HERMIT CRAB PHYLOGENY: A REAPPRAISAL AND ITS "FALL-OUT"

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ABSTRACT

The hypothesis of monophyly in Paguroidea and the relationship of this superfamily to the other three superfamilies of Anomura have been reassessed using current cladistic methods and computer generated analysis. In the analysis, 79 external morphological characters were examined for an in-group consisting of the seven paguroid families, Pylochelidae, Coenobitidae, Diogenidae, Pylojacquesidae, Paguridae, Parapaguridae, and Lithodidae (divided into the subfamilies Lithodinae and Hapalogastrinae), three hippoid families, Blepharipodidae, Albuneidae, and Hippidae, five galatheoid families, Galatheidae, Chirostylidae, Kiwaidae, Aeglidae, and Porcellanidae, and the Lomisoidea's monotypic Lomisidae. The out-group was comprised of *Neoglyphea inopinata*, representing Fractosternalia, and the families Dromiidae and Dynomenidae representing Brachyura. This analysis has shown that Anomura indeed is a monophyletic infraorder, as is Hippoidea a monophyletic superfamily. However, while six of the paguroid families form a cohesive clade, the two subfamilies of Lithodidae form a distinct clade more closely related to the superfamily Hippoidea than to the other paguroids. Galatheoidea, as presently constituted, is polyphyletic. Aeglidae, like Lithodidae, is more closely related to Hippoidea than to the galatheoid clade formed by the families Galatheidae, Chirostylidae, and Porcellanidae. Kiwaidae is also distinct from Galatheoidea sensu stricto, but its relationship, and that of Lomisoidea, to the remainder of the anomuran taxa are unresolved in the present analysis. As a result of this reappraisal, we propose that Lithodidae be removed from Paguroidea sensu lato and elevated to superfamily rank with families Lithodidae and Hapalogastridae. Similarly, we propose that Galatheoidea be restricted to the families Galatheidae, Chirostylidae, and Porcellanidae, whereas Kiwaidae and Aeglidae are each to be elevated to superfamily rank. Anomura will then consist of seven superfamilies, Hippoidea, Lithodoidea, Aegloidea, Lomisoidea, Kiwaoidea, Galatheoidea sensu stricto, and Paguroidea sensu stricto.

INTRODUCTION

A review entitled "Hermit crabs–are they really polyphyletic?—A reappraisal 22 years later", was prepared for the Sixth International Crustacean Congress in Glasgow in 2005. Subsequent to that presentation, our attention has been drawn to several weaknesses in our arguments and, as a consequence, our thesis is broadened to ask not only if Paguroidea, as defined by Martin and Davis (2001), is a monophyletic superfamily, but how do paguroids relate to the rest of Anomura. There appears to be a consensus that the infraorder Anomura is a monophyletic taxon (Martin and Abele, 1986; Scholtz and Richter, 1995; Schram, 2001; Dixon et al., 2003; Ahyong and O'Meally, 2004) and is the sister clade to Brachyura, forming the composite taxon Meiura of Scholtz and Richter (1995). However, agreement does not yet extend to superfamilial or inter-familial relationships. Consequently, we have examined the phylogenetic relationships among the four presently recognized superfamilies of Anomura, Hippoidea, Galatheoidea, Lomisoidea, and Paguroidea, focusing our investigation at the family level.

Historical Background

Anomura, or Anomala of numerous authors, has at one time or another in carcinological history contained an assortment of decapod crustaceans. Anomala of Latreille (1816), for example, included the families Hippidae, Paguridae, and Galatheidae, but not the genus *Lithodes* Latreille, 1806, whereas H. Milne Edwards' (1837) Anomura was comprised of a large group that included the dromiids, homolids, lithodids, *Lomis* H. Milne Edwards, 1837, raninids, porcellanids, hippids, and pagurids, but not the galatheids. Anomala of De Haan (1841) consisted of Galatheidea, Porcellanidea, Hippidea, Paguridea, and Lithodeacea (Lithodidae). However, Boas (1880b) grouped these five taxa into three large families, Paguridae, Galatheidae, and Hippidae. Although he noted the absence of the crista dentata and maxillipodal epipods in *Porcellana* Lamarck, 1801, the one genus of porcellanids he examined closely, Boas (1880b) considered those and other differences between *Porcellana* and *Galathea* Fabricius, 1798 minor and not at all justification for the separation of the porcellanids in a distinct major taxon, as had been the practice of previous carcinologists. Henderson's (1888) classification of Anomura followed Boas' (1880b), but Henderson (1888) expanded the latter's "sectional" ranking to that of families and "tribes." Of the porcellanids, Henderson remarked that they must be regarded as highly specialized galatheids, which have to a certain extend assumed brachyuran characteristics. A. Milne-Edwards and Bouvier (1894), addressing only the classification of the galatheids, included Porcellanidae, Aeglidae, Galatheidae and their newly established Chirostylidae (as Diptychinés), all as subfamilies, in their family Galatheidae.

While Boas (1880b) had derived his "Anomala" from the Thalassinidea, Borradaile (1906) included that major taxon, together with Paguridae, Galatheidae, and Hippidae, in his "Anomala". In contrast, Bouvier (1940) excluded Thalassinidea from Anomura, and divided the three remaining "Tribes" into families and subfamilies. In his Tribe Paguridea, Bouvier recognized the families Pylochelidae, Paguridae, including the subfamilies Paguridinae (as Eupagurinae) and Diogeninae (as Pagurinae), Lomisidae and Lithodidae. Bouvier's Galatheidea was still comprised of Aeglidae, Chirostylidae (as Uroptychidae), Galatheidae, and Porcellanidae, while Hippidea consisted of the families Albuneidae and Hippidae.

The hierarchical position of *Lomis* (Lomisidae) was equally controversial. The genus was proposed by H. Milne Edwards (1837) for *L. hirta* (Lamarck, 1818), a species that had been assigned to the porcellanid genus, *Porcellana* by Lamarck (1818) because of its superficial resemblance to porcelain crabs. H. Milne Edwards (1837) allied *L. hirta* to the lithodids, a proposition rejected by Bouvier (1894a, 1895b), who derived the taxon from a form intermediate between the paguroid genera *Mixtopagurus* A. Milne-Edwards, 1880 and *Paguristes* Dana, 1851. Boas (1924) suggested that *L. hirta* had originated from the oldest of Pylochelidae, but later (Boas, 1926) speculated that the taxon might best be regarded as a galatheid. After reviewing the hypotheses of these earlier carcinologists, Pilgrim (1965) concluded that *L. hirta* could not be assigned to Porcellanidae, Pylochelidae, or the Galatheidae, but found no one character that excluded the taxon from Paguridea. In subsequent studies a quarter century later, McLaughlin (1983a) removed Lomisidae (as Lomidae) from Paguridea and elevated the family to superfamily rank, an action supported by the spermatological evidence of Tudge (1997).

MacDonald et al. (1957), on the basis of limited larval data, suggested that Paguridea actually represented two distinct evolutionary lineages that independently had adopted the gastropod shell as a protective device. These authors proposed superfamily rank for Coenobitoidea, in which they included the families Coenobitidae and Diogenidae, and Paguroidea for the families Paguridae, Parapaguridae, and Lithodidae; Lomisidae was not considered in their evaluation. This polyphyly of Paguridea was challenged by McLaughlin (1983b) who did not find MacDonald et al.'s (1957) hypothesis convincing. At that time, there were 21 genera assigned to Coenobitoidea and 63 assigned to Paguroidea. Cladistics was in its infancy, at least when applied to crustaceans, and McLaughlin's (1983b) analysis was manual and intuitive, perhaps even ancestral by current standards. The classification of Crustacea by Bowman and Abele (1982) published a year prior to McLaughlin's query, reflected the MacDonald et al. (1957) viewpoint. Subsequently, Forest (1987), although accepting McLaughlin's (1983b) argument of monophyly in hermit crabs, still believed that the morphologies of coenobitoids and paguroids indicated two evolutionary lineages. He resolved the apparent hierarchical conflict by recognizing a classification that included the Section Paguridea, with superfamilies Coenobitoidea and Paguroidea. In a more recent classification, Martin and Davis (2001) rejected the section Paguridea,

accepting instead McLaughlin's (1983b) original proposition that a single, monophyletic superfamily Paguroidea included the families Pylochelidae, Coenobitidae, Diogenidae, Paguridae, Parapaguridae, and Lithodidae.

The hypothesis that hermit crabs (pagurids) gave evolutionary rise to king crabs (lithodids) dates back more than a century and it is a hypothesis that has been difficult to abandon. Although Martin and Abele (1986) suggested that the theory of a close phylogenetic relationship between the pagurids and the lithodids might be erroneous, they acknowledged that their study was not of sufficient detail to do more than offer a proposition for subsequent testing. McLaughlin and Lemaitre (1997) stated emphatically that there was no evidence that carcinization (evolving a crab-like body form) had provided a direct transition from a pagurid to a lithodid, and McLaughlin et al. (2004) demonstrated conclusively that the theorized developmental pathways of such a transition were incorrect. Nonetheless, these authors did not challenge the entrenched concept of a pagurid-lithodid evolutionary relationship. Despite the separation of Lithodidae from the remaining Paguroidea that was obtained in the recent analysis by Dixon et al. (2003), those authors were reluctant to accept the results as accurate. Instead, they suggested that, in view of the persuasive evidence for interfamilial affinities gleaned from the DNA results of Cunningham et al. (1992), the micro- and macro-morphological study of Richter and Scholtz (1994), the spermatozoan morphology of Tudge et al. (1998), and gene rearrangements of Morrison et al. (2002), the Dixon et al. (2003) contradictory results might have been influenced by what they considered to be the remarkably derived form of Lithodidae. Credible as the aforementioned studies were, those of Richter and Scholtz (1994) and Tudge et al. (1998) lacked rigorous analyses; synapomorphies were determined intuitively. The analysis of Cunningham et al. (1992), although cladistic in methods, was handicapped by very limited sample size and paucity of paguroid input. Supplemental support for their "hermit to king" hypothesis, obtained by their "molecular clock" calculations, placing the divergence of king crabs some 50 million years after that of shell-dwelling hermits was similarly weak. Specifically, the Cunningham et al. results were obtained from DNA extracted from ten species: four species from the polyphyletic genus *Pagurus* Fabricius, 1775, one species each from two additional genera of Paguridae, one species each from two genera of Lithodidae and one species from each of the families Diogenidae and Coenobitidae. The out-group was not even a malacostracan, let alone a close or distantly related decapod. Additionally, in view of the criticisms of molecular clock calculations (Shaul and Graur, 2002; Graur and Martin, 2004; Heads, 2005), the accuracy of Cunningham et al.'s (1992) clock, based on three hypothesized geological dates of divergence is highly doubtful. Porter et al. (2005), using 16S mtDNA, 18S and 28S RNA, and the histone H3 gene molecular data, and Bayesian analysis and Yang's (2004) likelihood heuristic rate-smoothing algorithm, and *Lithodes santolla* (Molina, 1782) as the paguroid representative, placed the anomuran radiation more than 325 million years ago. Sample size in the Morrison et al. (2000) study, although appreciably increased, still dealt

with just 26 taxa, of which only one represented Lithodidae and two belonged to Paguridae. Nonetheless, in addition to confirming the parallel evolution of the crab-like body form, the authors somehow found support for the "hermit to king" hypothesis of earlier authors. An apparent conflict between molecular and morphological data emerged in the recent investigation by Ahyong and O'Meally (2004). Although their scope was a phylogeny of reptant decapods in general, data from their three molecular loci nested *Pagurus* (Paguridae) with *Lithodes* (Lithodidae), whereas their morphological data nested *Pagurus* with *Calcinus* Dana, 1851 (Diogenidae); *Lithodes* was distantly removed. The authors discussed their results only in the broad terms of support of monophyly in Anomura. However, despite their rather extensive database, the Ahyong and O'Meally phylogeny of Paguroidea was determined from only five paguroid and two lithodid taxa.

All of the analyses disputing the relationship of Lithodidae and Paguridae, have, for the most part, not had that particular relationship as a focal point. The findings of Martin and Abele's (1986) study, based on 54 characters scored for numerous representatives of 13 anomuran and five thalassinid families was undertaken primarily to ascertain the phylogenetic position of the family Aeglidae. McLaughlin and Lemaitre (1997) and McLaughlin et al. (2004) addressed the question of carcinization as a viable theory. While McLaughlin and Lemaitre (1997) utilized 37 morphological characters to assess potential pathways of carcinization in 57 anomuran taxa, their employment of cladistic analyses was not for the purpose of determining relationships but rather for revealing conduits, if such existed. McLaughlin et al. (2004) also used cladistic analyses in an unconventional way. Their purpose was to show, with the use of 27 megalopal and juvenile characters for 11 pagurid and 15 lithodid species, the inaccuracies in the theory of lithodid pleonal plate development. Like Ahyong and O'Meally (2004), Dixon et al. (2003) were attempting to resolve the ongoing debate over relationships within the order Decapoda. Their analysis of 70 characters for 60 taxa resulted in a proposed reclassification based on a tree generated that included the removal of Lithodidae from Paguroidea, although these authors made no formal changes in the superfamily. However, again, the paguroids (including lithodids) accounted for only seven of the 60 taxa examined.

Of the few initial recent studies of anomuran phylogeny, the findings of Martin and Abele (1986), in their analysis of the phylogenetic position of Aeglidae, resulted in the removal of both Lomisidae and Lithodidae from Paguroidea, although these authors did not concur with McLaughlin's (1983a) superfamily rank of Lomisoidea. Martin and Abele (1986) instead suggested Lomisidae simply represented an early offshoot of the lithodid line. The only morphological study, other than McLaughlin's (1983b), to deal exclusively with paguroid relationships was that of Richter and Scholtz (1994). And unlike McLaughlin (1983b), Richter and Scholtz (1994) constructed their "frame" of a phylogenetic system on Hennig's (1966) principles of what at the time were thought to be shared

apomorphies, but without the benefit of more modern cladistic methodologies and computer manipulations. Richter and Scholtz (1994) concluded that while Paguroidea was indeed a monophyletic taxon, the "symmetrical" hermit crabs of the family Pylochelidae probably were paraphyletic. Their assessment of the "asymmetrical" hermit crabs was that their phylogenetic relationships were unresolved and complex. Even the monophyletic status of each of the remaining five families was considered uncertain.

Recent evaluations of relationships within Anomura have been made, as indicated above, in the broader context of overall decapod phylogenies. For example, of the 43 taxa included by Scholtz and Richter (1995) in their analysis of reptant relationships, data from only 13 anomuran taxa were employed. Scholtz and Richter found little reason to doubt the monophyly of Anomura (as Anomala). As previously noted, the investigation by Dixon et al. (2003), using 60 taxa, produced a new hypothesis of the phylogeny of the entire Decapoda. From the data gleaned from 14 anomuran species, the authors found four "unambiguous" characters that united Anomura (also as Anomala). However, within Anomura, Dixon et al. considered only Hippoidea and the monotypic Lomisoidea monophyletic. Ahyong and O'Meally (2004) incorporated 13 anomurans into their phylogenetic appraisal of reptant decapods. These latter authors corroborated the general findings of most previous authors, but surprisingly suggested that Pylochelidae ("symmetrical" hermit crabs of Richter and Scholtz, 1994) was a sister group not to other paguroids, but to Galatheoidea, excluding Aeglidae.

