (5 M & 5F)	northeast Pacific: Washington, U.S.A.: 20	north Pacific Ocean: Japan; Alaska to Washington, U.S.A.: 3-412 (Jensen 1995)
Pagurus longicarpus Say 1817	Smithsonian	USNM 43413: (5 M & 8 F)	northwest Atlantic: Pots Harbor, Casco Bay, Maine, U.S.A.	northwest Atlantic Ocean: Nova Scotia, Canada to Gulf of Mexico, U.S.A.: intertidal to 45 (Gosner 1978)

P. bernhardus, Benedict 1892	Smithsonian	USNM 156410: (5 M & 5 F)	northeast Atlantic: found near Plymouth, Devon, England: 37	northeast Atlantic Ocean: intertidal to 140 (Hayward & Ryland 1995)
Clibanarius vittatus Bosc 1802	Smithsonian	USNM 557; 18991: (5 M & 10 F)	northwest Atlantic: Little Sarasota Bay, Florida and Casco Bay Maine, U.S.A.: intertidal	northwest Atlantic Ocean: Virginia to North Carolina, U.S.A: intertidal to 45 (Gosner 1978)
Emerita analoga, Stimpson 1857	Smithsonian & B.C. Provincial Museum	USNM 17589: cat # 984-294-02: (5 F)	northeast Pacific: Long Beach, Vancouver Island, B.C., Canada	east Pacific Ocean: Kodiak Island, Alaska to Baja California, U.S.A. and Peru, Chile and Argentina: intertidal (Morris et al. 1980)

* AMNH = American Museum of Natural History in New York City
BCPM= Royal British Columbia Provincial Museum
MV= Museum of Victoria in Australia
PC = personal collection obtained through donations
USNM= United States National Museum of Natural History, Washington, D.C., U.S.A.

** Depths for some collection material was unavailable.

*** See Table 1-1 and Dawson 1989 for a more extensive distribution list.

Table 4-2. Species character matrix for five outgroup taxa of the infraorder Anomura (*Emerita analoga*, *Clibanarius vittatus*, *Pagurus bernhardus*, *P. longicarpus*, *Labidochirus splendescens*), and 29 species (15 genera) of Lithodidae. Definitions of the 170 characters and character states (0-4) can be found in Appendix 4-1 and Figs. 4-2 & 4-3. Question mark (?) denotes inapplicable character scores for *E. analoga*.

	1	1111111112	2222222223	3333333334	4444444445	5555555556	6666666667
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890
Emerita analoga	0000000021	0000000000	0011000100	0110002100	0000000010	0000??????	??????????
Clibanarius vittatus	0000000021	0000100000	0011000000	0012002100	0000000010	0110100000	1100110001
Pagurus longicarpus	0000000021	0000100000	0011000000	0011002100	0000000010	0000100000	0100110001
Pagurus bernhardus	0000000021	0000000000	0011000000	0012002100	0000000010	0000100000	1100110001
Labidochirus splendesce	0000001021	0000000000	0011000100	0010002100	0000000010	0000100000	0100110001
Oedignathus inermis	0000010011	0000100100	0011020100	0011002100	1001100111	0111010031	0111111110
Hapalogaster mertensii	0000111121	0000100000	0011020100	0011002100	1001000101	0111010011	0111011110
Hapalogaster dentata	0000111121	0400100000	0011020100	0011002100	1001100101	0111010031	0111111110
Hapalogaster grebnitzki	0000111121	0000100000	0011020100	0011002100	1002210110	0011010011	0111111010
Hapalogaster cavicauda	0000011121	0000100000	0010020100	0011002100	1001000110	0111011011	0111011010
Dermaturus mandtii	0000010021	0000100200	0011020100	0011002100	1001100110	0000011031	0110112110
Acantholithodes hispidu	0021110011	1000100001	0001110100	0011002110	2001101010	1001011011	0011102110
Placetron wosnessenskii	1000010001	0000100200	0001021100	0011002100	3001101010	0000011021	0100112110
Neolithodes grimaldii	0022110031	1200110001	1001011100	0001102110	3002201000	1002011031	0101102110
Rhinolithodes wosnessen	1000100031	2011001110	0101111100	0001102001	1022201010	1002001030	0011002110
Phyllolithodes papillos	1000100000	1011001110	0101110101	0001100001	3002211010	1002011030	0011002110
Lopholithodes mandtii	2011100010	2111101110	0101020100	0011102000	2022211010	0002011011	0011002110
Lopholithodes foraminat	2011100010	2111100110	1101020100	0011102110	2022211010	0002011011	0011002110
Glyptolithodes cristati	2000000000	2110101110	0101120100	0011102100	2022201010	0002011031	0011102110
Paralomis multispina	1021110031	2110100000	0001110100	0001102111	3002211010	1002011011	0011102110
Paralomis birsteini	1011110011	1110100000	0001010100	0011102110	3002211010	0002011031	0011002110
Paralomis verrilli	1010110011	2110100110	0001010100	0001102110	3022221010	0002011011	0011002110
Paralomis granulosa	1000000011	0000100100	0001010100	0011102111	2112201010	0002011031	0011102110
Paralithodes rathbuni	1022011011	2210130001	1001111100	0001101112	3102221010	1002011031	0111002110
Paralithodes californie	1022011011	2210130001	1001111100	0001101112	3102221010	0002011031	0111002110
Paralithodes brevipes	1011110011	1310120001	1001011100	0001102112	3112211010	0002011131	0110102010
Paralithodes camtshatic	1021110011	1310120001	1001011100	0001102112	3112211010	1002011131	0110102110
Lithodes aequispinus	1021110011	2010100001	1001111100	0011101112	3102221010	0002011031	0110002110
Lithodes couesi	1021111011	2210100001	1001111100	0001101112	3112221010	0002011031	0111002110
Lithodes maja	1022110011	1210100101	1001011100	0001102112	3102211010	0002011031	0111102110

	1 1234567890	1111111112 1234567890	2222222223 1234567890	3333333334 1234567890	4444444445 1234567890	5555555556 1234567890	6666666667 1234567890
Lithodes longispina	1022010011	2210110101	1001011100	0001101101	3102211010	0002011031	0111002110
Cryptolithodes sitchens	3100100000	2010100100	0000000111	1110111000	3002201000	0002011020	1111100010
Cryptolithodes typicus	3100100000	2010100100	0000000111	1110111000	3002201000	0002011020	1111100010
Sculptolithodes derjug	1000100000	2011101110	0101000100	0001112000	3002211010	0002011031	0011002110

			1	1111111111	1111111111	1111111111	1111111111
	7777777778	8888888889	9999999990	0000000001	1111111112	2222222223	3333333334
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890
Emerita analoga	???0101001	1001022100	0000101210	1112120001	3020000221	0000???00?	00000000?0
Clibanarius vittatus	0010100000	0000000000	0000000000	0000000000	0100000110	0001110100	0000000101
Pagurus longicarpus	0010100000	0000000000	0000000000	0000000000	0100000010	0001101101	0000000000
Pagurus bernhardus	1010101001	0001022100	0000000000	0000000000	1100000110	1001101101	0000000000
Labidochirus splendesce	0010101000	0000000000	0000000000	0000000000	0100000010	1011111100	0000000110
Oedignathus inermis	0110101101	0002000000	1100000000	0001020100	1100011200	1000001100	1010011101
Hapalogaster mertensii	0111101001	0002000000	1100010000	0201020100	3000000200	1111011100	0011110001
Hapalogaster dentata	0110101001	0002001000	1100010000	0201020102	2000000220	1111001110	0010131100
Hapalogaster grebnitzk	0110102001	0002001000	1100010000	0201020102	2000000220	1011001110	0010031111
Hapalogaster cavicauda	0110102001	0102001000	1100010000	0201020102	2000000220	1001101100	0010031111
Dermaturus mandtii	0210102011	1002101000	1200000020	0201310102	2000011220	1001101100	0111010101
Acantholithodes hispid	0201110001	1012101000	1200010020	0201311012	2001100220	1011111000	0111041111
Placetron wosnessenskii	0211101101	1012112000	1200120020	1201220102	2000000110	1011111000	0101010111
Neolithodes grimaldii	0201111101	1012122010	1210120121	1101211010	2011111110	1011111000	0001040010
Rhinolithodes wosnessen	0201001101	1112122120	2210121121	1111221011	3010111010	1011111000	0101141111
Phyllolithodes papillo	0201001101	1112122121	2201121121	1111221011	3010111010	1011111000	0101141111
Lopholithodes mandtii	0201001101	1111122121	1211121121	1111221021	3011111001	1011111000	1111031111
Lopholithodes foramina	0201001101	1111122121	1211121121	1111221021	3011111001	1011111000	1111031111
Glyptolithodes cristat	0201001111	1111122121	2211121121	1111221021	3010011110	1011111000	1011130010
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Paralomis granulosa	0201001101	1011122121	2311121121	1111211011	3010011011	1011111000	1011011000
Paralithodes rathbuni	0201011111	1012122212	1212122120	1121221011	3011111110	1011111000	0101041011
Paralithodes californi	0201011111	1012122212	1212122120	1121221011	3011111110	1011111000	0001041010
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Paralithodes camtschati	0201011111	1012122212	2212122121	1121221011	3011111110	1011111000	0101041011
Lithodes aequispinus	0201011111	1012122212	1212122120	1121221011	3011111110	1011111000	0000041011
Lithodes couesi	0201001111	1012122212	1212122120	1121221001	3011111110	1011111000	0000041010
Lithodes maja	1201011111	1011122212	1212122121	1121221011	3010111110	1011111000	0101041010
Lithodes longispina	1201001111	1012122212	1212122120	1121221011	3011111110	1011111000	0000041011
Cryptolithodes sitchens	0000001101	1011122122	2302121210	1112120001	3010000000	1001100000	0010001101
Cryptolithodes typicus	0000001101	1111122122	2302121210	1112120001	3010000000	1001110000	0010001101
Sculptolithodes derjugi	0201001101	1011122121	1311120121	1112221011	3010011000	1001111000	1100110111

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	4444444445	5555555556	6666666667
	1234567890	1234567890	1234567890
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Pagurus longicarpus	0100000000	2000010020	0001001002
Pagurus bernhardus	0100000000	2000011020	0001001002
Labidochirus splendescens	0100000000	2001100010	0001001002
Oedignathus inermis	0011010101	0000111000	1102001000
Hapalogaster mertensii	0111000101	2121011000	1102001001
Hapalogaster dentata	0111000101	0021011000	1102001000
Hapalogaster grebnitzkii	0111000101	0011011000	1102001000
Hapalogaster cavicauda	0111000101	0021011000	1102001000
Dermaturus mandtii	1111010101	2001211010	1100001001
Acantholithodes hispidus	0011000001	2100011000	1102111100
Placetron wosnessenskii	0011000001	2110211000	1110001002
Neolithodes grimaldii	0011001001	2100011001	1110001100
Rhinolithodes wosnessenskii	1011000001	0120011001	1102101100
Phyllolithodes papillosus	1011000001	0130011001	1102011100
Lopholithodes mandtii	1112220111	1000111101	1102101100
Lopholithodes foraminatus	1112220111	1000111101	1102101100
Glyptolithodes cristatipes	1112220111	2120011010	1102101100
Paralomis multispina	0010000001	2130011000	1102101100
Paralomis birsteini	0111100001	2120011011	1102001100
Paralomis verrilli	0111010101	2120011010	1102101100
Paralomis granulosa	1012100101	0120111011	1101111100
Paralithodes rathbuni	0010001001	2130010001	1111001000
Paralithodes californiensis	0010000001	2130010001	1111001000
Paralithodes brevipes	0010000001	2120011001	1111011100
Paralithodes camtschaticus	0010000001	2120011001	1111001100
Lithodes aequispinus	1010000001	2120010001	1111001000
Lithodes couesi	0010000001	2120010001	1111001000
Lithodes maja	0011001001	2120010001	1111001000
Lithodes longispina	0011001001	2130010001	1112001000
Cryptolithodes sitchensis	1112200110	0000011000	1102000010
Cryptolithodes typicus	1112200110	0000011000	1102000010
Sculptolithodes derjugini	1112010001	0020111010	1100000110

Table 4-3. Statistics for most parsimonious trees (mpt) generated from parsimony analyses of morphology with and without the questionable outgroup *Emerita analoga* (Figs. 3-4 & 3-6). pic= phylogenetically informative characters, ci= consistency index, ri= retention index.

data set	number of characters	pic	mpt	length	ci	ri
with *E. analoga*	170	170	48	630	0.378	0.731
without *E. analoga*	170	168	144	602	0.367	0.708

FIGURE LEGENDS

Figure 4-1: Worldwide localities of lithodid genera based on references from Table 4-1. Intertidal lithodids are in bold. All other lithodids are shallow sub-tidal to abyssal in distribution.

Figure 4-2: Dorsal carapace regions and spine locations (modified from Macpherson 1988b).

Figure 4-3: Abdominal somites of lithodid females (modified from Macpherson 1988b). (a) abdomen of *Paralithodes*, showing somite, telson and nodule locations (b) abdomen of *Paralomis* showing abdominal plate locality and intercalary rods (c) abdomen of *Cryptolithodes* (d) abdomen of *Hapalogaster* depicting plate outline and uncalcified nodules.

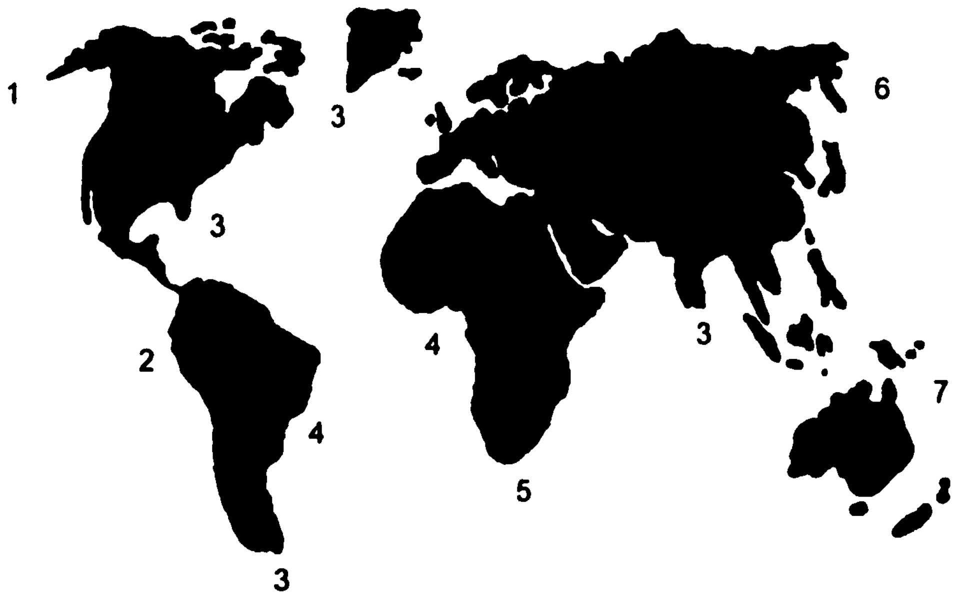
Figure 4-4: Parsimony analysis of 170 phylogenetically informative morphological characters using *Emerita analoga, Labidochirus splendescens, Clibanarius vittatus, Pagurus longicarpus*, and *P. bernhardus* as outgroups. Bootstrap values (1000 replicates) are indicated above branches and decay indices are shown in parentheses below. The tree is one of the 48 best trees of length 630, CI= 0.39, RI= 0.73. A= family Lithodidae, B and OL= subfamily Lithodinae Ortmann 1901, C and PH= proposed subfamily Hapalogastrinae, OH= subfamily Hapalogastrinae Ortmann 1901, D= *Dermaturus*, E and PL= proposed subfamily Lithodinae, F= subfamily Lithodinae with fused abdominal plates, G= subfamily Lithodinae with medial nodules on the abdomen, H= *Lopholithodes* and *Glyptolithodes*.

Figure 4-5: Phylogram of parsimony analyses of 170 phylogenetically informative morphological characters investigating the genus-level relationships of family Lithodidae (see Fig. 4-4 for bootstrap and decay values).

Figure 4-6: Parsimony analysis of 170 morphological characters (168 are phylogenetically informative) repeated with *Emerita analoga* removed from the outgroup. Bootstrap values (1000 replicates) are indicated above the branches, and decay indices are in parentheses. The tree is one of 24 most parsimonious trees having length of 602, CI=0.37, RI=0.71. O= outgroup, *Clibanarius* (family Diogenidae), *Pagurus* and *Labidochirus* (family Paguridae), H+L= family Lithodidae, H= subfamily Hapalogastrinae, L= subfamily Lithodinae, H+L+O= superfamily Paguroidea.

Figure 4-7: Phylogram of parsimony analyses of 168 phylogenetically informative morphological characters investigating the genus level relationships of family Lithodidae but with *E. analoga* removed. Numbers above branches indicate distances. Bootstrap values and decay indices are found in Fig. 4-6.

Figure 4-8: Bouvier's (1897) transition hypothesis concerning lithodid genus-level evolution based on differences in abdominal calcification. Abdominal drawings modified from Macpherson 1988b or originals by SDZ. Elements defined in Fig. 4-3.



1 **Oedignathus,**
Hapalogaster,
Cryptolithodes,
Dermaturus
Acantholithodes,
Placetron,
Paralomis,
Lithodes, Glyptolithodes,
Lopholithodes,
Rhinolithodes, Phyllolithodes,
Neolithodes

2 Paralomis,
Lithodes,
Glyptolithodes,
Lopholithodes

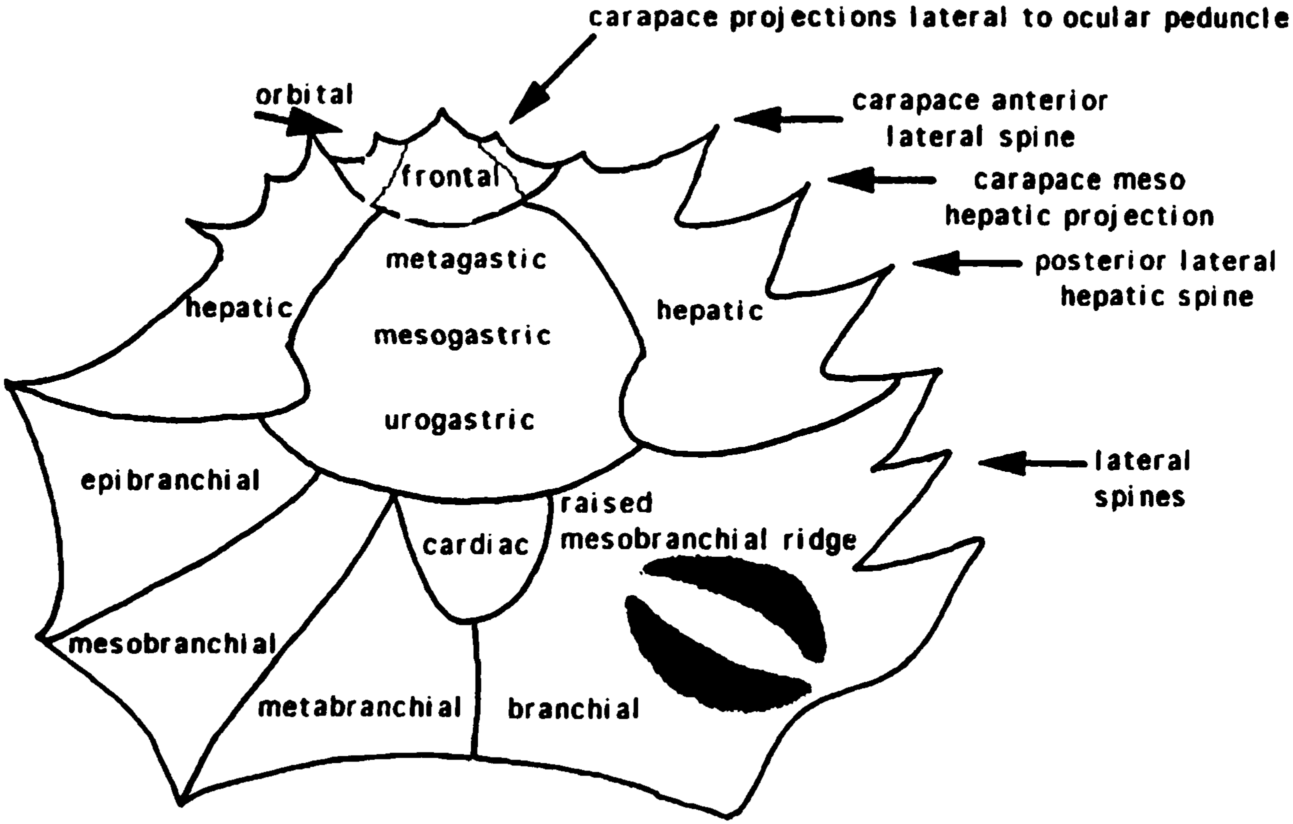
3 Paralomis, Neolithodes,
Lithodes

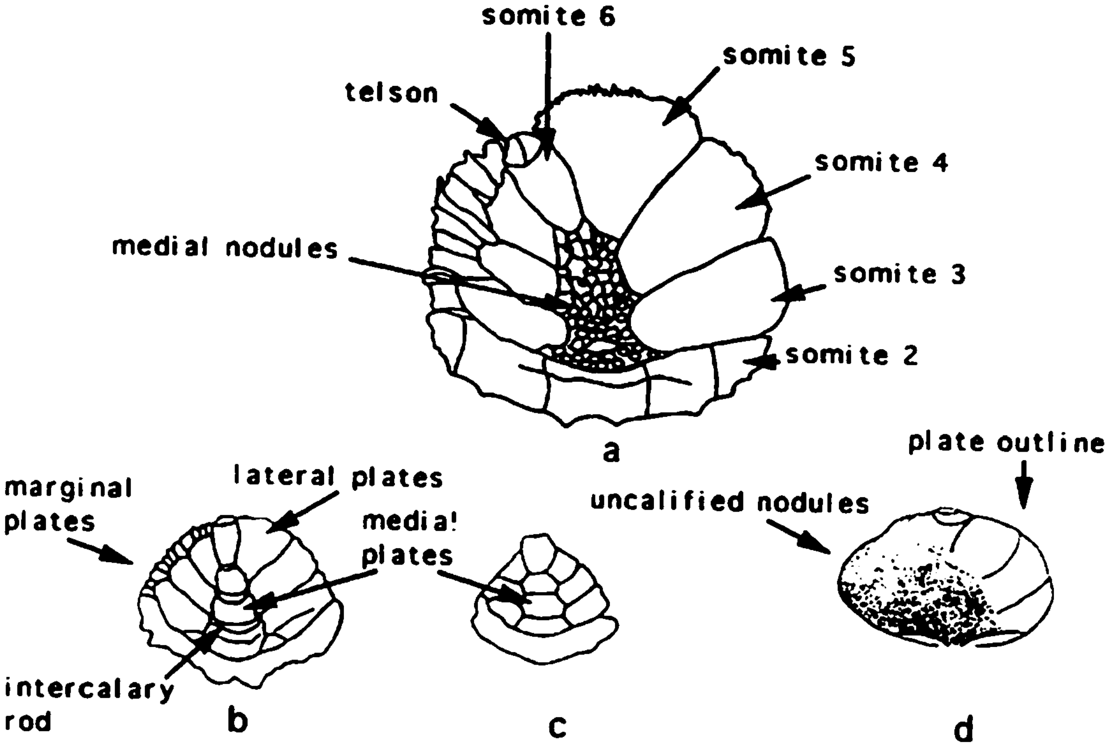
4 Paralomis,
Neolithodes,
Lithodes

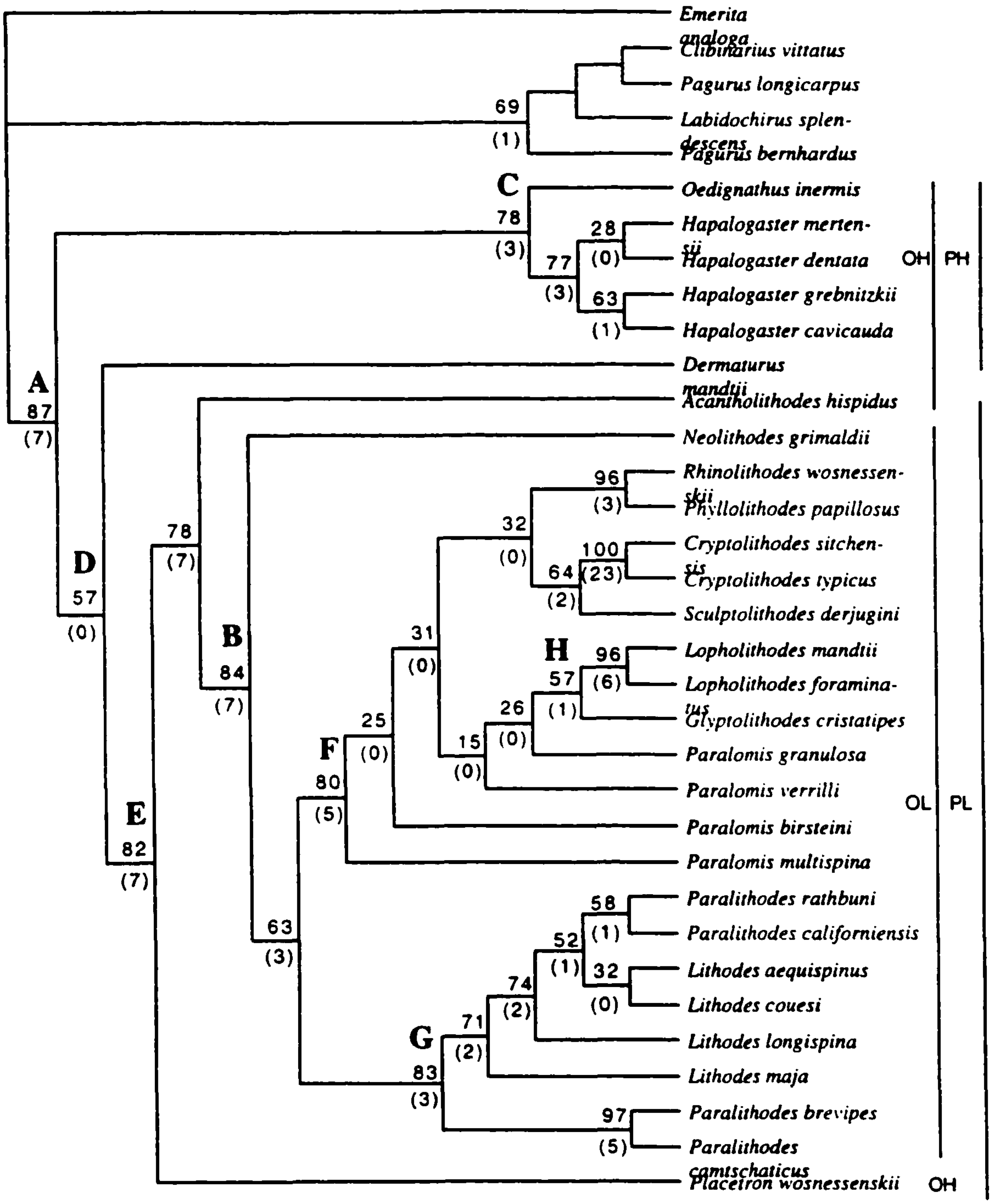
5 Neolithodes
Lithodes

6 **Dermaturus,**
Acantholithodes,
Hapalogaster,
Cryptolithodes
Acantholithus,
Paralomis,
Paralithodes,
Lithodes,
Sculptolithodes

