

Recent Advances and Conflicts in Concepts of Anomuran Phylogeny (Crustacea: Malacostraca)

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> Abstract

In the debate over phylogenetic relationships within the Decapoda that has raged for more than a century, the Anomura has been the source of many “conflicts”, including disagreements over which taxa belong in this morphologically diverse infraorder, and even what name is appropriate (Anomura or Anomala). The Anomura currently includes 17 families, 222 genera, and about 2,469 species, although 54% of the genera and 43% of the species are paguroids. A number of studies have summarized the traditional as well as recent concepts of the infraorder that were based on morphology. This review addresses modern studies on systematics of this group over the last two decades that have been based on molecular as well as morphological data, and which have continued to add controversy to concepts of anomuran phylogeny. The landmark study by C.W. Cunningham and co-workers (published in ‘Nature’ in 1992), proclaiming that molecular data confirmed the traditional hypothesis on the evolution of king crabs from hermit crabs, was the catalyst for several studies on anomuran evolution that followed, and is the starting point of this review. Modern studies are divided as follows, and discussed: 1) morphological, larval and molecular phylogenies exclusively of the Paguroidea and/or Anomura; 2) spermatologically derived phylogenies; 3) information from the fossil record; 4) phylogenetic assessments of anomuran taxa included in general decapod analyses; and 5) auxiliary information pertaining to the Paguroidea in general, and Pylochelidae in particular. These studies have made useful contributions to understanding the “big picture” of anomuran relationships but they also have limitations. It is concluded that the Anomura remains today as much a source of discord as it was a century ago, and “conflicts” in analyses will continue to cloud the landscape until more basic, complete information is gathered for all members of this intriguing and varied infraorder.

> Key words

Anomura, phylogenetic relationships, modern concepts, conflicts, review.

1. Introduction

In the debate over phylogenetic relationships within the Decapoda Latreille, 1802 that has continued for more than a century, the Anomura has been the source of many of the “conflicts.” Not only have disagreements flared over which taxa belong in this infraorder, but even what name is appropriate. McLAUGHLIN & HOLTHUIS (1985) reviewed the historical aspects and ultimately concluded that this major taxon should be comprised of the superfamilies Galatheoidea Sa-

mouelle, 1819, Hippoidea Latreille, 1825, Lomisoidea Bouvier, 1894 (as Lomoidea) (not 1895 as cited by MARTIN & DAVIS 2001), and Paguroidea Latreille, 1802 and bear the name Anomura MacLeay, 1838 in preference to older, but less frequently used, Anomala Latreille, 1816. Both the name and the hierarchy within the infraorder have yet to gain complete acceptance. And, as TAVARES (2003) pointed out, the lingering uncertainties about the ‘primitive crabs’ remain a per-

manent threat to the higher classification of both the Anomura and Brachyura. We begin this review by initially accepting the Anomura as proposed by MARTIN & DAVIS (2001). Recent advances in several avenues of systematics, however, have resulted in continuing controversies regarding our concepts of anomuran phylogeny. Although our focus is on modern conflicts and concepts, a brief summary of the more prominent classification schemes used in the past to define the Anomura provides an informative prelude to our discussion (see Appendix).

A historical background of the taxa that have been at one time or another included in the Anomura or Anomala was provided by McLAUGHLIN et al. (2007), although they did not mention, for the most part, the various characters used to propose the different classifications. To define their classifications, early carcinologists used characters such as: pleon type, whether it was straight and well developed or folded under the cephalothorax (LATREILLE 1816) or intermediate between straight and folded (H. MILNE EDWARDS 1837), mouthpart morphology (DE HAAN 1841), or degree of cephalization (DANA 1853). Based on mode of life, BOAS (1880) placed the Anomala in his Reptantia or "creepers". BORRADAILE (1906) derived the Anomala from the Thalassinidea based on six characters that in his view separated these two groups from other decapods: reduction of the pleon, free carapace not fused to the epistome, presence of a movable antennal scale, shape of endopod of first maxilliped, presence of 'appendices internae' on pleopods, and third pair of maxillipeds not covering the mouth. BOUVIER (1940) used: separation of epistome from the carapace and lack of its clear fusion to the first pleonal somite; presence of 'linea anomurica'; reduced or non-existent rostrum; narrow endopod of the first maxilliped; epipods reduced or absent on first and third maxillipeds, absent on second maxilliped; reduced fifth pereopod terminating in chela or subchela; and larval characteristics. Larval characters were also used by GURNEY (1942) and MACDONALD et al. (1957). The classifications used by WATERMAN & CHACE (1960) and BOWMAN & ABELE (1982) in two major treatises on crustacean biology were each based on up-to-date advances at the time, whereas DE SAINT LAURENT'S (1979) was based on her phyletic re-evaluation of the Decapoda as a whole, and SCHRAM'S (1986) incorporated fossil evidence.

2. Modern concepts

The first challenges to the traditional classification of the Anomura as given by BOWMAN & ABELE (1982) were those of McLAUGHLIN (1983a,b) and MARTIN

& ABELE (1986). McLAUGHLIN (1983a) removed the monotypic Lomisidae Bouvier, 1894 (as Lomidae) from the Paguroidea, elevating it to its own superfamily. McLAUGHLIN (1983b) suppressed the superfamily Coenobitoidea Dana, 1851, uniting the six then recognized hermit crab families, Pylochelidae Bate, 1888, Coenobitidae Dana, 1851, Diogenidae Ortmann, 1892, Paguridae Latreille, 1802, Parapaguridae Smith, 1882 and Lithodidae Samouelle, 1819, under the superfamily Paguroidea. In contrast, MARTIN & ABELE (1986) found the families Lomisidae (as Lomidae) and Lithodidae (Hapalogastrinae and Lithodinae) to be sister group to the remaining Paguroidea. However, it was the startling proclamation "From a hermit to a king" on the cover of the February 6, 1992 issue of the journal 'Nature' that propelled paguroid phylogeny into the arena of major scientific interest. In an article in that issue entitled "Evolution of king crabs from hermit crab ancestors", CUNNINGHAM et al. (1992) alleged that their molecular data proved not only the traditional hypothesis that hermit crabs (Paguridae) gave rise to king crabs (Lithodidae) through carcinization and peramorphosis (ALBERCH et al. 1979), but that the relationship was so close that king crabs were nested in the common hermit crab genus *Pagurus* Fabricius, 1775 (see Fig. 1). CUNNINGHAM et al.'s (1992) data also disassociated the diogenid species *Clibanarius vittatus* (Bosc, 1802) and an unidentified species of the terrestrial coenobitid genus, *Coenobita* Latreille, 1829 from the other paguroids. Interestingly, in a similar molecular study, SPEARS et al. (1993) found the dromiid *Hypoconcha arcuata* Stimpson, 1858 more closely related to *C. vittatus* than to a second dromiid, *Cryptodromiopsis antillensis* (Stimpson, 1858), raising not only the question of the relationship of the primitive crabs to the Anomura, but the accuracy of mitochondrial DNA as an indicator of phylogenetic relationships, at least when too few taxa were utilized in the analyses. CUNNINGHAM et al. (1992) strengthened their molecularly based hypothesis with implications of morphological, larval and fossil support. This landmark study was the catalyst for the numerous analyses of phylogenetic relationships within the Anomura and among reptant decapods that have followed. Although several avenues subsequently have been explored in some detail, the resulting phylogenies rarely have been congruent. We will first review the methods and results of post-CUNNINGHAM et al. (1992) phylogenetic studies that have focused directly on the Anomura in general and the Paguroidea in particular, and then consider the conflicts that have arisen when only few exemplars have been taken as representative of one or more of the anomuran superfamilies during the examination of decapod relationships.

