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## EVOLUTIONARY HISTORY OF DECAPOD GROUPS: ANOMURA

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### INTRODUCTION AND OVERVIEW

Anomura is a large infraorder exhibiting high disparity in body forms, which include squat lobsters with elongate pleons, porcelainid crabs with reduced pleons, burrowing mole crabs, king crabs, and symmetrical and asymmetrical hermit crabs. Anomuran habitats are equally diverse and variable, and they encompass freshwater and terrestrial locations in addition to most marine ecosystems. Despite this wide variation in form and habitat, Anomura is monophyletic in all recent analyses and sister to Brachyura (BRACKEN-GRISSOM & others, 2013; WOLFE & others, 2019; DAVIS & others, 2022) (FIG. 1). A key character uniting the group is the reduced fifth pereopod (POORE & AHYONG, 2023). Although monophyly is well-supported, relationships between and among anomurans are resolved variably. Understanding anomuran origins, relationships, and evolution has been complicated further by evolutionary convergence and repeated parallel evolutionary patterns within the group (TAN & others, 2018). The fossil record for Anomura is inconsistent; for example, galatheoid squat lobsters have a reasonably strong record, whereas hippoid mole crabs are unknown as fossils (SCHWEITZER, FELDMANN, & FRAAIJE, 2023; SCHWEITZER & others, 2023) (FIG. 2). Because of the lack of fossils for some groups, testing evolutionary hypotheses is difficult.

Anomurans generally are recognized as exhibiting four major body forms (FIGS. 3 and 4). Most hermit crabs have a weakly calcified and/or reduced pleon that is sheltered by a shell or other object; however, some hermit crab families have well-calcified pleons, and some do not carry objects. Squat lobsters, as the name suggests, are lobster-like in form with an elongate pleon that is partially folded under the carapace, and they usually bear long chelipeds. Many anomurans exhibit a crab-like form, with a pleon carried ventrally under the body and with a wide, flattened carapace (TSANG & others, 2011). Mole crabs are longer than wide and adapted to burrowing, with flattened pereopods to facilitate digging. It is important to note that these body forms evolved independently in Anomura more than once, in most cases, and similar morphologies have evolved in other decapod lineages.

Examples of multiple body forms evolving in one anomuran lineage may be found among the two superfamilies of squat lobsters, Chirostyloidea and Galattheoidea. In these two clades, similar, convergent evolutionary pathways to carcinization seem to have developed. Most phylogenies recover the symmetrical hermit crab family Pylochelidae as polyphyletic, with one branch associated with Chirostyloidea and another with Galattheoidea (AHYONG, SCHNABEL, & MAAS, 2009; TSANG & others, 2011; AHYONG, SCHNABEL, & MACPHERSON, 2011; BRACKEN-

GRISSOM & others, 2013, molecular only). In Chirostyloidea, an evolutionary pathway from pylochelid hermit crab to chirostyloid squat lobster to carcinized Lomisidae was proposed (AHYONG, SCHNABEL, & MACPHERSON, 2011). In Galatheoidea, a separate clade of pylochelid hermit crab was associated with galatheoid squat lobsters and the carcinized Porcellanidae (AHYONG, SCHNABEL, & MACPHERSON, 2011). These possible instances of convergent and parallel evolution within superfamilies of the same infraorder compound interpretations of anomuran evolution.

SCHRAM and KOENEMANN (2021) summarized three major evolutionary hypotheses about the origin of Anomura: from a hermit crab-type ancestor, a squat lobster-like ancestor, or a crab-like ancestor. The earliest fossils currently referred to Anomura, Eocarcinoidea, suggest the squat lobster-like ancestor is most likely, based on their gross morphology with an elongate cephalothorax, a pleon partially held under the body, and elongate pereopods—all similar to squat lobster morphology. The eocarcinoids are the oldest forms currently referred to the group and were considered as a generalized stem form for Anomura (SCHRAM & KOENEMANN, 2021). Notably, early hermit crabs of Schobertellidae also exhibit these features, albeit with shorter pereopods. Thus, a squat-lobster-like ancestral form is supported by the preponderance of evidence at this time.