7 Paralomis,
Acantholithus,
Neolithodes,
Lithodes


carapace projections lateral to ocular peduncle
orbital
carapace anterior lateral spine
frontal
carapace meso hepatic projection
metagastic
posterior lateral hepatic spine
hepatic
mesogastric
hepatic
urogastric
epibranchial
lateral spines
raised mesobranchial ridge
cardiac
mesobranchial
metabranchial
branchial


somite 6
somite 5
telson
somite 4
medial nodules
somite 3
somite 2
a
plate outline
marginal plates
lateral plates
medial plates
uncalified nodules
intercalary rod
b
c
d


Emerita analoga
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Pagurus longicarpus
Labidochirus splendescens
Pagurus bernhardus
Oedignathus inermis
Hapalogaster mertensii
Hapalogaster dentata
Hapalogaster grebnitzkii
Hapalogaster cavicauda
Dermaturus mandtii
Acantholithodes hispidus
Neolithodes grimaldii
Rhinolithodes wosnessenskii
Phyllolithodes papillosus
Cryptolithodes sitchensis
Cryptolithodes typicus
Sculptolithodes derjugini
Lopholithodes mandtii
Lopholithodes foraminatus
Glyptolithodes cristatipes
Paralomis granulosa
Paralomis verrilli
Paralomis birsteini
Paralomis multispina
Paralithodes rathbuni
Paralithodes californiensis
Lithodes aequispinus
Lithodes couesi
Lithodes longispina
Lithodes maja
Paralithodes brevipes
Paralithodes camtschaticus
Placetron wosnessenskii
OH
PH
OL
PL
OH
A 87 (7)
B 84 (7)
C 78 (3)
D 57 (0)
E 82 (7)
F 80 (5)
G 83 (3)
H 57 (1)
69 (1)
77 (3)
28 (0)
63 (1)
78 (7)
63 (3)
96 (3)
32 (0)
100 (23)
64 (2)
31 (0)
96 (6)
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32 (0)
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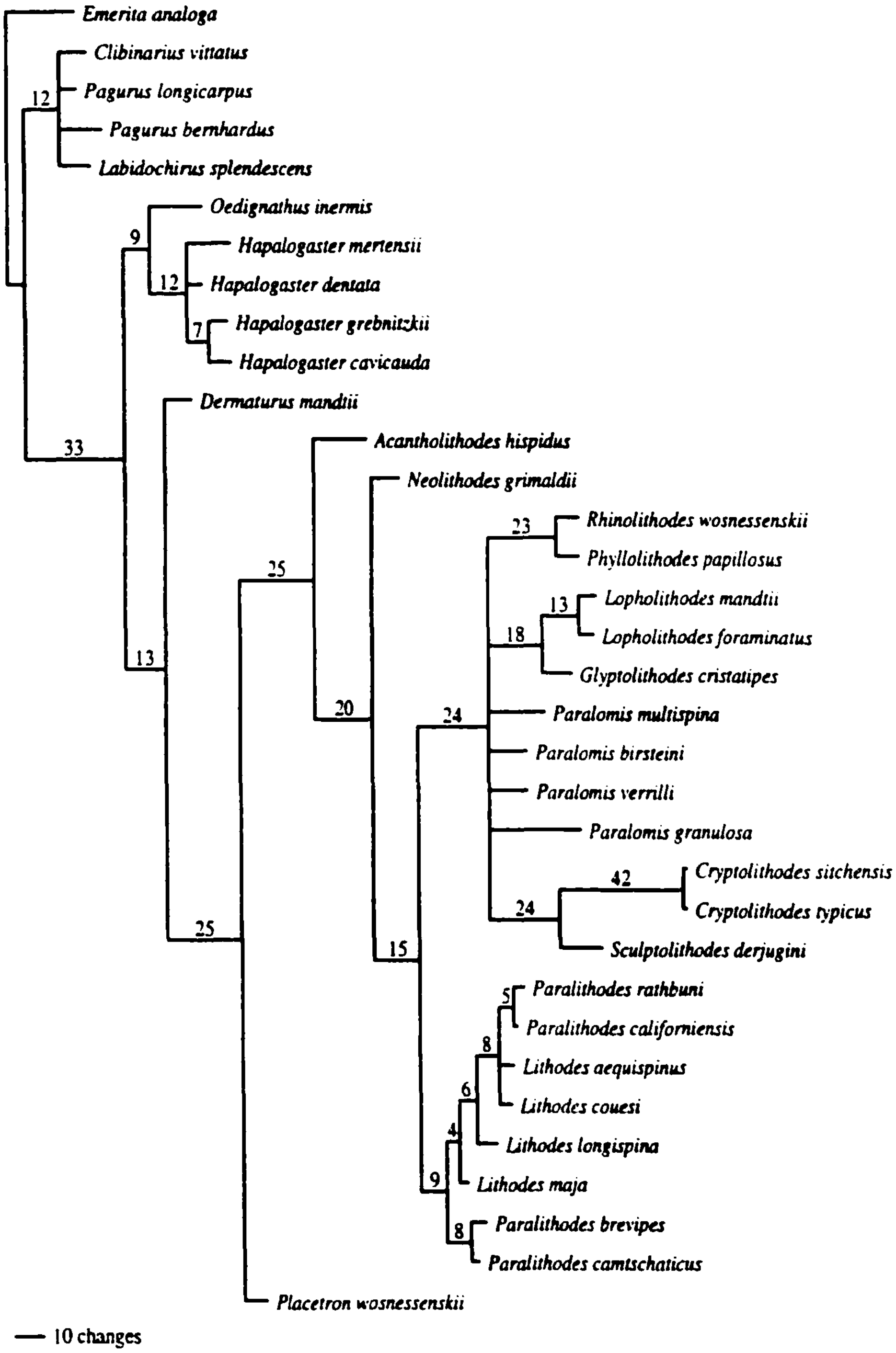
71 (2)
97 (5)


Emerita analoga
Clibinarius vittatus
Pagurus longicarpus
Pagurus bernhardus
Labidochirus splendescens
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Oedignathus inermis
Hapalogaster mertensii
Hapalogaster dentata
Hapalogaster grebnitzkii
Hapalogaster cavicauda
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Dermaturus mandtii
33
Acantholithodes hispidus
Neolithodes grimaldii
Rhinolithodes wosnessenskii
Phyllolithodes papillosus
23
Lopholithodes mandtii
Lopholithodes foraminatus
Glyptolithodes cristatipes
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Paralomis multispina
Paralomis birsteini
Paralomis verrilli
Paralomis granulosa
Cryptolithodes sitchensis
Cryptolithodes typicus
Sculptolithodes derjugini
42
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Paralithodes rathbuni
Paralithodes californiensis
Lithodes aequispinus
Lithodes couesi
Lithodes longispina
Lithodes maja
Paralithodes brevipes
Paralithodes camtschaticus
5
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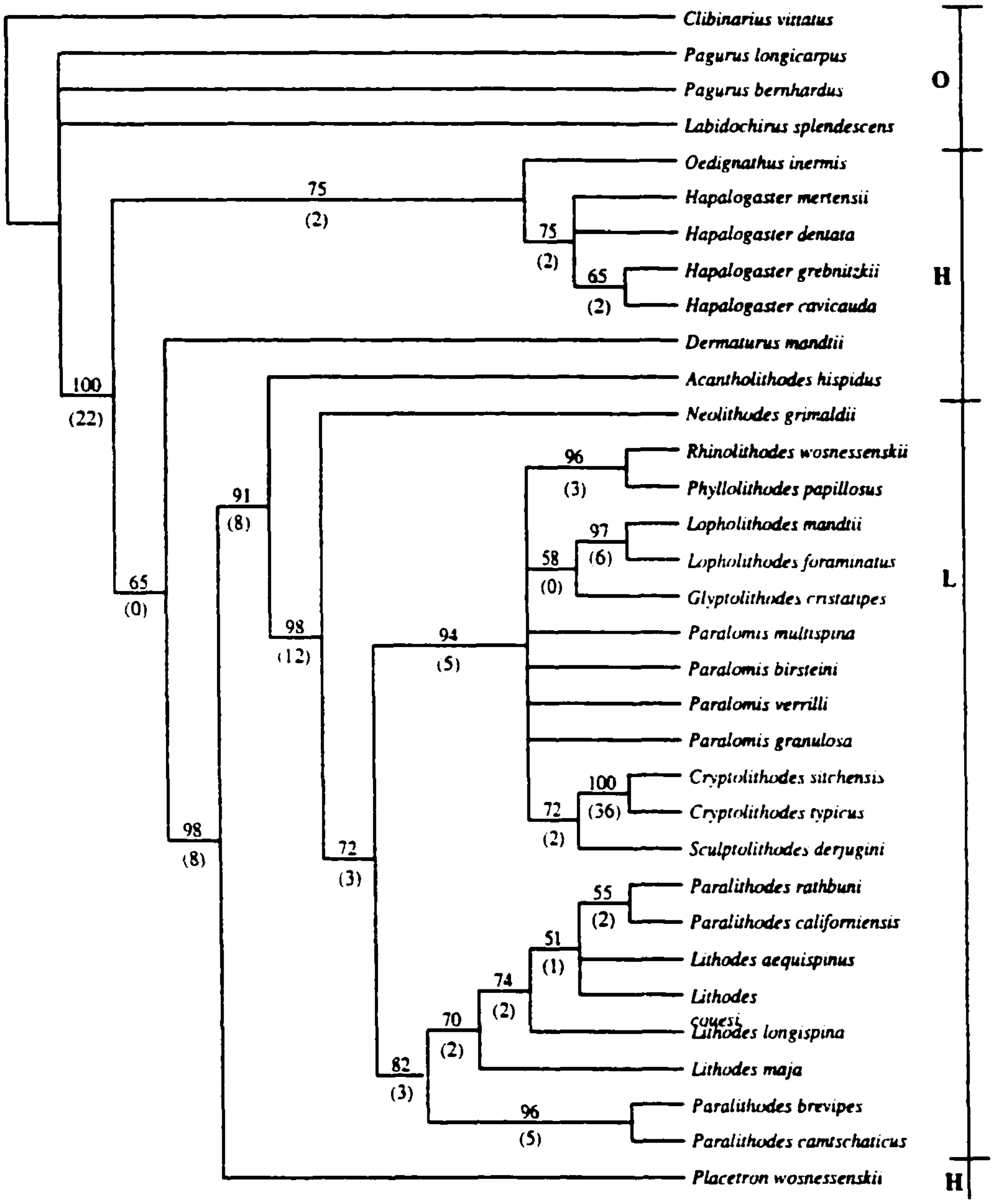
Placetron wosnessenskii
10 changes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Hapalogaster grebnitzkii
Hapalogaster cavicauda
Dermaturus mandtii
Acantholithodes hispidus
Neolithodes grimaldii
Rhinolithodes wosnessenskii
Phyllolithodes papillosus
Lopholithodes mandtii
Lopholithodes foraminatus
Glyptolithodes cristatipes
Paralomis multispina
Paralomis birsteini
Paralomis verrilli
Paralomis granulosa
Cryptolithodes sitchensis
Cryptolithodes typicus
Sculptolithodes derjugini
Paralithodes rathbuni
Paralithodes californiensis
Lithodes aequispinus
Lithodes couesi
Lithodes longispina
Lithodes maja
Paralithodes brevipes
Paralithodes camtschaticus
Placetron wosnessenskii
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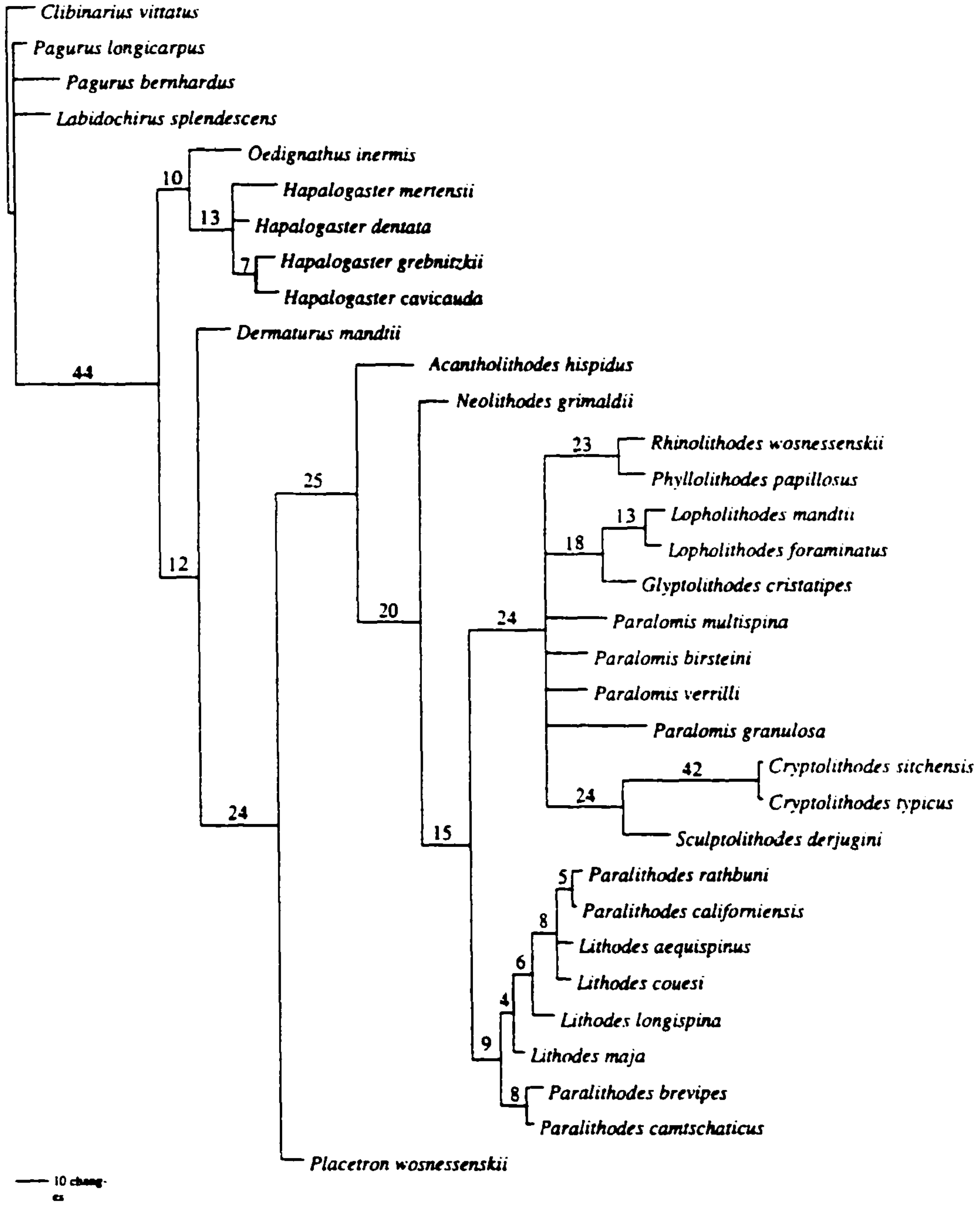
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Hapalogaster grebnitzkii
Hapalogaster cavicauda
Dermaturus mandtii
Acantholithodes hispidus
Neolithodes grimaldii
Rhinolithodes wosnessenskii
Phyllolithodes papillosus
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Lopholithodes foraminatus
Glyptolithodes cristatipes
Paralomis multispina
Paralomis birsteini
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Cryptolithodes sitchensis
Cryptolithodes typicus
Sculptolithodes derjugini
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Paralithodes californiensis
Lithodes aequispinus
Lithodes couesi
Lithodes longispina
Lithodes maja
Paralithodes brevipes
Paralithodes camtschaticus
Placetron wosnessenskii
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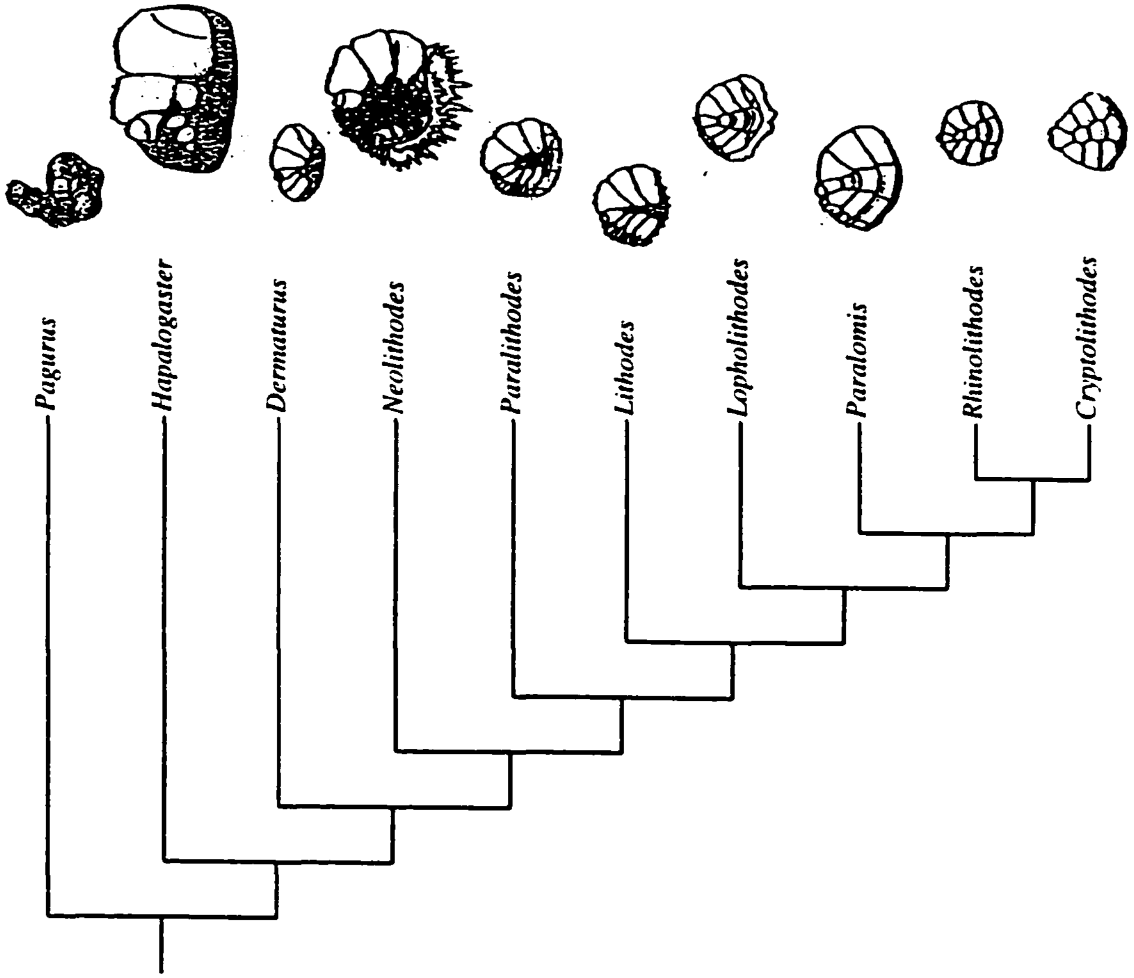
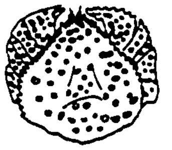
9
8
24
10 changes

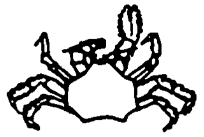

Pagurus
Hapalogaster
Dermaturus
Neolithodes
Paralithodes
Lithodes
Lopholithodes
Paralomis
Rhinolithodes
Cryptolithodes

Appendix 4-1: Annotated list of character names and states, with both written and pictorial descriptions, that are used in the phylogentic analysis of twenty-nine species of lithodids. Additional anatomical drawings are found in Figs. 4-2 and 4-3. Each character is numbered and each species' character state is indicated in Table 4-2. Drawings are modified from Sakai (1976), Morris et al. (1980), Dawson and Yaldwyn (1985), Macpherson (1988), or are originals by the author.

1. Carapace shape


(0) pear


(1) broadly triangular


(2) octagonal


(3) CW> CL

A pear shaped carapace is shared by the outgroup, most Hapalogastrinae (except *Placetron wosnessenskii*), and *Neolithodes grimaldii*. Lithodinae generally have broadly triangular carapaces except the octagonal *Lopholithodes* and *Glyptolithodes*. The carapace width is only larger than the carapace length is found only in genus *Cryptolithodes*. Bouvier (1895) suggested carapace widening occurred throughout lithodid evolution as a protective measure for pereopod bases.

2. Carapace anterior versus posterior width: (0) narrower, (1) equal

The width of the anterior carapace is equal to the posterior width only in *Cryptolithodes*. All remaining carapaces have a narrower anterior width than posterior.

3. Carapace dorsal spines:


(0) absent


(1) sparse


(2) dense

Dorsal spines may be a defensive mechanism used to protect deep-sea species living in unprotected environments. Dorsal spines are absent in outgroup taxa and intertidal and shallow subtidal inhabitants of subfamily Hapalogastrinae (except *Acantholithodes*). Dorsal spines are found in Lithodinae, except those species with thickened carapaces and substantial topological relief of the dorsal carapace (*Rhinolithodes, Phyllolithodes, Sculptolithodes*, and *Glyptolithodes*), and those inhabitants of shallower environments (*Paralomis granulosa*, and *Cryptolithodes*).

4. Carapace spine length:

(0) absent

(1) < 10% of carapace depth

(2) >10% of carapace depth

Spines are absent in outgroup taxa, hapalogastrinids (except *Acantholithodes* which has a dense carpet of short spines), and in some Lithodinae taxa. Spines are less that ten percent of carapace depth in *Rhinolithodes, Phyllolithodes, Glyptolithodes, Paralomis multispina, Paralomis verrilli, Paralomis granulosa, Cryptolithodes*, and *Sculptolithodes*. The remaining spines are greater than ten percent of the carapace depth. The greatest spine to carapace depth ratios are found in *Lithodes maja*, and *Lithodes longispina*.

5. Carapace lateral spines:

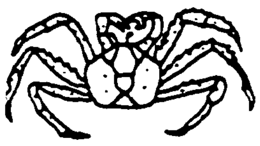
(0) absent

(1) present

Carapace lateral spines or pointed projections are found on the carapace's marginal edges. They are not synonymous with carapace spines as they do not occur on the dorsal surface of the carapace. Lateral spines are absent in outgroup taxa, *Oedignathus, Hapalogaster cavicauda, Dermaturus*, and *Placetron wosnessenskii*. These spines are present in *Hapalogaster* (except *Hapalogaster cavicauda*) *Acantholithodes*, and most, but not all, of the Lithodinae. Lateral spines are absent in *Glyptolithodes, Paralomis granulosa, Paralithodes rathbuni, Paralithodes californiensis* and *Lithodes longispina*).