2.1. Morphological, larval and molecular phylogenies exclusively of the Paguroidea and/or Anomura

The first was the morphologically based phylogenetic analysis by RICHTER & SCHOLTZ (1994), again with the focal point being the relationship between hermit crabs and lithodids (Fig. 2). Using a Hennigian approach, these authors concluded that while the “symmetrical” hermit crab family Pylochelidae was paraphyletic, the remaining paguroid families constituted a monophyletic taxon of “asymmetrical” hermit crabs. They included taxa from all hermit crab groups and used as outgroup members of Galatheoidea, Hippoidea, Lomoidea and Reptantia. Their study addressed CUNNINGHAM et al.’s (1992) carcinization and peramorphosis only in their conclusion that the lithodid characters they had considered reflected a change toward a free-living habit. RICHTER & SCHOLTZ (1994) emphasized the asymmetrical pleopod loss and pleonal asymmetry, fusion of the last thoracic and first pleonal sternites, division of the second through fifth pleonal tergites, fusion of the basal articles and displaced sensory hairs of the antennular flagellum, and the presence of accessory teeth on the ischium of the third maxilliped as apomorphies uniting the families Paguridae and Lithodidae.

Also using only morphological evidence, McLAUGHLIN & LEMAITRE (1997) addressed the matter of carcinization, asking whether the phenomenon actually occurred as had been hypothesized since its introduction in the late nineteenth century as a means of explaining the transformation of a shell-dwelling hermit crab into a free roaming lithodid. They applied cladistic methods in an unusual way to show evolutionary pathways of a set of adult morphological characters, rather than phylogenetic relationships; however, their results had implications suggestive of relationships (Fig. 3). McLAUGHLIN & LEMAITRE (1997) argued that for any hypothesis to be tenable the assumption had to be made that hermit crabs ancestrally had membranous pleons that were protected by dextral (although they mistakenly stated “sinistral”) gastropod shells. They then asked how, if a shell or some other protective covering for a soft and membranous pleon conferred a survival advantage, could not owning one provide a greater advantage? McLAUGHLIN & LEMAITRE (1997) reasoned that for the traditional hypotheses of carcinization to be correct, either the shell dwelling hermits for some inexplicit reasons chose to forsake safe mobility, or that an unexplainable disappearance of shells compelled some hermit crabs to adapt to adverse conditions by becoming free-living. They suggested that there was no factual evidence that hermit crabs were first and foremost shell-dwelling crustaceans. As we