Anomuran generic diversity pre-Holocene peaked in the Tithonian, the Ypresian, and the Priabonian, in part associated with the carbonate reefs in Europe during these times (FIG. 5) (PERRIN, 2002; KLOMPMAKER & others, 2013). Overall, the anomuran percentage of the total decapod fauna (approximately 11%) has remained relatively consistent since the Late Triassic (SCHWEITZER & FELDMANN, 2015). The group also has exhibited a strong preference for coral reef and higher energy environments, at least in the fossil record (SCHWEITZER

& FELDMANN, 2015). No non-paguroid anomuran families became extinct at the end of the Cretaceous, whereas a quarter of paguroid families did (SCHWEITZER & FELDMANN, 2023). Many more genera became extinct at that time, including approximately half of non-paguroid and almost two-thirds of paguroid anomuran genera (SCHWEITZER & FELDMANN, 2023). Overall, families and genera within Anomura have moderately long ranges as compared with other decapods. Their ranges are longer than brachyurans but shorter than shrimps and most lobsters (SCHWEITZER & FELDMANN, 2023). The overall longevity of lineages and consistent proportion of Anomura making up the entire decapod fauna may be a result of the broad diversity and disparity within it, as well as the specializations within various superfamilies (SCHWEITZER & FELDMANN, 2023).

Because Anomura is disparate and diverse, each major clade is discussed separately.

## EOCARCINOIDEA

The earliest anomurans belong to Eocarcinoidea, which includes two monotypic families, Eocarcinidae and Platykottidae (FIG. 2). They exhibit an elongate cephalothorax, with the pleon extending posterior to the carapace (FIG. 3.3). Platykottidae was recovered from Late Triassic limestones of what is now the Arabian Peninsula. The Early Jurassic *Eocarcinus* WITHERS, 1932, recovered from clays of the UK, retains a chela in the position of the second pereopod on two separate specimens (FELDMANN & SCHWEITZER, 2010), which is unusual but not unknown among Anomura. Subchelate appendages other than pereopod one are known among Munidopsidae (AHYONG, ANDREAKIS, & TAYLOR, 2011). The association of the second chelae with the specimens has been debated, but it seems most parsimonious to consider them as belonging to the animal rather than as dissociated claws from another chelate organism that are serendipitously present on two separate specimens. Its enigmatic

form has led to *Eocarcinus* being regarded as a stem-brachyuran (SCHOLTZ, 2020), but we retain it within Anomura, following the discussion of characters by FELDMANN and SCHWEITZER (2010). The body plan of Eocarcinoidea suggests that the squat lobster body plan was the earliest to appear among Anomura, at least based on the current fossil record.

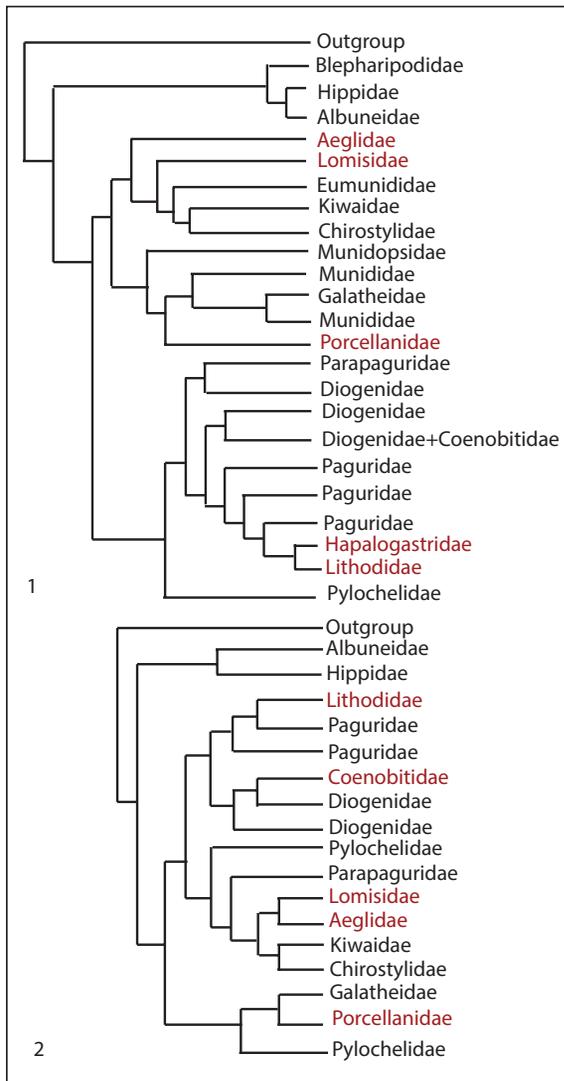


FIG. 1. Phylogenies for anomuran families. 1, adapted from BRACKEN-GRISOM & others (2013, morphology). 2, adapted from TSANG & others (2011). The red indicates carcinized forms.