In the years since McLaughlin (1983b) asked whether or not hermit crabs were really polyphyletic, the genera assigned to Coenobitidae and Lithodidae have remained constant. However, a seventh family, Pylojacquesidae, has been erected in the superfamily; two additional genera have been added to Pylochelidae, bringing its total to seven, and genera described in Diogenidae have increased from 14 to 20. More dramatic has been the expansions in Paguridae (from 44 to 74 genera) and Parapaguridae (from 5 to 10). Additionally, the long held concepts of Boas (1880a, b, 1924), Bouvier (1894b, c, 1895a, 1897), Borradaile (1916), Wolff (1961), Cunningham et al. (1992), Gould (1992); Richter and Scholtz (1994), Morrison et al. (2002) that shell-dwelling hermit crabs (pagurids) gave evolutionary rise to free-living king crabs (lithodids) through carcinization was challenged by McLaughlin and Lemaitre (1997) on the basis of adult morphology and McLaughlin et al. (2004) on developmental evidence.

Of the remaining anomuran superfamilies, Lomisoidea is still monotypic, but in Hippoidea, three families, Blepharipodidae, Albuneidae, and Hippidae, are now recognized (Boyko, 2002). Within Galatheoidea, a host of new species have been described and a new family, Kiwaidae, has been proposed as being closely related to the family Chirostylidae (Macpherson et al., 2005), whereas the inclusion of Aeglidae in Galatheoidea has been seriously questioned (Pérez-Losoda et al., 2002a, b, 2004; Tudge and Scheltinga, 2002; Ahyong and O'Meally, 2004). With the increases in our knowledge and understanding of morphological attributes, their transformations and distributions, together with

Table 1.   Data matrix (Hap, Hapalogastrinae; Lit, Lithodinae).

Taxon/Node	1 1234567890	1111111112 1234567890	2222222223 1234567890	3333333334 1234567890	4444444445 1234567890	5555555556 1234567890	6666666667 1234567890	777777777 123456789
N. inopinata	0000100000	0010000000	0000000000	0000000000	0000000000	0000000001	0011000000	000000000
Dromiidae	1413010011	0200001021	1100000100	0000031013	0200000012	0310020002	0011000130	000032000
Dynomenidae	1433000041	0200001021	1100011100	0000030001	0200000000	0220020002	0022000120	000032000
Blepharipodidae	0122000023	1000000011	1012210000	0021010124	1100001100	0130010012	0000001331	100012001
Albuneidae	0122100022	1011000011	1012210000	1021011124	2100001100	0130010002	0000001331	100012000
Hippidae	0002100032	0000000031	1110210110	2021001134	3000001100	0130020002	0002001331	100010000
Galatheidae	0222000023	1100011031	1010110000	0100011112	0200000000	0030010002	0000000101	100000211
Chirostylidae	0201020020	1100000011	0010010000	0102011132	0200020000	0030010011	0011010131	100011011
Kiwaidae	0323100021	0001000030	0110011100	010201????	?200020000	0130010001	001100010?	????11011
Aeglidae	0323000022	1000100030	0110001000	0101010124	0200020000	0130210001	0000001331	100012101
Porcellanidae	1213110030	0100011131	1010210110	0101011131	0201000000	0130020001	0011001131	030002211
Lomisidae	1313120021	0010000030	0011010000	0101011122	0201020000	0130010001	0011000130	000042000
Pylochelidae	0013100022	0000100011	1010000001	0021031122	0200020011	1031010002	0011010100	000021011
Coenobitidae	0213100040	0020100021	1010200010	0021011135	0210110011	1031130012	1122011331	021251011
Diogenidae	0213101021	0000100011	1011000000	0021021132	0210110011	1031031012	2222111211	021151011
Pylojacquesidae	0213101031	0000100010	0010011000	0011031132	1220120011	1011001012	2222111310	021121001
Paguridae	0213102121	0000100011	1010010001	0021231132	2220120011	1031332022	2222111311	021151011
Parapaguridae	0213101131	0000100001	1010210000	0021131132	2220120011	1031031022	1222110111	011151001
Lithodidae (Hap)	1321110022	1000000011	1010010001	0111111132	2220110000	0130021112	1222001330	021162000
Lithodidae (Lit)	1330000002	1000000001	1010010001	0111101132	2220110000	0130020102	0022001330	021162000

the advances in cladistic methods and computer generated analyses, it seems appropriate again to test the evolutionary hypothesis regarding paguroids and their relationships with the other major anomuran taxa.

MATERIALS AND METHODS

Morphology

Morphological data for each of the families, or subfamilies in the case of Lithodidae, have been gathered from reviews of the descriptions of the documented genera and species assigned to each family, the published monographic reviews of Boas (1880b), A. Milne-Edwards and Bouvier (1894, 1897), Bouvier (1895b, 1896), Alcock (1901), Makarov (1938, 1962), Pike (1947), Haig (1960), Pilgrim (1965), Forest and de Saint Laurent (1981, 1989), Forest (1987, 1995), Macpherson (1988), Martin and Abele (1988), Baba (1988, 1989, 2005), McLay (1993, 1999), McLaughlin and Lemaitre (2001b), Boyko (2002), McLaughlin (2003), Macpherson et al. (2005), the authors personal knowledge of the majority of species comprising the paguroid families, and/or direct examinations of the type and other representative species for less familiar taxa. The specimens examined are those deposited in the National Museum of Natural History, Smithsonian Institution, Washington DC; Muséum national d'Histoire naturelle, Paris; or collections of the first author. In view of the problems inherent in dealing with missing data in cladistic analyses (Maddison, 1993, Wilkinson, 1995; Strong and Lipscomb, 1999), we have, with one exception, excluded characters for which information is unavailable for one or more of the families of the in-group and/or out-group. That exception is certain data for the galatheid family Kiwaidae, a taxon that currently is based on a single male specimen.

Cladistic Analysis

Parsimony analyses were conducted in PAUP version 4.0 beta 10b (Swofford, 2002) using heuristic and branch-and-bound search options. Seventy-nine characters were considered; all were unordered and unweighted. Other settings were as follows: optimality criterion = parsimony; initial "Maxtrees" = 100 (auto-increased by 100), branches collapsed (creating polytomies) if maximum branch length is zero, "Multrees" option in effect, topological constraints not enforced; unrooted trees rooted using out-group method; character-state optimization; Accelerated transformation (ACCTRANS); random sequence addition; TBR 1000 replications holding 10 trees. Bremer support indices were obtained through heuristic searches. The data matrix (Table 1) originated in MacClade version 3 (Maddison and

Maddison, 1992), and was comprised of 20 taxa, three of which made up the out-group.

PARAMETERS OF THE ANALYSIS

Because of the morphological diversity exhibited by anomurans in general, the majority of the characters are multistate, and many are taxonomically polymorphic (Nixon and Davis, 1991). Wiens (1998a, b) and Simmon and Geisler (2002), among others, have proposed solutions to the coding problems caused by the use of polymorphic characters that involve supraspecific terminals. Of the coding methods tested by Simmon and Geisler, those authors found that the best way to deal with polymorphic characters was to use the IAS (Inferring Ancestral States) method. However, when phylogenies for within-group relationships were not available, as is the case in the anomurans, majority coding performed very well. We have not scored characters for the families and subfamilies on the basis of individual genera or species within those taxa, but rather on the states exhibited by the majority of genera within each family, unless such data were insufficiently documented and therefore could not be tabulated. Specifically, when characters exhibited taxonomic polymorphisms, such as development of the external lobe of the maxillulary endopod, disagreement between presence and absence, as in the case of maxillipedal flagella, or male pleopod development, we scored each character on the basis of the condition found in the majority ($\geq 50\%$) of the genera in the family, as suggested by Wiens (1995).

We recognize that majority rule scoring can be problematical because the most common state does not always represent the state found in the stem lineage. However, within Decapoda, stem-lineage states are still a matter of controversy (Porter et al., 2005). Had we selected one or two genera within each family as representative of character states of the family as has been done previously, we very well could have introduced unacceptable bias. For example,

selection of the genera *Pylocheles* A. Milne-Edwards, 1880 and/or *Cheiroplatea* Bate, 1888 as representative of Pylochelidae for the character accessory tooth on the crista dentata would have led us to score the family as lacking an accessory tooth as did Ahyong and O'Meally (2004). However, when species in four of the seven genera were found to possess an accessory tooth, scoring was reversed. Similarly, had we selected the genera *Munidopsis* White-aves, 1874 and/or *Shinkaia* Baba and Williams, 1998 as representative of Galatheidae, we would have scored the family as lacking a flagellum on the first maxilliped, when species in the vast majority of the genera in the family do have a flagellate first maxilliped. The choice of one or more of 13 particular galatheid genera rather than the majority of 16 would have resulted in scoring of Galatheidae as lacking male first pleopods. Likewise, our scoring of Porcellanidae would have been quite different had we used only one or two representatives of the genus *Petrolisthes* Stimpson, 1858, or *Pisidia* Leach, 1820, exemplars of previous studies, rather than applying the majority rule. For instance, the carapace shape of *Petrolisthes* is described as round or subquadrate (Haig, 1960); in the majority of genera the carapace shape is subovate to ovate; the dorsal integument in both of the former genera is spinose, tuberculate or marked with transverse striae, whereas smooth and unarmed is the condition described for the majority of the genera. Additionally, the carapace margins in species of both *Petrolisthes* and *Pisidia* usually are armed with spines or spinules; in the majority the margins are unarmed. Therefore, although majority rule scoring has certain drawbacks, the use of exemplars as an alternative also has limitations and potential for misleading results. The in-group in the present study consists of all families of Anomura, but because of numerous major morphological dissimilarities, the subfamilies Haplogastrinae and Lithodinae of Lithodidae are treated individually.

Out-groups

Out-group selection has been based on the rationale proposed by Nixon and Carpenter (1993) and includes *Neoglyphea inopinata* Forest and de Saint Laurent, 1975 representing the Fractosternalia of Scholtz and Richter (1995). *Neoglyphea inopinata* was believed to be the sole representative of this distinctive genus until just recently when a second generally similar species was assigned (Richer de Forges, 2006). However, there is uncertainty regarding this assignment (J. Forest, personal communication), thus we continue to regard *Neoglyphea* as monotypic. McLaughlin and Lemaitre (1997) used *N. inopinata* as the out-group in their carcinization study because it shared with Paguroidea and the other anomuran superfamilies the synapomorphy of reduced fifth pereiopods. In their analysis of phylogenetic relationships among reptant decapods, Scholtz and Richter (1995) suggested that the morphology of *N. inopinata* indicated it should be included in their Fractosternalia, together with Astacida [not the Astacidea of Martin and Davis (2001)], Thalassinidea, Anomura (as Anomala) and Brachyura. That placement of *N. inopinata* was corroborated by Schram (2001) and reaffirmed by Schram and Ahyong (2002), but Fractosternalia was

abandoned by Dixon et al. (2003). *Neoglyphea inopinata* has been found not to be the primitive reptant suggested by McLaughlin and Lemaitre (1997). Nevertheless, *N. inopinata*, as a member of Fractosternalia that is related, albeit distantly, to Anomura, meets the out-group criterion. However, also recognizing the value of selecting out-group members from the sister group of Anomura, we also have included two of the "primitive" crab families, Dromiidae and Dynomenidae representing Brachyura, the sister clade of Anomura (Scholtz and Richter, 1995; Dixon et al., 2003; Ahyong and O'Meally, 2004).

Characters and Coding

Most characters and character states are self explanatory, but there are some that have required clarification or re-interpretation and these are incorporated into the following listing.

1. Body form:—not crab-like (0); crab-like (1).
2. Carapace shape:—subcylindrical (0); subquadrate (1); subovate to ovate; (2); subtriangular (3); subglobose (4).

The interpretation of carapace shape differs from author to author. In the present analysis, we have considered the carapace to be subcylindrical (considerably, but evenly, longer than broad); subquadrate; subovate to ovate (slightly and roundly longer than broad); subtriangular; or subglobose (as used by McLay, 1993, 1999). Carapaces in Porcellanidae vary from subcylindrical to subcircular, but the family has been scored as subovate to ovate because the majority of taxa approach that generalized description.

3. Carapace regions (e.g., hepatic, gastric, cardiac, branchial):—absent (0); not well defined (1); weakly delineated (2); distinctly delineated (3).
4. Carapace dorsal integument:—covering of spines or tubercles (0); scattered spines, spinules or tubercles (1); distinct transverse grooves or furrows (2); smooth or nearly so (3).
5. Carapace margins:—armed with spines, tubercles, granules or protuberances (0); unarmed (1).
6. Cervical groove:—clearly distinct (0); weakly delineated (1); obsolete or absent (2).
7. Posterior portion of carapace:—well calcified throughout (0); weakly calcified or with areas of calcification (1); chitinous or membranous (2).
8. Anterior portion of carapace:—well calcified throughout (0); moderately or partially calcified (1).
9. Rostrum (median lobe):—simple, elongate (0); tridentate (1); moderately long to short, triangular or subtriangular (2); broadly rounded, broadly and weakly subacute, or lobate (3); obsolete or absent (4).

Rostra in the family Hippidae vary from obsolete through a bi- or tri-lobed, rounded median projection to a small, but distinct, acute, triangular rostrum. However, as the majority of species within two of the three genera have a lobate rostral prominence, we have scored the rostrum broadly rounded, broadly and weakly subacute, or lobate for the family.

10. Lateral projections (extra-orbital, supraorbital, post-

orbital or outer orbital spines):—obsolete or absent (0); weakly developed (1); moderately well developed (2); prominent (3).

The anterior margins of anomuran carapaces are variously shaped and armed and the terminology applied to that spination is similarly variable. To our knowledge, no detailed comparisons have been made among the various families, consequently homology can only be presumed. For the purpose of this study, we recognize a rostrum or rostral lobe (anterior marginal carapace midpoint when the rostrum is absent), and equate the pagurid lateral projections to the extra-orbital, supraorbital, postorbital or outer orbital spines of authors for other taxa.

11. Anterolateral (antero-external) spine(s):—absent (0); present (1).

An anterolateral or antero-external spine is defined as a spine arising at the junction of the anterior and lateral margins of the carapace.

12. Ocular orbits:—absent (0); weakly or partially developed (1); well developed (2).

Dixon et al. (2003) considered an ocular orbit (orbito antennularis fossa) present when the base of the eyestalk was surrounded by a ridge of the carapace and/or the basal articles of the antennules or antennae. These authors scored the porcellanid *Pisidia longicornis* (Pennant, 1777) as lacking ocular orbits because the bases of the peduncles were not surrounded by complete rings. However, Henderson (1888) described Galatheidae as having weakly developed ocular orbits. McLaughlin and Lemaitre (1997) scored *Galathea* as having weakly developed orbits and *Munida* Leach, 1820 and *Munidopsis* as varying between no orbits and weak orbital development. Henderson (1888), Bouvier (1940), Haig (1960), and McLaughlin and Lemaitre (1997) all reported orbital development in Porcellanidae. We consider weak or partial orbital development as transitional from no development to well developed orbits.

13. Ocular peduncular shape:—cylindrical (0); dorsoventrally flattened (1); laterally compressed (2).
14. Corneal development:—large to moderate (0); markedly reduced or absent (1).
15. Ocular acicles:—absent (0); present (1).