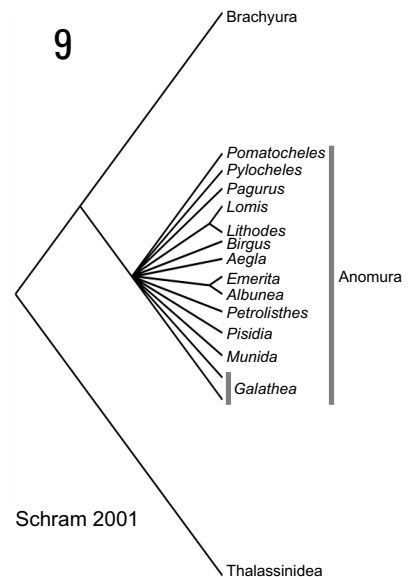
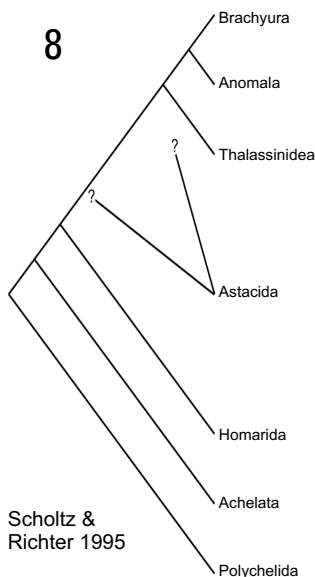
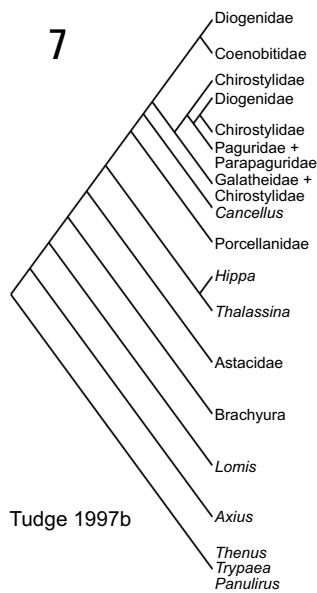
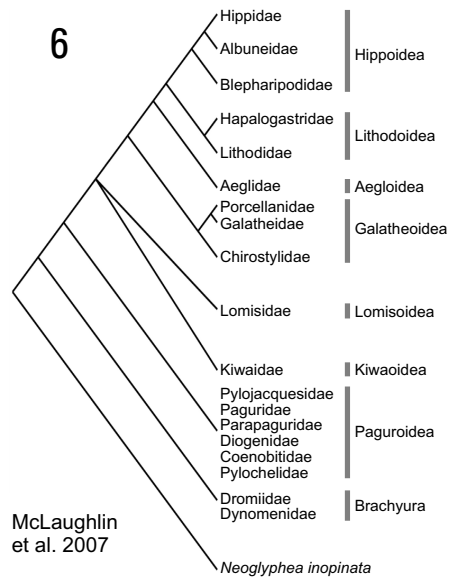
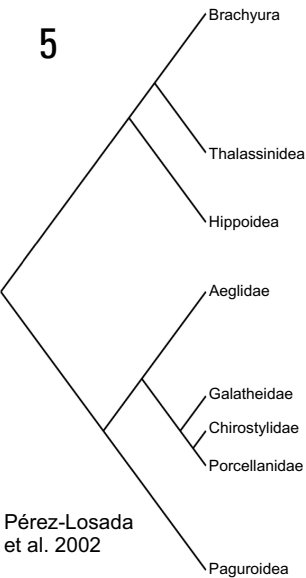
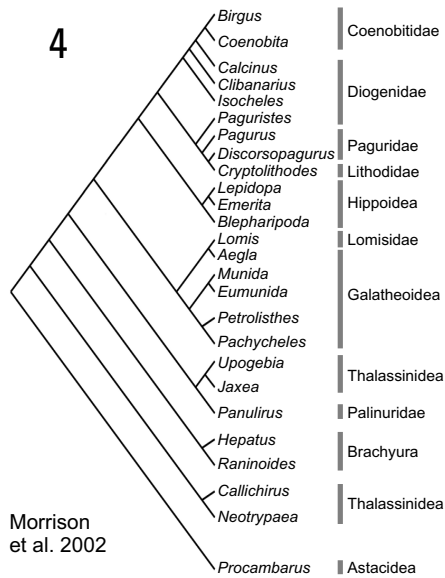
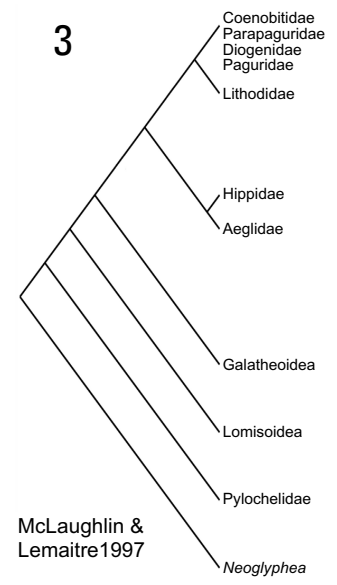
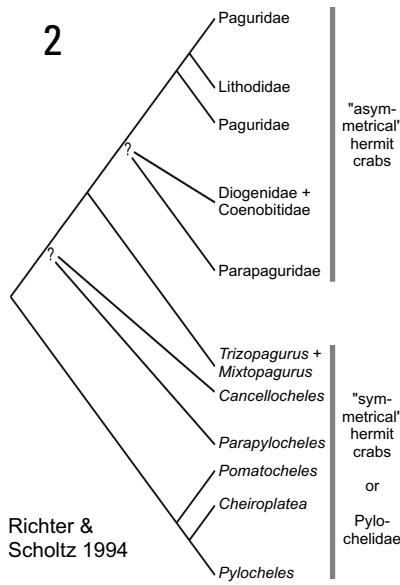
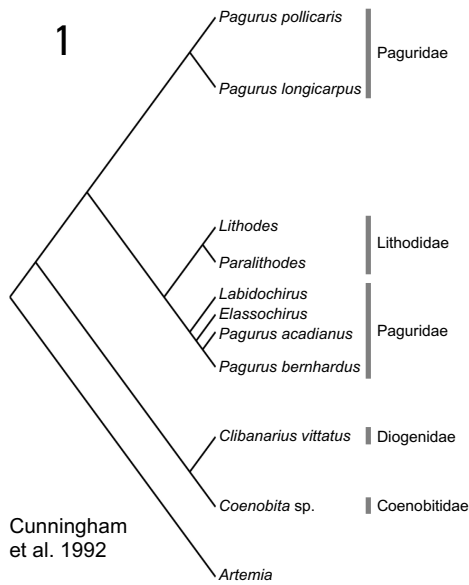
will describe shortly, the fossil record now provides some information that was not available to McLAUGHLIN & LEMAITRE (1997).

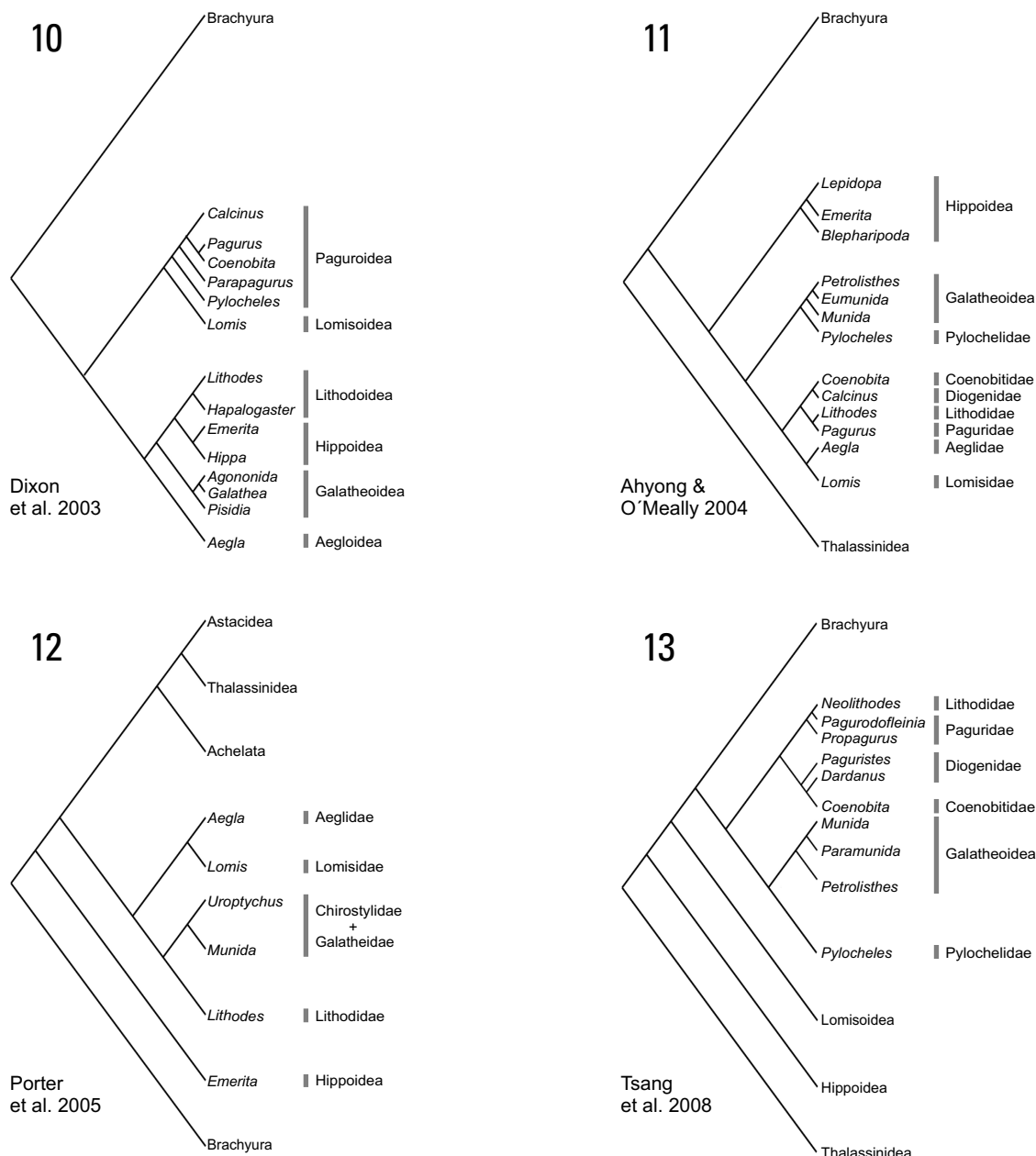
Although their emphasis was on the Paguroidea and the relationship between lithodids and pagurids, McLAUGHLIN & LEMAITRE (1997) also examined the evidence of carcinization in the other major taxa of the Anomura. While disputing the claim of CUNNINGHAM et al. (1992) that hermit crabs gave rise to lithodids through carcinization, they acknowledged that the acquisition of a crablike body form had been achieved independently in several anomuran groups.