6. Carapace branchial outline (see fig. 2):

(0) absent



(1) present

An outline of the branchial region (Fig. 2, based on Dawson and Yaldwyn 1985, Macpherson 1988) on the dorsal carapace is absent in outgroup taxa and found in some, but not all, Lithodidae. Branchial outlines are absent in lithodids with large carapace relief, making the branchial region hard to distinguish (*Rhinolithodes*, *Phyllolithodes*, and *Sculptolithodes*), and absent in lithodids with smooth dorsal carapaces (*Lopholithodes*, *Glyptolithodes*, and *Paralomis granulosa*, and *Cryptolithodes*).

7. Carapace epibranchial outline: (0) absent, (1) present (see fig. 2)

The epibranchial region is not outlined in outgroup taxa (except *Labidochirus*), hapalogastrinids (except *Hapalogaster*), and Lithodinae (except *Paralithodes rathbuni*, *Paralithodes californiensis*, and *Lithodes couesi*).

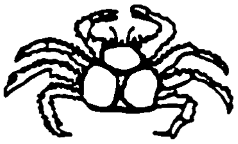
8. Carapace mesobranchial outline: (0) absent, (1) present (see fig. 1)

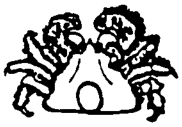
The mesobranchial region of the carapace is observed only in genus *Hapalogaster*.

9. Carapace lines:


(0) absent

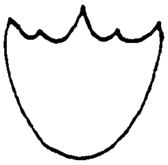

(1) faint


(2) clear


(3) furrows

Faint lines along the dorsal carapace are present in *Oedignathus*, *Acantholithodes*, *Lopholithodes*, *Paralomis*, *Paralithodes*, and *Lithodes*. The outgroup taxa and the remaining hapalogastrinids have clear demarcations. Observable furrows on the dorsal carapace are shared by *Neolithodes grimaldii*, *Rhinolithodes*, and *Paralomis multispina*. The remaining taxa have no carapace lineations.

10. Carapace cervical groove:


(0) absent


(1) present

The cervical groove separates the posterior and ventral carapace. It is found in all taxa except *Phyllolithodes*, *Lopholithodes*, *Glyptolithodes*, *Cryptolithodes*, and *Sculptolithodes*. The term linea transversalis follows McLaughlin (1974:11, fig 2).

11. Carapace gastric region convexity: (0) absent, (1) subtle, (3) prominent (see fig. 1)

Crabs living on the continental slope have branchial chambers that are more inflated than those of crabs living on the shelf. The degree of branchial inflation is quantified by Takeshita et al. (1978) for *Paralithodes camtschaticus*, *Lithodes longispina*, and *Paralomis verrilli*. The gastric region in Hapalogastrinae (except the more subtidal *Placetron wosnessenskii*) is flush (absent) with the rest of the carapace. It is convex in Lithodinae (except for the shallow water inhabitant *Paralomis granulosa*).

12. Carapace gastric spine: (0) absent, (1) single spine, (2) box of spines, (3) multiple spines, (4) bumps (see fig. 2)

Gastric region carapace spines are absent in the outgroup and, Hapalogastrinae (except gastric bump bearing *Hapalogaster dentata*). They are present in the Lithodinae (except *Rhinolithodes*, *Phyllolithodes*, *Paralomis granulosa*, *Lithodes aequispinus*, *Cryptolithodes*, and *Sculptolithodes*). The spines are either single, grouped in 4-6 spines paired in a box-like fashion, or occur in pairs throughout the region.

13. Carapace branchial region raised: (0) absent, (1) present (see fig. 1)

Crabs living on the continental slope have branchial chambers that are more inflated than those of crabs living on shallower depths of the shelf (Takeshita et al. 1978). The branchial region is flush with the remaining regions of the carapace in outgroup taxa and sub-family Hapalogastrinae (both intertidal or shallow subtidal inhabitants), but distinctly convex in Lithodinae (except shallow water inhabitant *Paralomis granulosa*).

14. Carapace cardiac bump: (0) absent, (1) present (see fig. 1)

A cardiac bump, or a raised area in the medial posterior carapace, is found only in the Lithodinae, specifically *Rhinolithodes*, *Phyllolithodes*, *Lopholithodes*, *Glyptolithodes*, and *Sculptolithodes*.

15. Carapace cardiac outline: (0) absent, (1) present (see fig. 1)

The cardiac region on the dorsal carapace is found in some outgroup taxa (*Clibanarius vittatus*, and *Pagurus longicarpus*) and the majority of Lithodidae (except *Rhinolithodes*, and *Phyllolithodes*).

16. Carapace hepatic spine box: (0) absent, (1) box, (2) rectangle, (3) bumps (see fig. 2)

Spines in the shape of a rectangle or a box located on in the carapace region are found only in some Lithodinae. *Neolithodes grimaldii*, and *Lithodes longispina* have spines in a box-shape. *Paralithodes brevipes* and *Paralithodes camtschaticus* have a rectangle shape to their spines. *Paralithodes rathbuni* and *Paralithodes californiensis* have bumps in the hepatic region.

17. Carapace relief:

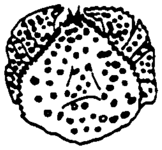
(0) absent

(2) present

There are large dorsal protuberances or carapace topological relief on the dorsal carapace in *Rhinolithodes, Phyllolithodes, Lopholithodes mandtii, Glyptolithodes*, and *Sculptolithodes*.

18. Carapace tubercle/scales:

(0) absent



(1) tubercles

(2) scales

The carapace is covered by scales (arch-like design) in *Dermaturus*, and *Placetron wosnessenskii*, and by tubercles in *Oedignathus, Rhinolithodes, Phyllolithodes, Lopholithodes, Glyptolithodes, Paralomis verrilli, Paralomis granulosa, Lithodes maja, Lithodes longispina, Cryptolithodes*, and *Sculptolithodes*.

19. Carapace posterior elevations: (0) absent, (1) present

There is a posterior ridge of bumps or tubercles on the carapace in *Rhinolithodes, Phyllolithodes, Lopholithodes, Glyptolithodes, Paralomis verrilli*, and *Sculptolithodes*.

20. Carapace posterior pinched-ridge: (0) absent , (1) present (see fig. 1)

There is a raised posterior edge on the carapace of *Acantholithodes, Neolithodes grimaldii, Paralithodes*, and *Lithodes*.

21. Carapace posterior spine ridge: (0) absent, (1) present (see fig. 1)

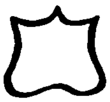
There a ridge of spines on the posterior edge of the dorsal carapace in *Lopholithodes foraminatus, Neolithodes grimaldii, Paralithodes*, and *Lithodes*.

22. Carapace mesobranchial ridge: (0) absent, (1) present (see fig. 1)

There is a protruding ridge in the medial area of the carapace's branchial region in *Rhinolithodes, Phyllolithodes, Lopholithodes, Glyptolithodes*, and *Sculptolithodes*.

23. Carapace posterior indentation:

(0) absent



(1) present

There is an invagination on the dorsal carapace's posterior edge in the outgroup and Hapalogastrinae (except *Acantholithodes* and *Placetron wosnessenskii*).

24. Carapace projection lateral to the ocular peduncle: (0) absent, (1) present (see fig. 2)

A projection that distally emerges from the anterior edge of the carapace lateral to the ocular peduncle. This projection is found in all outgroup taxa, hapalogastrinids (except *Hapalogaster cavicauda*) and Lithodinae (except *Cryptolithodes*).

25. Carapace hepatic medial projection: (0) absent, (1) present (see fig. 2)

A medial projection located between the ocular lateral projection and the anterior hepatic projection on the anterior edge of the carapace. This projection is observed in *Acantholithodes*, *Rhinolithodes*, *Phyllolithodes*, *Glyptolithodes*, *Paralomis multispina*, *Paralithodes rathbuni*, *Paralithodes californiensis*, *Lithodes aequispina*, and *Lithodes couesi*.

26. Carapace anterior hepatic protrusion: (0) absent, (1) spine, (2) projection (see fig. 2)

Projections or spines occur on the carapace's lateral edge of the anterior hepatic region in hapalogastrinids and Lithodinae (except *Cryptolithodes* and *Sculptolithodes*). They are absent in the outgroup. A projection, as defined here, is broader at the base than a spine and may or may not end in a point.

27. Carapace posterior-lateral hepatic spine: (0) absent, (1) present (see fig. 2)

A latterally projected spine on the posterior edge of the hepatic region. This character is shared by *Placetron wosnessenskii*, *Neolithodes grimaldii*, *Rhinolithodes*, *Paralithodes*, and *Lithodes*.

28. Carapace posterior calcified: (0) absent, (1) present

The posterior carapace region (posterior to the linea anomurica; from McLaughlin 1974 p.11, fig. 2a) of hermit crabs is uncalcified. This region is calcified in "missing link" pagurid taxon, *Labidochirus*, as well as mole-crab *Emerita analoga*, and Lithodidae.

29. Carapace anterior to posterior ridge:

(0) absent

(1) present

This character defines the ridge extending anterio-posteriorly on the dorsal carapace. This trait is only observed in *Cryptolithodes*.

30. Carapace posterior lateral ridge:

(0) absent

(1) present

The posterior lateral ridge is a crest protruding laterally across the posterior region of the carapace. This character is shared by *Phyllolithodes* and *Cryptolithodes*.

31. Carapace anterior lateral ridge:

(0) absent

(1) present

The anterior lateral ridge is a crest protruding laterally across the anterior region of the carapace. This character only occurs in *Cryptolithodes*.

32. Carapace obscures pereopods :

(0) absent

(1) present

The carapace obscures the dorsal view of pereopods in *Cryptolithodes*. *Cryptolithodes* possess a protective shield-like carapace which overhangs the full body including the pereopods, and thus obscures their view as well as dorsal movement. All other lithodids, including some capable of mass migrations, are unrestricted by their dorsal carapace (Somerton 1981).

33. Carapace ocular peduncle invagination:

(0) absent

(1) present

Paired anterior carapace invagination, near the ocular peduncles, occur in all outgroup taxa, Hapalogastrinae and some Lithodinae (*Lopholithodes*, *Glyptolithodes*, *Paralomis birsteini*, *Paralomis granulosa*, *Lithodes aequispinus*, and *Cryptolithodes*).

34. Carapace overhangs branchiostegite: (0) carapace overhangs branchiostegite, (1) the branchiostegite is flush with carapace, (2) branchiostegite can be viewed dorsally

The dorsal carapace overhangs the branchiostegites in *Emerita analoga*, *Labidochirus* and *Cryptolithodes*. The lateral edge of the carapace is flush with branchiostegites in *Pagurus longicarpus*, Hapalogastrinae, and remaining Lithodinae. The branchiostegite can be viewed dorsally in *Clibanarius vittatus* and *Pagurus bernhardus*.

Rostrum

35. Rostrum:

(0) subtle

(1) present

Bouvier (1895, 1896) suggested subfamily Hapalogastrinae was closely related to hermit crabs and cited *Hapalogaster cavicauda* 's small triangular rostrum with no subterminal prominence as evidence. A subtle rostral projection is observed in outgroup taxa and Hapalogastrinae and a more prominent rostrum is found in Lithodinae.

36. Rostral ridge: (0) absent, (1) present

A ridge on the rostrum's dorsal surface is shared by *Cryptolithodes* and *Sculptolithodes*.

37. Rostrum plane of projection:

(0) dorsal

(1) ventral

(2) lateral

The rostrum's plane of projection is dorsal for *Phyllolithodes*; ventral in *Paralithodes rathbuni*, *Paralithodes californiensis*, *Lithodes aequispinus*, *Lithodes couesi*, *Lithodes longispina*, and *Cryptolithodes*; and lateral in outgroup taxa, Hapalogastrinae, and remaining Lithodinae.

38. Rostrum ends in point:

(0) absent

(1) present

The rostrum has a blunt terminus in *Rhinolithodes*, *Phyllolithodes*, *Lophotithodes mandtii*, *Cryptolithodes*, and *Sculptolithodes*. The rostrum has a pointy terminus in outgroup taxa, hapalogastrinids, and remaining Lithodinae.

39. Rostrum dorsal spine:

(0) absent

(1) present

Dorsal spines are absent on the rostrum in outgroup taxa, in Hapalogastrinae (except *Acantholithodes*), and some Lithodinae (*Rhinolithodes*, *Phyllolithodes*, *Lopholithodes mandtii*, *Glyptolithodes*, *Lithodes longispina*, *Cryptolithodes*, and *Sculptolithodes*).

40. Rostrum ventral spine :


(0) absent


(1) present


(2) prominent

Ventral spines are absent on the rostrum in all outgroup taxa, sub-family Hapalogastrinae, and *Neolithodes grimaldii*. Rostral ventral spine is present in *Rhinolithodes, Phyllolithodes, Paralomis multispina, Paralomis granulosus*, and *Lithodes longispina*. It is prominent in *Paralithodes*, and *Lithodes* (except *Lithodes longispina*).

41. Rostral spine length with respect to ocular peduncle:


(0) absent


(1) shorter


(2) equal


(3) longer

The rostral spine is absent in the outgroup. The rostrum is shorter than the ocular peduncle in hapalogastrinids (except *Acantholithodes*, and *Placetron wosnessenskii*), and *Rhinolithodes*. The rostrum is equal in length in and *Lopholithodes, Acantholithodes, Glyptolithodes*, and *Paralomis granulosa*. The remaining Lithodinae have longer rostrums than ocular peduncles.

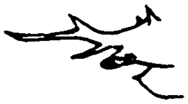
42. Rostral spine bifurcate:

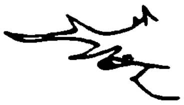

(0) absent


(1) present

The rostral distally bifurcates in *Paralomis granulosa, Paralithodes*, and *Lithodes*.

43. Rostrum ventral keel:


(0) absent


(1) subtle


(2) prominent

A keel-like projection on the rostrum's ventral side. It is subtly present in *Paralomis granulosa, Paralithodes brevipes, Paralithodes camtschaticus*, and *Lithodes couesi*. The keel is prominantly present in *Rhinolithodes, Lopholithodes, Glyptolithodes*, and *Paralomis verrilli*. The outgroup, hapalogastrinids, and remaining Lithodinae do not posses keels.

Branchiostegites

44. Branchiostegite anterior calcified: (0) soft, (1) dorsal only, (2) present

Branchiostegites are calcified plates which are located perpendicularly to the carapace and protect the gills and internal organs. These plates emerge at the anterior lateral edge of the carapace and extend posteriorly to the intersection of pereopod four and the carapace. The anterior region can be soft, meaning malleable. This character state distinguishes the fully calcified Lithodidae from the outgroup taxa's soft branchiostegites. The dorsal edge of the branchiostegites can be more calcified then the ventral region as found in Hapalogastrinae (except *Hapalogaster grebnitzkii*). Sub-family Lithodinae have full calcification.

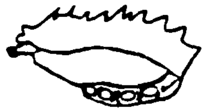
45. Branchiostegite with posterior calcified: (0) absent, (1) partially, (2) present

The branchiostegite's posterior section is non-calcified in outgroup taxa, *Hapalogaster mertensii*, and *Hapalogaster cavicauda*, partially calcified (i.e. soft to the touch) in hapalogastrinids and fully calcified in *Hapalogaster grebnitzkii*, and Lithodinae.

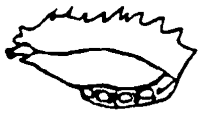
46. Branchiostegite raised anterior lip: (0) absent, (1) subtle, (2) present

A prominently raised edge, or lip, may occur on the anterior region of the branchiostegite. The anterior lip is absent in outgroup taxa, hapalogastrinids (except *Hapalogaster grebnitzki*), *Neolithodes grimaldii, Rhinolithodes, Glyptolithodes, Paralomis granulosus*, and *Cryptolithodes*. The anterior lip is subtly present in *Hapalogaster grebnitzkii, Phyllolithodes, Lopholithodes, Paralomis multipspina, Paralomis birsteini, Paralithodes brevipes, Paralithodes camtschaticus, Lithodes maja, Lithodes longispina*, and *Sculptolithodes*. The branchiostegite lip is present in all remaining taxa.

47. Branchiostegite anterior spine:



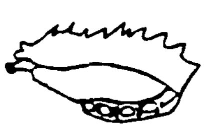
(0) absent



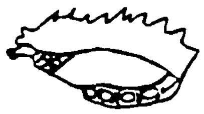
(1) present

This character is an anteriorly directed spine on the anterior margin of the branchiostegites. This spine is observed in subfamily Lithodidae and the more calcified hapalogastrinids, *Acantholithodes*, and *Placetron wosnessenskii*.

48. Branchiostegite triangular plates:



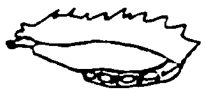
(0) absent



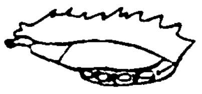
(1) present

The branchiostegite area can be composed of smooth, large contiguous plates or a small patchwork of triangularly outlined calcified regions as observed in genera *Hapalogaster*, *Oedignathus*, and *Dermaturus*.

49. Branchiostegite sulcus verticalis:



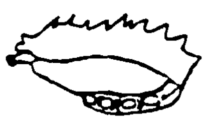
(0) absent



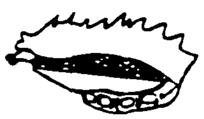
(1) present

The sulcus verticalis is a distinctive vertical line that separates the anterior and posterior region of the branchiostegite. This character is shared by the outgroup, and most lithodids. The sulcus verticalis is absent in *Hapalogaster mertensii*, *Hapalogaster dentata*, *Neolithodes grimaldii*, and *Cryptolithodes*.

50. Branchiostegite ventral/dorsal delineation:



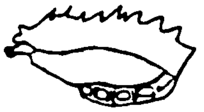
(0) absent



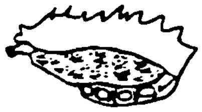
(1) present

The branchiostegite can be divided vertically (character 49) or horizontally. This horizontal delineation is not as apparent as the sulcus verticalis. This character is shared by *Oedignathus*, *Hapalogaster mertensii*, and *Hapalogaster dentata*.

51. Branchiostegite spines:



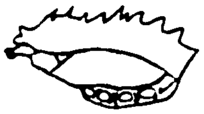
(0) spines absent



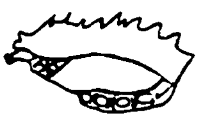
(1) spines present

The branchiostegite is often protected by an overhanging carapace or by proximal flexion of the pereopods. However, protective spines are found on a phylogenetic spattering of lithodids. Although I am unsure of this character's phylogenetic significance, it does serve to distinguish at the species level. Branchiostegite spines are present in *Acantholithodes*, *Neolithodes grimaldii*, *Rhinolithodes*, *Phyllolithodes*, *Paralomis multispina*, *Paralithodes rathbuni*, and *Paralithodes camtschaticus*. Generally, those with branchiostegite spines also possess spines throughout the body.

52. Branchiostegite anterior number of plates:



(0) few



(1) multiple

The branchiostegite anterior number of plates are those found before the sulcus verticalis (character 49). Few means less than three. Multiple plates are found in the outgroup taxon *Clibanarius vittatus* and in some hapalogastrinids (*Oedignathus*, *Hapalogaster mertensii*, *Hapalogaster dentata* and *Hapalogaster cavicauda*). All remaining taxa have few anterior plates.

53. Posterior section of the branchiostegite (i.e. the section associated with the pereopods).

(0) few (1) multiple

This character indicates the number of plates found in the posterior region of the branchiostegite. Few means less than three plates. Multiple posterior plates are found in *Clibanarius vittatus*, *Oedignathus*, and *Hapalogaster*.

54. Pereopod three's branchiostegite plates: (0) absent, (1) soft, (2) calcified

Pereopod three is the most distal walking leg in most anomurans. The branchiostegite region associated with pereopod three is either calcified (hard to touch) as observed in all Lithodinae, or soft as observed in *Oedignathus*, *Hapalogaster*, and *Acantholithodes*.

Sternites

55. Chelae proximally abutting:

(0) separated (1) abutting

Chelae are either separated by a ventral sternite or the proximal edge of chelae's coxa abut. This character distinguishes paguroids (lithodids and pagurids) from *Clibanarius vittatus*. *Emerita analoga* does not possess any sternites, thus character is defined as missing throughout.

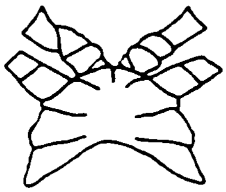
56. Sternite 1 medial slit:

(0) absent

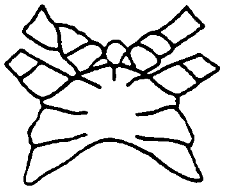
(1) present

Sternite one is a symmetrically paired sternite associated with the chelae. Sternite one is slit medially in all lithodids, except *Rhinolithodes*.

57. Sternite 3rd maxilliped raised:



(0) absent



(1) present

The sternite associated with the third maxilliped may either be a raised bump or flattened. It is raised in all Lithodinae and *Hapalogaster cavicauda*, *Dermaturus*, *Acantholithodes*, and *Placetron wosnessenskii*.

58. Sternite distal edges flared:

(0) flush

(1) flared

The sternites margins may have a flared or raised distal edge. This character is only shared by two of the four *Paralithodes* (*Paralithodes brevipes* and *Paralithodes camtschaticus*).

59. Sternite 1 anterior edge:

(0) absent

(1) raised medially

(2) raised distally

(3) straight

Each chela's associated sternite is either absent as the chelae are abutting, or the anterior edge is raised medially, distally or not raised (straight; Macpherson 1988b). Sternites are absent in the outgroup. The anterior edge is raised medially in *Hapalogaster mertensii*, *Hapalogaster grebnitzkii*, *Hapalogaster cavicauda*, *Acantholithodes*, *Lopholithodes*, *Paralomis multispina*, and *Paralomis verrilli*. The anterior edge is raised distally in *Placetron wosnessenskii*, *Cryptolithodes*, and is straight in *Oedignathus*, *Hapalogaster dentata*, *Dermaturus*, *Neolithodes grimaldii*, *Rhinolithodes*, *Phyllolithodes*, *Glyptolithodes*, *Paralomis birsteini*, *Paralomis granulosa*, *Paralithodes*, *Lithodes*, and *Sculptolithodes*.

60. Sternite 1 & 2 form a clover-like shape:

(0) absent

(1) present

An anterior medial slit in sternite one along with a posterior medial slit in sternite two, and an incomplete vertical slit separating sternite one and two produces a clover-like feature. This character is shared by all lithodids except *Rhinolithodes*, *Phyllolithodes*, and *Cryptolithodes*.

61. Sternite 1 & 2 with a protrusion between:

(0) absent

(1) present

An intercalary rod is an additional calcified region that separates sternites one and two. This character is observed in the outgroup taxa *Clibanarius vittatus*, *Pagurus bernhardus*, and ingroup taxon *Cryptolithodes*.

62. Sternite 2 medial slit:

(0) absent

(1) present

A slit occurring medially and running anterior to posterior in sternite two. This character is shared by outgroup taxa, hapalogastrinids (except *Acantholithodes*), and lithodinids *Neolithodes grimaldii*, *Paralithodes*, *Lithodes*, and *Cryptolithodes*.

63. Sternite 2 overlaps sternite 1:

(0) absent

(1) present

A distal overlap of sternite two on sternite one's marginal edge. This character is absent in the outgroup and present in all lithodids except *Placetron wosnessenskii* and *Neolithodes grimaldii*.

64. Sternite 2 distally wraps around 3:

(0) absent

(1) present

The distal posterior margin of sternite two wraps around the distal anterior margin of sternite three. This character is shared by all lithodids except *Dermaturus*, *Placetron wosnessenskii*, *Paralithodes brevipes*, *Paralithodes camtschaticus*, and *Lithodes aequispinus*.

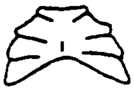
65. Sternite 3 anterior lobe:

(0) absent

(1) present

An anteriorly placed lobe contiguous with sternite three (described as a lobe by Lemaitre 1995 for *Xylopagurus* A. Milne Edwards). Can also be described as an intercalary rod between sternites two and three. This character is observed in hapalogastrinids (except *Hapalogaster mertensii*, *Hapalogaster cavicauda*), and lithodinids (except *Rhinolithodes*, *Phyllolithodes*, *Lopholithodes*, *Paralomis birsteini*, *Paralomis verrilli*, *Paralithodes rathbuni*, *Paralithodes californiensis*, *Lithodes aequispinus*, *Lithodes couesi*, *Lithodes longispina*, and *Sculptolithodes*).

66. Sternite 3 medial slit:



(0) absent (1) present

A medial slit in sternite three (sternite associated with pereopod two). This character is shared by outgroup taxa, and hapalogastrinids (except *Acantholithodes*).