## GASTRODOROIDEA

Another enigmatic group, Gastrodoroidae, the sole family within Gastrodoroidea, ranged from Middle Jurassic to early Late Cretaceous. Members exhibited an elongate carapace with moderately to well-developed carapace regions and weak orbits (FIG. 4.4). Gastrodoroidae is known exclusively from carbonates of what is now Europe. There

is no consensus on the position of Gastrodoroidae among decapods; FRAAIJE and others (2022) considered it to be a hermit crab, but others have placed it within Anomura unrelated to hermit crabs (KLOMPMAKER & others, 2011) or even as a brachyuran (FELDMANN & SCHWEITZER, 2009). Herein they are considered as carcinized anomurans, with enigmatic affinities, because no extant hermit crabs or other anomurans have a similar carapace (TUDGE, ASAKURA, & AHYONG, 2012).

## HIPPOIDEA

Extant hippoids are burrowing forms with an elongate carapace and pereopods adapted for digging. They are commonly encountered on beaches and consequently, familiarly referred to as “mole crabs” or “sand crabs” (POORE & AHYONG, 2023) (FIG. 3.1). Of the extant Anomura, they are the most basal clade and recovered as sister to all other anomurans (AHYONG, SCHNABEL, & MAAS, 2009; TSANG & others, 2011; BRACKEN-GRISOM & others, 2013; POORE & AHYONG, 2023) (FIG. 1). The fossil record of hippoids belies this apparent early divergence because the oldest known fossil is Late Cretaceous (Maastrichtian), which is much later than several other anomuran lineages appeared (FIG. 2). The

habitat of the extant animals might explain their poor fossil record because modern forms inhabit the surf zone (Hippidae) and intertidal to shallow subtidal environments (Albuneidae and Blepharipodidae) (TUDGE, ASAKURA, & AHYONG, 2012; POORE & AHYONG, 2023). Their delicate carapaces likely would break apart in such high energy environments; conversely, their burrowing habit might promote fossilization as seen in axiidean and gebiidean decapods. Hippidae is unknown in the fossil record, probably because of their very shallow, littoral habitat from 0- to 13-m depth (POORE & AHYONG, 2023). Extant forms inhabit circum-Pacific and western Atlantic coastal areas (POORE & AHYONG, 2023).

Albuneidae and Blepharipodidae, on the other hand, have limited but well-documented fossil records in the Paleogene (FIG. 2). Their habitat preferences in modern oceans differ from those of hippids because they range into deeper sublittoral habitats, up to approximately 100 m (POORE & AHYONG, 2023), which may explain their fossilization potential. The earliest albuneid occurrence is in lime sand of the Late Cretaceous (Maastrichtian) (FRAAIJE, 2002). Eocene albuneid occurrences are reasonably abundant in limestones and volcanoclastics of Italy and in Atlantic and Pacific coastal North America. Oligocene and Miocene occurrences are in siliciclastics. A shift to the siliciclastic sandy environments in which they are found today occurred by Oligocene and Miocene time in Europe, where fossils are found in siliciclastic rocks (MÜLLER, 1978). Albuneidae was suggested to have originated in the Indo-Pacific (BOYKO & HARVEY, 2009), but a Tethyan origin may be more likely based on Cretaceous and Eocene fossil occurrences in Europe (SCHWEITZER & others, 2023). Blepharipodidae are well-represented in siliciclastic sediments of the Eocene and Oligocene of western North America (NYBORG & VEGA, 2008), which supports the hypothesis that the group originated in the eastern Pacific in similar environments to those the group inhabits

today and later dispersed to the Indo-Pacific (TUDGE, ASAKURA, & AHYONG, 2012; POORE & AHYONG, 2023). Most fossil blepharipodids are referred to the extant *Lophomastix* BENEDICT, 1904, whereas 60% of fossil albuneids are referred to extant genera. Morphologically, Albuneidae and Blepharipodidae exhibit conservative carapace morphology across geologic time, and their distinctive shape and ornamentation makes them readily referable to their respective families.