Unbeknown to McLAUGHLIN & LEMAITRE (1997) at the time, VON STERNBERG (1996), in a little quoted discourse, similarly had supported the CUNNINGHAM et al. (1992) concept of lithodid evolution from a hermit crab ancestor. Quoting SLUYS (1989), VON STERNBERG (1996) referred to carcinization in the Anomura as representing a ‘rampant’ process of parallelism. Specifically, VON STERNBERG (1996: 154), was of the opinion that “the carcinization events which have occurred in the Anomura thus represent true homoplasies, i.e., parallelisms genetically and ontogenetically uncoupled from each other and with the unique carcinization event characterizing the brachyurans”. In his proposed model of carcinization based on *Hox* gene expression, VON STERNBERG suggested that anomuran carcinization represented complete expression (e.g. lithodids), partial expression (e.g. the parapagurid *Probeebei* Boone, 1926) and repression (e.g. *Pagurus*) of *Hox* and homeotic gene regulatory circuitry. However, he presented no data, and as far as we know, his model has not been tested.

A similar series of parallel pathways for carcinization was provided by the molecular analysis of MORRISON et al. (2002), although their Anomura included the Thalassinidea Latreille, 1831, as well as the superfamilies Galatheoidea, Hippoidea, Paguroidea and Coenobitoidea. In addition to the conclusion that the crab-like body form evolved independently in several anomuran taxa, these authors found molecular support for the monophyly of the Anomura exclusive of the Thalassinidea (Fig. 4). Within the Anomura, the Aeglididae Dana, 1852 grouped with the Lomisidae rather than the other Galatheoidea; the distinctiveness of the Hippoidea was supported, as was the monophyly of “asymmetrical” hermit crabs, including lithodids. However, representatives of “symmetrical” hermit crabs were not included in their study.

MORRISON et al. (2002) were not the only investigators to question the inclusion of the Aeglididae in the Galatheoidea. In a series of molecularly based investigations, PÉREZ-LOSADA et al. (2002a,b, 2004) examined the intra- and interfamilial relationships of the monotypic Aeglididae and other galatheoids (Fig. 5). These authors found strong evidence to sug-





Figs. 1–13. Phylogenetic relationships of anomuran groups as proposed or inferred by various recent studies. Presumed basal groups are on lower sides of cladograms.

gest that *Aegla* Leach, 1820 was a polyphyletic genus and that the conflicting results between gene trees and alpha taxonomy might represent unrecognized species. Their results also demonstrated a clear separation of the Aeglididae from other galatheoid families. MACPHERSON et al. (2005) similarly found unquestionable molecular separation of the Aeglididae from the remaining Galatheoidea as well as from their own new family, Kiwaidae Macpherson, Jones & Segonzac, 2005. Nevertheless, none of these authors formally removed the Aeglididae from the Galatheoidea.

Unlike the conflicts seen among analytical results derived from morphological, molecular, larval and

spermatological studies, several molecular studies also have been used successfully to differentiate taxa within the Galatheoidea. For example, MANTELATTO et al. (2006) convincingly demonstrated, through the use of partial fragment analysis of 16S DNA, the genetic distinctiveness of the monotypic paguroid genus *Loxocheloes* Forest, 1964, which had been suggested as possibly being a junior synonym of *Isocheles* Stimpson, 1858 by FOREST & DE SAINT LAURENT (1968) and others. Within the Galatheoidea, MACPHERSON & MACHORDOM (2001) and JONES & MACPHERSON (2007), found from comparisons of morphological characters and molecular sequences, corroboration such that the

sequence divergences confirmed the specific values of certain morphological characters in the genus *Raymunida* Macpherson & Machordom, 2000 and in Eastern Pacific species of *Munidopsis* Whiteaves, 1874. MACPHERSON & MACHORDOM (2004) used a similar combination of methods to detect cryptic speciation in the genus *Munida* Leach, 1820 and CABEZAS et al. (2008) were able to confirm the monophyly of a new genus of galatheids with molecular evidence.

Despite its "longevity", the Hippoidea had received little taxonomic or phylogenetic attention until quite recently. BOYKO & HARVEY (1999) and BOYKO (1999, 2000) published descriptive accounts of regional species from the Indo-West Pacific, Hawaiian and Marquesas Islands. But in a monographic study of the Albuneidae Stimpson, 1858 sensu lato worldwide, BOYKO (2002) provided the morphological information that will allow future phylogenetic studies addressing the relationships among albuneids, between this group and other hippoids, and among other anomurans. However, in one of the few molecular studies of intrageneric relationships in the family Hippidae Latreille, 1825, HAYE et al. (2002) found conflicts between the genetic and morphological concepts of the family, once again demonstrating that anomuran relationships often are not easily evaluated.

At the time that molecular and morphological evidence appeared to be providing momentum for the "hermit to king" hypothesis, the morphological arguments of McLAUGHLIN & LEMAITRE (1997) against this evolutionary scenario received some much needed support from the larval sector. Three studies on the megalopal and very early juvenile development of five species of lithodids (CRAIN & McLAUGHLIN 2000a,b; McLAUGHLIN & LEMAITRE 2001a) provided the first evidence that the long standing proposed evolution of the pleonal tergites of king crabs was not as it had been hypothesized. Specifically, as previously noted, RICHTER & SCHOLTZ (1994) were of the opinion that the Lithodidae retained divided pleonal tergites from their hermit-crab-like ancestors and in members of one subfamily, the intervening gaps were filled by secondary calcification, either as nodules as in *Lithodes maja* (Linnaeus, 1758), or segmental plates as in *Paralomis granulosa* (Jacquinot, in Hombron & Jacquinot, 1846). Even with the limited data available, McLAUGHLIN & LEMAITRE (2001a) were able to demonstrate that lithodid pleonal tergite structure was the result of decalcification and sundering, not secondary calcification and fusion. But only when the tergal changes occurring through the first six or more lithodid juvenile stages had been documented (McLAUGHLIN et al. 2001; McLAUGHLIN & PAUL 2002; McLAUGHLIN et al. 2003) could McLAUGHLIN et al. (2004) confidently reject the traditional hypotheses regarding pleonal tergite transformations. Similarly, carcinization and

peramorphosis, as the causal factor in the evolution from "hermit to king" (CUNNINGHAM et al. 1992) had been shown to be a convergent phenomenon throughout the Anomura (McLAUGHLIN & LEMAITRE 1997; MORRISON et al. 2002). However, several of RICHTER & SCHOLTZ's (1994) apomorphies presumably uniting pagurids and lithodids remained unchallenged.