67. Sternite 3 distal/anterior brace:

(0) absent (1) round (2) triangular

An anterior wrapping of sternite three around the posterior edge of sternite two. This character is shared by all lithodids except *Cryptolithodes*. It is round in hapalogastrinids (except *Dermaturus*, *Acantholithodes*, and *Placetron wosnessenskii*) and triangular in lithodinids.

68. Sternite 3 braced around 4th sternite:

(0) absent (1) present

A distal/posterior wrapping of sternite three around the anterior region of sternite four. This character is shared by all lithodids except *Hapalogaster grebnitzkii*, *Hapalogaster cavicauda*, *Paralithodes brevipes*, and *Cryptolithodes*.

69. Sternite 3:

(0) thin line (1) present

Pereopod two's associated sternite three is present as a thin line only in outgroup taxa or present as a full structure in hapalogastrinids and Lithodinae.

70. Sternite 3 & 4 with a separating uncalcified region: (0) absent, (1) present

A membranous and flexible region between sternites three and four exists only in outgroup taxa.

71. Sternite 4 medial slit:

(0) absent

(1) present

A medial slit in pereopod three's associated sternite four. This medial slit is found in *Pagurus bernhardus*, *Lithodes maja*, and *Lithodes longispina.*

72. Sternite 4 distal/anterior brace:

(0) absent

(1) round

(2) triangular

A distal/anterior projection of sternite four which is wrapped around the distal/posterior region of sternite three. It is absent in the outgroup and present in all lithodids except *Cryptolithodes.* The brace is round in all hapalogastrinids (except *Dermaturus*, *Acantholithodes*, and *Placetron wosnessenskii*), and triangular in all Lithodinae.

73. Sternite continuous slit:

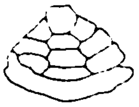
(0) absent

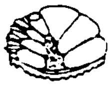
(1) present

A continuous, medial slit running anteriorly/posteriorly from sternite one through to sternite four. This character is found in all outgroup taxa, and hapalogastrinids (except *Acantholithodes*).

Abdomen, Telson and Pleopods

74. Abdominal nodules:


(0) absent


(1) present

Nodules are repetitive calcified rounded bumps which are continuous but not contiguous as they are often separated by non-calcified membranous areas. This character is absent in the outgroup and hapalogastrinids (except *Hapalogaster mertensii*, *Acantholithodes*, and *Placetron wosnessenskii*), and present in Lithodinae (except in *Cryptolithodes*).

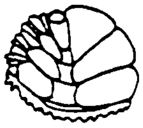
75. Abdomen viewed dorsally:

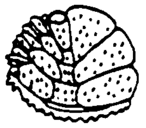

(0) absent


(1) present

Visibility of the abdomen from a dorsal perspective. A character shared by the outgroup, all hapalogastrinids, and *Neolithodes grimaldii*.

76. Abdominal spines:

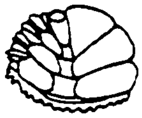

(0) absent

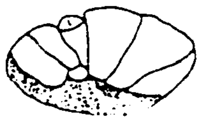

(1) present

Spines found on the abdomen's dorsal surface. Abdominal spines are found in *Acantholithodes*, *Neolithodes grimaldii*, *Paralomis multispina*, *Paralithodes*, *Lithodes aequispinus*, and *Lithodes maja*.

77. Abdominal tergite 1 calcified:


(0) membranous


(1) calcareous


(2) partially calcareous

Boas (1880a,b), Bouvier (1894, 1897) and Makarov (1962), noted differences in calcification levels when comparing families Lithodidae and Paguridae. They suggested limited calcification was most likely associated with the shell-wearing habit in family Paguridae. They also suggested that the limited amount of calcification found in sub-family Hapalogastrinae was a remnant of their pagurid ancestry. Calcification is absent in *Clibanarius vittatus*, *Pagurus bernhardus*, and *Acantholithodes*. All Lithodinae, *Oedignathus*, *Hapalogaster mertensii*, *Hapalogaster dentata* have a fully calcareous abdominal tergite one. *Hapalogaster grebnitzkii*, *Hapalogaster cavicauda*, and *Dermaturus* are partially calcareous.

78. Abdominal tergite 2 perpendicular to first: (0) absent (1) present (fig. 3)

The presence of a perpendicular plane of articulation between abdominal tergites one and two. This character is absent in hapalogastrinids (except *Oedignathus*, and *Placetron wosnessenskii*) and present in lithodinids.

79. Abdominal projection between tergites 1 & 2:

(0) absent

(1) present

This character is a dorsally raised projection between tergites one and two. This character is shared by *Dermaturus*, *Glyptolithodes*, *Paralomis verrilli*, *Paralithodes*, and *Lithodes*.

80. Abdominal tergite 2 calcified: (0) absent, (1) present (see fig. 3)

The presence of a calcareous plate on the second abdominal somite. Portions of abdominal tergite two are calcareous in all ingroup members, *Pagurus bernhardus*, and *Emerita analoga*.

81. Abdominal tergite 2 plates abut:

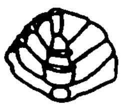
(0) absent

(1) present

Abdominal tergite two can consist of several calcareous plates. These plates are separated by a membranous region in most Hapalogastrinae. These plates are contiguously abutting in *Emerita analoga*, *Dermaturus*, *Acantholithodes*, *Placetron wosnessenskii*, and all Lithodinae.

82. Abdominal tergite 2 medial protrusion or bump:


(0) absent


(1) present

Abdominal tergite two's protrusion or bump is a medially located raised region. This character is shared by *Hapalogaster cavicauda*, *Rhinolithodes*, *Phyllolithodes*, *Lopholithodes*, *Glyptolithodes*, *Paralomis* (not *Paralomis granulosa*), and *Cryptolithodes typicus*.

83. Abdominal tergite 2 with lateral invagination:


(0) absent

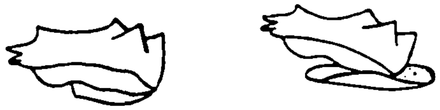

(1) present

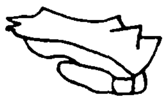
There is a paired invaginated region located latterly on tergite two. These invaginations are found in *Acantholithodes* and, *Placetron wosnessenskii*, and subfamily Lithodinae.

84. Abdominal tergite 2 number of plates: (0) none, (1) one, (2) multiple (fig. 3)

Abdominal tergite two can consist of a number of easily distinguished plates. There are no calcareous plates in *Clibanarius vittatus*, *Pagurus longicarpus*, and *Labidochirus* as abdominal tergite two is membranous. There are multiple plates in hapalogastrinids, *Neolithodes grimaldii*, *Rhinolithodes*, *Phyllolithodes*, *Paralithodes*, and *Lithodes* (except *Lithodes maja*). All other taxa possess only one plate.

85. Abdominal tergite 2 perpendicular to 3:


(0) absent


(1) present

A perpendicular bend between abdominal tergites two and three. This character is absent in hapalogastrinids (except *Dermaturus*, *Acantholithodes*, and *Placetron wosnessenskii*), and present in lithodinids.

86. Abdominal tergite 3 calcified (males): (0) absent, (1) partially, (2) present (see fig. 3)

Calcification of abdominal tergite three is absent in most outgroup taxa (except *Emerita analoga*, and *Pagurus bernhardus*), and in hapalogastrinids (except *Placetron wosnessenskii*). Calcification is partial in *Placetron wosnessenskii* as an outline is apparent and there are two symmetric circular nodules present instead of lateral plates. Calcification of abdominal tergite three is observed in *Emerita analoga, Pagurus bernhardus*, and all Lithodidae.apparent for the remaining hapalogastrinids (except *Placetron wosnessenskii*). Tergite three is calcified for all Lithodinae, and *Placetron wosnessenskii.*

87. Abdominal tergite 3 calcified (females): (0) absent, (1) outline, (2) present (fig. 3)

Abdominal tergite three is membranous in *Clibanarius vittatus, Pagurus longicarpus, Labidochirus, Oedignathus*, and *Hapalogaster mertensii*. An outline is apparent for the remaining hapalogastrinids.

88. Abdominal tergite 3 medial plate: (0) absent, (1) present, (2) nodules (see fig. 3)

Abdominal tergite three is membranous and lacks plates in *Clibanarius vittatus, Pagurus longicarpus, Labidochirus*, Hapalogastrinae, and *Neolithodes grimaldii*. A calcareous medial plate exists in *Emerita analoga, Pagurus bernhardus, Rhinolithodes, Phyllolithodes, Lopholithodes, Glyptolithodes, Paralomis, Cryptolithodes*, and *Sculptolithodes*. The medial area is present in a rounded continuous calcareous form, called nodules, as in *Paralithodes* and *Lithodes*.

89. Abdominal tergite 3 number of medial plates: (0) absent, (1) nodules, (2) 1-5 plates (see fig. 3)

There are no medial plates in the outgroup and hapalogastrinids. Medial nodules are found in *Neolithodes grimaldii, Paralithodes*, and *Lithodes*. Between one to five plates are found in the remaining Lithodinae.

90. Abdominal tergite 3 & 4 separated by intercalary rod: (0) absent, (1) present, (2) outline (see fig. 3)

An intercalary rod, or an elongate calcified region, can separate abdominal tergites three and four. Intercalary rods are absent in the outgroup, hapalogastrinids, *Neolithodes grimaldii*, and *Rhinolithodes*. Intercalary rods are outlined in *Paralithodes, Lithodes*, and *Cryptolithodes*. Intercalary rods exist in *Phyllolithodes, Lopholithodes, Glyptolithodes, Paralomis*, and *Sculptolithodes*.

91. Abdominal tergite 3 with lateral and marginals fused (males): (0) absent, (1) unfused, (2) fused (see fig. 3)

Marginal and lateral plates of abdominal tergite three in males are absent in the outgroup. These plates are present and unfused in hapalogastrinids *Neolithodes grimaldii*, *Lopholithodes*, *Paralithodes rathbuni*, *Paralithodes californiensis*, *Paralithodes brevipes*, *Lithodes*, and *Sculptolithodes*. They are present and fused in the remaining Lithodinae.

92. Abdominal tergite 3 with lateral and marginals fused (females): (0) absent, (1) unfused, (2) left fused, (3) both fused (see fig. 3)

Marginal and lateral plates of abdominal tergite three in females are absent in the outgroup. These plates are present and unfused in *Oedignathus*, and *Hapalogaster*. The plates are present and fused on the left side in *Dermaturus*, *Acantholithodes*, *Placetron wosnessenskii* and most Lithodinae. These plates are fully fused on both the left and right sides in *Paralomis granulosa*, *Cryptolithodes*, and *Sculptolithodes*.

93. Abdominal tergite 3 & 4 with nodules at crossroads of lateral and medial plates: (0) absent, (1) present (see fig. 3)

Nodules, calcified rounded segments, are found at the corner intersection of lateral and medial plates in Lithodinae except *Phyllolithodes*, *Paralomis birsteini*, and *Cryptolithodes*.

94. Abdominal tergite 4 & 5 separated by intercalary rod: (0) absent, (1) present, (2) outline only (see fig. 3)

A calcified rod (intercalary rod) separates abdominal tergites four and five in Lithodinae except *Neolithodes grimaldii*, and *Rhinolithodes*. Outlines of the intercalary rod are observed in *Paralithodes*, *Lithodes*, and *Cryptolithodes*.

95. Abdominal tergite 4 calcified (males): (0) absent, (1) present (see fig. 3)

All abdominal plates, which in *Pagurus* are hardly chitinized, are well calcified in *Lithodes* (Makarov 1962). Abdominal tergite four is calcified in male *Emerita analoga*, *Placetron wosnessenskii*, and all Lithodinae.

96. Abdominal tergite 4 calcified (females): (0) absent, (1) outline only, (2) present (see fig. 3)

Calcification of abdominal tergite four is observed in female *Placetron wosnessenskii* and Lithodinae. Abdominal tergite four is outlined in *Hapalogaster*, and *Acantholithodes* females.

97. Abdominal tergite 4 medial plate fusion: (0) absent, (1) present, (2) nodules (see fig. 3)

Abdominal tergite four medial region is either non calcified in the outgroup (except *Emerita analoga*), hapalogastrinids, *Neolithodes grimaldii*, and *Sculptolithodes*. Abdominal tergite four is fused in *Emerita analoga*, *Rhinolithodes*, *Phyllolithodes*, *Lopholithodes*, *Glyptolithodes*, *Paralomis*, and *Cryptolithodes* or it is present as large nodules (*Paralithodes*, and *Lithodes*).

98. Abdominal tergite 4 with laterals and marginals fused (males): (0) absent, (1) unfused, (2) fused (see fig. 3)

Lateral and marginal plates are absent in outgroup taxa (except *Emerita analoga*) and, hapalogastrinid males. Lateral and marginal plates are present but

99. Abdominal tergite 4 with laterals and marginals fused (females): (0) absent, (1) present, (2) left side only (see fig. 3)

Lateral and marginal plates are absent in the outgroup (except *Emerita analoga*), *Oedignathus*, and *Hapalogaster* males. The plates are present and fused in *Cryptolithodes*. The plates are fused on the left side only in *Dermaturus*, *Acantholithodes*, *Placetron wosnessenskii*, and remaining Lithodinae.

100. Abdominal tergites 4 & 5 with nodules at lateral and medial crossroads: (0) absent, (1) present (see fig. 3)

Nodules, calcified rounded areas, are found at the corner intersection of lateral and medial plates of abdominal tergites four and five in Lithodinae (except *Paralithodes rathbuni*, *Paralithodes californiensis*, *Lithodes aequispinus*, *Lithodes couesi*, *Lithodes longispina*, and *Cryptolithodes*).

101. Abdominal tergite 5 calcified (males): (0) absent, (1) present (see fig. 3)

Calcification of abdominal tergite five occurs in *Emerita analoga*, *Placetron wosnessenskii*, and Lithodinae males.

102. Abdominal tergite 5 calcified (females): (0) absent, (1) present, (2) outline only (see fig. 3)

Calcification of abdominal tergite five occurs in *Emerita analoga* and Lithodinae females. An outline of plate five occurs in *Hapalogaster*, *Dermaturus*, *Acantholithodes*, and *Placetron wosnessenskii*.

103. Abdominal tergite 5 medial plate fused: (0) absent, (1) present, (2) nodules (see fig. 3)

Medial plate is absent in outgroup (except *Emerita analoga*), hapalogastrinids, and, *Neolithodes grimaldii*. The medial plate is fused in *Rhinolithodes*, *Phyllolithodes*, *Lopholithodes*, *Glyptolithodes*, *Paralomis*, *Cryptolithodes*, and *Sculptolithodes*. Enlarged nodules, instead of a plates, exist in the abdominal tergite five medial region in *Paralithodes* and *Lithodes*.

104. Abdominal tergite 5 with lateral and marginal fused (males): (0) absent, (1) unfused, (2) fused (see fig. 3)

Lateral and marginal plates in the fifth abdominal region of males are absent in outgroup taxa (except *Emerita analoga*). Abdominal tergite five's lateral and marginal plates are unfused in Hapalogastrinae and Lithodinae (except *Cryptolithodes* and *Sculptolithodes*, whose plates are fused).

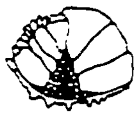
105. Abdominal tergite 5 with lateral and marginals fused (females): (0) absent, (1) present, (2) left only, (3) left outline only (see fig. 3)

Lateral and marginal plates in the fifth abdominal region of females are absent in the outgroup (except *Emerita analoga*), *Oedignathus*, and *Hapalogaster*. The plates are fused in *Cryptolithodes*, are fused only on the left side in Lithodinae (except *Cryptolithodes*). Plates are outlined in *Dermaturus*, and *Acantholithodes*.

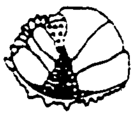
106. Abdominal tergite 6 calcified: (0) absent, (1) partially, (2) present (see fig. 3)

Abdominal tergite six is membranous in outgroup taxa (except *Emerita analoga*). It is partially calcareous (soft to the touch) in *Dermaturus*, *Acantholithodes*, *Neolithodes grimaldii*, and *Paralomis granulosa*. Tergite six is fully calcified in all other taxa.

107. Abdominal tergite 6 spines:



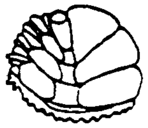
(0) absent



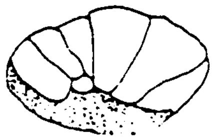
(1) present

Abdominal spines on tergite six are absent in outgroup and hapalogastrinid taxa (except *Acantholithodes*). They are present in Lithodinae (except *Paralomis birsteini*, and *Cryptolithodes*).

108. Telson location:



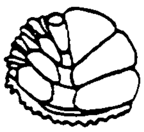
(0) dorsally



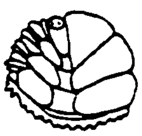
(1) wrapped under

The telson is easily viewed dorsally in all ingroup taxa, except *Oedignathus*, *Hapalogaster*, *Dermaturus*, and *Placetron wosnessenskii* where the telson is wrapped ventrally under the abdominal flap.

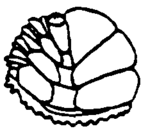
109. Telson spines:



(0) absent



(1) present

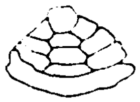


(2) tubercles

Spines on the telson are absent in the outgroup and hapalogastrinid taxa (except *Acantholithodes*), *Paralithodes brevipes*, *Lithodes couesi*, and *Cryptolithodes*. Spines are present in the remaining Lithodinae except those possessing tubercles (*Lopholithodes mandtii*, *Glyptolithodes*, and *Paralomis* (except *Paralomis granulosa*).

110. Abdominal plates (males):

(0) absent



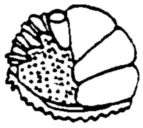
(1) present

(2) outline visible

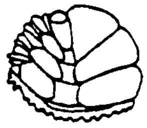
In males the abdominal plate outline is absent in outgroup taxa (except *Emerita analoga*), *Oedignathus*, *Hapalogaster mertensii*, and *Neolithodes grimaldii*. Abdominal plates are present in lithodinids and partially present in the remaining Hapalogastrinae.

111. Abdominal plates outlines (females):

(0) absent



(1) partially (2) left only



(3) present

In females abdominal plate outlines are absent in outgroup taxa (except *Pagurus bernhardus*, and *Emerita analoga*). Partial plate outlines are found in *Pagurus bernhardus*, and *Oedignathus*. Abdominal plate outlines are found only on the left in *Hapalogaster* (not *Hapalogaster mertensii*), *Placetron wosnessenskii*, *Dermaturus*, *Acantholithodes*, and *Neolithodes grimaldii*. Plate outlines are fully present in lithodinids, and *Hapalogaster mertensii*.

112. Abdominal asymmetry (males): (0) absent, (1) present

Abdominal asymmetry in males is present in outgroup taxa (except *Emerita analoga*) and ingroup taxon *Oedignathus*. Asymmetry is absent in all remaining taxa.

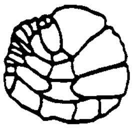
113. Abdominal laterals and medial plates fused: (0) absent, (1) unfused, (2) fused (see fig. 3)

Abdominal lateral and medial plates are absent in outgroup taxa (except *Emerita analoga*) and hapalogastrinids. The plates are unfused in Lithodinae and fused in *Emerita analoga*.

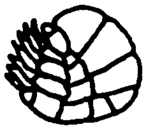
114. Abdominal spines on outer edge (males): (0) absent, (1) present (see 113)

Abdominal spines refer to marginal plate spines or to a pointed continuum of the marginal plates. They are absent in outgroup taxa males, hapalogastrinids (except *Acantholithodes*) and present in Lithodinae (except *Rhinolithodes*, *Phyllolithodes*, *Lopholithodes foraminatus*, *Glyptolithodes*, *Paralomis multispina*, *Paralomis verrilli*, *Paralomis granulosa*, *Lithodes maja*, *Cryptolithodes*, and *Sculptolithodes*).

115. Abdominal spines on outer edge (females):



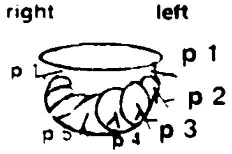
(0) absent



(1) present

Abdominal spines refer to marginal plate spines or to a pointed continuum of the marginal plates. Abdominal spines are absent in outgroup taxa females, hapalogastrinids (except *Acantholithodes*), and present in Lithodinae (except *Lopholithodes foraminatus*, *Paralomis multispina*, *Paralomis verrilli*, *Paralomis granulosa*, *Cryptolithodes*, and *Sculptolithodes*).

116. Pleopod 1 left (females): (0) absent, (1) present



Makarov (1962) stated that all lithodid females have pleopods on the left side of each of the second to fifth abdominal segments and reduced paired pleopods (both right and left) on the first abdominal somite. However, Boas (1880a) stated that genus *Hapalogaster* does not have paired pleopods on the first abdominal somite, and Hart (1965) did not observe paired pleopods on the first abdominal somite of *Cryptolithodes*. Herein, I have scored the first paired pleopods as present in *Oedignathus*, *Dermaturus*, and Lithodinae females. I scored first paired pleopods as absent in *Cryptolithodes*, *Hapalogaster*, *Placetron wosnessenskii*, and *Acantholithodes* as I did not observe the first paired pleopod. The scoring of these characters was confirmed by viewing ovigerous females. However, it should be noted that although *Oedignathus* and *Dermaturus* have paired pleopod one they did not carry eggs on these pleopods.

117. Pleopod 1 right (females): (0) absent, (1) present (see 116)

Chela

The dactyl and propodus of the chelipeds do not form functional chelae in *Emerita analoga*, thus the characters are often scored as missing (?).

118. comparitive lengths of the right chela to the right pereopods: (0) equal, (1) shorter, (2) longer

This character compares the relative length of the right chela and pereopods. Takeda (1974) noted modifications in pereopod length and width in deep sea lithodids. The right chela length is equal to pereopod length in *Pagurus longicarpus*, *Labidochirus splendescens*, *Rhinolithodes*, *Phyllolithodes*, *Lopholithodes*, *Paralomis granulosa*, *Cryptolithodes*, and *Sculptolithodes*. The right chela is shorter than the pereopods in *Clibanarius vittatus*, *Pagurus bernhardus*, *Placetron wosnessenskii*, *Neolithodes grimaldii*, *Glyptolithodes*, *Paralomis* (except *Paralomis granulosa*), *Paralithodes*, and *Lithodes*. The right chela is longer than pereopods in the remaining hapalogastrinids (*Oedignathus*, *Hapalogaster*, *Dermaturus*, and *Acantholithodes*).

119. comparitive lengths of the left chela to the left pereopods: (0) equal, (1) shorter, (2) longer

This character compares the relative length of the right chela and pereopods. The left chela is similar length to chela in *Oedignathus*, *Hapalogaster mertensii*, *Lopholithodes*, *Cryptolithodes* and *Sculptolithodes*. The chela is shorter than the pereopods in the outgroup (except *Emerita analoga*), *Placetron wosnessenskii*, *Neolithodes grimaldii*, *Rhinolithodes*, *Phyllolithodes*, *Glyptolithodes*, *Paralomis*, *Paralithodes*, and *Lithodes*. The left chela is longer than pereopods in *Emerita analoga*, *Hapalogaster dentata*, *Hapalogaster grebnitzkii*, *Hapalogaster cavicauda*, *Dermaturus*, and *Acantholithodes*.

120. Carapace and appendages form a tight bond:

(0) absent

(1) present

When pereopods and chelae are folded they interlock with each other and the carapace in *Lopholithodes*, and *Paralomis granulosa*.

121. Chelae are asymmetric: (0) absent, (1) present

The chelae are symmetric only in *Emerita analoga*, *Clibanarius vittatus*, and *Pagurus longicarpus*, all other taxa have larger right than left chela.

122. Cheliped serrated ridge clusters on the dorsal surface:

(0) absent

(1) present

Hapalogaster mertensii and *Hapalogaster dentata* possess a serrated ridge on their chelae's dorsal surface. When Boas (1880a) suggested relationships between Pagurids and the genera *Nematopagurus* and *Pylopagurus* with *Lithodes*, he suggested homologies pertaining to the armature of cheliped dactyl.

123. Chelae with spines: (0) absent, (1) present

Chelae spines are absent in the outgroup (except *Labidochirus*), *Oedignathus*, *Hapalogaster cavicauda*, *Dermaturus*, *Cryptolithodes*, and *Sculptolithodes*.

124. Chela right with dactyl teeth:

(0) absent

(1) present

Molar-like projections on the dactyl's ventral margin are present in all taxa except *Emerita analoga*, and *Oedignathus*.

125. Chela right setose row beside teeth:

(0) absent

(1) present

A row of setae beside the molar-like projections on the ventral surface of the dactyl occurs in all taxa except *Emerita analoga*, *Oedignathus*, and *Hapalogaster* (except *Hapalogaster cavicauda*).

126. Chela right fused differentially colored tip:


(0) absent


(1) present

The dactyl and propodus of the right chelae possess a distinctive colored tip (either red or brown) of hardened, scleritized protein along the distal edge. This fused biting tip is found in *Clibanarius vittatus*, *Labidochirus*, *Hapalogaster mertensii*, *Acantholithodes*, *Placetron wosnessenskii*, and family Lithodinae (except *Cryptolithodes sitchensis*).