## GALATHEOIDEA

This superfamily is composed of squat lobsters and porcelain crabs and was recovered as monophyletic based on analysis of extant families (Munididae, Galatheidae, Munidopsidae, Porcellanidae) (AHYONG, SCHNABEL, & MAAS, 2009; TSANG & others, 2011; BRACKEN-GRISSOM & others, 2013; TAN & others, 2018; WANG & others, 2023) (FIG. 1). There are two additional extinct families, Catilloalatheidae and Paragalatheidae. Subsequent work suggests that Galatheidae, in addition to several speciose genera of galatheoids, are not monophyletic (RODRÍGUEZ-FLORES & others, 2023). PALERO and others (2017) examined extant taxa referable to Munididae and Galatheidae, and they suggested that these two families diversified during the Miocene in the Indo-Pacific region. The fossil record neither supports nor refutes this hypothesis because the record for Galatheidae primarily is European, and the record for Munididae is broad but does not include Indo-Pacific occurrences, except Japan. Examination of members of a single genus within Galatheidae showed that included species moved into deeper habitats as early as the Cretaceous while also maintaining shallower representatives, based on molecular clock estimates (RODRÍGUEZ-FLORES & others, 2022). The extinct Cretaceous genus *Eomunidopsis* VÍA, 1981, exhibits a similarly broad array of depositional environments, which indicates that broad environmental tolerances appeared early in lineages within the family. Such eurytopic adaptations within a single