There has been considerable disagreement on what actually constitutes an ocular acicle. Boyko and Harvey (1999), for example, argued that only the spinose projection represented the acicle, whereas Forest et al. (2000) considered the ocular plates of some of the pylochelids homologous with the ocular acicles of other paguroids. Dixon et al. (2003) stated that they were unable to differentiate between "true ocular acicles" and "pieces of the ocular plate", and consequently scored any structure that resembled an ocular acicle as being one. However, they scored both *Aegla* sp. and *Pylocheles* sp. as lacking ocular acicles, as did Ahyong and O'Meally (2004). We accept Forest et al.'s (2000) definition of the ocular acicles. A. Milne-Edwards and Bouvier (1894: 202, 239) suggested that the presence of ocular acicles in Aeglidae was one of several characters that demonstrated the original common

origin of Paguroidea and Galatheoidea. Although Martin and Abele (1986) scored Aeglidae as lacking ocular acicles, Martin and Abele (1988: fig. 5d-f) described and illustrated an ocular ring formed by individual calcified plates at the base of the peduncle in *Aegla uruguayana* Schmitt, 1942. We have scored Aeglidae as having ocular acicles. In contrast, while Martin and Abele (1986) scored Albuneidae as possessing ocular acicles, we have accepted Boyko's (2002) interpretation of ocular segmentation in Blepharipodidae and Albuneidae and because the ocular plates in these families appear, for the most part, to represent the basal ocular segments, we have scored the families of Hippoidea as lacking ocular acicles.

16. Antennular basal segment:—not notably expanded or enlarged (0); notably expanded or enlarged (1).
17. Antennal peduncle segmentation:—5 segments (0); fewer than 5 segments (1).

McLaughlin and Provenzano (1974) reported the presence of a "supernumerary" segment between the second and third antennal segments in paguroids, and the presence of such an element also was documented by Martin and Abele (1986) for several decapods. A similar structure may be present in *N. inopinata* (Forest and de Saint Laurent, 1981, fig. 15c). However, those authors cautioned against drawing conclusions regarding the complexity of the peduncular segmentation until the internal organization had been investigated. Such caution also seems appropriate for this study. Therefore, we have recognized only two character states, the basic reptant five-segmented peduncle (0), and a peduncle in which some segments have fused, leaving less than five segments (1).

18. Basal antennal segment:—movable, not fused to carapace or epistome (0); immovable, fused to carapace or epistome (1).
19. Scaphocerite (antennal acicle or scale):—elongate or broadened, articulated (0); moderate to short, articulated (1); moderate to short, fused to segment 2 (2); markedly reduced or vestigial or absent (3).
20. Mandibular cutting edge:—chitinous (0); calcified (1).
21. Mandibular dentition:—toothed (0); not toothed (1).

Toothed as used in this character refers to the mandibular margin that is cut into a series of acute or subacute projections (teeth), and giving a "saw-toothed" appearance. The one or two occasional tooth-like protuberance(s) described as teeth by Bokyo (2002) for the mandibles of Blepharodidae and Albuneidae do not meet this criterion. Hippoid mandibles are scored as not toothed.

22. Mandibular palp:—three-segmented (0); two-segmented (1).
23. Maxillulary endopod:—two-segmented (0); one-segmented (1).
24. Maxillulary endopodal external lobe:—reduced or absent (0); recurved (1); broadly inflated (2).
25. Flagellum of first maxilliped:—always present (0); present or absent (1); always absent (2).
26. Thoracic sternite IX (sternite of third maxillipeds):—narrow, with bases of corresponding appendages approx-

imate or nearly so (0); broad, with bases of corresponding appendages moderately to widely separated (1).

27. Thoracic sternite IX development:—without median projection (0); with median projection separating corresponding appendages (1).

28. Form of third maxillipeds:—pediform (0); broadly expanded or operculate (1).

29. Crista dentata of third maxilliped:—well developed (0) weakly developed or absent (1).

30. Accessory tooth:—absent (0); present (1).

On the basis of a species of *Pylocheles*, Dixon et al. (2003) and Ahyong and O'Meally (2004) scored Pylochelidae as lacking a tooth on the crista dentata. However, as members of four of the seven genera, and a majority of the species, do have one or more accessory teeth on this structure, we have scored Pylochelidae as having an accessory tooth.

31. Exopod of maxilliped 3:—present, with flagellum (0); present, without flagellum (1); absent (2).

32. Thoracic sternal plastron:—narrow (0); broadening posteriorly (1).

33. Thoracic sternite XII (sternite of third pereiopods):—completely fused to sternite XI (0); incompletely or indistinctly fused to XI (1); distinctly not fused to sternite XI (2).

34. Thoracic sternite XIV (sternite of fifth pereiopods):—well developed (0); distinctly reduced (1); absent (2).

35. Last thoracic and first pleonal somite:—not fused (0); partially fused (1); completely fused (2).

36. Branchiostegites (pterygostomial plates or flaps):—well calcified (0); partially calcified, divided by suture(s) or "fragmented" (1); weakly calcified throughout (2); primarily membranous (3).

37. Gill type:—trichobranchiate (0); phyllobranchiate (1).

In this study, we have recognized only two gill types, trichobranchiate and phyllobranchiate. There has been considerable confusion in the interpretation of gill types in reptant decapods. For example, Martin and Abele (1986) reported that trichobranchiate gills occurred in the pylochelids (as pomatochelids), some parapagurids, and *Aegla* Leach, 1820. These authors were basing their differentiation between trichobranchiate and phyllobranchiate gills on the form of the lamellae, tubular as opposed to flattened and leaf-like. However, the late Michèle de Saint Laurent (McLaughlin and de Saint Laurent, 1998: 161), after an in depth study of decapod gill structure, determined that it was not the shape of the gill elements so much as their insertion on the rachis of the gill that determined gill type. In true trichobranchiate gills, the tubercular elements are equal or unequal, but inserted in order or disorder around the axis, or in regular transverse rows along the axis. In contrast, the elements of phyllobranchiate gills always are inserted biserially in regular pairs along the rachis. The misinterpretation of trichobranchiate led McLaughlin and Lemaitre (1997), Dixon et al. (2003) and Ahyong and O'Meally (2004) to score several anomuran taxa as having trichobranchiate gills, when in fact their gills were actually quadriserial phyllobranchiae. The gills of *Lomis hirta* were called trichobranchiate by the aforementioned authors as

well; however, Bouvier (1895b: 200, pl. 13, fig. 15) clearly described and illustrated quadriserial gills in this taxon. Of Aeglidae, Martin and Abele (1988: 23) said simply that the gills resembled trichobranchiate gills distally in that the filament were long, finger-like tubes; the proximal portion resembled that of the brachyuran phyllobranch in having plate-like lamellae. These authors illustrated a quadriserial lamella and referred to the lamellar arrangement as being serial; however, Boyko (2002: 7) emphasized what he considered the truly trichobranch morphology of the gills of Blepharipodidae and Aeglidae. Phyllobranch gill structure is seen in members of Albuneidae, Hippidae Porcellanidae, Galatheidae, and Chirostylidae; it is not known for Kiwaidae. Of the out-groups, the gill structure in *N. inopinata* is trichobranch and phyllobranch in the Dromiidae. The gill structure in genera of Dynomenidae appears to vary from trichobranch to phyllobranch, but based on the descriptions presented by McLay (1999), we have scored Dynomenidae as having a trichobranch gill structure.

38. Podobranchs:—1 or more present (0), absent (1).

39. Epipod number:—5-7 (0), 3 or 4 (1); 1 or 2 (2); 0 (3).

40. Arthrobranch formula:—rudiment mxp1; 1 mxp2; 2 mxp3; 2(P1); 2(P2); 2(P3); 2 (P4), 0(P5) (0); 0,1,1,2,2,2,2,0 (1); 0,0,2,2,2,2,2,0 (2); 0,0,2,2,2,2,1,0 (3); 0,0,1,2,2,2,2,0 (4); 0,0,0,0,2,2,0 (5).

Boyko (2002) reported the arthrobranch formula for the family Blepharipodidae as having one arthrobranch plus a rudiment on the third maxilliped and two arthrobranchs on pereiopods 1-4 . In keeping with our system, we have scored this family, like Albuneidae, as having only one arthrobranch on maxilliped 3.

41. Pleurobranch formula:—0,0,0,0,1(P2),1(P3),1(P4), 1(P5) (0); 0,0,0,0,1,1,1,0 (1); 0,0,0,0,0,0,1,0 (2); absent (3).

42. Pereiopod 1 (cheliped) termination:—simple (0); subchelate (1); chelate (2).

43. Pereiopod 1 symmetry:—equal or subequal (0); left distinctly larger (1); right distinctly larger (2).

44. Structure of pereiopods 1:—generally subcylindrical (0); dorsoventrally flattened (1).

45. Armament of pereiopods 1:—similar (0); dissimilar (1).

46. Pereiopod 1 dactylar orientation:—vertical (0) oblique (1); horizontal (2).

In *N. inopinata* and in the family Hippidae, where the dactyls of the first pereiopods are simple, the scoring vertical refers to the articulation of the dactyls with the propodal segments. In all other taxa where subchelate or chelate appendages develop, the orientation refers to the articulations of the dactyls with the fixed fingers of the palms or propodi.

47. Dactyls of pereiopods 2-4:—generally subcircular (0); laterally compressed and dorsoventrally expanded (1).

Perusal of the literature has shown that numbering of the pereiopods differs among authors. Lemaitre (1996, 1999, 2004), for example, referred to the second and third pereiopods as the first and second walking legs. McLay (1993) described the chelipeds and four pereiopods of Dromiidae, but pereiopods 1-5 in the family Dynomenidae

(McLay, 1999). Similarly, we refer to the five pairs of thoracic appendages as pereiopods 1-5.

48. Tips of dactyls of pereiopods 2-4:—with corneous claws (0); without corneous claws (1).
49. Pereiopod 4:—developed as walking or digging leg (0); reduced and not used for walking or digging (1).
50. Pereiopod 4 termination:—simple (0); semichelate (1); subchelate (2).
51. Propodal rasp of pereiopod 4:—not developed (0); developed (1).
52. Pereiopod 5 carriage:—carried externally (0); carried under carapace (1); carried horizontally (2); carried dorsally or subdorsally (3).

Scholtz and Richter (1995) stated that one apomorphy uniting all anomurans was the reduced fifth pereiopods that, with the exception of shell dwelling hermit crabs, were kept in the branchial chamber and used as cleaning appendages. That the fifth pereiopods are used to clean the gills has been documented for several anomuran species including shell-dwelling hermits by Bauer (1981). However, as pointed out by McLaughlin and Lemaitre (1997), not all non shell-dwelling paguroids carry the fifth pereiopods under the carapace any more than shell-dwelling species do, and neither do all galatheoids. Bouvier (1940) described the fifth pereiopods of Galatheidea as being capable of "returning to the gill chambers" for the purpose of cleaning. The color and black and white photographs of Macpherson (1993, 1994, 1995), Baba and Williams (1998), and Baba (2005) clearly show that the galatheid fifth pereiopods are reduced, but are not routinely carried in the gill chambers.

53. Pereiopod 5 termination:—simple (1); subchelate (1); semichelate (2); chelate (3).
54. Pereiopod 5 rasp:—absent (0); well developed (1).
55. Pereiopod 5 coxal modification:—none (0): calcified short papilla(e) or tube(s) (1); vas deferens coupled externally with membranous coxal lobe (2); membranous papilla(e) or short to long tube(s) (3).

A character not considered by previous authors is the development of sexual tubes in males. That the coxal segments of the fifth pereiopods are modified for sperm transfer is considered a homology shared by Aeglidae, Coenobitidae, and Paguridae, but the modifications differ among the three families. Consequently, we have scored coxal modifications as three distinct states. Although coxal modifications in Aeglidae are moderately well documented (Lopretto, 1979, 1980a, b, 1981), it is only recently that the extent of this developmental phenomenon in Paguroidea has been more than superficially investigated (Tudge and Lemaitre, 2004, 2006). Nonetheless, because of its occurrence in more than 50% of coenobitid and pagurid genera, the families have been scored as having sexual modified coxae present.

56. Pleon flexion:—carried straight (0); slightly or weakly flexed (1); strongly flexed and carried closely applied to ventral thorax (at least in males) (2); elongate or short, not flexed, but distinctly twisted (3).

Dixon et al. (2003) differentiated between a straight pleon and pleonal flexion as generalized for either anomurans or brachyurans, whereas, Ahyong and O'Meally (2004) scored only two positions, straight or ventrally flexed. We have taken into account the variability demonstrated within Anomura. Specifically, we consider the elongate, but twisted, pleon of many paguroids quite distinct from the elongate, but straight, pleons of glypheids and muscular differences substantiate this view (Alexandrowicz, 1952; Pilgrim, 1960; Chapple, 1966, 1969a-c, 1973; Stephens, 1986). Similarly, the weak flexion of the pleon seen in the aeglids, galatheids, chirostylids, pylochelids, or the majority of the hippoids, where the pleon is simply bent under the more anterior pleonal somites, is not equivalent to the flexion seen in *Lomis*, the lithodids, the porcellainids, or the hippids where the pleon is flexed to such a great extent that it is pressed against the thorax.

57. Pleonal segmentation:—clearly defined (0); weakly defined (1); not defined (2).
58. Pleonal tergite dimorphism:—absent (0); present (1).

Under their character 50, symmetry, Dixon et al. (2003) grouped chela symmetry/asymmetry with pleon symmetry/asymmetry, accompanied by the explanation that hermit crabs and their putative descendants had asymmetrical pleons, apparently in order to conform to asymmetrical mollusk shells. The authors went on to explain that hermits also frequently had asymmetrical chelae, and then noted that the lithodids were unusual in having symmetrical males and asymmetrical females. However, Dixon et al. scored the lithodid *Hapalogaster dentata* (De Haan, 1844) as having asymmetrical chelae and a symmetrical abdomen, but *Lithodes santolla* (Molina, 1782) as having an asymmetrical female and symmetrical male. Actually, both lithodid species used by Dixon et al. (2003) have asymmetrical chelae and dimorphic pleonal tergites (Makarov, 1938, 1968; Mc-Laughlin and Lemaitre, 2001a). The female pleonal tergite development in *H. dentata* simply isn't as obvious as it is in *L. santolla*, but in both species the female pleon, unlike the male, is markedly asymmetrical. We also disagree with the scoring of Ahyong and O'Meally (2004) in regarding the pleonal sexual dimorphism in *Lithodes* as being slight.

59. Pleonal tergite 1:—well calcified (0); partially calcified (1); chitinous or membranous (2).
60. Pleura of tergite 1:—well developed (0); weakly developed (1); absent (2).
61. Pleonal tergite 2:—well calcified (0); partially or weakly calcified (1); chitinous or membranous (2).
62. Pleonal tergites 3-5:—well calcified (0); partially or weakly calcified (1); chitinous or membranous (2).
63. Pleura of tergite 2:—distinctly delineated (0); weakly or partially delineated (1); not delineated (2).
64. Pleura of tergites 3-5:—distinctly delineated (0); weakly or partially delineated (1); not delineated (2).
65. Pleonal tergite 6:—well calcified (0); weakly calcified, chitinous or membranous (1).
66. Pleomere 6 tergal margins:—entire (0); with transverse groove(s), furrow(s) or incisions (1).
67. Male paired pleopod 1:—present and modified (0); absent (1).