127. Chela right with dactyl underbite compared to propodus:


(0) absent


(1) present

The propodus is elongate compared to the shortened dactyl in the right chela of all outgroup taxa (except *Clibanarius vittatus*), and lithodids (except *Cryptolithodes*).

128. Chela right propodus mid-dorsal tooth:


(0) absent


(1) present

A pointed projection emanating medially from the propodus' ventral margin. A mid-dorsal tooth is found in all outgroup taxa (except *Emerita analog*), *Oedignathus*, *Hapalogaster*, and *Dermaturus*. The mid-dorsal tooth is absent in all remaining taxa.

129. Chela propodus ventral pad:


(0) absent


(1) present

A discolored elliptical region is located on the outer surface of each chela's propodus. This character is found only in *Hapalogaster dentata* and *Hapalogaster grebnitzkii*.

130. Chela right biting angle:

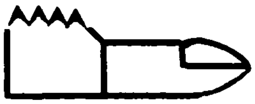
(0) downward

(1) crossed

The propodus and dactyl of the right chela either contact directly or cross as in *Pagurus longicarpus*, and *Pagurus bernhardus*.

131. Chela right carpus flare:

(0) absent

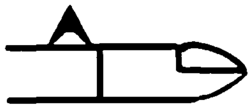


(1) present

A flared projection that extends from the right chela's carpus. This character is found in *Oedignathus*, *Lopholithodes*, *Glyptolithodes*, *Paralomis granulosa*, and *Sculptolithodes*.

132. Chela right carpus spine:

(0) absent



(1) present

A prominent spine that extends from the dorsal edge of chela's right carpus. This character is absent in the outgroup and found in *Dermaturus*, *Acantholithodes*, *Placetron wosnessenskii*, *Rhinolithodes*, *Phyllolithodes*, *Lopholithodes mandtii*, *Paralomis multispina*, *Paralomis birsteini*, *Paralithodes rathbuni*, *Paralithodes brevipes*, *Paralithodes camtschaticus*, *Lithodes maja*, and *Sculptolithodes*.

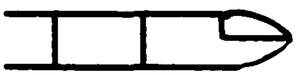
133. Chela right merus ridge protrusion:

(0) absent

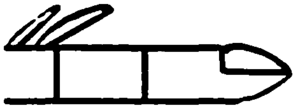
(1) present

An extensive ridge that protrudes from the right chela's merus. This character is absent in the outgroup and is found in hapalogastrinids (except *Placetron wosnessenskii*), *Lopholithodes*, *Glyptolithodes*, *Paralomis granulosa*, and *Cryptolithodes*.

134. Chela right merus prominent spines:



(0) absent



(1) present

A prominent spine projecting from the merus of the right chela. This character is absent in the outgroup. This character is shared by *Hapalogaster mertensii*, *Dermaturus*, *Acantholithodes*, and *Placetron wosnessenskii*, and Lithodinae (except *Paralomis multispina*, *Paralomis verrilli*, *Lithodes aequispinus*, *Lithodes couesi*, *Lithodes* longispina, *Cryptolithodes*, and *Sculptolithodes*).

135. Chela setal cup when bent: (0) absent, (1) present

When the chelae are bent, between the carpus and merus, and towards the carapace, a settling carpet for potential food is produced by the seta. This character is absent in the outgroup. This character shared by *Hapalogaster mertensii*, *Hapalogaster dentata*, *Rhinolithodes*, *Phyllolithodes*, and *Sculptolithodes*.

136. Chela left placement of spines: (0) absent, (1) dorsal, (2) ventral, (3) dorsal/ventral lines only, (4) everywhere

Spines are absent on left chela for outgroup taxa and in *Cryptolithodes*. Left chela spines exist solely on the dorsal edge of *Oedignathus*, *Hapalogaster mertensii*, *Dermaturus*, *Placetron wosnessenskii*, *Paralomis granulosa*, and *Sculptolithodes*. Spines occur on both the dorsal and ventral edge of the left chelae in *Hapalogaster dentata*, *Hapalogaster grebnitzkii*, *Hapalogaster cavicauda*, *Lopholithodes*, *Glyptolithodes*, *Paralomis birsteini*, and *Paralomis verrilli*. Spines exist throughout the left chela on *Acantholithodes*, *Neolithodes grimaldii*, *Rhinolithodes*, *Phyllolithodes*, *Paralomis multispina*, *Paralithodes*, and *Lithodes*.

137. Chela left dactyl dorsal bump:

(0) absent

(1) present

A dorsal bump on the proximal edge of the chela's left dactyl occurs in *Oedignathus*, *Hapalogaster* (except *Hapalogaster mertensii*), *Acantholithodes*, and Lithodinae (except *Neolithodes grimaldii*, *Glyptolithodes*, and *Sculptolithodes*).

138. Chela left dactyl teeth:

(0) absent

(1) present

Teeth-like protrusions exist on the dorsal edge of chela's left dactyl in *Clibanarius vittatus*, *Labidochirus*, hapalogastrinids (except *Hapalogaster mertensii*), *Rhinolithodes*, *Phyllolithodes*, *Lopholithodes*, *Paralithodes brevipes*, *Cryptolithodes*, and *Sculptolithodes*.

139. Chela left dactyl underbite compared to propodus: (0) absent, (1) present (see character 127)

The propodus is elongate compared to the shortened dactyl in the left chela in *Labidochirus*, *Hapalogaster grebnitzkii*, *Hapalogaster cavicauda*, *Acantholithodes*, *Placetron wosnessenskii*, and Lithodinae (except *Paralomis granulosa*, and *Cryptolithodes*).

140. Chela left propodus teeth: (0) absent, (1) present

Teeth-like protrusion on the dorsal surface of the left chela are found in *Clibanarius vittatus*, hapalogastrinids (except *Hapalogaster dentata*), and lithodinids (except *Neolithodes grimaldii*, *Glyptolithodes*, *Paralomis granulosa*, *Paralithodes californiensis*, *Lithodes couesi*, and *Lithodes maja*).

141. Chela left biting angle: (0) straight, (1) downward

Contact between the propodus and dactyl of the left chela is either downward as in *Dermaturus*, *Rhinolithodes*, *Phyllolithodes*, *Lopholithodes*, *Glyptolithodes*, *Paralomis granulosa*, *Lithodes aequispinus*, *Cryptolithodes*, and *Sculptolithodes* or straight across as observed in outgroup taxa, the majority of hapalogastrinids, and remaining Lithodinae.

142. Chela left propodus dorsal ridge:

(0) absent

(1) present

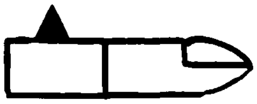
A dorsal ridge, on the non-pinching region of the left chela's propodus, is observed in outgroup taxa (except *Emerita analoga*), hapalogastrinids (except *Oedignathus*, *Acantholithodes*, *Placetron wosnessenskii*), *Lopholithodes*, *Glyptolithodes*, *Paralomis birsteini*, *Paralomis verrilli*, *Cryptolithodes*, and *Sculptolithodes*.

143. Chela left setae around teeth: (0) absent, (1) present (see 125)

A setose line alongside the left chela's teeth-like protrusions, occur in all lithodids, and is absent in all outgroup taxa.

144. Chela left carpus bumps:

(0) absent



(1) spine

(2) bump

Spines are found on the dorsal surface of the left chela's carpus in hapalogastrinids, *Neolithodes grimaldii*, *Rhinolithodes*, *Phyllolithodes*, *Paralomis birsteini*, *Paralomis verrilli*, *Lithodes maja*, and *Lithodes longispina*. Bumps are present in *Lopholithodes*, *Glyptolithodes*, *Paralomis granulosa*, *Cryptolithodes*, and *Sculptolithodes*.

145. Chela left carpus flare: (0) absent, (1) subtle, (2) prominent (see 131)

A frill-like protuberance extends on the dorsal edge of chela's left carpus. A subtle flare occurs in *Paralomis birsteini*, and *Paralomis granulosa*. This flare is prominent in *Lopholithodes*, *Glyptolithodes*, and *Cryptolithodes*.

146. Chela left merus bumps:

(0) absent

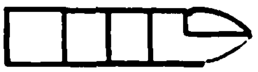
(1) subtle (2) prominent

Prominent bumps occur on the dorsal edge of the left chela's merus in *Glyptolithodes*, *Lopholithodes*. Subtle bumps occur in *Oedignathus*, *Dermaturus*, *Paralomis verrilli*, and *Sculptolithodes*.

147. Chela width compared to spine length: (0) spines less than or equal to chela width, (1) spines greater than chela width

Chela spines are longer than chela width in *Neolithodes grimaldii*, *Paralithodes rathbuni*, *Lithodes maja*, and *Lithodes longispina*. All remaining taxa's spines are less than the chela length.

148. Chela left merus ridge on dorsal edge:



(0) absent

(1) present

A left merus ridge is absent in the outgroup, *Acantholithodes*, *Placetron wosnessenskii*, *Neolithodes grimaldii*, *Rhinolithodes*, *Phyllolithodes*, *Paralomis multispina*, *Paralomis birsteini*, *Paralithodes*, *Lithodes*, and *Sculptolithodes*. All remaining taxa have this ridge.

149. Chela left ishium ridge on dorsal edge: (0) absent, (1) present (see 153)

On the dorsal edge of the left chela's ishium is an extended ridge in *Lopholithodes*, *Glyptolithodes*, and *Cryptolithodes*.

150. Chela coxal -basis setal tuft: (0) absent, (1) present

There are setal tufts on the chela's coxal and basis region in lithodids (except *Cryptolithodes*), which are absent for outgroup taxa.

Pereopods

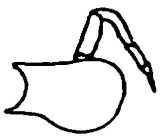
151. Pereopod to carapace ratio: (0) equal, (1) smaller, (2) greater

Pereopods are equal to carapace width in *Emerita analoga*, *Oedignathus*, *Hapalogaster dentata*, *Hapalogaster grebnitzkii*, *Hapalogaster cavicauda*, *Rhinolithodes*, *Phyllolithodes*, *Paralomis granulosa*, *Cryptolithodes*, and *Sculptolithodes*. They are longer in all remaining taxa. Takeda (1974) noticed the pereopod length is greater in deeper-living lithodids.

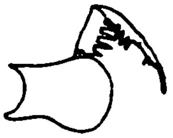
152. Pereopod spines: (0) absent, (1) present

Spines are present on pereopods of *Hapalogaster mertensii*, *Acantholithodes*, *Placetron wosnessenskii*, and Lithodinae (except *Lopholithodes*, *Cryptolithodes*, and *Sculptolithodes*).

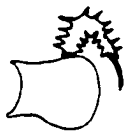
153. Pereopod spine lines:



(0) absent



(1) dorsal spine



(2) ventral and dorsal spine line

(3) everywhere

Spine ridges are absent in the outgroup, *Oedignathus*, *Dermaturus*, *Acantholithodes*, *Neolithodes grimaldii*, *Lopholithodes*, and *Cryptolithodes*. There is a dorsal spine line in *Hapalogaster grebnitzkii*, *Placetron wosnessenskii*. There are dorsal and ventral spine lines in *Hapalogaster* (except *Hapalogaster grebnitzkii*), *Rhinolithodes*, *Glyptolithodes*, *Paralomis* (except *Paralomis multispina*), *Paralithodes brevipes*, *Paralithodes camtschaticus*, *Lithodes* (except *Lithodes longispina*), and *Sculptolithodes*. The remaining taxa have spines throughout their pereopods.

154. Pereopod setose ridges:

(0) absent

(1) present

There is a ridge of setae along the ambulatory pereopods of *Emerita analoga*, *Clibanarius*, *Labidochirus*, *Hapalogaster*, and *Dermaturus* which does not exist in the remaining Lithodidae.

155. Pereopod tubercles or scales:

(0) absent

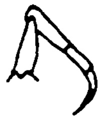
(1) tubercles

(2) scales

There are pereopod tubercles (rough, calcareous bumps) on *Labidochirus*, *Oedignathus*, *Lopholithodes*, *Paralomis granulosa*, and *Sculptolithodes*. There are pereopod scales on *Dermaturus*, and *Placetron wosnessenskii*.

156. Pereopod hard dactyl points:

(0) absent



(1) present

On the distal walking edge, or dactyl, of each ambulatory pereopod, there are hardened differentially colored (often red or brown) points in all taxa except *Emerita analoga*, and *Labidochirus*.

157. Pereopod hardened dactyl tufts:

(0) absent

(1) present

Tufts of hardened scleritized setae on the posterior/distal edge, or dactyl, of the ambulatory pereopods are observed in *Pagurus bernhardus*, hapalogastrinids and family Lithodinae (except *Paralithodes rathbuni*, *Paralithodes californiensis*, and *Lithodes*).

158. Pereopod ishium and coxal shelves: (0) absent, (1) present

The ventral region of the ishium or coxa of the ambulatory pereopods have a squared shape and are shelf-like in appearance. This is only observed in *Lopholithodes*.

159. Pereopod dactyl to propodus ratio: (0) d<p, (1) d=p, (2) d>p

Ambulatory pereopods with shorter dactyl segments than propodal segments are found in hapalogastrinids (except *Dermaturus*) Lithodinae (except *Glyptolithodes*, *Paralomis birsteini*, *Paralomis verrilli*, *Paralomis granulosa*, and *Sculptolithodes* – all of whose dactyl length is the same length as that of the propodus). Dactyl length is greater than propodal length in the outgroup (except *Labidochirus* whose dactyl and propodus lengths are equal).

160. Pereopod dactyl proximal projection:

(0) absent

(1) present

There is a multi-peaked projection surrounding the proximal edge of the dactyl in ambulatory pereopods in *Neolithodes grimaldii*, *Rhinolithodes*, *Phyllolithodes*, *Lopholithodes*, *Paralomis birsteini*, *Paralomis granulosa*, *Paralithodes*, and *Lithodes*. This character is absent in all outgroup taxa, hapalogastrinids and remaining lithodinids.

161. Pereopod 3 reduced: (0) reduced, (1) not reduced

The third pereopod is non-ambulatory and reduced in outgroup taxa (except *Emerita analoga*), and ambulatory and not reduced in all lithodids.

162. Pereopod 5 placement: (0) dorsal (wrapped over the carapace), (1) ventral (wrapped under the carapace)

Pereopod 5 is reduced and wrapped over the dorsal edge of the carapace in the outgroup (except *Emerita analoga*), and ventrally wrapped under the carapace and used as gill cleaners in all lithodids.

163. Pereopod distal propodus projection:

(0) absent

(1) present

There is a multi-peaked projection surrounding the distal edge of the propodus in *Placetron wosnessenskii*, *Neolithodes grimaldii*, *Paralithodes*, and *Lithodes*.

Ascicle, Ocular peduncle and Antenna

164. Ascicle:

(0) absent

(1) subtle

(2) present

The ascicle is absent in *Dermaturus*, *Placetron wosnessenskii*, *Neolithodes grimaldii*, and *Sculptolithodes*. The ascicle is subtly present in the outgroup, *Paralomis granulosa*, *Paralithodes*, and *Lithodes*. The ascicle is present in all remaining taxa.

165. Ascicle spinious:

(0) absent

(1) present

The ascicle is spinious in *Acantholithodes*, *Rhinolithodes*, *Lopholithodes*, *Glyptolithodes*, *Paralomis multispina*, *Paralomis verrilli*, and *Paralomis granulosa*.

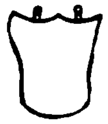
166. ascicle multi-branched:

(0) absent

(1) present

The ascicle is multi-branched in *Acantholithodes*, *Phyllolithodes*, *Paralomis granulosa*, and *Paralithodes brevipes*.

167. Ascicle viewed dorsally:



(0) absent

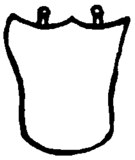
(1) present

The ascicle can be easily viewed dorsally, i.e. the carapace does not overlie the ascicle in all taxa except *Cryptolithodes* and *Sculptolithodes*.

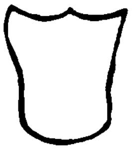
168. Ocular peduncle spines: (0) absent, (1) present

There are spines on the ocular peduncle of *Acantholithodes*, and Lithodinae (except *Paralithodes rathbuni*, *Paralithodes californiensis*, *Lithodes*, and *Cryptolithodes*).

169. Carapace overlaps ocular peduncle



(0) absent



(1) present

The ocular peduncle can be observed dorsally in all taxa excepting *Cryptolithodes*, and *Sculptolithodes*.

170. Antennal length: (0) shorter than carapace, (1) equal to carapace, (2) longer than carapace

The antennae are shorter than the carapace in *Oedignathus*, *Hapalogaster dentata*, *Hapalogaster grebnitzkii*, *Hapalogaster cavicauda*, and *Acantholithodes*, and all family Lithodinae. The antennae are equal to the carapace length in *Emerita analoga*, *Hapalogaster mertensii*, and *Dermaturus*. The antennae are longer than the carapace in the outgroup (except *Emerita analoga*), and *Placetron wosnessenskii*.

CHAPTER 5

A case of reversed asymmetry in *Lithodes maja* (Linnaeus, 1758) (Decapoda, Anomura, Lithodidae).

Zaklan, S. D. 2000. A case of reversed asymmetry in *Lithodes maja* (Linnaeus, 1758) (Decapoda, Anomura, Lithodidae). Crustaceana 78:1019-1022.

Introduction, Results and Discussion

A fundamental characteristic of the family Lithodidae is the conspicuous abdominal asymmetry in females. Left lateral plates of somites 3-5 are distinctively larger than the opposing right plates resulting in a medial line of symmetry directed to the right. Corresponding to the lateral plate asymmetry is medial asymmetry, represented either by plates, nodules or membranous tissue (genus dependent). Marginal plates are only located on the right side, associated with the smaller right lateral plates, left marginal plates are either absent or fused to the left lateral plates. Pleopod asymmetry is also observed, with lithodids bearing a full complement of pleopods only the left side of the abdomen. Thus, egg bearing is associated with larger left lateral plates. Finally, chela asymmetry is also apparent, the right being larger than the left. In general this asymmetry is thought to be a vestigial characteristic from a hypothetical hermit crab ancestry (e.g., Bouvier, 1895; Cunningham et al., 1992; but see McLaughlin & Lemaitre, 1997): morphological residuals from inhabiting an asymmetric and generally dextrally coiled gastropod shell.

In December of 1998, while working in the American Museum of Natural History, I observed a female specimen of *Lithodes maja* (Linnaeus, 1758) that was collected and identified by J. C. Armstrong in 1939, from George's Bank in the northwestern Atlantic Ocean (42°N 65°W). This female presented a total reversal of the normal abdominal asymmetry (fig. 5-1a) and corresponding pleopods as well as chela asymmetry reversal (fig. 5-1b). The lateral plates on the right in somites 3-5 were substantially larger than those on the left, there were no right marginal plates, and the corresponding medial nodules were found concentrated on the left rather than the normal right side. Chela asymmetry reversal could potentially be due to autotomy and regrowth of the chela (in this case the right chela; for review see Hartnoll, 1982).

The specimen is deposited in the collections of the American Museum of Natural History in New York (Number 9354) and has the following dimensions: carapace length (excluding the rostrum) 46.19 mm; rostrum 22.73 mm; maximum height of carapace (excluding the spines) 24.86 mm; small right chela length 23.41 mm; height right chela 6.85 mm; length of large left chela 28.30 mm; height of left chela 10.20 mm; mass is unknown as it was a dried specimen. The specimen was not gravid.

Although this is the first reported case of abdominal asymmetry and associated pleopod position reversal in *Lithodes maja*, there have been two prior reports of lithodid abdominal reversals; *Paralomis granulosa* Jacquinot, 1852 (Campodonico, 1978) and *Lithodes nintokuae* Sakai, 1978 (Dawson & Yaldwyn, 1985). Although no species were mentioned, Campodonico (1978) noted that other crustacean researchers (Dr. Janet Haig, University of Southern California; and Dr. Guy C. Powell, Department of Fish and Game, Kodiak, Alaska) had also observed this phenomenon. The frequency of this anomaly is unknown, but presumed low for *Lithodes*, as well as other king crabs. Campodonico (1978) estimated that 2.5% of the population of *P. granulosa* in the Porta Zenteno region of Chile (52° 47'S 70° 44'W) possessed chelae asymmetry reversal. This is the first time that reversal in abdominal asymmetry with an associated chela asymmetry reversal has been reported.

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FIGURE LEGEND

Fig. 5-1: Ventral view of a female *Lithodes maja* (Linnaeus, 1758), showing reversed chela (a) and abdominal plate asymmetry (b). Left chela and left plates are viewed on the reader's right.


a
b

CHAPTER 6

An investigation into carcinization using a combined morphological and DNA-based phylogeny of the king crab family Lithodidae (Crustacea: Anomura: Paguroidea)

ABSTRACT

DNA sequences and morphological characters were combined to examine the evolutionary history of the king crab family Lithodidae, as well as its relationship to the hermit crab family Paguridae. A total of 2577 characters comprised 2374 bp of neucleotide data (mtDNA: 12S, 16S, COI, COII, and nuclear DNA: 28S), of which 532 are phylogenetically informative, and 170 phylogenetically informative morphological characters. An inferred phylogeny, based on 14 of 104 species in the Lithodidae representing 10 of 16 described lithodid genera, indicates that the family Lithodidae, the subfamilies Lithodinae and Hapalogastrinae, and four genera (*Cryptolithodes*, *Hapalogaster*, *Lithodes*, and *Paralithodes*) are monophyletic at the current taxon sampling. The family Paguridae (represented by ingroup genera *Pagurus* and *Labidochirus*) was found to be paraphyletic with respect to the subfamily Lithodidae. There was a large degree of concordance between my phylogeny and some (Boas 1880 a,b, Bouvier 1894 a,b, 1897, Cunningham et al. 1992, Richter and Schultz 1994, Chapters 3 and 4), but not all (Martin and Abele 1986, McLaughlin and Lemaitre 1997, 2000), published accounts of lithodid evolution. Number of pleopods and their use in egg-bearing was mapped on the combined phylogeny, revealing an ancestral state of three left egg-bearing pleopods in the hermit crab genus *Pagurus*, and derived states of four left egg-bearing pleopods in the subfamily Hapalogastrinae and the genus *Cryptolithodes*, and six egg-bearing pleopods in the subfamily Lithodinae (five left and one right). This shift in the use of egg-bearing appendages may have acted as selective pressure toward becoming a fully calcified crab (=carciniaed) as observed in the subfamily Lithodinae.

Key words: king crabs, hermit crabs, carcinization, combined analysis, Lithodidae, Paguridae, character mapping, pleopods

INTRODUCTION

Although crustaceans are defined by their hardened exoskeletons, they are not all fully protected by their exoskeleton. For example, many taxa within the infraorder Anomura bear soft abdomens, including the hermit crab families Pylochelidae, Diogenidae, Coenobitidae, Parapaguridae, Paguridae and the lithodid subfamily Hapalogastrinae (Table 6-1). Of these taxa, lithodids are the only anomurans with soft abdomens and a crab-like form. Carcinization, or the process of becoming a crab through the broadening and hardening of the carapace and tucking under of the abdomen, was first described by Borradaile (1916). At least five independent developments of carcinization have been detected, four times in the infraorder Anomura (the families Porcellanidae, Lomidae, Lithodidae and genera *Birgus* and *Probeebei*, Przibram 1907, Harms 1932, Reese 1968, Wolff 1961) and once in the true crab infraorder Brachyura (Morrison et al. submitted). Although the repeated conversion to a crab-like forms suggests a large fitness advantage (Morrison et al. submitted), experimental and observational work supporting this hypothesis is limited.

Hermit crabs generally house their soft abdomen in the protective casing of a dextrally spiraled and asymmetric gastropod shell, or in other forms of acquired protection such as bivalve shells, sabellid or serpulid tubeworm casings, tooth shells or sponges. However, the subfamily Hapalogastrinae, which have soft abdomens, are free living intertidal crustaceans that are independent of gastropod shells, and instead wrap their unprotected soft abdomen beneath them. The persistence of naked abdomens in crabs that do not bear gastropod shells, coupled with asymmetries in their abdominal appendages, strongly suggests that hapalogastrine crabs were derived from hermit crab ancestors and likely represent an early stage in the radiation of lithodids (Boas 1880a,b, Bouvier 1894a,b, Makarov 1962). Although this hypothesis has been widely accepted, phylogenetic relationships among lithodid taxa remain poorly resolved and strongly debated (McLaughlin and Lemaitre 1997, 2000).