In a reappraisal of hermit crab phylogeny, McLAUGHLIN et al. (2007) specifically addressed the long standing assumption that asymmetry was an apomorphy uniting lithodids with paguroids (Fig. 6). These authors presented evidence strongly supporting their hypothesis that pleonal asymmetry in the two taxa was not homologous. Additionally, they pointed out, as PALMER (2004) had, that cheliped asymmetry could not be considered a strong synapomorphy of lithodids and paguroids because it was common to many decapods. Similarly, McLAUGHLIN et al. (2007) demonstrated that the partial pleopod loss seen in paguroids was not homologous with the total male and partial female pleopod loss of lithodids.

McLAUGHLIN & LEMAITRE's (1997) analysis was not limited to the Paguroidea. They also evaluated all of the anomuran superfamilies using families as terminal taxa. Their analysis, consisting of 79 characters for all 17 known anomuran families, and/or subfamilies, and three outgroup species resulted in a proposed new classification. Polyphyly of the Paguroidea resulted in the removal of the Lithodidae and subsequent elevation of that taxon to superfamily rank of Lithodoidea, with families Lithodidae and Hapalogastriidae Brandt, 1850. Polyphyly of the Galattheoidea similarly resulted in the removal of the Aeglididae and Kiwaididae and their elevation to superfamily ranks, the Aegloidea and Kiwaoidea respectively.

2.2. Spermatologically derived phylogenies of the Paguroidea and/or Anomura

In a relatively early study of spermatozoa ultrastructure as a tool of phylogenetic assessment in the Anomura, TUDGE (1992) presented a "branching tree" of hermit crab sperm types, based on data drawn from TUDGE & JAMIESON (1991) and HINSCH (1980). The two genera of the Coenobitidae were closely linked and showed similarities with the diogenid genera *Dardanus* Paulson, 1875 and *Diogenes* Dana, 1851; that clade was the sister group to the three species of *Clibanarius* Dana, 1852 included in the study. All were distantly remote from the only pagurid representative, *Pagurus bernhardus* (Linnaeus, 1758).

In a greatly expanded database of 42 anomuran and 9 non-anomuran taxa and 32 spermatozoal and spermatophore characters, TUDGE (1997b) produced an

interesting, albeit somewhat astonishing, cladogram of a 50% majority consensus tree (Fig. 7). In a previous study, TUDGE (1997a) had already concluded that on the basis of spermatological evidence there was no close relationship between the Lomisidae and the Lithodidae represented by *Lithodes maja* as described from light microscope drawings by RETZIUS (1909), but it was surprising to see *Lomis hirta* (Lamarck, 1818) in an unresolved relation with two brachyuran species. *Lithodes maja* was not included in TUDGE's (1997b) phylogenetic assessment, but its spermatozoal morphology subsequently was described in detail by TUDGE et al. (1998). Other surprising relationships in TUDGE's (1997b) analysis included *Hippa pacifica* (Dana, 1852) grouped with a thalassinid; a clade including species of Coenobitidae (*Diogenes*, *Dardanus*, *Calcinus* Dana, 1851 and *Strigopagurus* Forest, 1995), was distinctly separated from a second clade that included species of Diogenidae (*Clibanarius*), Paguridae (*Pagurus*, *Xylopagurus* A. Milne-Edwards, 1880, *Porcellanopagurus* Filhol, 1885), Parapaguridae (*Sympagurus* Smith, 1883), Chirostylidae Ortmann, 1892 (*Uroptychus* Henderson, 1888, *Eumunida* Smith, 1883), and species of Galatheidae (*Allogalatea* Baba, 1969, *Munida* Leach, 1820, *Munidopsis* Whiteaves, 1874). The diogenid genus *Cancellus* H. Milne Edwards, 1836 was distantly removed, as were species of the Porcellanidae Hayworth, 1825. In a more recent study, TUDGE et al. (2001) found the spermatozoal morphology of an unidentified species of the pylochelid subgenus *Pylocheles* (*Bathycheles*) Forest, 1987 like no other anomuran spermatozoa studied to date. The specimens of this "unidentified species" have recently been shown to represent a new species, *Bathycheles phenax* McLaughlin & Lemaitre (2009). TUDGE et al. (2001) were of the opinion that the differences exhibited by this species when compared to other anomurans were as great as the differences observed between the spermatozoa of primitive brachyuran crabs and those of the more advanced families. Although phylogenetic relationships determined by spermatozoal evidence seem, at least in part, as contentious as those obtained by morphological and molecular methods, the recent study by TIRELLI et al. (2008) indicated spermatological monophyly in at least the diogenid genera *Calcinus* and *Clibanarius*. The spermatozoal morphology of three examined species of hippoids also provides additional evidence of monophyly of the Hippoidea (TUDGE et al. 1999). Similarly, spermatozoal evidence from the aeglid *Aegla longirostris* Bond-Buckup & Buckup, 1994 confirmed the distinctness of the family Aeglididae and supported its separation from the Galatheoidea (TUDGE & SCHELTINGA 2002). Additionally, spermatozoal evidence (TUDGE & JAMIESON 1996a,b) also supports the dichotomy in the Porcellanidae suggested by LEBOUR

(1943), GORE (1971), and others based on larval differences.

2.3. Information from the fossil record

Using temporal scaling, CUNNINGHAM et al. (1992) estimated that king crabs diverged from their pagurid ancestors in the lower Miocene, and ZAKLAN (2002) suggested such divergence may have been enhanced through protection provided by recently evolved canopy-producing kelp. Although CUNNINGHAM et al.'s (1992) molecular clock methodology has been criticized (SHAUL & GRAUR 2002; GRAUR & MARTIN 2004; HEADS 2005), the discovery by FELDMANN (1998) of a fossil species of *Paralomis* White, 1856 from the Miocene of New Zealand might support their proposition, although Feldmann expressed the belief that the lithodid fossil record extended well beyond the Miocene; those fossils simply had not been found yet.