68. Male pleopod 2:—paired and modified (0); unpaired (1); markedly reduced or absent (2).

Modification of the second pleopods in *N. inopinata* is less pronounced than in genera of Dromiidae and Dynomenidae; however, the presence of appendix masculinae in *N. inopinata* suggests that this pair of appendages is involved in sperm transfer as it is in many carideans.

69. Male pleopods 3-5:—paired (0); unpaired (1); reduced (2); vestigial or absent (3).

Ahyong and O'Meally (2003) did not distinguish between male and female pleopods, and as a result scored *Petrolisthes* as having uniramous pleopods 2-5. However, among the galatheid families, pleopods 3-5 are reduced or absent in males of the majority of genera of Porcellanidae and Chirostylidae. They are also vestigial in Aeglidae.

70. Female paired pleopod 1:—present (0); absent (1).
71. Female pleopods 3-4 development:—biramous (0); uniramous (1).
72. Female pleopod 2:—symmetrically paired (0); asymmetrically paired (1); unpaired (2); absent (3).

Again, because Ahyong and O'Meally (2003) did not distinguish between male and female pleopods, these authors scored female pleopods 2-5 as paired and uniramous for *Petrolisthes*. However, female porcellanids lack second pleopods.

73. Female pleopods 3-4:—paired (0); unpaired (1).
74. Female pleopod 5:—paired (0); unpaired (1); absent (2).
75. Uropods:—symmetrical, forming tail fan (0); symmetrical, not forming tail fan (1); symmetrical, specialized with rasps (2); symmetrical, reduced to dorsal or ventral plates (3); symmetrical in females, absent in males (4); asymmetrical, with rasps (5); absent in both sexes (6).

Dixon et al. (2003) scored the uropods of *L. hirta* as biramous, whereas Ahyong and O'Meally (2004) scored them as uniramous. While it is true that females of *L. hirta* have large, unequally biramous, but symmetrical uropods, this pair of appendages is absent in males as noted by Martin and Abele (1986). We consider this dimorphic loss as being potentially informative.

76. Telson development:—elongate, triangular or subtriangular (0); generally subquadrate or subrectangular (1); short, subtriangular to subsemicircular (2).
77. Telson dorsal surface:—undivided (0); divided by longitudinal suture (1); divided into several small plates (2).
78. Telson lateral margins:—entire (0), with transverse indentation(s), notches or incisions (1).
79. Telsonal terminal margin:—entire (0); with median cleft or concavity (1).

RESULTS

The data matrix included 79 morphological characters, of which 76 were parsimony-informative. The analysis produced four most parsimonious trees of 298 steps, with Consistency Index (CI) of 0.4866 and Homoplasy Index (HI) of 0.5134. The CI excluding uninformative characters = 0.4843; HI excluding uninformative characters = 0.5157; Retention Index (RI) = 0.5887; Rescaled Consistency Index (RC) = 0.2865. A strict consensus tree from these four trees (Fig. 1), and a majority rule tree were generated; the two trees show identical branching patterns, thus only the former is presented.

The results of the analysis, like those of Dixon et al. (2003), not only support the proposition by McLaughlin and Lemaitre (1997) and McLaughlin et al. (2004) that the hermit crabs did not give evolutionary rise to the king crabs, but the suggestion of Martin and Abele (1986) that neither Lithodidae nor Lomisoidea are closely related to other members of Paguroidea. Similarly, we confirm Ahyong and O'Meally's (2004) proposition that, as currently constituted, neither Paguroidea sensu lato (s.l.) nor Galatheoidea is monophyletic. In fact, our results show that both superfamilies are polyphyletic, but the Paguroidea sensu stricto (s.s.), that is, exclusive of Lithodidae, is monophyletic. We disagree with Ahyong and O'Meally's (2004) suggestion that Pylochelidae is the sister clade of Galatheoidea, excluding Aeglidae. Within Paguroidea s.s., the relationships among the families are well supported. However, the interfamilial relationships of Paguridae, Parapaguridae, and Pylojacquesidae cannot be resolved on the basis of the present data.

As may be seen in Fig. 1, two of the families of Galatheoidea s.l., Aeglidae and Kiwaidae represent separate and distinct superfamilies. The relationship between Kiwaidae and Lomisoidea is unresolved in the present analysis, but both are only distantly related to Galatheoidea s.s. Our results were identical regardless of which of the four most parsimonious trees was examined. In contrast with the findings of Morrison et al. (2002), Ahyong and O'Meally (2004), and Porter et al. (2005) that suggested Lomisoidea as the sister clade of Aeglidae, our analysis indicates a closer relationship between Aeglidae and Lithodidae. Interestingly, the Bayesian phylogenetic tree based on 2035 base-pairs of 18S rRNA presented by Macpherson et al. (2005) similarly aligned Aeglidae and Lithodidae both more closely to Hippoidea, than to Galatheoidea s.s. The family Kiwaidae was only distantly related to Galatheoidea s.s.; Lomisoidea was not considered in their molecular analysis. The molecular analysis of Pérez-Losada et al. (2002) suggested a closer relationship of Aeglidae to Hippoidea than Galatheoidea; neither Kiwaidae, nor Lomisoidea were included in their study. However, Lithodidae were distantly removed.

Four characters were cited by Dixon et al. (2003) as apomorphies uniting Anomura (as Anomala): 1) notch in the carapace to accommodate the basal segments of the antennae; 2) reversal of the coxosternal joints of the ambulatory legs; 3) the rotation of the cheliped to bring the dactyls into a horizontal position; and 4) the loss of the female first pleopods. Only dactylar orientation and the presence/absence of first female pleopods were considered in the current study. Contrary to Dixon et al.'s belief, female first pleopods are not absent in all anomurans, only some, although when present they are structurally different from the remaining pleopods. We did not find absence of female first pleopods a defining apomorphy of Anomura. However, we do concur that the horizontal carriage of the chelipeds is
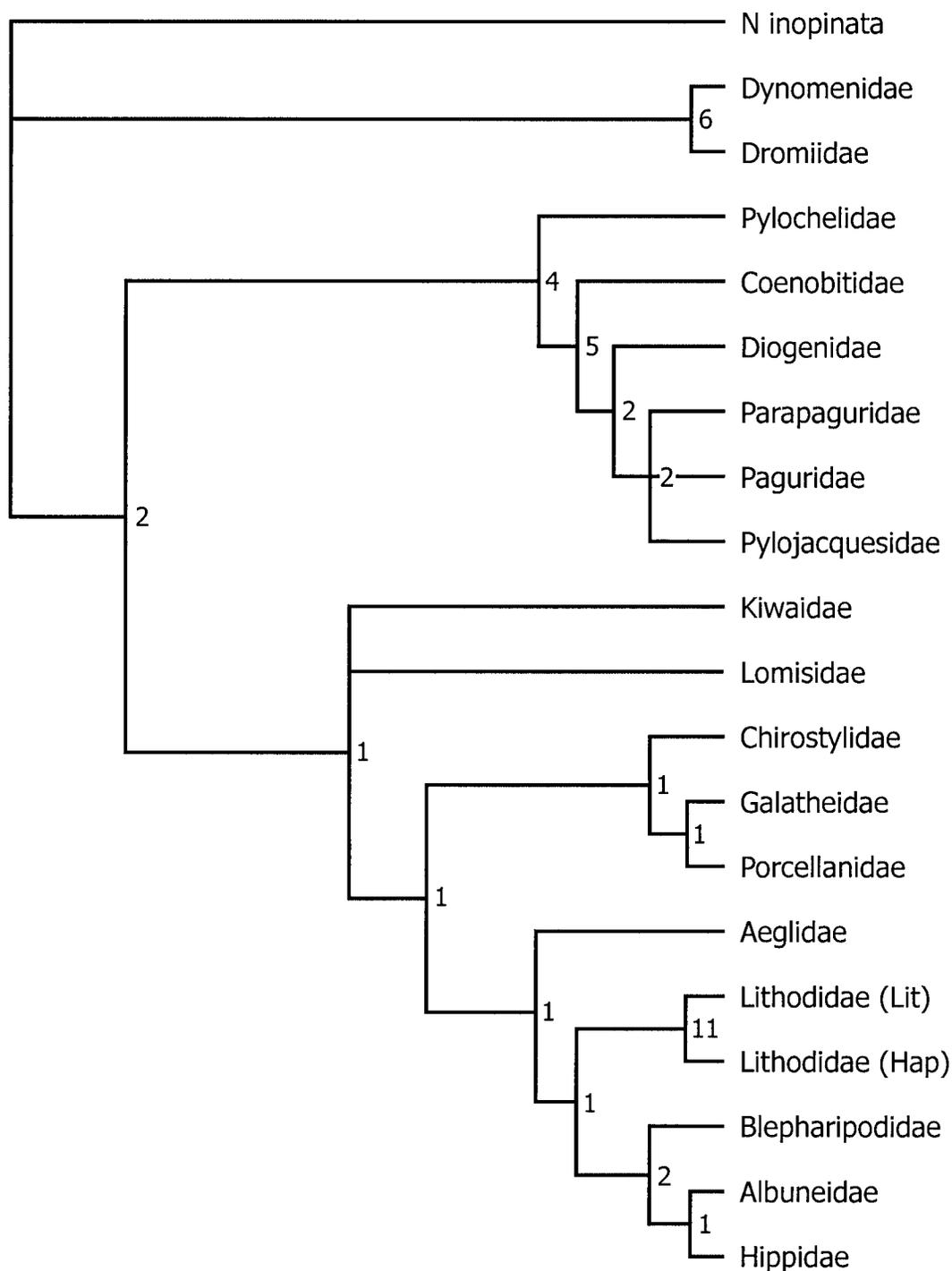
Fig. 1. Strict consensus cladogram of the four most parsimonious trees obtained from PAUP analysis using branch-and-bound search (298 steps, CI = 0.4866, RI = 0.5887, RC = 0.2865, HI = 0.5240), showing relationships of families of Anomura. Bremer support indices shown at resolved nodes. Lit = Lithodinae; Hap = Hapalogastrinae.

one of the apomorphies setting many of the anomurans apart from the out-group taxa. Nonetheless, cheliped carriage, like many other morphological characters, is highly variable, at least within Paguroidea s.s. We found five apomorphies that define Anomura. These include: 1) the reduction in the segmentation of the maxillulary endopod, 2) reduction in the sternite of the fifth pereiopod, 3) loss of podobranchs, 4) reduction and ultimate loss of epipods, and 5) the incised

terminal margin of the telson. McLaughlin and Lemaitre (1997) considered the reduction in the fifth pereiopods a unifying character of Anomura; but the fifth pereiopods are similarly reduced, albeit not similarly modified, in two of the out-group taxa. Nevertheless, if the proposition put forth by Porter et al. (2005) that Brachyura and Anomura are basal in decapod evolution is proven correct, our interpretations of character polarities could be significantly altered.

Resolution of the relative position of Anomura within Crustacea, other than accepting its sister clade relationship with Brachyura, is beyond to scope of the present investigation. Our focus has been on reappraisal of the phylogeny of Paguroidea s.l., the relationship of Paguroidea to the other major anomuran taxa, and theirs with one another. Six synapomorphies verify the monophyly of Paguroidea s.s.: 1) the lack of fusion of the sternites of the third and second pereiopods; 2) the reduction in the fourth pereiopods to non-ambulatory appendages; 3) the semichelate propodi and dactyls of that pair of appendages; 4) the development of propodal rasps on those propodi; 5) the development of rasps on the propodi of the fifth pereiopods; and 6) the incised or notched tergal margins of the sixth pleomere. From our reappraisal of interfamilial relationships within the superfamily, we concur with the proposition put forth by Richter and Scholtz (1994) that Pylochelidae is paraphyletic (sensu Hennig, 1966).

Kiwaidae, despite being monotypic and known from a single male specimen is separated from the remainder of Galethoidea by four apomorphies: 1) The reduction of the segmentation of the mandibular palp from three to two. This apomorphy is shared by the hippoid family Hippidae and Aeglidae, and may reflect convergent adaptation to specialized habitats. 2) The development of a median projection on thoracic sternite IX (third pereiopds). This apomorphy is shared with the similarly monotypic paguroid family Pylojacquesidae, and also may reflect convergent adaptation. The habitat of *Pylojacquesia colemani* McLaughlin and Lemaitre, 2001b is known only as tusk shells, whereas *Kiwa hirusta* Macpherson, Jones, and Segonzac, 2005 is found in association with hydrothermal vents. 3) The broadly expanded or opercular third maxilliped is an apomorphy also shared with Hippidae and with the galatheid family Porcellanidae and again may indicate convergent adaptation to food sources and/or specialized habitats. An apomorphy that Kiwaidae shares with the galatheid family Chirostylidae is the complete loss of thoracic stenite XIV (sternite of the fifth pereiopds). This apparently parallel (Wiley, 1981: 121) loss was one of the principal reasons for the assignment of Kiwaidae to Galatheidae by Macpherson et al. (2005).

Lomisoidea is also monotypic, but nonetheless is set apart from the other superfamilies by several apomorphies: 1) The development of a crab-like body form is shared by Porcellanidae and Lithodidae, and was one of the characters cited by older carcinologists for relating *Lomis hirta* to first Porcellanidae and later to Lithodidae. Evidence presented by McLaughlin and Lemaitre (1997) and Morrison et al. (2000) show convincingly that development of the crab-like body form in several major taxa is convergent. 2) The external obliteration of the cervical groove is an apomorphy that *L. hirta* shares not only with several other anomuran taxa, but also with one of the out-groups and similarly is viewed as convergence. 3) The dorsoventral flattening of the ocular peduncles reflects modification of the typical structure of the decapod ocular peduncle. Modifications also are seen in *Neoglyphea inopinata* and in Coenobitidae, but these clearly reflect distinctly different adaptations. 4) The broadening of the external lobe of the maxillulary endopod is an

apomorphy shared with the paguroid family Diogenidae, and is considered another example of convergence. 5) The dorsoventral flattening of the chelipeds of *L. hirta*, an apomorphy shared by the galatheid family Porcellanidae, is interpreted as a convergent adaptation to the cryptic shallow-water habitats occupied by both taxa. 6) An apomorphy unique to Lomisidae is the dimorphic loss of male uropods.

Galatheoidea s.s. is essentially paraphyletic. Despite the considerable morphological diversity of its members, one synapomorphy unites Galatheidae, Chirostylidae, and Porcellanidae in the superfamily. This is the progressive development of ocular orbits.

Four apomorphies support the removal of Aeglidae from Galatheoidea s.l. and two, at least, appear to reflect adaptations to particular environments. The reduction of the number of segments in the mandibular palp is an apomorphy shared with two other specialized taxa, Hippidae and Kiwaidae. The median projection that is developed on the sternite of the third maxillipeds is an apomorphy paralleled in Kiwaidae and the paguroid family Pylojacquesidae. As previously discussed, sexual modification of the coxae of the male fifth pereiopods is interpreted as homologous among the aeglids, coenobitids, and pagurids; however, the individual modifications are unique to each family. The longitudinal suture on the dorsal surface of the telson is exclusively an aeglid attribute. Additionally, considerable molecular evidence supporting superfamily status for this taxon has been presented by Pérez-Losoda et al. (2002a, b, 2004).