The family Lithodidae (Crustacea: Decapoda: Anomura) contains approximately 105 species (Chapter 2) belonging to 15 (if *Acantholithus* is part of *Paralomis*, Sakai 1976) or 16 genera (Dawson 1989). These anomurans are distributed in a variety of aquatic zones from the mid-intertidal region (the subfamily Hapalogastrinae) to the depths of the abyssal zone (the subfamily Lithodinae), typically anti-tropical, and most diverse in the north eastern Pacific Ocean (Chapter 2). Phylogenetic inference (Chapters 3 and 4) and distributional data (Chapter 2) suggest that lithodids most likely originated in the northeastern Pacific (Makarov 1962) between 13-25 mya (Cunningham et al. 1992, Feldmann 1998) and possibly co-evolved under the protection of the recently evolved (16-30 mya, Saunders and Druehl 1992) canopy-producing kelp, Laminariales (Chapters 2 and 3).

This paper has three main objectives. First, to employ a total evidence approach to derive a phylogeny for the family Lithodidae. This is done by combining molecular (mitochondrial DNA COI, COII, 16S, 12S, and nuclear DNA 28S; representing a total 2374 bp of which 532 are phylogenetically informative) and morphological data (170 phylogenetically informative characters) from 14 species representing 10 of a possible 16 genera of the family Lithodidae. When congruent data obtained from diverse sources provide a congruent signal, the validity of the phylogenetic hypothesis is stronger (Graham et al. 1998). Second, as McLaughlin and Lemaitre's (1997) data set requires a contrary stance to long held views on lithodid evolution, it is reanalyzed and subsequently compared to the combined topology. Finally, the use of egg-bearing appendages (pleopods), was mapped onto the combined phylogeny. This was done as it is plausible that gastropod shell confinement for housing of eggs and lack of suitable habitat may act as selective pressures towards the evolution of a crab-like form.

MATERIALS AND METHODS

Taxon Sampling:

All taxa included in this analysis are extant members of the Crustacean infraorder Anomura. The ingroup consists of 17 members of the superfamily Paguroidea. These include three hermit crabs of the family Paguridae (*Pagurus bernhardus*, and *Pagurus longicarpus*) and *Labidochirus splendescens* (Jensen 1995). The later is considered a 'missing link' between lithodids and pagurids. The remaining members of the ingroup include 14 of the approximately 105 species of the king crab family Lithodidae, including three species representing two genera of the subfamily Hapalogastrinae (*Oedignathus* and *Hapalogaster*) and 11 species representing eight genera of the subfamily Lithodinae (*Cryptolithodes*, *Phyllolithodes*, *Rhinolithodes*, *Lopholithodes*, *Glyptolithodes*, *Paralomis*, *Lithodes*, and *Paralithodes*; see Table 3-1 and Table 4-1 for sample origins). Outgroups were chosen based on previous hypotheses of Anomuran higher level phylogeny (Table 6-1 and Cunningham et al. 1992), and represent two closely related families, including the left-handed hermit crab *Clibanarius vittatus* (Bosc 1802, superfamily Paguroidea, family Diogenidae), and mole crab *Emerita analoga* (Stimpson 1857, superfamily Hippoidea, family Hippidae).

Data sets

Both morphological and molecular information were analyzed in this study. The 170 morphological characters are presented in Chapter 4, and include 12 morphological regions of the lithodid exoskeleton: carapace (34 of 170; 20.0% of characters), rostrum (9; 5.3%), branchiostegites (11; 6.5%), sternites (19; 11.1%), abdomen including telson (42; 24.7%), pleopods (2; 1.2%), chelae (33; 19.4%), pereopods (13; 7.6%), and ascicle, ocular peduncle and antenna region (7; 4.1%). Figures 4-2 and 4-3 and Appendix 4-1 in Chapter 4 provide visual depictions and written descriptions of each character and state. Previous treatises such as McLaughlin (1974), Sakai (1976), Macpherson (1988), and Sandberg and McLaughlin (1998) were referred to for anatomical definitions. The DNA sequences are from Chapter 3, and include sequences from mtDNA (COI, 406bp; COII, 418bp; 12S, 529bp; and 16S, 716bp) and nrDNA (28S, 300bp). Molecular methodology is outlined in Chapter 3 and Genbank (accession numbers Table 3-2). Due to limitations in material access, there are species that are found only in the DNA-based phylogeny (*Lithodes santolla*) or the morphologically-based phylogeny (*Hapalogaster grebnitzkii, Hapalogaster cavicauda, Dermaturus mandtii, Acantholithodes hispidus, Neolithodes grimaldii, Sculptolithodes derjugini, Lopholithodes foraminatus, Paralomis verrilli, Paralomis birsteini, Paralomis multispina, Paralithodes rathbuni, Paralithodes* *californiensis, Lithodes couesi, Lithodes longispina, Placetron wosnessenskii*) but not both. Only taxa found in both data sets were used in the combined analysis.

McLaughlin and Lemaitre (1997) investigated the possibility of repeated evolution of carcinization within the Anomura using a morphological data set of 37 characters scored for 59 taxa. This data set was entered into MacClade 4.0 (Maddison and Maddison 1992), and reanalyzed in PAUP* 4.08b (Swofford 2001).

Phylogenetic analysis

Phylogenetic analysis was performed using equally weighted maximum parsimony on the combined DNA (n=2374 of which 532 were phylogenetically informative; Chapter 3) and morphological (n=170; Chapter 4) data sets. Analyses for the combined data set and the reanalysis of data from McLaughlin and Lemaitre (1997), were performed using PAUP * 4.0b8 (Swofford 2001). MacClade 4.0 (Maddison and Maddison 1992) was used to map pleopod presence and reproduce the original tree from McLaughlin and Lemaitre (1997). Gaps were treated as 'missing', and starting trees were obtained via stepwise addition. Heuristic searches were carried out with 10 random-taxon-addition iterations. Only one tree was held at each step during stepwise addition, and tree-bisection and reconnection (TBR) was used as the branch-swapping algorithm. Branches were collapsed (creating polytomies) if maximum branch length was zero. Clade stability was estimated using two different parameters, either multiple bootstrap replicates (Felsenstein 1985) or decay indices (= Bremer support, Bremer 1994). Bootstrap values were generated in PAUP* from 1000 replicates, each with 10 random addition sequences. Bremer support values were also calculated in PAUP* by finding the length of the best tree that did not include each of monophyletic clades. Bremer support was calculated by subtracting the length of the best overall tree from the length of the tree which disallowed the monophyletic tree in question.

Combining Data sets

Three general approaches may be taken when analyzing data sets with multiple components (here mitochondrial DNA (16S, 12S, COI, COII), nuclear DNA (28S), and

170 morphological characters): (1) combining data sets to better maximize parsimony (Farris 1983, Nixon and Carpenter 1996), (2) keeping data sets separate then combining them via consensus trees, or (3) combining only non-contradictory data sets (reviewed in Swofford 1991, de Queiroz et al. 1995, Miyamoto and Fitch 1995, Huelsenbeck et al. 1996). Here, the latter methodology is followed as different data sets can potentially be viewed as independent indicators of phylogeny (de Queiroz et al. 1995) and the individual data sets are considered non-contradictory (see discussion below and label 'A' Figs. 1a-d). Several methods of assessing congruence between data sets were used and discussed below.

The partition homogeneity test (also known as the incongruence length difference (ILD) test; Mickevich and Farris 1981, Farris et al. 1995) may be used to evaluate whether data sets are significantly incongruent, and can be performed in PAUP* 4.0b8 (Swofford 2001). The test randomly repartitions characters from all data sets (here morphological and DNA) into new data sets of similar size. The shortest trees are then estimated for each rearranged data partition. If the sum of tree lengths for the rearranged data sets are significantly larger than the original length, the null hypothesis of congruence is rejected, meaning that one of the original data sets is different than the others (Farris et al. 1995).

The Shimodaira-Hasegawa (1999) test (=SH test) was used to assess similarities between most parsimonious trees derived from the morphological and DNA data sets. Neither the Kishino-Hasegawa (1989) test nor the Templeton (1983) test were used to assess similarities between the different trees. Both tests assume no tree topology is chosen *a priori*, and as the most parsimonious trees (i.e. trees that are chosen *a priori*) are compared when using these analyses, they may be invalid methods of investigating phylogenies (Goldman et al. 2000).

Partitioned Bremer support (Baker and DeSalle 1997) was calculated in accordance with procedures developed by Baker et al. (1998) to evaluate the support provided by the individual DNA and morphological data sets for the combined tree at each individual node. Analysis of a single data set combined with others may support phylogenetic relationships that are not evident when the data sets are individually analyzed. The partitioned Bremer support assesses the relative contribution of each data set, as well as conflicts between them and topology of the combined analysis. Each node's Bremer support value is divided between each data set (here morphological and DNA) included in the combined analysis. The partitioned Bremer support values can be positive or negative but the sum will be always equal the total Bremer support value for that node.

Character mapping of pleopod presence and use in egg-bearing

The presence or absence of pleopods used for egg-bearing for this study was obtained by observing between 2-10 ovigerous representatives of each taxon. Species were either freshly collected (personal collection; PC) or were preserved animals found in the United States National Museum of Natural History (USNM). Female lithodids observed include pagurid species *Pagurus bernhardus* (10 animals observed; obtained from PC), and *Pagurus longicarpus* (10; PC) as well as lithodid species, *Oedignathus inermis* (10; PC; 2 USNSM), *Hapalogaster dentata* (2 PC; 2 USNM), *Hapalogaster mertensii* (3 USNM), *Cryptolithodes sitchensis* (3 PC; 1 USNM), *Cryptolithodes typicus* (2 PC; 1 USNM), *Rhinolithodes wosnessenskii* (1 PC; 2 USNM), *Phyllolithodes papillosus* (4 PC), *Lopholithodes mandtii* (3 PC; 1 USNM), *Paralomis granulosa* (3 USNM), *Paralithodes camtschaticus* (4 USNM), *Paralithodes brevipes* (3 USNM), *Lithodes maja* (2 USNM), and *Lithodes aequispinus* (1 PC; 3 USNM). The number of pleopods used in carrying eggs were then mapped onto the combined phylogeny using MacClade 4.0 (Maddison and Maddison 1992).

RESULTS

Phylogenetic analysis

For DNA sequence data see Chapter 3 (GenBank accession numbers Table 3-2). DNA sequences were combined into one data set, as individually each gene region produced unresolved, but non-conflicting nodes (Chapter 3). Two trees of length 2121 were found (CI=0.57, RI=0.53, RC=0.30, HI=0.43 and G-Fit = -461.13, Fig. 6-1a).

For morphological characters, definitions and states see Chapter 4 (Appendix 4-1 and Figs. 4-2 and 4-3). Four most parsimonious trees of length 411 were found and combined (Fig. 6-1b; CI=0.54, RI= 0.76, RC=0.41, HI=0.46, G-fit=-199.0). As missing characters (symbolized by "?" due to the absence of grasping chelae and abdominal sternites) may influence tree topology (Nixon and Davis 1991), *E. analoga* was removed from the second of two analyses. When *E. analoga* was removed, ten most parsimonious trees of length 391 were found (Fig. 6-1c; CI=0.57, RI=0.77, RC=0.44, HI=0.433, G-Fit=-129.8).

All 2539 characters in the combined analysis were unordered and had equal weight. 1468 DNA characters were constant and 415 variable DNA characters were parsimony uninformative. The number of parsimony informative characters was 656 (170 morphological characters and 486 DNA characters). The most parsimonious trees (which included *Emerita analoga*) had a length of 2561 (Fig. 6-1d).

Total pairwise base differences ranged from 15% (*Pagurus longicarpus* and *Rhinolithodes*) to 2% (*Lithodes maja* and *Lithodes aequispinus*) in the ingroup. Tree length distributions were derived from a sample of 10 000 random trees and g1 skewness values were significant ($p < 0.05$) in both the DNA and morphological data sets, suggesting the presence of significant phylogenetic signal (Hillis 1991, Hillis and Huelsenbeck 1992).

The partition homogeneity test (or ILD test) was performed to evaluate the degree of incongruence between the DNA and morphological data sets. Significant incongruence between morphological characters and the combined DNA data set was detected both with or without *Emerita analoga* in the outgroup ($p = 0.01$).

The likelihood-based Shimodaira-Hasegawa (SH test, 1999) test was performed to test incongruence between the two most parsimonious DNA based trees and the four most parsimonious morphological based trees. Significant differences were observed ($p < 0.05$). However, visual comparison of each node on the individual trees, revealed only one well-supported nodal difference (label 'A' Figs. 1a-c). The SH test was re-performed with the successive removal of these taxa. Tree incongruence was still observed with the individual removal of *Glyptolithodes cristatipes* ($p < 0.05$), *Lopholithodes mandtii* ($p < 0.05$), and *Paralomis granulosa* ($p = 0.038$). However, incongruence was not observed when both *P. granulosa* and *G. cristatipes* ($0.328 < p < 0.712$) were removed, nor when *Paralomis granulosa* and *L. mandtii* were removed ($0.451 < p < 0.837$).

Partitioned Bremer support assesses the relative contribution of individual data sets to the support found in the combined data analysis tree (Baker et al. 1998). Using the combined analysis tree as a constraint, the morphological tree was length 439 (compared to the most parsimonious length of 411) and the DNA tree was length 2122 (compared to the most parsimonious tree length of 2121). The 170 morphological characters contributed to 42.6%, whereas the 486 phylogenetically informative DNA characters contributed to 57.4% of the decay values (Fig. 6-1d). Thus, each informative morphological character represented 0.25%, and each informative DNA character represented 0.12% of the final decay values.

Analysis of McLaughlin and Lemaitre 1997

McLaughlin and Lemaitre (1997) used their original morphological data set to investigate the possibility of repeated evolution of carcinization within the Anomura. Overall, they concluded, using a majority rule concensus of 17 000 best trees, that repeated carcinization within infraorder Anomura did not occur and that the family Lithodidae was basal to family Paguridae. However, my reanalysis of the McLaughlin and Lemaitre (1997) data set suggests different conclusions. Overall, my analyses produced 660,732 trees of length 473, with all 37 characters being parsimony informative. However, bootstrapping of the 50% majority rule consensus tree produced only one well supported clade (bootstrap 66% for *Pylocheles*, *Cheiroplatea*, and *Mixtopagurus*), with all remaining clades having bootstrap values < 50%. This reanalysis suggests little or no phylogenetic resolution can be obtained from McLaughlin and Lemaitre's 1997 data set, and thus conclusions regarding the evolution of carcinization should be treated with caution.

Character mapping of pleopods

Pagurus bernhardus and *Pagurus longicarpus* use three left anterior pleopods (of a possible four left pleopods) to carry eggs. Female lithodids have between four and six pleopods. *Hapalogaster mertensii*, *Hapalogaster dentata*, *Cryptolithodes sitchensis*, and *Cryptolithodes typicus* all possess and use four left pleopods to carry eggs (in agreement with Hart 1965, but see Makarov 1962). *Oedignathus inermis* possesses six pleopods (five left and one right), but only uses four left pleopods to carry eggs. *Lopholithodes mandtii*, *Paralomis granulosa*, *Phyllolithodes papillosus*, *Rhinolithodes wosnessenskii*, *Paralithodes brevipes*, *Paralithodes camtschaticus*, *Lithodes maja*, and *Lithodes aequispinus* each possess and use six pleopods (five left and one right). Overall, this suggests that the ancestral state is the use of 3 left pleopods, and there is an evolutionary progression towards a greater number of symmetrically placed pleopods.

DISCUSSION

DNA sequences (mitochondrial DNA (16S, 12S, COI, COII), nuclear DNA (28S)), and 170 morphological characters were analyzed separately (Figs. 1a, b,c) and then combined (Figs. 1d, e). This combined analysis strongly supports the monophyly of the Lithodidae (bootstrap 100%, decay 34) and the subfamilies Hapalogastrinae (100%, 14) and the Lithodinae (100%, 23; Fig. 6-1d) at this level of taxon sampling (but see Chapter 4). Genera of the family Lithodidae with more than one representative species were also found to be monophyletic including *Hapalogaster* (100%, 30), *Cryptolithodes* (100% , 51), *Lithodes* (78%, 3), and *Paralithodes* (53%, 0). Although monophyly was supported at each taxonomic level, at most two representatives of each genus were analyzed and not all lithodid genera were represented. This is important to note as morphological evidence suggests that subfamily Lithodinae should be redefined to include *Acantholithodes* and *Placetron* (Chapter 4), and the position of *Dermaturus* is unknown. Genera which are not included in this phylogeny are: *Acantholithodes*, *Dermaturus*, *Placetron* (subfamily Hapalogastrinae), *Neolithodes*, and *Sculptolithodes* (subfamily Lithodinae). Overall, my phylogeny agrees with most previous reconstructions of the family Lithodidae (Boas 1880a,b, 1924, Bouvier 1894a,b, 1897, Martin and Abele 1986, Cunningham et al. 1992, Richter and Scholtz 1994, McLaughlin and Lemaitre 1997, Chapter 3).

Although the ILD test revealed significant incongruence, this may not indicate noncombinability. Recently, systematists have been interpreting the ILD test with caution as its statistical properties have not yet been thoroughly explored (Crespi et al. 1998) and significance may indicate a high amount of noise or homoplastic morphological characters (Graham et al. 1998). In early versions of PAUP the partition homogeneity test was called "combinability". However, name changes were implemented after questioning the appropriateness for assessing combinability (Yoder et al. 2001). Although, investigators have continued to test for noncombinability using this method, the test's perceived sensitivity has steadily declined. Originally, Farris recommended $P < 0.05$ as the threshold for determining noncombatibility when applying the ILD test. More recently, investigators have suggested that P-values as low as 0.001 (as found in this study) should not necessarily preclude the combination of different data sets (Sullivan 1996, Cunningham 1997a,b, DeSalle and Brower 1997, Sidall 1997, Davis et al. 1998, Flynn and Nedbal 1998, Messenger and McGuire 1998, Yoder 2001).

Visual comparisons of cladistic groups reveal only one well supported (bootstrap > 70) difference between the separate DNA (label 'A', Fig. 6-1a) and morphological data sets (label 'A', Figs. 1b,c) and the combined data set (label 'A', Fig. 6-1d). *Glyptolithodes cristatipes* and *Lopholithodes mandtii* form a well supported monophyletic clade in the morphological phylogeny (71%, 2; Figs. 1b,c), whereas this clade is not found in either the DNA (Figs. 1a) or the combined analyses (Figs. 1d,e). Instead, *G. cristatipes* and *Paralomis granulosa* form a well supported monophyletic clade in both the DNA analysis (96%, 9; Fig. 6-1a), and in the combined analysis (91%, 9; Fig. 6-1d). However, *L. mandtii*, *G. cristatipes*, and *P. granulosa* form a well supported clade in the DNA analysis (100%, 13; Fig. 6-1a) and the combined analysis (bootstrap (99%, 13; Fig. 6-1d) which is unresolved in the separate morphological analyses (Figs. 1b,c). The SH test (Shimodaira and Hasegawa 1999) was redone with the problematic taxa removed. First, *P. granulosa* was removed, then *P. granulosa* in combination with either *L. mandtii* or *G. cristatipes*. I found that incongruence between data sets was marginally insignificant when *P. granulosa* was removed, and insignificant when *P. granulosa* with either *L.*

mandtii or *G. cristatipes* were removed. Perhaps these topological differences (label 'A,' Figs. 1a-d) confirm morphological continuum of characters that may have lead to unclear taxonomic distinctions between these three genera (Takeda and Ohta 1979). They may also indicate extreme convergence of morphological characters or possible misinterpretations of character states.

At a basal level, the combined analysis indicates that ingroup family Paguridae (represented by genera *Pagurus* and *Labidochirus*) is not monophyletic but instead a basal paraphyletic assemblage to lithodids. Thus, the family Lithodidae are derived pagurids. Morphologists have long suspected this close genealogical tie between the hermit crab family Paguridae and the king crab (or stone crab) family Lithodidae, since the hermit crab's abdomen is modified to coil within a gastropod shell and the asymmetric abdomen possessed by king crabs appears to be a remnant of hermit crab ancestry (Boas 1880a,b, Bouvier 1894a,b). Recent morphological observations (Richter and Scholtz 1994, Chapter 4) and DNA phylogenetic data sets (Cunningham et al. 1992, Chapter 3, Morrison et al. submitted) have corroborated this hypothesis.

However, some modern morphologists using cladistic analysis disagree with this proposal. Martin and Abele (1986) suggest that lithodids are sister taxa to the superfamily Lomoidea and distantly related to the family Paguridae. On the other hand, McLaughlin and Lemaitre (1997, 2000), argue that king crabs are basal to the derived hermit crabs, and suggest that the lithodid crab-like body form gave rise to uncarcinized hermit crabs via calcium loss, habitat change and subsequent morphological adaptations. They suggest Bouvier's hypothesis, that states an evolutionary trajectory from a crab bearing an abdomen that is soft and asymmetrical to a crab bearing a calcified and symmetrical abdomen, should be applied in reverse. They used a majority rule consensus tree of 17,000 most parsimonious trees (the analysis was stopped before all trees were found due to computational limitations, Fig. 6-2a) of 37 morphological characters scored for 59 taxa as evidence. However, re-analysis of this data set, using faster computers and a newer version of PAUP* (4.0b8 vs. 3.1), revealed little or no phylogenetic resolution (Fig. 6-2b). It is important to note that only 37 characters were provided for a taxa set of 59, thus limited cladistic resolution can be expected at best.

More recently, McLaughlin and Lemaitre (2000) used developmental observations from ten species representing eight genera of lithodids, to suggest that pagurids are derived lithodids. They observed that juvenile (megalopa, crab 1, crab 2) and adult hapalogastrinids (e.g. *Placetron* and *Hapalogaster*) possess abdomens that are calcified early (megalopa) and uncalcified later (crab 1 to adult) in development and suggest that this ontogenetic change reflects evolutionary history. However, three lines of evidence suggest that their conclusions are premature. First, Przibram (1907) showed that when hermit crab *Eupagurus* (now *Pagurus*) develops in absence of shells, they produce 'plate outlines' much like *Oedignathus*, *Hapalogaster*, and *Dermaturus* of the subfamily Hapalogastrinae. This suggests that abdominal calcification is a plastic character that is modified with respect to environmental conditions. Second, Harvey (1998) showed that when hermit crab *Clibanarius vittatus* develops in absence of gastropod shells, abdominal asymmetry is substantially reduced. This suggests that abdominal asymmetry is also a heavily influenced by environmental conditions. Finally, all crustacean megalopal stages have calcified abdomens throughout their development (for example: porcellanids, e.g. Gonor and Gonor 1973; pagurids, e.g. McLaughlin et al. 1992; galatheids, e.g. Gore 1979; brachyurans, e.g. Taishaku and Konishi 1995; Dromiidae, e.g. Tan et al. 1986; Anomurans, e.g. Hart 1937, Shenoy 1967; Peneids, Dobkin 1961). This suggests that megalopal calcification is an ancestral character, and all adults bearing non-calcified abdomens must go through a reduction in calcification during early crab stages. Hence, reduction in calcification during early ontogeny of lithodids may be a remnant of their pagurid ancestry.

Hermit crabs, such as *Pagurus bernhardus* and *P. longicarpus*, that protect their soft abdomens by wearing gastropod shells release their eggs onto three of four left pleopods. The hapalogastrinid genus, *Oedignathus* has a soft abdomen and releases eggs onto four of five left pleopods. A basal member of the subfamily Lithodinae, *Cryptolithodes*, also releases eggs onto all four of its left pleopods, compared to the remaining subfamily Lithodinae which release eggs onto all six (five left and one right) pleopods (up to 821 eggs found on *Paralithodes californiensis'* first pleopod, Rypien in litt.). This may suggest that gastropod shells do pose a constraining selective pressure on reproduction and could be a strong evolutionary impetus for habitat independence. Mapping this character onto the phylogeny suggests that few egg-bearing appendages is the ancestral state (Fig. 6-3), and may have had fitness consequences (Childress 1972) which forced the urlithodid out of its shell. However, further experimental work investigating the fitness consequences of shell-bearing is needed.

CONCLUSIONS

Combined analysis of partial sequences of five different genes (mtDNA COI, COII, 16S, 12S, and nrDNA 28S) and 170 morphological characters has added support to most but not all morphological theories concerning lithodid evolution and their relationships to pagurids. Based on the taxa sampled here, the Lithodidae are considered monophyletic, as are the subfamilies Lithodinae and Hapalogastrinae, and genera with more than one species sequenced (*Cryptolithodes*, *Hapalogaster*, *Lithodes*, and *Paralithodes*). The genus *Pagurus* is found to be paraphyletic to the Lithodidae, suggesting that lithodids are derived hermit crabs. Although McLaughlin and Lemaitre (1997) suggest that hermit crabs are derived lithodids, reanalysis of their data shows limited cladistic resolution in defense of their stance. Use of phylogenic inference and character mapping suggests that limitations of pleopod use may act as a selective pressure towards carcinization.