In contrast to the Brachyura Latreille, 1802, which has a substantial fossil record, relatively few anomuran fossils are known. Four genera in each of the superfamilies Galatheoidea and Paguroidea were cited by GLAESSNER (1969) as occurring as early as the Jurassic, with the Lomisoidea and Hippoidea reported Recent taxa. As may be seen by the review of SCHWEITZER & FELDMANN (2000) eight galatheid genera currently have fossil records dating back to the Middle or Upper Jurassic. The freshwater Aeglididae, until recently also included in the Galatheoidea, similarly was considered of fairly recent origin. However, FELDMANN (1984) described the first fossil aeglid from Late Cretaceous marine rocks in New Zealand, suggesting that its freshwater endemicity might be recently evolved. The geologic occurrence of the Aegloidea was moved even earlier, to the Early Cretaceous, and its range extended to the northern hemisphere by the discovery of a second fossil genus in the Tlayúa formation in Mexico (FELDMANN et al. 1998). Four confirmed fossil hippoids were reported by BOYKO (2002) dating back to the Middle and Late Eocene. AMATI et al. (2004) evaluated the phylogenetic relationships among decapod taxa using fossil and extant taxa, and although their focus was on astacid lobsters, their cladistic analysis showed the Paguridae (*Pagurus*) to be sister group to the Galatheidae (*Galathea*). These recent studies and discoveries might make it tempting to suggest that the ancestral anomuran was a galatheid-like decapod, however, anomuran fossil history is just beginning to unfold.

Unfortunately, the paguroids in the fossil record have been known primarily from isolated chelipeds (SCHWEITZER & FELDMANN 2001), making even generic placement uncertain at best, as discussed in detail by SCHWEITZER et al. (2005). Because of this difficulty,

the prior Jurassic occurrences of paguroids continue to be suspect. A few descriptions of in situ gastropod shell-inhabiting hermit crabs have placed paguroids in the Upper Cretaceous (MERTIN 1941; JAGT et al. 2000, 2006), Miocene (HYDEN & FOREST 1980; FELDMANN & KEYES 1992), and Oligocene (KARASAWA 2002), but only the specimen reported by HYDEN & FOREST (1980) was in sufficiently good condition to permit identification. It was described as *Pagurus clifdenensis* Hyden & Forest, 1980 and subsequently transferred to the genus *Diacanthurus* McLaughlin & Forest, 1997, by the latter authors. But the most interesting report of a paguroid fossil is that of FRAAIJE (2003) who described a perfectly preserved Early Cretaceous hermit crab found occupying the shell of an ammonite cephalopod. FRAAIJE (2003) suggested that the discovery of this hermit crab, apparently a diogenid judging from the description of the larger left cheliped, might explain the absence of hermit crabs in gastropod shells of Jurassic and Early Cretaceous ages. He noted that paleontologists may have focused their attentions on the wrong class of mollusks in their attempts to analyze the evolution of hermit crabs. However, VAN BAKEL et al. (2008) have just provided us with even more tantalizing data. These paleontologists report on the discovery of a series of Jurassic age carapaces that most convincingly belong to paguroids, including two that appear assignable to families of the Pylochelidae. These are the first examples of fossilized paguroid carapaces and the first positive confirmations of paguroid occurrence in the Jurassic period. More importantly, these first fossil records of pylochelids add a new dimension to the puzzle of “who begat whom.”

2.4. Phylogenetic assessments of anomuran taxa included in general decapod analyses

Having already reviewed relationships within the Anomura (RICHTER & SCHOLTZ 1994), SCHOLTZ & RICHTER (1995) then undertook an assessment of phylogenetic relations within the Decapoda Reptantia (Fig. 8). For the Anomura (as Anomala), these authors cited several apomorphies they believed demonstrated the monophyly of the infraorder. In addition, they discerned two higher monophyletic taxa within the anomuran infraorder, one comprised of the Galatheaidea and Hippoidea and the second represented by *Lomis* and the hermit crabs, including coenobitids and lithodids. However, when anomuran taxa are included in broader phylogenetic analyses, often quite unexpected relationships appear. For example, SCHRAM (2001) re-examined the reptant decapod character set of SCHOLTZ & RICHTER (1995). After converting their

raw data to a numerical matrix suitable for parsimony analysis, SCHRAM (2001) found only a few exceptions to the initial results of SCHOLTZ & RICHTER (1995), but a strict consensus of 32,700 trees resulted in a multitude of polychotomies (Fig. 9). Nevertheless, the Anomura again was found to be monophyletic, with *Lomis hirta* and *Lithodes maja* resolved as sister taxa. SCHRAM's (2001) matrix was then reconfigured with additional characters from BURKENROAD (1981), and while resolution by 50% majority rule was better for the overall relationships among reptants, *L. maja* was still distinctly separated from *Pagurus bernhardus*. Further data manipulations by SCHRAM (2001) produced other 50% consensus trees, all of which allied *L. maja* to the Galatheaidea and Aegliidae.

DIXON et al. (2003) also attempted to resolve the ongoing debate over relationships within the Decapoda (Fig. 10) using a suite of morphological characters. Their analysis was based on 70 characters for 60 taxa, which they treated as both unordered and ordered in generating majority rule consensus trees. In their unordered tree, the Galatheaidea, exclusive of the Aegliidae, was sister group to the Hippoidea; the Lomisoidea was sister group to the Paguroidea and the two representatives of the subfamilies of the Lithodidae were unresolved. When the analysis was ordered, a similar majority consensus again produced a tree in which the two families of Lithodidae were together sister group to the Hippoidea and that clade in turn was sister group to the Galatheaidea, exclusive of the Aegliidae; the relationships of the Lomisoidea and families of the Paguroidea remained unchanged. Given what they considered the convincing evidence presented by CUNNINGHAM et al. (1992), RICHTER & SCHOLTZ (1994) and MORRISON et al. (2002), DIXON et al. (2003) suggested that the separation of the Lithodidae from the remainder of the Paguroidea might have been caused by the remarkably derived form of the lithodids. However, as in those previous studies, sample sizes were small. In the DIXON et al. (2003) analysis, paguroids (including lithodids) accounted for only seven of the 60 taxa examined, while the entire anomuran representation was only 14 taxa.