Lithodidae share the apomorphic epipod loss with several other anomuran families, and the pronounced pleonal flexion with Hippidae and Porcellanidae; however, most apomorphies are shared only with one or more families of Paguroidea s.s. Before it was recognized that the majority of the pylochelids also were provided with one or more accessory teeth on the crista dentata of the third maxilliped, this character was one of the most significant attributes cited as confirmation of the close evolutionary relationship between Lithodidae and Paguridae. The fusion of the last thoracic and first pleonal sternites similarly was cited as demonstrating this relationship, although such fusion was found by McLaughlin and Lemaitre (1997) and McLaughlin et al. (2004) to be only partial in the parapagurids and lithodids but complete in the majority of pagurids. The most compelling evidence for the close lithodid-pagurid relationship was seen in the presumably apomorphic loss of female pleopod 2-5 on the right side of the pleon in paguroids other than the pylochelids and in all lithodids, and was interpreted as demonstrating the shared synapomorphies of cheliped and pleonal asymmetry. The rationale for proposing that these attributes are convergent, not homologous, in the two groups is presented in the discussion that follows. Two apomorphies set the lithodids apart from all other anomuran families. These are the pleonal tergite dimorphism and the complete loss of uropods in both sexes.

Two synapomorphies of Hippoidea distinguish this superfamily from the remainder of Anomura. These are the laterally compressed and dorsoventrally expanded dactyls of the second through fourth pereiopods, and dactylar termi-

nations that lack corneous claws. These apomorphies reflect specialized adaptations to the burrowing habits of these crustaceans. A third apomorphy, the loss of the flagellum of the first maxilliped is loss paralleled in Porcellanidae, Coenobitidae, and Parapaguridae. A synapomorphy of Hippoidea not considered in the present study, is the muscle [uropod return stroke muscle] arising from the dorsal surface of the telson that inserts dorsally on the uropodal coxa (Paul et al., 1985; Paul, 1989, 2003) and its accompanying telson stretch receptor.

As a result of this analysis, we propose the following revised classification of Anomura:

Infraorder Anomura
  Superfamily Paguroidea
    Family Pylochelidae
    Family Coenobitidae
    Family Diogenidae
    Family Pylojacquesidae
    Family Paguridae
    Family Parapaguridae
  Superfamily Kiwaoidea
    Family Kiwaidae
  Superfamily Lomisoidea
    Family Lomisidae
  Superfamily Galatheoidea
    Family Galatheidae
    Family Chirostylidae
    Family Porcellanidae
  Superfamily Aegloidea
    Family Aeglidae
  Superfamily Lithodoidea
    Family Hapalogastridae
    Family Lithodidae
  Superfamily Hippoidea
    Family Albuneidae
    Family Blepharipodidae
    Family Hippidae

DISCUSSION

Interfamilial Relationships

Paguroidea s.s.—Other than the six synapomorphies of Paguroidea previously mentioned, character transformations within the superfamily primarily reflect varying levels of morphological loss, which we interpret as indicative of evolutionary advancement. However, loss is heterochronic and most certainly not stepwise. For example, the loss of calcification in the posterior carapace seen beginning in Diogenidae, Pylojacquesidae, and Parapaguridae is much greater in Paguridae, whereas the same type of loss is more exaggerated in the anterior carapace (shield) in Parapaguridae than in the other families. The maximum number of epipods in Pylochelidae is three in *Mixtopagurus*, but two or one in other genera and/or subgenera of the family. A single epipod is present on each third maxilliped in nine of 20 genera of Diogenidae, but absent in all genera of the remaining families. Similarly, arthrobranch numbers are a maximum 14 pairs in Pylochelidae and some Diogenidae but reduced to 13, 12, or eight in other diogenid genera, and from 13 to nine in certain genera of Paguridae, with further reduction of functional gills in the coenobitids. Progressive reductions in both pleonal calcification and segmentation can be traced from Pylochelidae through Paguridae. The relatively basal, paraphyletic position of Pylochelidae is demonstrated not only by the plesiomorphic retention of paired third through fifth male

pleopods, but in the plesiomorphic states of all of the synapomorphic character states that unite the remaining paguroid families. In addition to those just mentioned, transformations include the tendency toward pereiopod 1 (cheliped) asymmetry; the tendency toward dissimilarity in cheliped armature; pleonal twisting; progressive loss of male paired first and second pleopods; progressive loss of female first pleopods; and asymmetrical loss of female second through fifth pleopods and male third through fifth pleopods. Male pleopod loss is complete in the coenobitids and several pagurid genera.

Five apomorphies set Coenobitidae apart from the remaining other four paguroid families: 1) lateral compression of the ocular peduncles; 2) loss of the flagellum of the first maxilliped; 3) extreme reduction of the crista dentata; 4) reduction in arthrobranch number; and 5) sexual modification of the coxae of the fifth pereiopods. Although there is a clear trend toward decrease in arthrobranchs throughout the paguroids, their marked reduction in the coenobitids appears to be an adaptation to terrestrial life that has evolved independently in numerous decapods (Bliss, 1968). The complete lost of the flagellum of the first maxilliped is an apomorphy shared with Parapaguridae, but a loss that has occurred independently in Hippoidea and to a lesser extent in Galatheoidea s.s. Reduction in the crista dentata also occurs in other paguroids, but it usually is a loss in the number of teeth comprising the structure. At least in *Coenobita clypeatus* (Fabricius, 1787), the crista dentata consists only of a row of minute corneous denticles. This type of reduction may also be an adaptation to changes in feeding habits in the terrestrial environment, although this possibility has not been investigated in any detail. Similarly, the lateral compression of the ocular peduncles may be a terrestrial adaptation in this group considered to possess a degree of adaptation superior to that of many other semiterrestrial decapods (Vannini, 1976). As previously stated, we have considered sexual modification of the male fifth pereiopds in Aegleoidea, Coenobitidae, and Paguridae homologous in the three taxa, but the specific modifications are quite different. Recent detailed anatomical studies (Tudge and Lemaitre, 2006) on the sexual tubes in the coenobitids show that the tubes are heavily calcified and strongly muscular prolongations of the coxal segments themselves, with the gonopores terminal in positions. In contrast, the tubes in the pagurids are, at last in the species studied to date, cuticular sheaths surrounding internal functional extensions of the vasa deferentia (Tudge and Lemaitre, 2004). That the coenobitid sexual tube development represents the precursor to the pagurid tube(s) has yet to be investigated.

Diogenidae share two synapomorphies with the three families of Paguridae: the continuing loss of segmental delineation of the pleon, and the progressive loss of calcification of the sixth pleonal tergite. One apomorphy, the recurved external lobe of the maxillulary endopod, sets Diogenidae apart from these pagurid families. Characters that are plesiomorphic in Pylochelidae, Coenobitidae, and Diogenidae, but apomorphic in Pylojacquesidae, Parapaguridae, and Paguridae include the breadth of thoracic sternite IX (sternite of the third maxillipeds), narrow in the

former trio and broad in the latter, and the reduction in pleurobranchs. The median projection of thoracic sternite IX of Pylojacquesidae is an apomorphy that sets this family apart from Parapaguridae and Paguridae, but it is a character that is paralleled in Kiwaoidea and Aegloidea. The apomorphic loss of the flagellum of the first maxilliped in Parapaguridae is, as previously mentioned, shared with Coenobitidae, Hippoidea, and some galatheoids. An apomorphy involving the last thoracic and first pleonal tergite is manifest as partial fusion in parapagurids and becomes complete in the pagurids. This fusion, however, appears to be a growth-related phenomenon (McLaughlin et al., 2004) and its similar occurrence in Lithodiodea is considered another example of convergence. Loss of pleonal segmentation, beginning as a loss in segmental delineation in Diogenidae, Pylojacquesidae, and Parapaguridae, is virtually complete in Paguridae. This apomorphy develops quite differently in the lithodoid family Hapalogastridae (McLaughlin et al., 2004), and it can only be considered a superficial similarity, perhaps associated with the similarly more reclusive habits of the hapalogastrids. The presence of one or more accessory tooth (teeth) on the crista dentata in the majority, but not all, genera of Paguridae is an apomorphy shared with the preponderance of Pylochelidae, suggesting heterochronic character evolution. Its coincidental occurrence in Lithodoidea has not been investigated developmentally, but clearly can no longer be considered a synapomorphy of the pagurids and lithodids. Although sexual modification of the male coxae of the fifth pereiopods is an apomorphy shared with Aegloidea and Coenobitidae, the unique development of membranous sexual tube(s) in Paguridae represents an evolutionary advancement that sets Paguridae apart from the other two taxa.

Body symmetry was not specifically addressed in the current study, but the overall symmetry of the majority of the pylochelids is in direct contrast to the general asymmetry seen in the remainder of the paguroids. The exception is the monotypic genus *Mixtopagurus*. *Mixtopagurus paradoxus* A. Milne-Edwards, 1880, while having symmetrical chelipeds, has paired but asymmetrical pleopods and uropods. That *Mixtopagurus* actually provides a phylogenetic link to the other families remains to be determined. Asymmetry has often been cited as evidence of the close relationship between the pagurids and lithodoids. In the present study, asymmetries of the chelipeds, pleon, pleopods and uropods were evaluated, and as might be expected, such asymmetry was found only in the paguroids, with the exception of most of the pylochelids, and in the lithodoids. However, is asymmetry really a synapomorphy uniting the paguroids and lithodoids? After applying the definition of similarity provided by Desutter-Grandcolas et al. (2005: 57) ["characters that have evolved to be so similar that they could not be recognized by immediate observation, but cannot meet usual criteria of homology statements"], we think not. The paguroids often have, and the lithodoids virtually always have, asymmetrical chelipeds. However, bilateral asymmetry of the chelipeds is common in many decapods (Palmer, 2004), thus certainly not a synapomorphy uniting the pagurids and lithodoids.

Pleon asymmetry is more restricted. Richter and Scholtz (1994) equated pleon asymmetry to pleopod loss in Parapaguridae, Paguridae, Diogenidae, and Coenobitidae with pleopod loss and tergal asymmetry in females of Lithodoidea. Asymmetry in the pleon occurs in the majority of genera of Paguroidea, except perhaps in Pylochelidae, but this asymmetry is not homologous with pleonal asymmetry seen in Lithodoidea. In Paguroidea s.s., it is principally internal and pertains to the muscular, circulatory and nervous systems (Chapple, 1966; Imafuku, 1993). Externally paguroid pleonal asymmetry is not addressed in this study as it has never been quantified. It is indicated primarily by the pleonal dextral twist (Pérez, 1934; Brightwell, 1951, fig. 1), which involves the entire pleon by tending to shorten the integument on the right side. Because of calcification loss, tergal identity is reduced in some paguroid genera and minimal in others. Only during the developmental stages is it possible to ascertain homologies. Like other decapods, all paguroid megalopae, at least initially, have straight, fully extended pleons with identifiable tergites (McLaughlin et al., 2004). During the molt to first or subsequent juvenile stages, in most "asymmetrical" paguroids tergal identity is reduced or disappears and the pleon develops its characteristic asymmetric torsion, whether or not small gastropod shells are provided (McLaughlin et al, 1989; McLaughlin et al., 1992; Crain and McLaughlin, 1994). This asymmetry, although reinforced by routine shell use, can be environmentally reduced if the habitat changes (Brightwell, 1952; Harvey, 1998; de Saint Laurent and McLaughlin, 2000).

In the lithodoids, asymmetry of the pleon is sexually dimorphic and concerns the development of only pleonal tergites 3-5 of females. The clarification of tergal development in several lithodid species presented by McLaughlin et al. (2004) repudiated the hypothetical homologies between lithodoid and paguroid tergites proposed by Boas (1880a, b, 1924) and Bouvier (1895b, 1897). The pleons of lithodoid megalopae are symmetrical, and remain symmetrical through the first four crab stages; tergal identity, when lost, is lost symmetrically on both sides of the pleon. In species of *Lithodes* and *Paralomis* White, 1856, that have been studied (McLaughlin et al., 2001; 2003 McLaughlin and Paul, 2002), marginal plate development begins at the fourth crab stage, and it is at this stage that sex is usually identifiable and asymmetry first becomes apparent. At crab stage 5 in *L. santolla*, *L. aequispinus* Benedict, 1895, and *Paralomis granulosa* (Jacquinot in Hombron and Jacquinot, 1846), sex is clearly determined because in females, but not in males, pleonal tergites 3-5 on the left side begin increasing in size. In these species, female marginal plate development does not continue on the left of the pleon as it does on the right and on both sides in males. Thus, while the paguroids of both sexes and female lithodoids exhibit pleonal asymmetry, the asymmetry and mechanisms causing it are similar, but not homologous.

Further disparity in ontogenetic asymmetry between the lithodoids and paguroids is seen the pleopods, which, in juvenile individuals, excludes pleopod development on pleomere 1. Richter and Scholtz (1994) stated that in the paguroid families (exclusive of Pylochelidae), pleopods are

present only on the left side of pleomeres 3-5, with still further loss in a few genera and all male lithodoids. Unpaired pleopods 3-5 in adult males are, for the most part, present in genera of these paguroid families. Adult female unpaired pleopods 2-5 occur on the left side of the pleon in the majority of genera of Paguridae, Diogenidae, and Coenobitidae, whereas a vestigial right second pleopod is still present in the majority of genera of Parapaguridae. Complete male pleopodal loss is not limited to the lithodoids, but also occurs in a few pagurid genera, and in all Coenobitidae, Hippoidea, and Aegloidea. All paguroid megalopae develop paired, biramous pleopods on pleomeres 2-5. With the molt to the first or subsequent juvenile stages, changes occur that may include immediate loss or reduction of both second pleopods, loss or reduction of only the pleopods on the right or perhaps initially only loss of some setation and endopodal reduction, with right pleopod loss occurring over several molts (review by McLaughlin et al., 1993). When loss includes the second left pleopod, redevelopment may occur rapidly or after several additional stages (review in McLaughlin et al., 2004). Data on megalopal and/or juvenile pleopod loss in paguroids in which adult male pleopods are absent is not available. However, McLaughlin (2000) reported that in *Porcellano-pagurus edwardsi* Filhol, 1885, pleopods on both sides of the pleon underwent drastic reduction with the molt to crab stage 1. Only very limited data are available for pleopod development in Parapaguridae, but despite their phylogenetic closeness to the pagurids, pleopod development in the parapagurids appears to proceed somewhat differently with symmetry retained in males over a longer juvenile period (Lemaitre and McLaughlin, 1992).

Pleopod loss and redevelopment, like pleonal tergite development, is dimorphic in lithodoids. In some taxa, all traces of megalopal pleopods are lost with the molt to first juvenile, although, as summarized by McLaughlin et al. (2003), stage loss of pleopods varied among genera. Pleopods remain entirely lacking in male lithodoids, but their redevelopment in females does not begin until after asymmetrical development of the tergites of pleomeres 3-5 has commenced. McLaughlin and Paul (2002) found that process to occur at crab stage 6 with minute buds appearing on pleomeres 2-4. Unlike paguroid pleopod development, the lithodoid data available suggest that female pleopod development in this superfamily is closely associated with sexual differentiation and female pleomere development. That lithodoid asymmetry may be under the control of a binary switch (Palmer, 2004) is suggested by the reports of reversed plate development in several lithodid species (Campodonico, 1978; Sandberg and McLaughlin, 1998; Zaklan, 2000; McLaughlin and Paul, 2002). Conversely, while pleopodal antisymmetry (Palmer, 1996) is documented in the diogenid genera *Cancellus* H. Milne Edwards, 1836 and *Paguropsis* Henderson, 1888, pleopodal directional asymmetry appears to be inherited universally in all but the pylochelids.