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Table 6-1: Anomuran Taxonomy **

Phylum Arthropoda
Sub-phylum Crustacea Pennant, 1777
Class Malacostraca Latreille, 1806
Order Decapoda Latreille, 1803

Infraorder Anomura (non-true crabs) Boas, 1880

Superfamily Galatheoidea Samouelle, 1819
- Family Aeglidae Dana, 1852
- Family Chirostylidae Ortmann, 1892
- Family Galatheidae Samouelle, 1819
- Family Porcellanidae Haworth, 1825

Superfamily Hippoidea Latreille, 1825
- Family Albuneidae Stimpson, 1858
- Family Hippidae Latreille, 1825
  - **Emerita analoga*

Superfamily Lomoidea Bouvier, 1895
- Family Lomidae Bouvier, 1895

Superfamily Paguroidea Latreille, 1803 (=superfamily of hermit crabs)
- +Family Coenobitidae Dana, 1851
- +Family Diogenidae Ortmann, 1892
  - **Clibanarius vittatus*
- +Family Lithodidae Samouelle, 1819
  - Subfamily Hapalogastrinae Ortmann, 1901
    - **Oedignathus inermis*
    - **Hapalogaster mertensii*
    - **Hapalogaster dentata*
    - *Dermaturus*
    - *Placetron*
    - *Acantholithodes*
  - Subfamily Lithodinae Ortmann, 1901
    - *Acantholithus* (synonomous with *Paralomis*?, Sakai 1976)
    - **Cryptolithodes sitchensis*
    - **Cryptolithodes typicus*
    - **Glyptolithodes cristatipes*
    - **Lithodes aequispinus*
    - **Lithodes maja*
    - **Lopholithodes mandtii*
    - *Neolithodes*
    - **Paralithodes brevipes*

        ***Paralithodes camtschaticus*
        ***Paralomis granulosa*
        ***Phyllolithodes papillosus*
        ***Rhinolithodes wosnessenskii*
        Sculptolithodes
+Family Paguridae Latreille, 1803
    **Labidochirus splendescens*
    **Pagurus bernhardus*
    **Pagurus longicarpus*
+Family Parapaguridae Smith, 1882
Family Pylochelidae (= Pomatochelidae Miers, 1879)

*=used in this analysis
+=asymmetrical hermit crabs
**= as per Sakai 1976, McLaughlin 1983 a, b, Martin and Abele 1986, Schram 1986, Richter and Scholtz 1994.

FIGURE LEGENDS

Figure 6-1: Phylogenetic trees using outgroup taxa *Emerita analoga* and *Clibanarius vittatus*. Bootstrap values (1000 replicates) are indicated above branches and decay indices are shown in parentheses. SP= superfamily Paguroidea. FP= family Paguridae. FL= family Lithodidae, SH= subfamily Hapalogastrinae, SL= subfamily Lithodinae. A= phylogenetic incongruence when comparing individual phylogenies.

6.1a: Phylogenetic tree of the DNA data set. The tree shown is a consensus of two most parsimonious trees of length 2121. CI = 0.59. RI = 0.421. RC = 0.25. HI = 0.41. G-Fit = -359.6.

6.1b: Phylogenetic tree obtained using only the morphological data. Outgroup taxa are *Emerita analoga* (superfamily Hippoidea) and *Clibanarius vittatus* (superfamily Paguroidea. family Diogenidae). Four most parsimonious trees of length 411 were found and the combined tree is shown. CI= 540, RI= 0.76, RC= 0.41. HI= 0.46. G-fit= -199.0.

6.1c: Phylogenetic tree obtained using only the morphological data and without *Emerita analoga* in the outgroup. Outgroup taxon is *Clibanarius vittatus* (superfamily Paguroidea, family Diogenidae). Ten most parsimonious trees of length 391 were found and combined. CI= 0.57. RI= 0.77. RC= 0.44. HI= 0.433. G-Fit= -129.8.

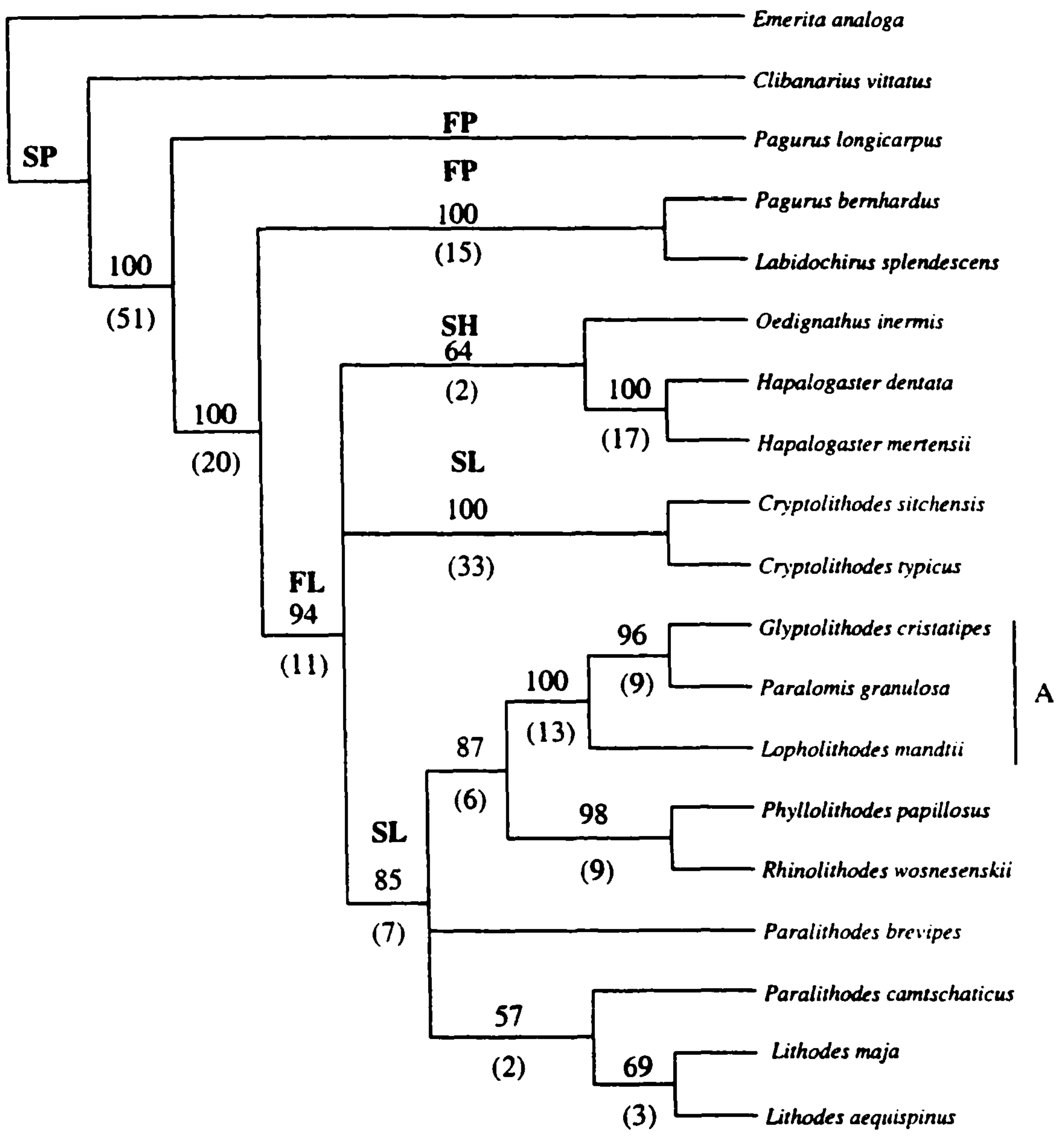
6.1d: Phylogenetic tree obtained by combining morphological and DNA analyses. The single most parsimonious tree of length 2561. CI= 0.57, RI= 0.53. RC= 0.30, HI= 0.43 and G-Fit = -461.13 is shown. Minimal possible length = 1481, maximum = 3799. Partitioned Bremer support decay indexes are shown below the branches (full decay/ partitioned morphological decay value/partitioned molecular decay value).

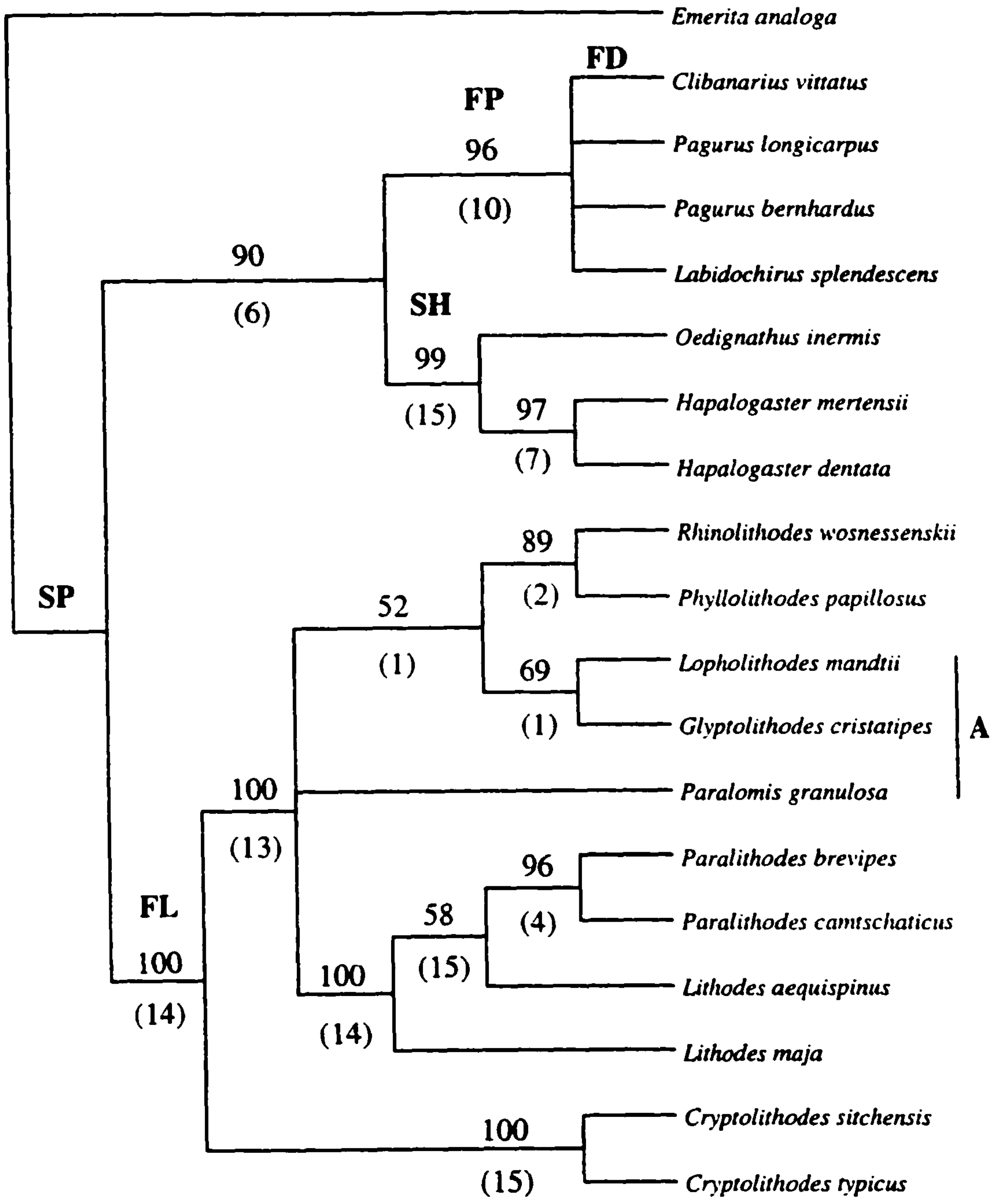
6-1e: Phylogram of the total evidence tree, numbers above branches indicate branch lengths.

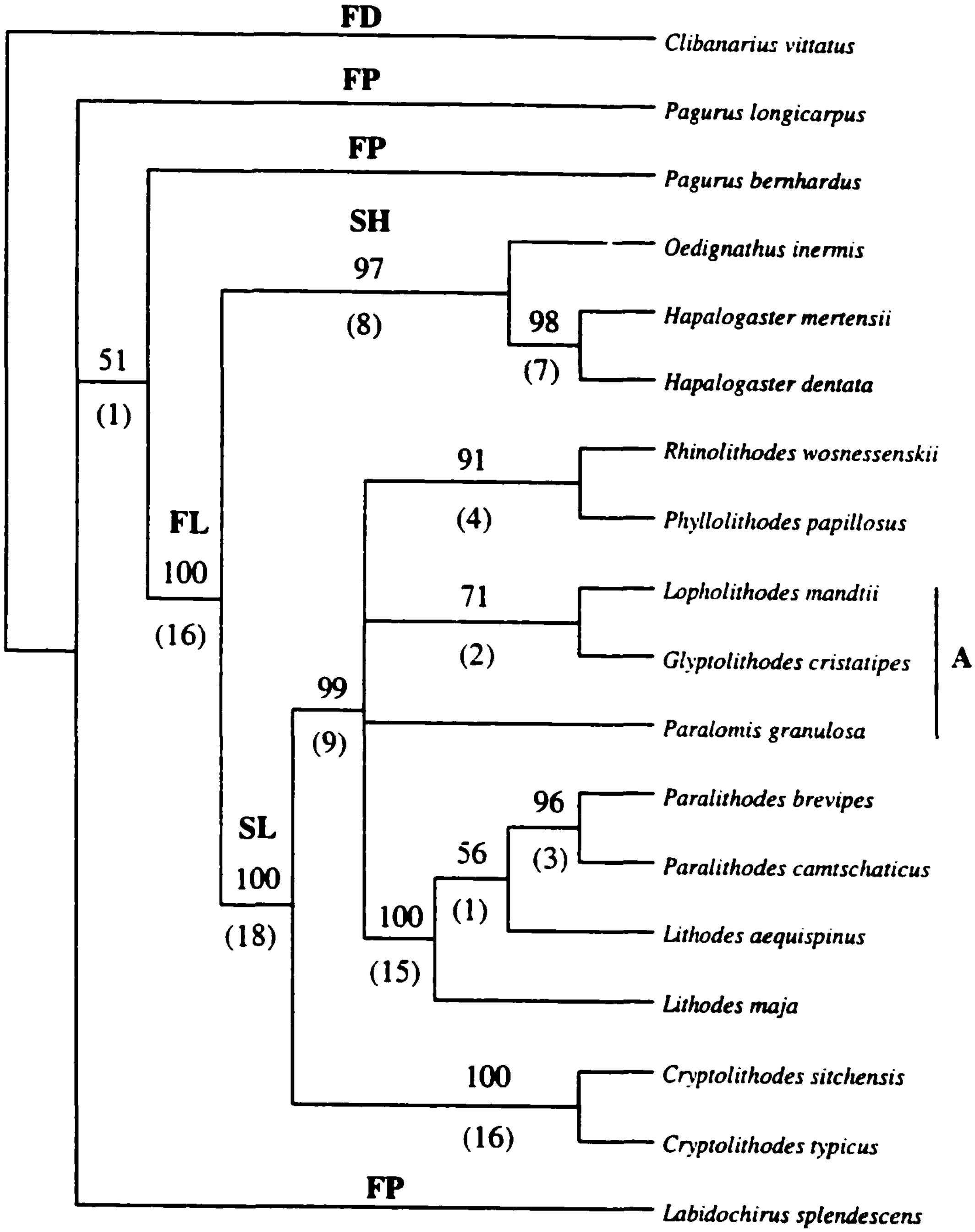
Figure 6-2a: McLaughlin and Lemaitre's (1997) majority rule consensus tree.

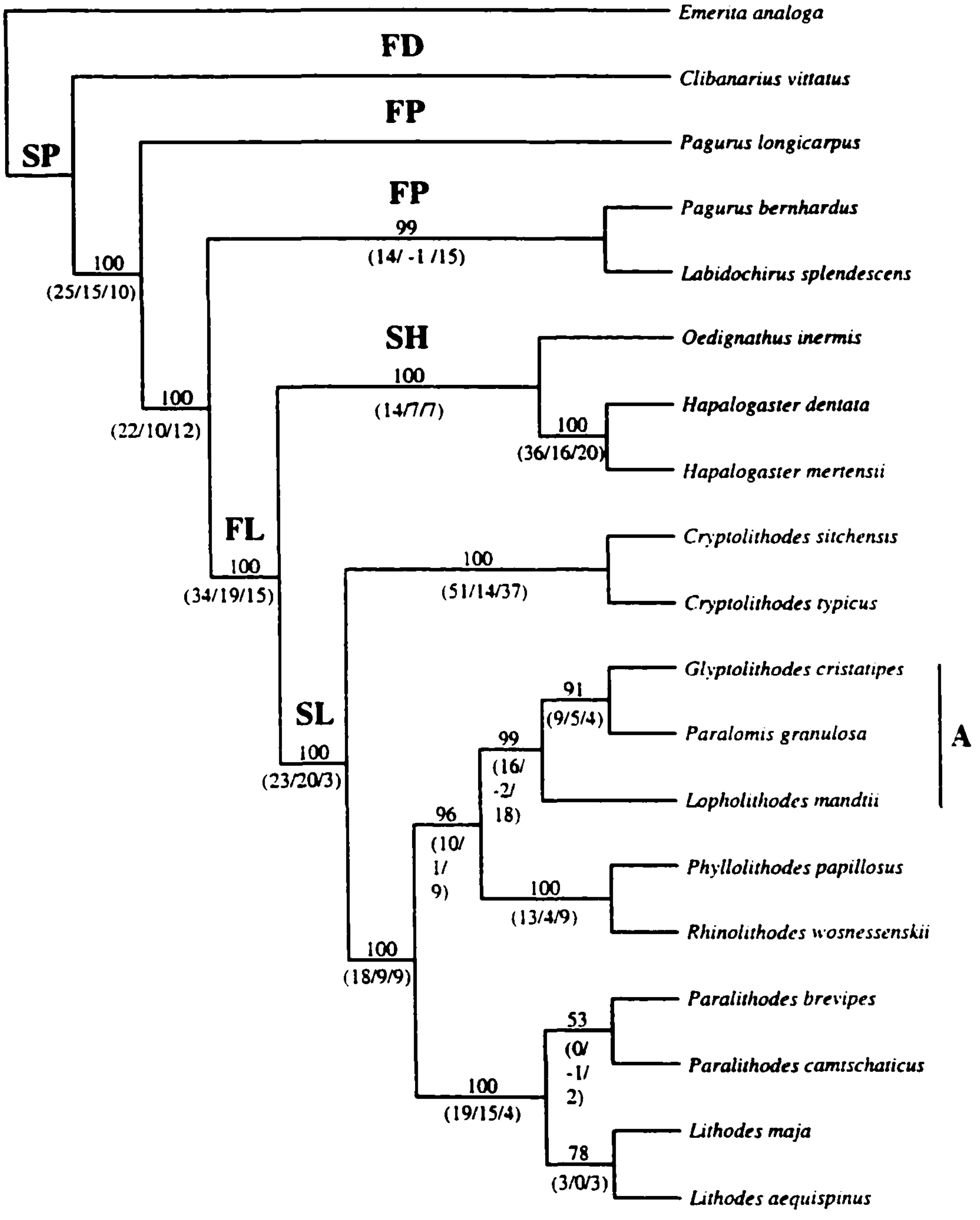
6-2b: Parsimony tree (bootstrap consensus) based on reanalysis of McLaughlin and Lemaitre's (1997) morphological data. P= family Paguridae, L= family Lithodidae

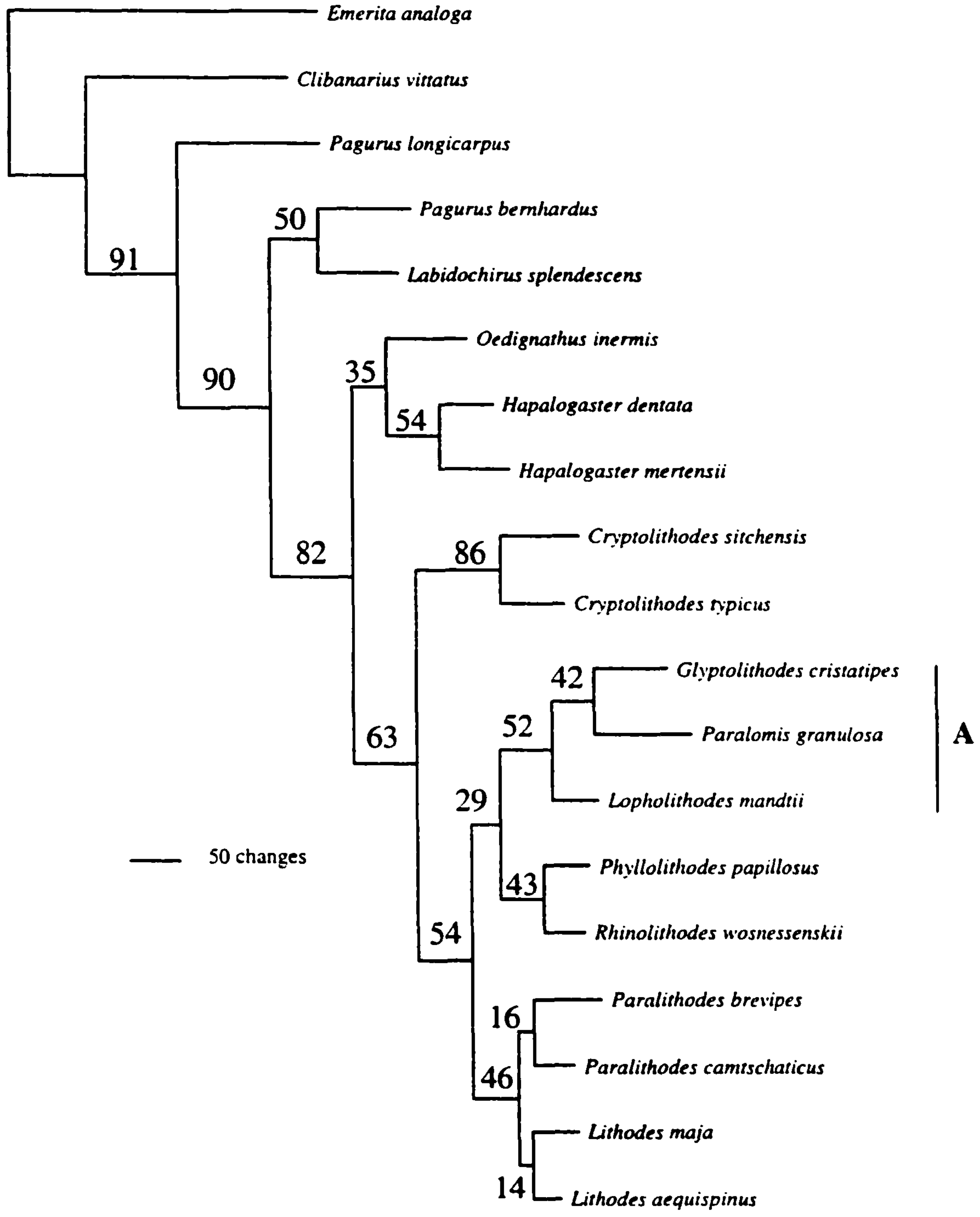
Figure 6-3: Phylogenetic tree based on the combined phylogeny (fig. 6.1d). Numbers at the basal nodes indicate the number of pleopods each lithodid taxon uses to carry eggs.