An apparent conflict between molecular and morphological data emerged in the recent investigation by AHYONG & O'MEALLY (2004) (Fig. 11). Although their scope again was a phylogeny of reptant decapods in general, data from their three molecular loci placed the Hippoidea as sister group to a weakly supported clade of *Lomis*, *Aegla*, *Lithodes* and *Pagurus*, whereas *Coenobita* and *Calcinus* were sister group to *Pylocheles* A. Milne-Edwards, 1880, and the Galatheaidea, exclusive of *Aegla*. In contrast, their morphological data produced a quite different strict consensus tree. With weak support for the positions of *Lomis* and *Lithodes*, the Anomura were displayed as three clades, the first

consisting of *Lomis*, *Lithodes*, *Pylocheles*, *Coenobita*, *Calcinus* and *Pagurus*, the second with the genus pair *Eumunida* and *Munida*, and the third with the genus pair *Aegla* and *Petrolisthes* Miers, 1876 sister group to the Hippoidea. However, when the data were combined and weighted for minimized incongruences, *Lomis* was paired with *Aegla*, the genus pair *Pagurus* and *Lithodes* was sister group to the genus pair *Calcinus* and *Coenobita*. *Pylocheles* and *Munida* were sister group to the genus pair *Eumunida* and *Petrolisthes*, and the Hippoidea formed a separate clade. Although AHYONG & O'MEALLY (2004) found strong support for the monophyly of the Anomura, they noted, correctly, that internal relationships were less stable and support for indicated patterns was weak. Particularly unexpected was the grouping of the Pylochelidae with the Galattheoidea, exclusive of the Aeglidae, rather than the Paguroidea. Nevertheless, their results, like those of previous studies, supported the separation of the Aeglidae from the Galattheoidea. Of the 44 taxa of the ingroup, 13 were anomurans, each representing one family.

Two molecularly based studies of decapod phylogeny have been published more recently and with even more diametrically opposed conclusions. The study by PORTER et al. (2005), while not including the Paguroidea in their sample of anomurans (as Anomala), placed the Brachyura and Anomura as basal reptant lineages, a position contradictory to all previous analyses (Fig. 12). These authors concluded that their hypothesis of reptant relationships would force re-interpretation of many of the morphological characters currently used to define decapod lineages. Additionally, they pointed out that their basal positions of the Brachyura and Anomura were supported by the current understanding of the fossil record, which well might be true, given the most recent additions to galatheid and paguroid fossils.

The latest published phylogeny of the Decapoda by TSANG et al. (2008) adds another dimension to the molecular playing field (Fig. 13). These authors called attention to the short comings of mitochondrial and nuclear ribosomal DNA markers, and suggested that the use of nuclear protein genes would provide a more reliable reconstruction of the phylogeny of the infraorders of the Decapoda. TSANG et al.'s (2008) results did not provide a robust phylogeny of the Anomura. Like the molecular results of AHYONG & O'MEALLY (2004) they found the Pylochelidae aligned with the Galattheoidea, which is not surprising since the same species, *Pylocheles* (*Xylocheles*) *macrops* Forest, 1987 was the molecular source for both studies. As additional support for this alignment, the authors of both papers cited TUDGE et al.'s (2001) report that sperm morphology of *Pylocheles* (*Bathycheles*) sp. differed from all other hermit crabs. What AHYONG & O'MEALLY (2004)

and TSANG et al. (2008) omitted from TUDGE et al.'s evaluation was the latter's observation, as previously noted, that the sperm of pylochelids, as represented by that one species, was not only different from all other hermit crabs but from all other studied anomurans and that difference was as great as the difference seen between primitive crabs and more advanced brachyurans. That a single species of *Pylocheles* can not accurately reflect the spermatological structure, molecular make up, or morphology of the family is discussed in the following section. In addition to the non-paguroid placement of the Pylochelidae, TSANG et al. (2008) found the Lithodidae nested within the Paguridae, and the Coenobitidae nested within the Diogenidae. These authors found that while their results supported the conclusions reached in earlier studies of the relationship between pagurids and lithodids, effectively challenging the superfamily rank proposed by McLAUGHLIN et al. (2007), they were unable to robustly resolve the positions of several major clades within the Anomura. The fact that TSANG et al.'s (2008) analysis was based on only 13 anomuran species might be a contributing factor to weakness of their results.

2.5. Auxiliary information pertaining to Paguroidea in general and Pylochelidae in particular

In a series of studies just completed, the phylogeny of the Pylochelidae has been investigated on morphological and to a lesser extent on developmental levels. A cladistic analysis of the family, with species or subspecies as terminal taxa, utilized 79 morphological characters for 42 of the 46 assigned taxa in the six subfamilies and confirmed the accurate assignment of the Pylochelidae to the Paguroidea (LEMAITRE et al. 2009; McLAUGHLIN & LEMAITRE 2009). However, of the six subfamilies proposed by FOREST (1987) only three were supported: Pylochelinae Bate, 1888, Pomatochelinae Stebbing, 1914 and Trizochelinae Forest, 1987. Clear distinctions separate these three subfamilies, both morphologically (McLAUGHLIN & LEMAITRE 2009) and developmentally (McLAUGHLIN & LEMAITRE 2008). Only minuscule larval, molecular and spermatological data currently are available. However, we have accumulated sufficient morphological data to recognize that differences among the three subfamilies, and among the tribes of the Trizochelinae, are of such magnitude that it is questionable that even a single exemplar of each subfamily will sufficiently represent its major taxon. For these reasons, a single species representing the entire Pylochelidae cannot give accurate input to any phylogenetic appraisal, be it morphological or molecular.

TSANG et al. (2008) also questioned the monophyly of the Diogenidae, and probably with merit. Although monophyly of the Paguroidea is hard to disavow when its numerous unique apomorphies are considered, it is highly probable that with further in-depth study of the other paguroid families, none, except perhaps the Coenobitidae and Pylojacquesidae McLaughlin & Lemaître, 2001b, will be found to be monophyletic. While it is always tempting to strive to solve the “big picture”, the Anomura remains today as much a source of discord as it was a century ago. Conflicts in analyses will continue to cloud the landscape until more basic information is gathered for all members of this infraorder.

3. Conclusions

In his progress review of the phylogeny of decapods SCHRAM (2001) stated that there is general agreement that the Decapoda is monophyletic. He also lamented, however, the lack of clarity in regard to which groups within the Decapoda were monophyletic. Indeed our review of recent concepts has shown that while some advancements have been made on deciphering the composition and relationships within the Anomura, there is still considerable controversy. The conclusions of several phylogenetic studies based on molecular data, in particular, are contradictory. That conflicts exist in modern studies is not surprising, given that not all have included all anomuran groups in their analyses, or have in some cases used taxa that can not accurately represent large or phylogenetically poorly known anomuran families. Furthermore, most studies have not focused exclusively on ascertaining the phylogenetic relationships of the Anomura, but instead have concentrated on larger groups within the decapods or the entire Decapoda. Thus, only a few conclusive statements can be made about the phylogenetic knowledge of anomurans specifically, and these can be summarized as follows:

- (1) Despite numerous studies, there is still conflicting evidence on the relationships between the Anomura and the “primitive crabs” or Podotremata (TAVARES 2003; AHYONG et al. 2007).
- (2) Most recent studies based on morphology and molecules conclude that the Anomura and Brachyura are monophyletic sister clades, the two forming the Meiura (SCHOLTZ & RICHTER 1995; SCHRAM 2001; DIXON et al. 2003; AHYONG & O’MEALLY 2004).
- (3) Several studies have consistently placed the Thalassinoidea outside of the Anomura, although there is still debate over whether the former are monophyletic or not (e.g., AHYONG & O’MEALLY 2004).
- (4) The Lomisoidea is monophyletic, although there is uncertainty as to which is its sister group (e.g., McLAUGHLIN et al. 2007).
- (5) The Hippoidea appear to be monophyletic but this needs rigorous phylogenetic testing.
- (6) There is solid evidence that the Aeglidae is outside the Galatheoidea, although it is unclear which is the sister group (e.g., MORRISON et al. 2002; PORTER et al. 2005; McLAUGHLIN et al. 2007).
- (7) The families Galatheidae, Chirostylidae, Porcellanidae of the Galatheoidea still need rigorous phylogenetic testing, as does the Kiwaidae, a taxon originally placed in the Galatheoidea and then elevated to superfamily rank by McLAUGHLIN et al. (2007), not an elevation accepted by BABA et al. (2008).
- (8) The composition of the Paguroidea *sensu lato* has been revised recently based on morphological and developmental evidence, and the family Lithodidae removed to its own superfamily (McLAUGHLIN et al. 2007).
- (9) Within the Paguroidea, LEMAITRE et al. (2009) confirmed the parapyly of the Pylochelidae originally proposed by RICHTER & SCHOLTZ (1994), although molecular studies are needed to explore the possible polyphyly of this family suggested by larval data, and other families still need to be fully analyzed.

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Appendix: influential classifications of the Anomura 1816–1986

LATREILLE (1816)

Section “Anomaux” or Anomalia

Albunées
Hippes
Remipèdes
Pagures
Porcellanes
Galathées

H. MILNE EDWARDS (1837)

Section Anomoures

Family Apterures
Tribe Dromiens
Tribe Homoliens [included
Lithodes, *Lomis*]
Tribe Raniniens
Tribe Pactoliens
Family Ptérygures
Tribe Porcellaniens
Tribe Hippiciens
Tribe Paguriens

DE HAAN (1841)

Anomala

Family Galatheidea
Family Porcellanidea
Family Hippidea
Family Paguroidea
Family Lithodeacea

STIMPSON (1858)

Anomoura

Teleosomi
Synopsis Dromideorum
[included Latreillidea,
Homolidea, Raninidea]
Schizosomi
Synopsis Porcellanideorum
Synopsis Hippideorum
Synopsis Lithodideorum
[included *Lomis*]
Synopsis Pagurideorum

DANA (1852)

Tribe Anomoura

Section I. Anomoura Superiora
Subtribe Dromidea
Families Dromidae, Cymopolidae
Subtribe Bellidea
Family Bellidae
Subtribe Raninidea

Family Raninidae
Section II. Anomoura Media
Subtribe Hippidea
Family Hippidae
Subtribe Porcellanidea
Family Porcellanidae
Section III. Anomoura Submedia
Subtribe Lithodea
Family Lithodidae
Section IV. Anomoura Inferiora
Subtribe Paguridea
Families Paguridae, Cenobitidae
Subtribe Aegleidea
Family Aeglidae
Subtribe Galatheidea
Family Galatheidae

BOAS (1880)

Section Anomala

Families Hippidae, Paguridae, Galatheidae

ORTMANN (1896)

Reptantia [abandoned use of Anomura]

Division Thalassinidea
Division Paguridea
Division Galatheidea
Division Hippidea
Division Dromiidea

BORRADAILE (1906)

Suborder Anomura

Tribe Hippidea
Tribe Galatheidea
Tribe Thalassinidea
Tribe Paguridea
Subtribe Pagurinea
Subtribe Lithodinea

BOUVIER (1940)

Section Anomura

Tribu I. Paguridea
Families Pylochelidae, Paguridae,
Lomisidae, Lithodidae
Tribu II. Galatheidea
Families Aeglidae, Chirostylidae,
Galatheidae, Porcellanidae
Tribu III. Hippidea
Families Albuneidae, Hippidae

GURNEY (1942)

Superfamily Galatheidea

Families Aeglidae, Galatheidae, Porcellanidae
Superfamily Paguridea
Families Paguridae, Lithodidae
Superfamily Hippidea
Superfamily Dromiacea

MACDONALD et al. (1957)

Suborder Anomura

Superfamily Thalassinoidea

Superfamily Coenobitoidea

Families Pylochelidae, Diogenidae,

Coenobitidae, Lomisidae

Superfamily Paguroidea

Families Paguridae, Lithodidae

WATERMAN & CHACE (1960)

Section Anomura

Superfamily Galatheoidea

Superfamily Paguroidea

Superfamily Hippidea

McLAUGHLIN (1983)

(included families only for Paguroidea)

Infraorder Anomala [replaced by Anomura

by McLAUGHLIN & HOLTHUIS 1985]

Superfamily Galatheoidea

Superfamily Lomoidea

Superfamily Hippoidea

Superfamily Paguroidea

Families Pomatochelidae, Diogenidae,

Coenobitidae, Paguridae, Parapaguridae,

Lithodidae

BOWMAN & ABELE (1982)

Infraorder Anomura

Superfamily Coenobitoidea

Superfamily Paguroidea

Superfamily Galatheoidea

Superfamily Hippoidea

SCHRAM (1986)

Infraorder Anomala

Families Pomatochelidae, Diogenidae,

Coenobitidae, Lomisidae, Paguridae,

Lithodidae, Parapaguridae, Galatheidae,

Aeglidae, Chirostylidae, Porcellanidae,

Albuneidae, Hippidae

Added in Proof

AHYONG et al. (2009) just published new insights into anomuran phylogeny that further accent both the advances and conflicts associated with anomuran studies whether they are morphological, spermatological, developmental, or molecular. With an abundantly expanded molecular database for the Galatheoidea the unexpected results the authors found have drastically undermined the currently accepted concepts of relationships within the superfamily. Thus it is not surprising that with only minimal additions to the paguroid molecular database catastrophic disarray is portrayed for this superfamily.

AHYONG, S.T., K.E. SCHNABEL & E.W. MAAS 2009. Anomuran phylogeny: new insights from molecular data. Pp. 399–414 *in*: J.W. MARTIN, K.A. CRANDALL & D.L. FELDER (eds.), Decapod Crustacean Phylogenetics; Crustacean Issues 18. CRC Press, Taylor & Francis Group, Boca Raton, London, New York.