Although uropodal symmetry is maintained in some paguroid genera other than the pylochelids (Gherardi and McLaughlin, 1995; Imafuku and Ando, 1999, for review), the symmetrical uropods of early stage paguroid megalopae

may begin to indicate impending asymmetry even prior to the molt to first juvenile (McLaughlin et al., 1992; Crain and McLaughlin, 1994). In a study of paguroid asymmetry and growth, Bush (1930) found that while the right uropod of *Pagurus prideaux* (Leach, 1815) (as *Eupagurus*) was always smaller than the left, it increased considerably in relative size during growth. Bush found that the right grew relatively faster than the rest of the body, while the left decreased in relative size, that is, grew relatively slower than the rest of the body. However, as shown by Rodrigues et al. (2002), uropod symmetry and asymmetry may be under environmental rather than genetic control. Males of *Calcinus verrillii* Rathbun, 1901 routinely occupy dextral gastropod shells and have asymmetrical uropods. On the contrary, females of this species commonly occupy tubular gastropod casings and have symmetrical uropods. Uropods may or may not be present in lithodoid megalopae, but if they are, they are markedly reduced, uniramous structures. All traces of uropods are lost at the molt to the first crab stage, and remain absent in both sexes throughout life.

The presumed reversals of the fourth pereiopods in the lithodoids, regarded as an atavism by Boas (1924), can not be substantiated. Richter and Scholtz (1994) suggested that the similarities in spine arrangements among the second through fourth pereiopods in the lithodids and hapalogastrids might indicate that a posteriorly directed genetic shift was responsible for the transformation of the typically modified hermit crab fourth pereiopod back to a functional ambulatory leg. There is no developmental evidence to support that atavism theory, and Scholtz (2004: 9) cautioned that it was not possible to infer the existence or quality of a morphological adult structure from early gene expression data alone.

The monotypic family Pylojacquesidae is most closely allied to Paguridae and Parapaguridae, but the relative relationships among the three taxa are unresolved based on the present characters. Nonetheless, the suggestion by McLaughlin and Lemaitre (2001b) that *Pylojacquesia colemani* is phylogenetically intermediate between Diogenidae and Paguridae is not supported by the present analysis. One character that led McLaughlin and Lemaitre to that conclusion, the separation of the bases of the third maxilliped by a median projection, was interpreted as being structurally intermediate between the approximate positions of the basal segments of the third maxillipeds in diogenids and the broadly separated bases of the appendages in pagurids. The similar development of a median projection on this sternite in Aegloidea and Kiwaoidea has not been investigated in detail, but is considered here to reflect convergence.

The sister relationship between Paguridae and Parapaguridae suggested by Martin and Abele (1986) is equivocal in the present analysis. As indicated above, the relationships among Paguridae, Parapaguridae, and Pylojacquesidae can not be determined on the basis of the generalized characters used at the family level. However, the parapagurid apomorphy, absence of the flagellum of the first maxilliped, appears, as previously indicated, to be a heterochronic tendency toward loss in Paguroidea and parallel losses in Hippoidea and Porcellanidae.

Kiwaiodea.—Two characters not considered in the present analysis appear to be unique apomorphies of Kiwaoidea, namely the structure of the chelae of the fifth pereiopods and the insertion of this pair of appendages on the body below the sternite of seventh somite. The relationship of this superfamily to the rest of Anomura cannot be resolved until gill structure and female morphology are known.

Lomisoidea.—The loss of male pleopods 3-5 is an apomorphy shared with Porcellanidea, Aegloidea, Lithodoidea and some pagurid genera. It is not viewed as parallelism or convergence, but simply as an incomplete and heterchronic loss within the infraorder. As with Kiwaoidea, the relationship of Lomisoidea to the rest of Anomura is unresolved in the present analysis.

Galatheoidea.—Within this major taxon, Galatheidae, like Pylochelidae within Paguroidea, is paraphyletic; however, the development of the carapace lateral projections is an apomorphy of Galatheidae that sets this family apart from the other two. Nonetheless, it is an apomorphy viewed as convergent in the hippoid family Blepharipodidae and the paguroid family Pylochelidae.

Several apomorphies unite the genera of Porcellanidae, some more inclusive than others. For example, the carapace margins are smooth in the majority of genera. but two of the more specious genera have spinose margins, a transformation that we interpret as transitional loss in the majority. The decrease in rostral prominence is an apomorphy shared with several major taxa and considered convergent loss. The fusion of the basal segment of the antennular peduncle is an apomorphy unique to the porcellanids, whereas the expanded or opercular third maxilliped is, as previously noted, is an apomorphy paralleled in Lomisoidea and may be an environmental adaptation in both taxa. The total loss of the crista dentata in porcellanids is further advanced than the loss seen in the coenobitids and may be influenced by differing environmental factors. As with Lomisoidea, the flattening of the chelipeds in the porcellanids is considered an apomorphic response to a specialized habitat. The loss of male first pleopods appears to be a heterochronic loss occurring throughout Anomura. Adult anomuran male first and second pleopods primitively are modified as copulatory structures, but often may be completely absent as is characteristic of the hippoids, lithodoids, and numerous genera of the paguroids. However, only in male porcellanids are the first pleopods always absent, the second frequently present and when so, reproductively modified, and the third through fifth usually rudimentary, vestigial or absent. Female pleopod loss is not common among anomurans, but has been reported in some pagurid genera. However, when female pleopod loss occurs in Paguridae, it is the left fifth pleopod that is usually absent. The complete loss of female second pleopods is an apomorphy unique to Porcellanidae.

Three apomorphies distinguish the family Chirostylidae. These include: 1) the external obliteration of the cervical groove, a loss convergently shared with Lomisoidea; 2) the complete loss of the sternite of the fifth pereiopods, a loss paralleled in Kiwaoidea; and 3) the grooved, furrowed or incised tergal margins of the sixth pleomere, an attribute

seen also in Paguroidea and interpreted as convergent in the two groups.

Aegloidea.—In the present analysis, the aegloids are seen as sister to Lithodoidea. This relationship is in conflict with the spermatological evidence Tudge and Scheltinga (2002) that related aegloids to *Lomis*. Morrison et al. (2002) using mitochondrial gene rearrangement data and Ahyong and O'Meally (2004) using combined molecular and morphological data also found Aegloidae sister to Lomisoidea. However, as indicated above, in our analysis, the relationship of Lomisoidea is unresolved.

Lithodoidea.—The apparent sister clade relationship of Lithodoidea and Hippoidea does not appear to be based on any particular shared synapomorphies. The carriage of the fifth pereiopod under the carapace is an apomorphy of Hippoidea and Lithodoidea that is also shared with Lomisoidea, Aegloidea, and Kiwaoidea. However, two synapomorphies unite the two lithodoid families, namely the sexually dimorphic pleon and the complete loss or uropods. The apomorphies supposedly shared by the lithodoids and paguroids have been discussed previously. Our analysis suggests that of the two lithodoid families, Lithodidae is paraphyletic, whereas Hapalogastridae is distinguished by the reduction in armature of the carapace margins, external obliteration of the cervical groove, weakly defined pleonal segmentation, reduction in calcification of the first pleonal tergite and virtually complete loss of calcification of pleonal tergites 2-5.

Hippoidea.—Within this superfamily, Blepharipodidae is distinguished from the sister clade Albuneidae-Hippidae by the reduction in calcification of pleonal tergite 1. However, this reduction occurs convergently in the lithodoid family Hapalogastridae, the galatheoid family Chirostylidae, and all the paguroid families except Pylochelidae. Albuneidae is set apart from the paraphyletic Hippidae by the reduction in the corneas of the ocular peduncle. This is an apomorphy also seen as parallel evolution in Kiwaoidea.

CONCLUSIONS

As pointed out by Carpenter (2005) the field of "cladistics" has matured in the last 20 or so years. The theory and philosophy of cladistics, so controversial initially, are now overwhelmingly resolved in favor of the phylogenetic point of view. The same may be said for general anomuran alpha taxonomy and the understanding of developmental pathways. The morphological and ontogenetic evidence amassed in the past few years convincingly supports the concept of monophyly in Anomura. The present investigation, based upon an extensive review of external morphological characters, provides the first comprehensive appraisal of overall anomuran phylogenetic relationships. Polyphyly in Paguroidea s.l. and Galatheoidea s.l. has been confirmed, resulting in the removal of Lithodidae from Paguroidea s.s., and Aeglidae and Kiwaidae from Galatheoidea s.s. Superfamilial rank is proposed for each of these three families, bringing the number of superfamilies recognized within the infraorder to seven.

Hypotheses of anomuran phylogenetic relationships will undoubted remain contentious until morphological and molecular studies produce harmonious results. The findings

of the current study must now be tested using markedly expanded molecular and spermatological studies, and perhaps even endophragmal and other internal anatomical attributes that as yet are not available for more than a relatively few representative species.

REFERENCES

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

Alcock, A. 1901. Catalogue of the Indian decapod Crustacea in the collection of the Indian Museum. Part 1. Brachyura. Fascicule I. Introduction and dromides or Dromiacea (Brachyura Primigenia). v-ix, 1-80. Indian Museum, Calcutta.

Alexandrowicz, J. S. 1952. Muscle receptor organs in the Paguridae. Journal of the Marine Biological Association of the United Kingdom 31: 277-286.

Baba, K. 1988. Chirostylid and galatheid crustaceans (Decapoda: Anomura) of the Albatross Philippine Expedition, 1907-1910. Researches on Crustacea, Special Number 2: 1-203.

———. 1989. Chirostylid and galatheid crustaceans of Madagascar (Decapoda, Anomura). Bulletin du Muséum National d'Histoire Naturelle, Paris (4)11 (A): 921-975.

———. 2005. Deep-sea chirostylid and galatheid crustaceans (Crustacea, Decapoda, Anomura) from the Indo-Pacific, with a list of species. Galathea Report 20: 1-317.

———, and A. B. Williams. 1998. New Galatheoidea (Crustacea, Decapoda, Anomura) from hydrothermal systems in the West Pacific Oceana: Bismarck Archipelago and Okinawa Trough. Zoosystema 20: 143-156.

Bate, C. S. 1888. Report on the Crustacea Macrura dredged by H.M.S. Challenger during the years 1872-76. Report on the scientific results of the voyage of H.M.S. Challenger during the years 1873-76. Zoology 24(52): i-xc, 1-942.

Bauer, R. T. 1981. Grooming behavior and morphology in the decapod Crustacea. Journal of Crustacean Biology 1: 153-175.

Benedict, J. E. 1895. Descriptions of new genera and species of crabs of the family Lithodidae with notes on the young of *Lithodes camtschaticus* and *Lithodes brevipes*. Proceedings of the United States National Museum 17: 479-488.

Bliss, D. E. 1968. Transition from water to land in decapod crustaceans. American Zoologist 8: 355-392.

Boas, J. E. V. 1880a. II. Wissenschaftliche Mittheilungen. 1. *Lithodes* und *Pagurus*. Zoologischer Anzeiger 3: 349-352.

———. 1880b. Studier over decapodernes Slægtskabsforhold. Kongelige Danske Videnskabernes Selskabs Skrifter, naturvidenskabelig og mathematisk Afdeling (5)6: 25-210.

———. 1924. Die verwandtschaftliche Stellung der Gattung *Lithodes*. Kongelige Danske Videnskabernes Selskabs Skrifter, Biologiske Meddelelser 4(4): 1-34.

———. 1926. Zur Kenntnis symmetrischer Paguriden. Kongelige Danske Videnskabernes Selskabs Skrifter, Biologiske Meddelelser 5 (6): 1-52.

Borradaile, L. A. 1906. On the classification and genealogy of the reptant decapods. In, J. S. Gardiner (ed.), The Fauna and Geography of the Maldive and Laccadive Archipelagoes, Being an Account of the Work Carried on and of the Collections made by an Expedition During the Years 1899 and 1900. 2: 690-699. University Press, Cambridge.

———. 1916. Crustacea. Part II. *Porcellanopagurus*: an instance of carcinization. In, British Antarctic (Terra Nova) Expedition, 1910. Natural history report. Zoology 3: 111-126.

Bouvier, E.-L. 1894a. Sur les caractères et l'évolution des Lomisinés, nouveau groupe de crustacés anomures. Comptes Rendus des Séances de l'Académie des Sciences 118: 1353-1355.

———. 1894b. Sur la signification de *Hapalogaster* dans l'évolution des Lithodinés. Compte Rendu Sommaire des Séances de la Société Philomathique de Paris 18: 1-5.

———. 1894c. Sur la transformation des Paguriens en crabes anomures de la sous-famille des Lithodinés. Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences 119: 350-352.

———. 1895a. Sur les Lithodinés hapalogastriques *Hapalogaster* et *Dermaturus*. Compte Rendu Sommaire des Séances de la Société Philomathique de Paris 18: 56.

———. 1895b. Recherches sur les affinités des *Lithodes* & des *Lomis* avec les Pagurides. Annales des Sciences Naturelles, Zoologie et Paléontologie (7)18: 157-213.

———. 1896. Sur l'origine homarienne des crabes: étude comparative des Dromiacés vivants et fossiles. Bulletin de la Société de la Philomathique, Paris, Sér. 8, 8: 34-110, figs. 1-43.

———. 1897. La transformation des Bernards l'Ermite en *Lithodes*. Naturaliste (2)19 (230): 41-43.

———. 1940. Faune de France. 37. Décapodes Marcheurs. Paul Lechevalier, Paris. 404 pp.

Bowman, T. E., and L. G. Abele. 1982. Classification of the Recent Crustacea. pp. 1-27. In, L. G. Abele (ed.), The Biology of Crustacea. Vol. 1. Systematics, the Fossil Record and Biogeography. Academic Press, New York.

Boyko, C. B. 2002. A worldwide revision of the Recent and fossil sand crabs of the Albuneidae Stimpson and Blepharipoididae, new family (Crustacea: Decapoda: Anomura: Hippoidea). Bulletin of the American Museum of Natural History 272: 1-396.

———, and A. W. Harvey. 1999. Crustacea Decapoda: Albuneidae and Hippidae of the tropical Indo-West Pacific region. In, A. Crosnier, (ed.) Résults des Campagnes MUSORSTOM. Vol. 20. Mémoirs du Muséum national d'Histoire naturelle 180: 379-460.

Brightwell, L. R. 1951. Some experiments with the common hermit crab (*Eupagurus bernhardus*) Linn. (sic), and transparent univalve shells. Proceedings of the Zoological Society of London 121: 279-283.

———. 1952. Further notes on the hermit crab *Eupagurus bernhardus* and associated animals. Proceedings of the Zoological Society of London 123: 61-64.

Bush, S. F. 1930. Asymmetry and relative growth of parts in the two sexes of the hermit crab *Eupagurus prideauxi*. Archiv für Entwicklung 123: 39-79.