Emerita analoga
Clibanarius vittatus
SP
FP
Pagurus longicarpus
FP
100
(15)
Pagurus bernhardus
Labidochirus splendescens
100
(51)
SH
64
(2)
Oedignathus inermis
100
(17)
Hapalogaster dentata
Hapalogaster mertensii
100
(20)
SL
100
(33)
Cryptolithodes sitchensis
Cryptolithodes typicus
FL
94
(11)
96
(9)
Glyptolithodes cristatipes
Paralomis granulosa
A
100
(13)
Lopholithodes mandtii
87
(6)
98
(9)
Phyllolithodes papillosus
Rhinolithodes wosnesenskii
SL
85
(7)
Paralithodes brevipes
57
(2)
Paralithodes camtschaticus
69
(3)
Lithodes maja
Lithodes aequispinus


Emerita analoga
FD
Clibanarius vittatus
Pagurus longicarpus
Pagurus bernhardus
Labidochirus splendescens
FP
96
(10)
90
(6)
SH
99
(15)
Oedignathus inermis
97
(7)
Hapalogaster mertensii
Hapalogaster dentata
89
(2)
Rhinolithodes wosnessenskii
Phyllolithodes papillosus
52
(1)
69
(1)
Lopholithodes mandtii
Glyptolithodes cristatipes
A
Paralomis granulosa
SP
100
(13)
96
(4)
Paralithodes brevipes
Paralithodes camtschaticus
58
(15)
Lithodes aequispinus
FL
100
(14)
100
(14)
Lithodes maja
100
(15)
Cryptolithodes sitchensis
Cryptolithodes typicus


FD
Clibanarius vittatus
FP
Pagurus longicarpus
FP
Pagurus bernhardus
SH
97
(8)
Oedignathus inermis
98
(7)
Hapalogaster mertensii
Hapalogaster dentata
51
(1)
91
(4)
Rhinolithodes wosnessenskii
Phyllolithodes papillosus
FL
100
(16)
71
(2)
Lopholithodes mandtii
Glyptolithodes cristatipes
A
99
(9)
Paralomis granulosa
96
(3)
Paralithodes brevipes
SL
100
(18)
56
(1)
Paralithodes camtschaticus
100
(15)
Lithodes aequispinus
Lithodes maja
100
(16)
Cryptolithodes sitchensis
Cryptolithodes typicus
FP
Labidochirus splendescens


Emerita analoga
FD
Clibanarius vittatus
FP
Pagurus longicarpus
SP
FP
99
(14/-1/15)
Pagurus bernhardus
Labidochirus splendescens
100
(25/15/10)
SH
Oedignathus inermis
100
(14/7/7)
Hapalogaster dentata
100
(22/10/12)
100
(36/16/20)
Hapalogaster mertensii
FL
100
(34/19/15)
Cryptolithodes sitchensis
100
(51/14/37)
Cryptolithodes typicus
Glyptolithodes cristatipes
91
(9/5/4)
Paralomis granulosa
A
SL
99
(16/-2/18)
Lopholithodes mandtii
100
(23/20/3)
96
(10/1/9)
Phyllolithodes papillosus
100
(13/4/9)
Rhinolithodes wosnessenskii
100
(18/9/9)
Paralithodes brevipes
53
(0/-1/2)
Paralithodes camtschaticus
100
(19/15/4)
Lithodes maja
78
(3/0/3)
Lithodes aequispinus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Clibanarius vittatus
Pagurus longicarpus
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Pagurus bernhardus
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Labidochirus splendescens
Oedignathus inermis
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Hapalogaster dentata
Hapalogaster mertensii
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Cryptolithodes sitchensis
Cryptolithodes typicus
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Glyptolithodes cristatipes
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Paralomis granulosa
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Lopholithodes mandtii
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Phyllolithodes papillosus
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Rhinolithodes wosnessenskii
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Paralithodes brevipes
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Paralithodes camtschaticus
Lithodes maja
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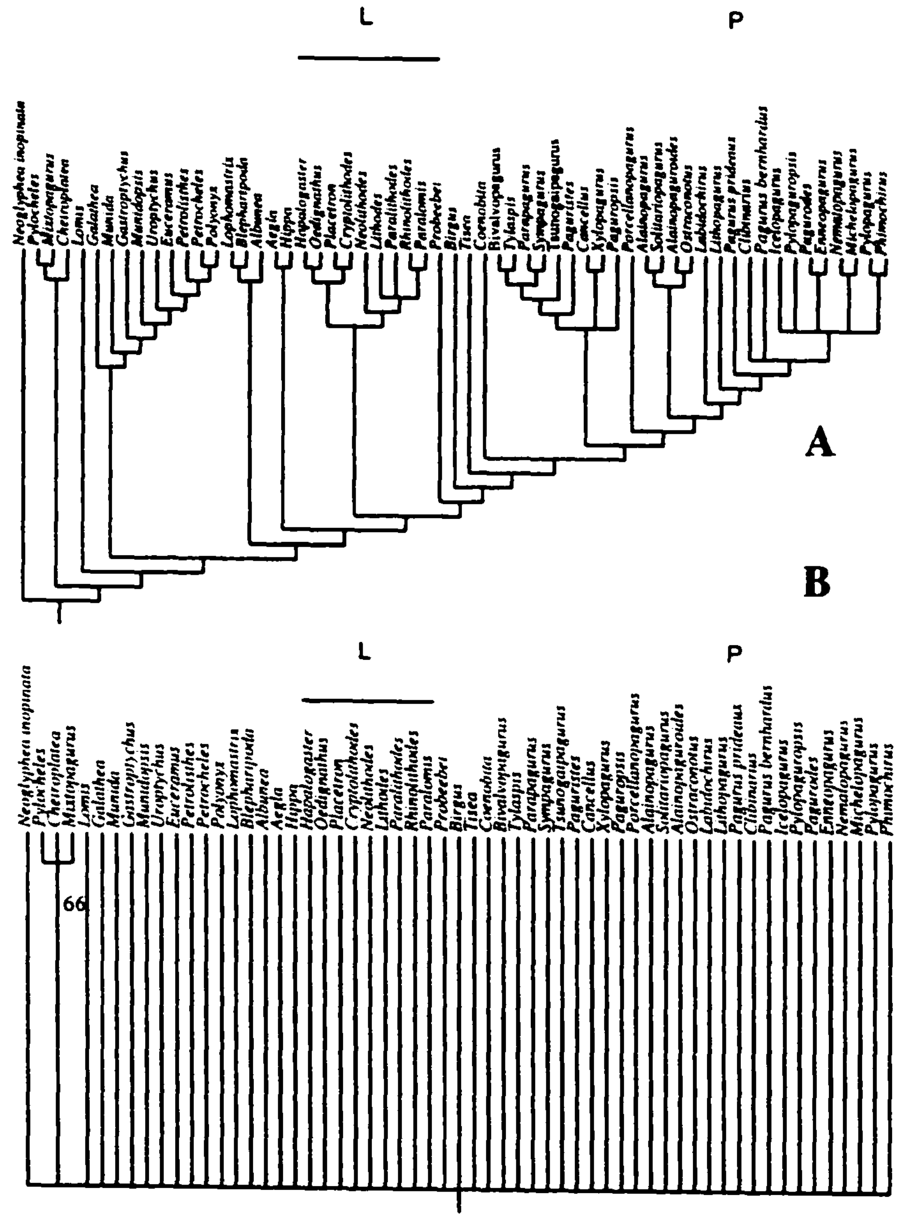
Lithodes aequispinus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Petrolisthes
Petrocheles
Polyonyx
Lophomastix
Blepharipoda
Albunea
Aegla
Hippa
Hapalogaster
Oedignathus
Placetron
Cryptolithodes
Neolithodes
Lithodes
Paralithodes
Rhinolithodes
Paralomis
Probeebei
Birgus
Tisea
Coenobita
Bivalvopagurus
Tylaspis
Parapagurus
Sympagurus
Tsunogaipagurus
Paguristes
Cancellus
Xylopagurus
Paguropsis
Porcellanopagurus
Alainopagurus
Solitariopagurus
Alainopaguroides
Ostraconotus
Labidochirus
Lithopagurus
Pagurus prideaux
Clibanarius
Pagurus bernhardus
Icelopagurus
Pylopaguropsis
Paguroides
Enneopagurus
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Enneopagurus
Nematopagurus
Michelopagurus
Pylopagurus
Phimochirus
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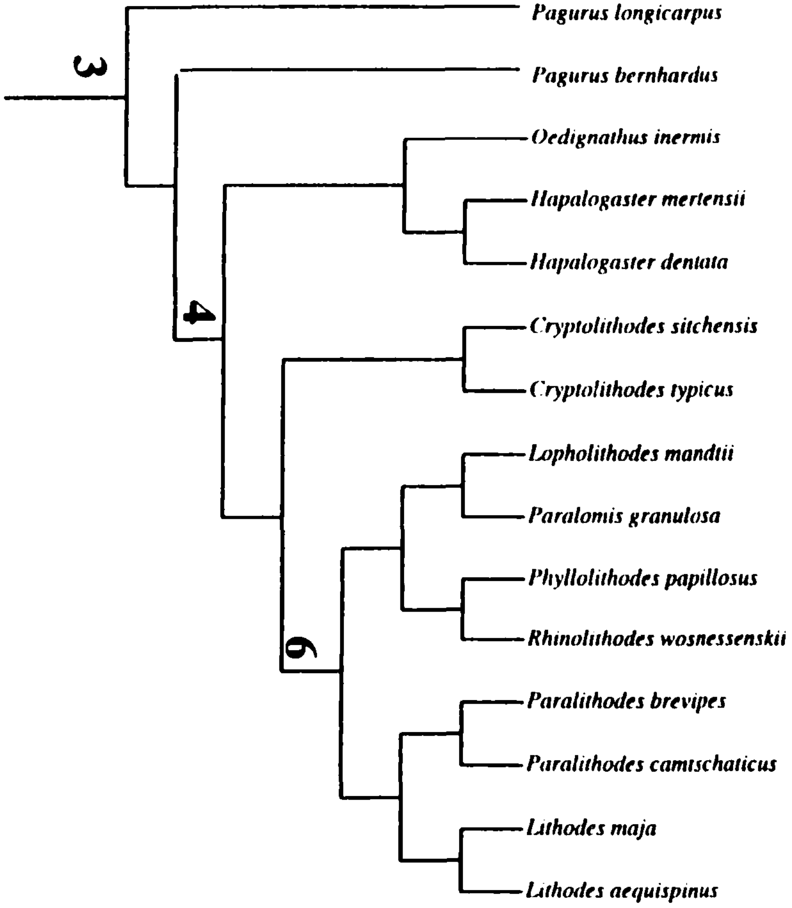
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Pagurus longicarpus
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Cryptolithodes typicus
Lopholithodes mandtii
Paralomis granulosa
Phyllolithodes papillosus
Rhinolithodes wosnessenskii
Paralithodes brevipes
Paralithodes camtschaticus
Lithodes maja
Lithodes aequispinus

CHAPTER 7

Thesis synopsis

This collection of scientific papers attempts to address three main objectives. First, it provides an overview of what is known about a diverse, charismatic, and speciose family Lithodidae (Crustacea, Anomura, Paguroidea). Second, it uses molecular and morphologically-based data to establish a phylogenetically robust hypothesis concerning genus level relationships using molecular and morphological data. Finally, through character mapping, it suggests a plausible evolutionary history, and compares these findings to other, well-established hypotheses.

Currently the family Lithodidae (Crustacea, Anomura, Paguroidea) is divided into subfamilies Hapalogastrinae and Lithodinae. The subfamily Hapalogastrinae consists of physically small species and has few representative taxa. These two features may be linked to a character rarely found in the phylum Arthropoda– the possession of an uncalcified abdomen. Presently, there are six genera and nine species of the subfamily Hapalogastrinae, whereas members of the subfamily Lithodinae, are large, fully calcified, and more speciose than the former subfamily. Lithodinids are represented by 9 or 10 genera (depending whether or not *Acantholithus* is equivalent to *Paralomis* as per Sakai 1976), with 96 species (Chapter 2). Perhaps the abyssal nature of the subfamily Lithodinae (depth averaged from Table 2-1 minimum and maximum depths: *Neolithodes* = 1570 m; *Lithodes* = 532 m; *Paralomis* = 821m; Table 2-1), along with a large protective exoskeleton (CW $\leq$ 300 mm, Table 2-4), group social dynamics, migratory abilities, large broods (up to 280 000 eggs, Matsuura et al. 1972), expansive larval dispersal capabilities (Table 2-5) and opportunistic foraging strategies, allowed them to spread into extreme habitats that offer little environmental protection from overhead predators (Table 2-6).

Climatic changes and geographic rearrangements during the past 20 million years apparently allowed for lithodid radiation from the northeast Pacific, through to the Atlantic, Arctic, and Indian Oceans (Makarov 1962, Vermeij 1991, Chapter 2). Interestingly, the radiation of the Lithodidae (13-25 mya Cunningham et al. 1992) took place in the context of the radiation of kelp (Laminariales) in the north Pacific 16-30 mya (Estes and Steinberg 1988, Saunders and Druehl 1992). *Oedignathus inermis*— which belongs to one of the two most basal lithodid genera and is certainly the least carcinized lithodid — is usually found in the canopy cover and under hold-fasts of the kelp *Hedophyllum sessile* (Zaklan pers. obs.). This is consistent with the hypothesis that kelp cover may have helped the ancestral lithodid compensate for the lack of protection afforded by a gastropod shell. The dramatic increase in size found within the genera *Paralithodes* and *Lithodes* was associated with movement to deeper water, beyond the protection of the kelp canopy cover.

Only weak evolutionary hypotheses can be based on the limited knowledge of fossil lithodids. At present time, only one fossil species has been discovered, *Paralomis debodeorum* (Feldmann 1998). However, information gleaned from this fossil conforms with projected evolutionary hypotheses proposed by other types of evidence. The age of the specimen (10 mya), fits well within the molecular estimations of lithodid origins of 13-25 mya (Cunningham et al. 1992). However, although a relatively old fossil in respect to estimated divergence time of the family, *P. debodeorum* possesses an apomorphic morphology, including fully calcified abdomen, no medial nodules, and extensive plate fusion. These characters, according to Bouvier (1897) and recent phylogenetic hypotheses (Chapters 3, 4 and 6), are considered highly derived. This fossil finding may lend credence to a punctuated radiation event (Gould and Eldredge 1977) at the beginning of their evolutionary history. *P. debodeorum* was uncovered in New Zealand, a great distance from the theoretical place of lithodid origin (northeast Pacific, Makarov 1962, Chapter 2), suggesting that members of family Lithodidae crossed the Pacific in a relatively short (3-12 million years) window of time. However, some lithodid species, such as *Paralithodes camtschaticus* have been known to migrate up to 13 km/day as adults (Marukawa 1933), and although not presently documented, zoea and glaucothoe may use currents to passively disperse into new niches. Thus, it is plausible that this vast journey has occurred during this potentially small (as little as 3 million years) time frame.

A literature review (Chapter 2) suggests an overall scarcity of information concerning those lithodid species that have limited economic importance. No single taxonomic key differentiating all lithodids is available, but good keys emphasizing the differences between lithodid genera are currently accessible (Table 2-3). Investigations into evolutionary relationships are just beginning at the genus level (Figs. 3-1, 4-4 to 4-7, Figs. 6-1a to 6-1e), and species level relationships remain very poorly understood. This is especially the case in the more speciose genera such as *Paralomis* (51 species), *Neolithodes* (10 species) and *Lithodes* (17 species: Table 2-1) where often only the type specimen is known (Table 2-4). Although there are presently 105 lithodid species, only 95 representative species of the entire family were known recently (Dawson 1989), suggesting that species numbers will keep expanding as we delve into the unexplored realms of our oceans. Knowledge of life history traits remains wanting, including such important ecological information as age of first reproduction (Table 2-5). Although predators, such as fish, are thought to be an important selective pressure, limited information is available on the specifics of these relationships, including the extent of population damage they incur and whether behavioral or morphological adaptations act as protective measures against these overhead predators. In general lithodids are thought to be opportunistic foragers but only a cursory view of lithodid prey types is currently available (Table 2-6). Lithodids are host to several damaging parasites including liparid fish, *Careproctus* spp., the rhizocephalan, *Briarosaccus callosus*, microsporidans producing "cottage cheese" disease, and brood parasites (nemerteans), – each of which is a source of mortality (Table 2-7).

Overall, family Lithodidae is a large and diverse group of poorly understood animals. A fundamental characteristic is the conspicuous abdominal asymmetry in females. Although, the general rule is left lateral plates of somites 3-5 are distinctly larger than the opposing right plates resulting in a medial line of symmetry directed to the right, reversals of asymmetry have been observed (Campodonico 1978, Dawson and Yaldwyn 1985, Chapter 5). Lithodids possess complex life-history patterns and live in environments that tend to be inhospitable and inaccessible to biologists. Behavior such as podding (Powell and Nickerson 1965, Dew 1990), female preference, sperm limitation (e.g. Paul and Paul 1997, Paul and Paul 2001), and slow growth rates (Paul 1992, Lovrich 1997) are important keys for fisheries management tools, as well as biodiversity estimates. Many species with high morphological similarity are only known from holotypes or a single gender, thus named species may represent natural intra-specific variation or may be indicative of the taxonomic infancy of this family. This is not a particularly unusual scenario, as there is most probably a serious underestimation of oceanic biological diversity (Miya and Nishida 1997, Etter et al. 1999). However, due to their abyssal life-styles, discerning valid species from variants that are merely natural morphological extremes is often a difficult task. In this age of molecular systematics and increased taxonomic interest, future genetic analysis may aid in the basic goals of understanding species numbers, diversity, distributions, and evolutionary history and trajectories of lithodids.

Phylogenetic inference

The Lithodidae are only one of several groups of hermit crabs that have reduced or lost dependence on gastropod shells. Each of these lineages has shown varying degrees of carcinization, including a broad carapace and a relatively smaller abdomen than most hermit crabs (Borradaile 1916; Harms 1932; Wolff 1961; Reese 1968). Of these hermit crab descendants, the Lithodidae are by far the most crab-like, with complete carcinization— characterized by symmetric abdomens (excluding pleopods) and fully articulated abdominal plates—having originated at least twice in the group (Fig. 3-2a).

The molecular phylogeny (based on partial sequences of mtDNA – COI, COII, 12S, 16S, and nuclear DNA 28S; sequenced for 15 lithodids, Chapter 3) suggests that two basal genera within the Lithodidae (*Oedignathus*, and *Hapalogaster*) share characteristics that help to reconstruct the circumstances of the loss of dependence on gastropod shells in the ancestral lithodid. Both genera are small, intertidal, and currently restricted to the north Pacific Ocean (Figure 2b-d).

A morphological data set was compiled comprising 170 characters, of which a large majority are newly defined (Chapter 4). Twenty-nine lithodid species were characterized and cladistic analysis added rigorous support to several generally accepted views of morphological evolution within Lithodidae. This included familial monophyly (also supported by the molecular tree, and the combined analysis). However, only the morphological data (which includes the only data for members of the subfamily Hapalogastrinae in question) suggests paraphyly of the subfamily Hapalogastrinae and thus the reassignment of *Placetron wosnessenskii* and *Acantholithodes hispidus* to the subfamily Lithodinae. The subfamilial placement of *Dermaturus mandtii* remains unclear, thus should remain in the subfamily Hapalogastrinae. The genera *Cryptolithodes*, *Hapalogaster*, and *Lopholithodes* were monophyletic, whereas the more speciose but sparsely sampled genera were either paraphyletic (*Lithodes*), polyphyletic (*Paralithodes*), or relationships remained unresolved (*Paralomis*), regardless of data origin. Based on morphological data I suggest the reassignment of *Paralithodes rathbuni* and *Paralithodes californiensis* to genus *Lithodes*, thus allowing both genera to retain monophyletic status (Figure 7-1).

Three general approaches may be taken when analyzing data sets with multiple components (here the five partially sequenced genes and 170 morphological characters): always combine data sets, always keep data sets separate then combine via consensus trees, or combine only non-contradictory data sets (reviewed in Swofford, 1991, de Queiroz et al., 1995, Miyamoto and Fitch, 1995, Huelsenbeck et al., 1996). As there was a large degree of concordance between individual data sets and combined data sets, non-contradictory data sets were combined and used to investigate the lithodid evolutionary hypothesis proposed by McLaughlin and Lemaitre (1997). Although they suggest hermit crabs are derived lithodids, my data concur with early morphologists claim that lithodids are derived hermit crabs. I also use phylogenic inference and character mapping to suggest that limitations of pleopod use may act as a selection pressure towards carcinization.

Molecular (Chapter 3), morphological (Chapter 4) and the total evidence phylogenetic analyses (Chapter 6) suggest that Bouvier (1894, 1897) was correct in arguing that the range in extent of carcinization of lithodids reflects a gradual transition from the soft, asymmetric abdomens of hermit crabs to symmetrical abdomens with fully articulated abdominal plates (Fig. 3-2a). This observed progression— in addition to the phylogenetic placement of the Lithodidae within several groups of hermit crabs —strongly supports Bouvier's theory that the lithodids are descended from hermit crab ancestors.

We know relatively little about the phylogenetic relationships of many living things. The crabs (Anomura and Brachyura) are no exception (e.g. Schram 1986). As phylogenetic trees are being produced at a faster rate, an increase breadth of taxa is being investigated. These include taxa of generalized interest to evolutionary biologists, such as presented here, as we finally begin to build large phylogenetic databases based upon morphological, molecular, and combined analyses.

Some suggestions for future investigation:

During a thesis, questions emerge which, due to time constraints, are inevitably left on the back burner to be picked up in another life time. Thus, I would like to leave a few thoughts for future investigators. First, I have spent many hours observing *Lopholithodes mandtii* nocturnal and diurnal movements in the lab. Overall, movement seems to be confined to nocturnal wanderings, they often possess specified home territories in the protection of crevices, and I have never observed them in social aggregations. However, is this true in their natural habitat? My diving observations merely suggest they are solitary individuals, cryptic inhabitants of cliff faces during the day; however, no nocturnal field observations were made.

Second, I think investigation into the molting of *Cryptolithodes* would prove to be a wonderful observational experience. This genus is fondly known as the butterfly, turtle or umbrella crab, as its carapace is winglike as it spreads over the pereopods covering the entire body much like an umbrella does on a rainy day. It is also, by far, the smallest member of the subfamily Lithodinae (Table 1-4). Observing the backward progression through the ecdysal plate and the subsequent extension of its new carapace may provide some insight into possible size constraints.

Third, I have observed pairing of *Oedignathus inermis* for only specific parts of the year (August, in Barkley Sound, Canada). Are these paired assemblages mates, and how long do they stay together? How are mates chosen? Are these choices body size dependent, territory dependent, and/or proximity dependent? Is there competitive exclusion for mates or is a serial monogamy observed in some of the older, and potentially larger males?

Fourth, are reproductive constraints truly a selective pressure in the evolution of carcinization within family Lithodidae? I think this can be investigated from at least two different angles. The first through experimental manipulation of hermit crabs during egg eclosion. I would suggest observing the use of pleopods with and without the potential constraint of a confining home. It is possible that the general observation that they use only three of their pleopods to hold eggs, may be related to the narrow confinement of the spiraling when the gastropod shell is removed. Another potential investigative angle is to compare abdominal carrying capacity of the egg mass size between lithodids and other crabs, through observation. It is possible that egg mass is limited by the construction (i.e. lack of calcification and plate fusion) of the lithodid abdomen, and thus may be a selective pressure towards symmetry and plate reduction. Most crabs (i.e. Brachyura) have a few rows of plates which are fully calcified and exist as single units across the lateral plane. However, lithodid abdomens are not as simple in their construction, as abdomens range dramatically, from uncalcified to fully calcified. For example, they can be uncalcified (e.g. *Oedignathus inermis*), partially calcified (e.g. *Placetron wosnessenskii*), possess medial nodules instead of plates (e.g. *Lithodes* and *Paralithodes*, and *Neolithodes*), have partial fusion of marginal and lateral plates (*Paralomis*, *Lopholithodes*, *Glyptolithodes*, *Rhinolithodes*, *Phyllolithodes*), or full fusion of marginal and lateral plates (*Cryptolithodes*) can exist.

Overall, systematics provide a strong framework that biologists can use to understand evolutionary relationships, ensure taxonomic groups are clades, and to map characters so as to understand character evolution as well as predict possible characteristics that are presently unknown. In this thesis I present a genus-level phylogeny of the family Lithodidae and suggest this information be used for three broad-based purposes. First, phylogenies may be used in a predictive manner. Mapping characters onto the proposed lithodid phylogeny may allow fishery biologists to predict important reproductive features that can be used for future management purposes. Second, I have presented an example of macroevolutionary transitional changes within one superfamily. These changes extend from members of the family Paguridae that posses small, soft, asymmetrical abdomens, to the members of the king crab subfamily Hapalogastrinae that possess small, partially calcified, asymmetrical abdomens, and to the members of the most derived king crab subfamily Lithodinae that possess calcified, asymmetrical abdomens. Third, I have used these phylogenies to suggest that two taxa, *Placetron wosnessenskii* and *Acantholithodes hispidus* should be reassigned to the subfamily Lithodinae as they form a clade with this taxon.

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Table 7-1. Proposed taxonomy for members of family Lithodidae.

Phylum Arthropoda
Sub-phylum Crustacea Pennant, 1777
Class Malacostraca Latreille, 1806
Order Decapoda Latreille, 1803
Infraorder Anomura Boas, 1880
Superfamily Paguroidea Latreille, 1803

Family Lithodidae Samouelle, 1819
- Subfamily Hapalogastrinae Ortmann, 1901
  - *Oedignathus inermis*
  - *Hapalogaster mertensii*
  - *Hapalogaster dentata*
  - *Hapalogaster grebnitzkii*
  - *Hapalogaster cavicauda*
  - *Dermaturus mandtii*

- Subfamily Lithodinae Ortmann, 1901
  - **Acantholithodes hispidus* (presently in subfamily Hapalogastrinae)
  - *Acantholithus hystrix*
  - *Cryptolithodes sitchensis*
  - *Cryptolithodes typicus*
  - *Glyptolithodes cristatipes*
  - *Lithodes aequispinus*
  - *Lithodes couesi*
  - *Lithodes longispina*
  - *Lithodes maja*
  - **Lithodes rathbuni* Benedict, 1894 (presently *Paralithodes*)
  - **Lithodes californiensis* Benedict, 1894 (presently *Paralithodes*)

Lopholithodes mandtii

Lopholithodes foraminatus

Neolithodes grimaldii

Paralithodes brevipes

Paralithodes camtschaticus

Paralomis birsteini

Paralomis granulosa

Paralomis verrilli

Paralomis multispina

Placetron wosnessenskii (presently in subfamily Hapalogastrinae)

Phyllolithodes papillosus

Rhinolithodes wosnessenskii

Sculptolithodes derjungini

* suggested taxonomic shifts