Campodonico, G. I. 1978. Un caso de inversión en la asimetría abdominal de las hembras de *Paralomis granulosa* (Jacquinot) (Decapoda, Anomura, Lithodidae). Anales del Instituto de la Patagonia 9: 231-232.

Carpenter, J. 2005. Editorial. Cladistics 21: 1.

Chapple, W. D. 1966. Asymmetry of the motor system in the hermit crab *Pagurus granosimanus* Stimpson [sic]. Journal of Experimental Biology 45: 65-81.

———. 1969a. Postural control of shell position by the abdomen of the hermit crab, *Pagurus pollicarus* [sic] I. Morphology of the superficial muscles and their nerves. Journal of Experimental Zoology 171: 397-408.

———. 1969b. Postural control of shell position by the abdomen of the hermit crab, *Pagurus pollicarus* [sic] II. Reflex control of the ventral superficial muscles. Journal of Experimental Zoology 171: 409-416.

———. 1969c. Postural control of shell position by the abdomen of the hermit crab, *Pagurus pollicarus* [sic] III. Analysis of movements and calculations of forces exerted by the muscles. Journal of Experimental Zoology 171: 417-424.

———. 1973. Role of the abdomen in the regulation of shell position in the hermit crab *Pagurus pollicarus* [sic]. Journal of Comparative Physiology 82: 317-332.

Crain, J. A., and P. A. McLaughlin. 1994. Larval, postlarval, and early juvenile development in *Pagurus venturensis* Coffin, 1957 (Decapoda: Anomura: Paguridae) reared in the laboratory, with a redescription of the adult. Bulletin of Marine Science 53 [1993]: 985-1012.

Cunningham, C. W., N. W. Blackstone, and L. W. Buss. 1992. Evolution of king crabs from hermit crab ancestors. Nature, London 355: 539-542.

Dana, J. D. 1851. Conspectus crustaceorum quae in orbis terrarum circumnavigatione, Carolo Wilkes e classe reipublicae foederatae duce, lexit et descripsit. (Preprint from) Proceedings of the Academy of Natural Sciences, Philadelphia 5: 267-272.

De Haan, W. 1833-1850. Fauna Japonica auctore Ph. Fr. De Siebold. Crustacea. Lugduni Batavorum. 244 pp.

Desutter-Grandcolas, L., F. Legendre, P. Grandcolas, T. Robillard, and J. Murienne. 2005. Convergence and parallelism: is a new life ahead of old concepts? Cladistics 21: 51-61.

Dixon, C. J., S. T. Ahyong, and F. R. Schram. 2003. A new hypothesis of decapod phylogeny. Crustaceana 76: 935-975.

Fabricius, J. C. 1775. Systema entomologiae, sistens Insectorum classes, ordines, genera, species, adjectis synonymis, locis, descriptionibus, observationibus. Officina Lebraria Kortii, Flensburgi et Lipsiae, xxxii + 832 pp.

———. 1787. Mantissa Insectorum sistens eorum species nuper detectas adjectis characteribus denericis, differentiis specificis, endemdationoibus, observationibus.1: i-xx, 1-348. C. G. Proft, Hafniae.

———. 1798. Supplementum. Entomologia Systematica emendate et aucta . . . adjectis synonymis, locis, observationibus, descriptionibus. Proet et Storch, Hafniae. 572 pp.

Filhol, H. 1885. Considérations relatives à la faune des Crustacés de la Nouvelle-Zélande. Bibliothèque de l'École des Hautes Études, Section des Sciences Naturelles 30(2): 3-60.

Forest, J. 1987. Les Pylochelidae ou "Pagures symetriques" (Crustacea Coenobitoidea). In: Résultats des campagnes MUSORSTOM. Mémoires du Muséum National d'Histoire Naturelle, Série A, Zoologie 137: 1-254.

———. 1995. Crustacea Decapoda Anomura: révision du genre *Trizopagurus* Forest, 1952 (Diogenidae), avec l'établissement de deux genres nouveaux. In, A. Crosnier (ed.), Résultalts des Campagnes MUSORSTOM. Vol. 13. Mémoires du Muséum national d'Histoire naturelle 163: 9-149.

———, and M. de Saint Laurent. 1975. Présence dans la faune actuelle d'un représentant du groupe mésozoïque des Glyphéides: *Neoglyphea inopinata* gen. nov., sp. nov. (Crustacea Decapoda Glypheidae). Compte Rendus Hebdomadaire des Séances de l'Académie des Sciences Paris, série D 281: 155-158.

———, and ———. 1981. La morphologie externe de *Neoglyphea inopinata*, espèce actulle de Crustacé Décapode Glyphéide. In, Résultats des Campagnes MUSORSTOM, 1. Philippines (18-28 mars 1976). Mémoires de ORSTOM 91: 51-84.

———, and ———. 1989. Nouvelle observations à la connaissance de *Neoglyphea inopinata* Forest & de Saint Laurent, à propos de la description de la femelle adulte. In, J. Forest (ed.), Résultats des Campagnes MUSORSTOM. Vol 5. Mémoires du Muséum national d'Histoire naturelle (A) 144: 74-92.

———, ———, P. A. McLaughlin, and R Lemaitre. 2000. The marine fauna of New Zealand: Paguridea (Decapoda: Anomura) exclusive of the Lithodidae. NIWA Biodiversity Memoir 114: 1-250.

Gherardi, F., and P. A. McLaughlin. 1995. Larval and early juvenile development of the tube-dwelling hermit crab *Discorsopagurus schmitti* (Stevens) (Decapoda: Paguridae) reared in the laboratory. Journal of Crustacean Biology 15: 258-279.

Gould, S. J. 1992. We are all monkeys' uncles. Natural History 6/92: 14-21.

Graur, D., and W. Martin. 2004. Reading the entrails of chickens: molecular timescales of evolution and the illusion of precision. Trends in Genetics 20: 80-86.

Haig, J. 1960. The Porcellanidae (Crustacea Anomura) of the Eastern Pacific. Allan Hancock Pacific Expeditions 24: 1-440.

Harvey, A. W. 1998. Genes for asymmetry easily overruled. Nature 392: 345-346.

Heads, M. 2005. Dating nodes on molecular phylogenies: a critique of molecular biogeography. Cladistics 21: 62-78.

Hennig, W. 1966. Phylogenetic Systematics. University of Illinois Press, Urbana.

Henderson, J. R. 1888. Report on the Anomura collected by H.M.S. Challenger during the years 1873-76. Scientific Results of the Exploratory Voyage of HMS Challenger, (Zoology) 27: 1-xi, 1-221. Her Majesty's Stationary Office, Edinburgh etc.

Hombron, J. B., and H. Jacquinot. 1846. Atlas d'Histoire Naturelle Zoologie par MM. Hombron et Jacquinot, chirurgiens de l'expedition, in Voyage au Pôle sud et dans l'Océanie sur les corvettes l'Astrolabe et la Zélée exécuté par ordre du roi pendant les années 1837-1839-1840 sous le commandement de M. Dumont-D'Urville capitaine le Vaisseau publié sous les auspices du departement de la marine et sous la direction superieure de M. Jacquinot, capitaine de Vaisseau, commandant de la Zélée. Dix-Huitième Livraison. Oiseaux pl. 21; Crustaces pls. 3, 4; Insectes coléoptèrez pls. 16, 17. Gide et Baudry, Paris.

Imafuku, M. 1993. Observations on the internal asymmetry of the sternal artery and the cheliped asymmetry in selected decapod crustaceans. Crustacean Research 22: 35-43.

———, and T. Ando. 1999. Behaviour and morphology of pagurid hermit crabs (Decapoda, Anomura) that live in tusk shells (Mollusca, Scaphopoda). Crustaceana 72: 129-144.

Lamarck, J. B. P. A. 1801. Système des Animaux sans Vertèbraes, ou Tableau général des classes des orders et des genres de ces animaux; présentant leurs caractères essentiels et leur distribution, d'après la considération de leur rapports naturels et de leur organization, et suivant l'arrangement établi dans le galéries du Muséum d'Hist. Naturelle parmi leurs dépouilles conservées; précédé du discourse d'ouverture du Cours de Zoologie, donné dans le Muséum National d'Histoire Naturelle l'an 8 de la République. Chez L'auteur, au Muséum d'Hist. Naturelle, Paris. Déterville, Libraire, Paris, viii + 432 pp.

———. 1818. Histoire Naturelle des Animaux sans Vertèbraes, présentant leurs caractères généraux et partiiculaires de ces animaux, leur distribution, leurs classes, leurs familles, leurs genres, et la citation des principales espèces qui s'y rapportent; précédée d'une introduction offrant la détermination des caractères essentieles de l'Animal, sa distinction du végétal et des autres corps naturels, enfin, l'Exposition des Principes fondamentaus de la Zoologie. 5: 1-612. Déterville and Verdiére, Paris.

Latreille, P. A. 1806. Genera Crustaceorum et Insectorum secundum Ordinem naturalem in Familias disposita, Iconibus Exemplisque plurimis explicata. 1: 1-302 Apud Amand Koenig Bibliopolam, Parisiis et Argentorati.

———. 1816. Les Crustacés, les Arachnides et les Insectes. Vol. 3. In, G. Cuvier (ed.), Le Regne Animal, distribué d'après son Organisation, pour server de Base à l'Histoire naturelle des Animaux et de l'Introduction à l'Anatomie Comparée. Déterville, Paris.

Leach, W. E. 1815. Malacostraca Podophthalmata Britanniae: or descriptions of such British species of the Linnean genus *Cancer* as have their eyes elevated on footstalks. James Sowerby, London. 124 pp.

———. 1820. Galathéadées. Dictionnaire des Sciences Naturelles 18: 49-56. F. G. Levrault, Strasbourg.

Lemaitre, R. 1996. Hermit crabs of the family Parapaguridae (Crustacea: Decapoda: Anomura) from Australia: species of *Strobopagurus* Lemaitre, 1989, *Sympagurus* Smith, 1883 and two new genera. Records of the Australian Museum 48: 163-221.

———. 1999. Crustacea Decapoda: a review of the species of the genus *Parapagurus* Smith, 1879 (Parapaguridae) from the Pacific and Indian Oceans. In, A. Crosnier (ed.), Résultats des Campagnes MUSORSTOM. Vol. 20.Mémoires du Muséum national d'Histoire naturelle 180: 303-378.

———. 2004. Crustacea Decapoda: A worldwide review of the hermit crab species of the genus *Sympagurus* Smith, 1883. In, B. Marshall and B. Richer de Forges (eds.), Tropical Deep-Sea Benthos, 23. Mémoires du Muséum national d'Histoire naturelle 191: 85-149.

———, and P. A. McLaughlin. 1992. Descriptions of megalopa and juveniles of *Sympagurus dimorphus* (Studer, 1883), with an account of the Parapaguridae (Crustacea: Anomura: Paguroidea) from Antarctic and Subantarctic waters. Journal of Natural History 26: 745-768.

Lopretto, E. C. 1979. Estudio comparative del quinto par de pereiópodos en los representantes del gênero *Aegla* de la Patagonia Argentina (Crustacea Anomura). Neotropica 25(73): 9-22.

———. 1980a. Análisis de las características del quinto pereiópodos en las especies de *Aegla* del grupo "*platensis*" (Crustacea Anomura Aeglidae). Physis B 39(96): 37-56.

———. 1980b. Clave para la determinación de la especies del gênero *Aegla* del la República Argentina en base al studio comparative del quinto par de pereiópodos masculinos (Crustacea Anomura Aeglidae). Limnobios 1: 431-436.

———. 1981. Consideraciones sobre la estructura apendicular vinculada al dimorfismo sexual en los machos de la especies de *Aegla* del noroeste Argentino (Crustacea, Anomura, Aeglidae). Acta Zoologica Lilloana 36(2): 15-35.

MacDonald, J. D., R. B. Pike, and D. I. Williamson. 1957. Larvae of the British species of *Diogenes*, *Pagurus*, *Anapagurus* and *Lithodes* (Crustacea, Decapoda). Proceedings of the Zoological Society of London 128: 209-257.

Macpherson, E. 1988. Revision of the family Lithodidae Samouelle, 1819 (Crustacea, Decapoda, Anomura) in the Atlantic Ocean. Monografías de Zoología Marina 2: 1-153.

———. 1993. Crustacea Decapoda: species of the genus *Paramunida* Baba, 1988 (Galatheidae) from the Philippines, Indonesia and New Caledonia. In, A. Crosnier (ed.), Résultats des Campagnes MUSORSTOM. Vol. 10. Mémoires du Muséum national d'Histoire naturelle 156: 443-473.

———. 1994. Crustacea Decapoda: Studies on the genus *Munida* Leach, 1820 (Galatheidae) in New Caledonian and adjacent waters with descriptions of 56 new species. In, A. Crosnier (ed.), Résultats des Campagnes MUSORSTOM. Vol. 12. Mémoires du Muséum national d'Histoire naturelle 161: 421-569.

———. 1995. Crustacea Decapoda: Species of the genus *Munida* Leach, 1820 and *Paramunida* Baba, 1988 (Galatheidae) from the seas around the Wallis and Futuna Islands. In, A. Crosnier (ed.), Résultats des Campagnes MUSORSTOM. Vol. 15. Mémoires du Muséum national d'Histoire naturelle 168: 387-421.

———, W. Jones, and M. Segonzac. 2005. A new squat lobster family of Galatheoidea (Crustacea, Decapoda, Anomura) from the hydrothermal vents of the Pacific-Antarctic Ridge. Zoosystema 27: 709-723.

Maddison, W. P. 1993. Missing data versus missing characters in phylogenetic analysis. Systematic Biology 42: 576-581.

———, and D. R. Maddison. 1992. MacClade, version 3. Analysis of phylogeny and character evolution. Sinauer Associates, Inc., Sunderland, Massachusetts.

Makarov, V. V. 1938. Rakoobraznyey. Anomura. [Crustaces Decapodes anomures]. In, A. A. Shtakel'berg (ed.), Fauna SSSR, (n. ser.) 16, (10) (3): i-x, 1-324. Akademii Nauk SSSR, Moscow and Leningrad.

———. 1962. Fauna of U.S.S.R. Crustacea, Anomura 10(3): 1-278 Jerusalem: Israel Program for Scientific Translation. Published for the National Science Foundation and Smithsonian Institution, Washington, D.C. [English translation.]

Martin, J. W., and L. G. Abele. 1986. Phylogenetic relationships of the genus *Aegla* (Decapoda: Anomura: Aeglidae), with comments on anomuran phylogeny. Journal of Crustacean Biology 6: 576-616.

———, and ———. 1988. External morphology of the genus *Aegla* (Crustacea: Anomura: Aeglidae). Smithsonian Contributions to Zoology 453: 1-46.

———, and G. E. Davis. 2001. An updated classification of the Recent Crustacea. Natural History Museum of Los Angeles County, Science Series 39: 1-124.

McLaughlin, P. A. 1983a. A review of the phylogenetic position of the Lomidae (Crustacea: Decapoda: Anomala). Journal of Crustacean Biology 3: 431-437.

———. 1983b. Hermit crabs—are they really polyphyletic? Journal of Crustacean Biology 3: 608-621.

———. 2000. Megalopal and early crab stages of *Porcellanopagurus edwardsi* Filhol Decapoda: Anomura: Paguridea). Proceedings of the Biological Society of Washington 113: 721-730.

———. 2003. Illustrated keys to the families and genera of the superfamily Paguroidea (Crustacea: Decapoda; Anomura), with supplemental diagnoses of the genera of the Paguridae. In, R. Lemaitre and C. C. Tudge (eds.), Biology of the Anomura. Proceedings of a symposium at the Fifth International Crustacean Congress, Melbourne, Australia, 9-13 July 2001. Memoirs of Museum Victoria 60: 111-144.

———, and R. Lemaitre. 1997. Carcinization—fact or fiction? I. Evidence from adult morphology. Contributions to Zoology 67: 79-123.

———, and ———. 2001a. Aspects of evolution in the anomuran superfamily Paguroidea. One larval prospective. Invertebrate Reproduction and Development 38: 159-169.

———, and ———. 2001b. A new family for a new genus and new species of hermit crab of the superfamily Paguroidea (Decapoda: Anomura) and its phylogenetic implications. Journal of Crustacean Biology 21: 1062-1076.

———, and J. M. Paul. 2002. Abdominal tergite and pleopod changes in *Lithodes aequispinus* Benedict, 1895 (Decapoda: Anomura: Lithodidae) from megalopa to juvenile. Proceedings of the Biological Society of Washington 115: 138-147.

———, and A. J. Provenzano, Jr. 1974. The genus *Paguristes* (Crustacea: Decapoda: Diogenidae) from the western Atlantic. Part I. The *Paguristes tortugae* complex, with notes on variation. Bulletin of Marine Science 24: 165-234.

———, and M. de Saint Laurent. 1998. A new genus for four species of hermit crabs heretofore assigned to the genus *Pagurus* Fabricius (Decapoda: Anomura: Paguridae). Proceedings of the Biological Society of Washington 111: 158-187.

———, J. A. Crain, and R. H. Gore. 1992. Studies on the *provenzanoi* and other pagurid groups: VI. Larval and early juvenile stages of *Pagurus ochotensis* (Brandt) from the eastern North Pacific reared under laboratory conditions. Journal of Natural History 26: 507-531.

———, R. H. Gore, and W. R. Buce. 1989. Studies on the *provenzanoi* and other pagurid groups: III. The larval and early juvenile stages of *Pagurus kennerlyi* (Stimpson) (Decapoda: Anomura: Paguridae) reared in the laboratory. Journal of Crustacean Biology 9: 626-644.

———, R. Lemaitre, and C. C. Tudge. 2004. Carcinization in the Anomura—Fact or Fiction? Part II. Evidence from larval, megalopal and early juvenile morphology. Contributions to Zoology 73: 165-205.

———, F. A. Siddiqui, and J. A. Crain. 1993. Larval and early juvenile development in *Pagurus stevensae* Hart, 1971 (Decapoda: Anomura: Paguridae) reared in the laboratory. Journal of Crustacean Biology 13: 322-342.

———, K. Anger, A. Kaffenberger, and G. A. Lovrich. 2001. Megalopal and early juvenile development in *Lithodes santolla* (Molina) (Decapoda: Anomura: Paguroidea: Lithodidae), with notes on zoeal variation. Invertebrate Reproduction and Development 40: 53-67.

———, ———, ———, and ———. 2003. Larval and early juvenile development in *Paralomis granulosa* (Jacquinot) (Decapoda: Anomura: Paguroidea: Lithodidae), with emphasis on abdominal changes in megalopal and crab stages. Journal of Natural History 37: 1433-1452.

McLay, C. L. 1993. Crustacea Decapoda: the sponge crabs (Dromiidae) of New Caledonia and the Philippines with a review of the genera. In, A. Crosnier (ed.), Résultats des Campagnes MUSORSTOM. Vol. 10. Mémoires du Muséum national d'Histoire naturelle 156: 111-251.

———. 1999. Crustacea Decapoda: revision of the family Dynomenidae. In, A. Crosnier (ed.), Résultats des Campagnes MUSORSTOM. Vol. 20. Mémoires du Muséum national d'Histoire naturelle 180: 427-569.

Milne-Edwards, A. 1880. Report on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico, and in the Caribbean Sea, 1877, 78, 79, by the United States Coast Survey steamer "Blake", Lieut.-Commander C. D. Sigsbee, U.S.N., and Commander J. R. Bartlett, U.S.N., commanding. VIII. Études préliminaires sur les Crustacés. Bulletin of the Museum of Comparative Zoology, Harvard College 8(1): 1-68.

———, and E.-L. Bouvier. 1894. Considérations générales sur la famille des Galathéidés. Annales des Sciences Naturalles, Zoologie et Paléontologie 16: 191-327.

———, and ———. 1897. Report on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico, and in the Caribbean Sea, 1877, 78, 79, by the United States Coast Survey steamer "Blake", Lieut.-Commander C. D. Sigsbee, U.S.N., and Commander J. R. Bartlett, U.S.N., commanding. XXXV. Description des Crustacés de la Famille des Galathéidés recueillis pendant l'Expedition. Bulletin of the Museum of Comparative Zoology, Harvard College 19: 1-68.

Milne Edwards, H. 1836. Observations zoologiques sur les Pagures et description d'un nouveau genre de la tribu des Paguriens. Annales des Sciences Naturelle Zoologie, Paris (2)6: 257-288.

———. 1837. Histoire naturelle des Crustacés, comprenant l'anatomie, la physiologie et la classification de ces animaux. 2: 1-532 Librairie Encyclopédique de Roret, Paris.

Molina, G. I. 1782. Saggio sulla storoia naturale del Chile. Bologna. 367 pp.

Morrison, C. L., A. W. Harvey, S. Lavery, K. Tieu, Y. Huang, and C. W. Cunningham. 2002. Mitochondrial gene rearrangements confirm the parallel evolution of the crab-like body form. Proceedings of the Royal Society, London 269: 345-350.

Nixon, K. C., and J. M. Carpenter. 1993. On outgroups. Cladistics 9: 413-426.

———, and J. I. Davis. 1991. Polymorphic taxa, missing values and cladistic analysis. Cladistics 7: 233-242.

Palmer, A. R. 1996. From symmetry to asymmetry: phylogenetic patterns of asymmetry variation in animals and their evolutionary significance. Proceedings of the National Academy of Science USA 93: 14279-14286.

———. 2004. Symmetry breaking and the evolution of development. Science 306: 828-833.

Paul, D. H. 1989. A neurophylogenetist's view of decapod crustaceans. Bulletin of Marine Science 45: 487-504.

———. 2003. Neurobiology of the Anomura (Crustacea: Decapoda). In, R. Lemaitre and C. C. Tudge (eds.), Biology of the Anomura. Proceedings of a symposium at the Fifth International Crustacean Congress, Melbourne, Australia, 9-13 July 2001. Memoirs of Museum Victoria 60: 3-11.

———, A. M. Than, and D. S. Magnuson. 1985. Evolution of the telson neuromusculature in decapod Crustacea. Biological Bulletin 168: 106-124.

Pennant, T. 1777. Crustacea. Mollusca. Testacea. Vol. 4. vii + [12], 1-136. In, British Zoology. Fourth edition. [1776-1777]. Benjamin White, London.

Pérez, C. 1934. Exposés de biologie zoologique. I. Les Pagures ou Bernard l'ermite (un example d'adaptation). Actualités scientifiques et industrielles, Paris 101: 1-33.

Pérez-Losada, M., C. G. Jara, G. Bond-Buckup, and K. A. Crandall. 2002a. Phylogenetic relationships among the species of *Aegla* (Anomura: Aeglidae) freshwater crabs from Chile. Journal of Crustacean Biology 22: 304-313.

———, ———, ———, M. L. Porter, and K. A. Crandall. 2002b. Phylogenetic position of the freshwater anomuran family Aeglidae. Journal of Crustacean Biology 22: 670-676.

———, ———, ———, and K. A. Crandall. 2004. Molecular systematics and biogeography of the southern South American freshwater "crabs" *Aegla* (Decapoda: Anomura: Aeglidae) using multiple heuristic tree search approaches. Systematic Biology 53: 767-780.

Pike, R. B. 1947. *Galathea*. Liverpool Marine Biology Committee Memoirs 34: 1-138.

Pilgrim, R. L. C. 1960. Muscle receptor organs in some decapod Crustacea. Comparative Biochemistry and Physiology 1: 248-257.

———. 1965. Some features in the morphology of *Lomis hirta* (Lamarck) (Crustacea: Decapoda) and a discussion of its systematic position and phylogeny. Australian Journal of Zoology 13: 545-557.

Porter, M. L., M. Pérez-Losada, and K. A. Crandall. 2005. Model-based multi-locus estimation of decapod phylogeny and divergence times Molecular Phylogenetics and Evolution 37: 355-369.

Rathbun, M. J. 1901. Recent papers relating to the fauna of the Bermuda. American Journal of Science (4)11: 328.

Richter, S., and G. Scholtz. 1994. Morphological evidence for a hermit crab ancestry of lithodids (Crustacea, Decapoda, Anomala, Paguroidea). Zoologischer Anzeiger 223: 187-219.

Richter de Forges, B. 2006. Découverte en mer du Corail d'une deuxième espèce de glyphéide (Crustacea, Decapoda, Glypheoidea). Zoosystema 28: 17-29.

Rodrigues, L. J., D. W. Dunham, and K. A. Coates. 2002. The effect of shelter type on uropod symmetry in *Calcinus verrilli* [sic] (Anomura: Diogenidae). Journal of Crustacean Biology 22: 298-303.

Saint Laurent, M. de, and P. A. McLaughlin. 2000. Superfamily Paguroidea, Family Paguridae. In, J. Forest, M. de Saint Laurent, P. A. McLaughlin, and R. Lemaitre (eds.), The Marine Fauna of New Zealand: Paguridea (Decapoda: Anomura) Exclusive of the LithodidaeNIWA Biodiversity Memoir 114: 104-209.

Sandberg, L., and P. A. McLaughlin. 1998. Crustacea, Decapoda, Paguridea. Marine Invertebrates of Scandinavia 10: 1-113. Universitetsforlaget, Oslo.

Schmitt, W. L. 1942. The species of *Aegla*, endemic South American freshwater crustaceans. Proceedings of the United States National Museum 91: 431-520.

Scholtz, G. 2004. Introduction. In, G. Scholtz (ed.), Evolutionary Developmental Biology of Crustacea Crustacean Issues 15: 3-16. A. A. Balkema. Lisse.

———, and S. Richter. 1995. Phylogenetic systematics of the reptantian Decapoda (Crustacea, Malacostraca). Zoological Journal of the Linnean Society 113: 289-328.

Schram, F. R. 2001. Phylogeny of decapods: moving towards a consensus. Hydrobiologia 449: 1-20.

———, and S. T. Ahyong. 2002. The higher affinities of *Neoglyphea inopinata* in particular and the Glypheoidea (Decapoda, Reptantia) in general. Crustaceana 75: 629-635.

Shaul, S., and D. Graur. 2002. Playing chicken (*Gallus gallus*): methodological inconsistencies of molecular divergence data estimates due to secondary calibration points. Gene 300: 59-61.

Simmons, N. B., and J. H. Geisler. 2002. Sensitivity analysis of different methods of coding taxonomic polymorphism: an example from higher-level bat phylogeny. Cladistics 18: 571-584.

Stephens, P. J. 1986. The fused thoracic-abdominal ganglion of the hermit crab (*Pagurus pollicaris*): neuromuscular relationships in the thoracic and abdominal flexor muscles. Journal of Experimental Biology 123: 201-216.

Stimpson, W. 1858. Prodromus descriptionis animalium evertebratorum, quae in expeditione ad oceanum Pacificum septentrionalem, a Republica Federate missa, Cadwaldaro Ringgold et Johanne Rodgers ducibus, obseravit et descripsit. VII. [Preprint (December 1858) from] Proceedings of the Academy of Natural Sciences of Philadelphia 1858: 225-252.

Strong, E. E., and D. Lipscomb. 1999. Character coding and inapplicable data. Cladistics 15: 363-371.

Swofford, D. L. 2002. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Sinauer Associates, Inc., Sunderland, Massachusetts.

Tudge, C. C. 1997. Spermatological evidence supports the taxonomic placement of the Australian endemic hairy stone crab, *Lomis hirta* (Decapoda: Anomura: Lomidae). Memoirs of the Museum of Victoria 56: 235-244.

———, and R. Lemaitre. 2004. Studies of male sexual tubes in hermit crabs (Crustacea, Decapoda, Anomura, Paguroidea). I. Morphology of the sexual tube in *Micropagurus acantholepis* (Stimpson, 1858), with comments on function and evolution. Journal of Morphology 259: 106-118.

———, and ———. 2006. Studies of male sexual tubes in hermit crabs (Crustacea, Decapoda, Anomura, Paguroidea). II. Morphology of the sexual tube in the land hermit crabs, *Coenobita perlatus* and *C. clypeatus* (Coenobitidae). Crustacean Research, Special Number 6: 121–131.

———, and D. M. Scheltinga. 2002. Spermatozoal morphology of the freshwater anomuran *Aegla longirostris* Bond-Buckuup & Buckup, 1994 (Crustacea: Decapoda: Aeglidae) from South America. Proceedings of the Biological Society of Washington 115: 118-128.

———, B. G. M. Jamieson, L. Sandberg, and C. Erséus. 1998. Ultrastructure of the mature spermatozoon of the king crab *Lithodes maja* (Lithodidae, Anomura, Decapoda): further confirmation of a lithodid-pagurid relationship. Invertebrate Biology 117: 57-66.

Vannini, M. 1976. Researches on the coast of Somalia. The shore and the dune of Sar Uanle. 7. Field observations on the periodical transdunal migrations of the hermit crab *Coenobita rugosus* Milne Edwards. Monitore Zoologico Italiano, n.s. supplemento 7(3): 145-185.

White, A. 1856. Some remarks on Crustacea of the genus *Lithodes*, with a brief description of a species apparently hitherto unrecorded. Proceedings of the Zoological Society of London 1856: 132-135.

Whiteaves, J. F. 1874. Report on further deep-sea dredging operations in the Gulf of St. Lawrence. American Journal of Science (3)7: 210-219.

Wiens, J. J. 1995. Polymorphic characters in phylogenetic systematics. Systematic Biology 44: 482-500.

———. 1998a. The accuracy of methods for coding and sampling higher-level taxa for phylogenetic analysis: a simulation study. Systematic Biology 47: 398-413.

———. 1998b. Testing phylogenetic methods for tree congruence: phylogenetic analysis of polymorphic morphological characters in phrynosomatid lizards. Systematic Biology 47: 427-444.

Wiley, E. O. 1981. Phylogenetics. The Theory and Practice of Phylogenetic Systematics. John Wiley and Sons, New York, etc. 439 pp.

Wilkinson, M. 1995. A comparison of two methods of character construction. Cladistics 11: 297-308.

Wolff, T. 1961. Description of a remarkable deep-sea hermit crab with notes on the evolution of the Paguridae. Galathea Report 4: 11-32.

Yang, Z. 2004. A heuristic rate smoothing procedure for maximum likelihood estimation of species divergence times. Acta Zoologica Sinica 50: 645-656.

Zaklan, S. D. 2000. A case of reversed asymmetry in *Lithodes maja* (Linnaeus, 1758) (Decapoda, Anomura, Lithodidae). Crustaceana 73: 1019-1022.