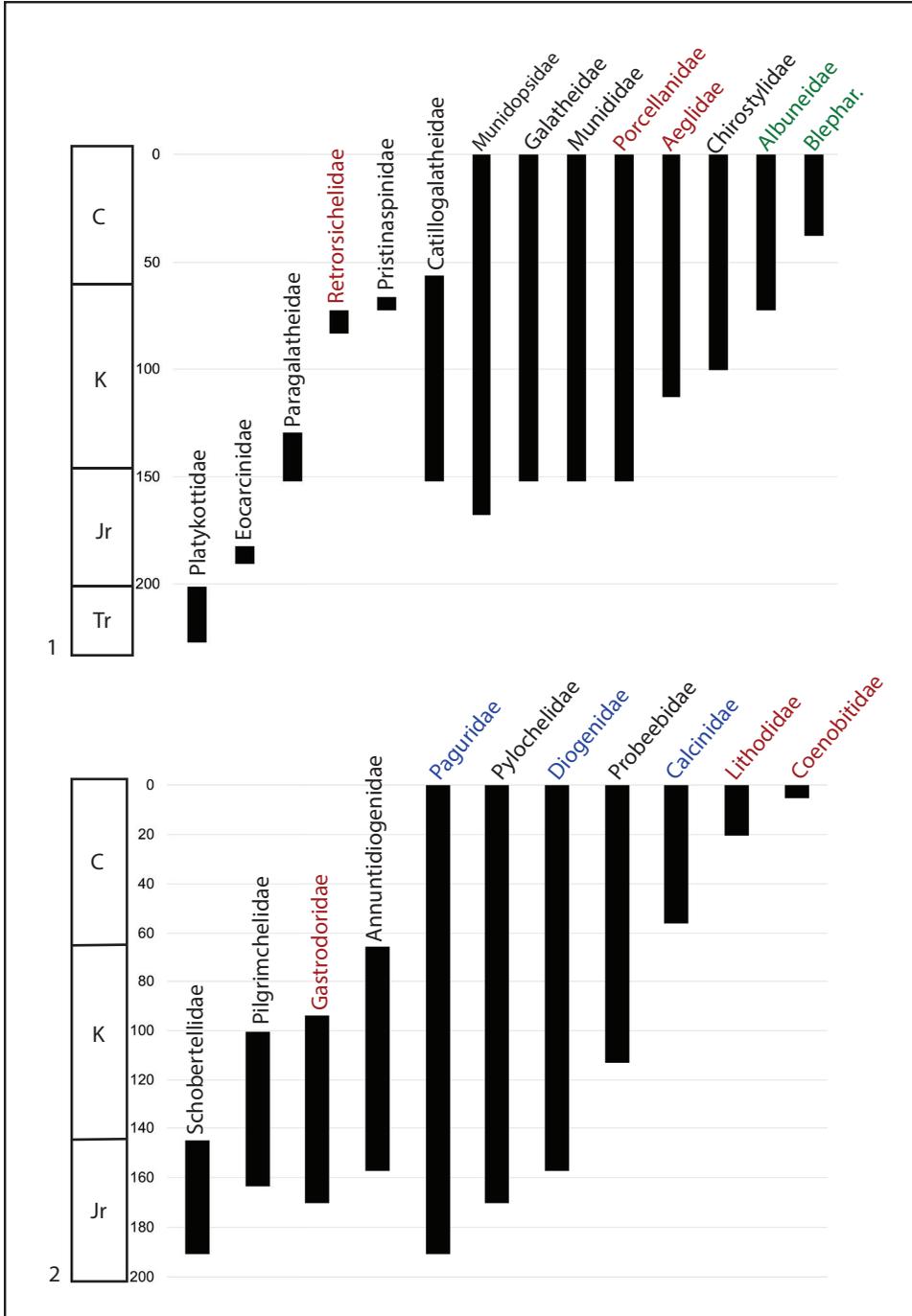


FIG. 2. Geologic ranges of anomuran families with fossil records, in millions of years before present. Tr = Triassic, Jr=Jurassic, K=Cretaceous, C=Cenozoic, Blephar=Blepharipodidae. The red indicates carcinized forms; green, mole crabs; blue, paguroid with reduced plesion.

genus may explain the robust fossil record and evolutionary success of the group.

Galatheaidea is perhaps the best represented group among anomurans in the fossil record, with the possible exception of disarticulated paguroid-type chelipeds. Galatheaidea originated in the Middle Jurassic and diversity exploded in the Late Jurassic (FIGS. 2, 5.2). All extant families have a fossil record. One family exhibits carcinization. It is important to note that fossil membership in each family of Galatheaidea has not yet been confirmed phylogenetically, and referral of fossils to families largely has been based on carapace ornamentation.

The oldest galatheid family is Munidopsidae, which appeared in the Middle Jurassic. Jurassic forms are preserved almost exclusively in limestones with corals. Fossils are referred to this family based on possession of a circumgastric groove, a branchiocardiac groove, well-defined gastric regions, and a keeled rostrum (ROBINS, FELDMANN, & SCHWEITZER, 2013). Munidopsidae peaked in fossil diversity in the latest Jurassic and maintained moderate generic diversity of between one and four genera into the Cenozoic, with five extant genera with over 250 species (POORE & AHYONG, 2023). Paleogene and Neogene species inhabit an array of habitats, including slope siliciclastics and coral limestones. *Shinkaia* BABA & WILLIAMS, 1998, inhabited cold seeps as long ago as the Eocene in the northern Pacific, where it is found today. Fossils of *Shinkaia* are found in large numbers, and the genus is gregarious in modern oceans, which suggests conservative habitat, behavioral, and geographic preferences in the lineage (SCHWEITZER & FELDMANN, 2008; POORE & AHYONG, 2023) (FIG. 3.4). Otherwise, members of the family now generally prefer outer shelf to deep water habitats (POORE & AHYONG, 2023); thus, a shift in habitat preferences from mostly coral-associated habitats to shelf siliciclastics occurred sometime during the Paleogene. The majority of fossil occurrences of munidopsids are

in Europe, with exceptions for species in Japan, West coastal North America, Brazil, and Antarctica. Extant forms are cosmopolitan, including *Munidopsis* WHITEAVES, 1874, the only extant genus with a fossil record besides *Shinkaia* (OBIS, 2023). Fossil species of *Munidopsis* also are widely distributed, with occurrences in Antarctica, Bosnia-Herzegovina, Canada, Japan, Slovakia, and Slovenia (SCHWEITZER & others, 2023).

Other galatheid families appeared in the Late Jurassic. The extinct Catillogalatheidae was reasonably diverse until the Late Cretaceous, when it was reduced to one genus. Membership in this family is based on possession of distinct epigastric regions, a deep cervical groove, and a broad, flat rostrum (ROBINS & others, 2016). Most occurrences of this family are in coral-associated limestones (ROBINS & others, 2016), with only a few exceptions in shales or lithographic limestones (FRANȚESCU, 2014; GARASSINO, DE ANGELI, & PASINI, 2014). Nearly all occurrences are in Europe, with some in USA (Texas), Mexico, Japan, and Morocco. Catillogalatheidae survived the end-Cretaceous event in Northern Europe, in the reefal refugia there (SCHWEITZER & FELDMANN, 2023), and became extinct in the Paleocene (YOST, FELDMANN, & SCHWEITZER, 2023).

Galatheaidea, a diverse extant family, is questionably known from the Late Jurassic with confirmed occurrences in the Early Cretaceous (Barremian). The family achieved low but stable diversity (1–3 genera) in the Cretaceous, with a peak in the early Eocene (five genera), and then diminished in fossil occurrences through the remaining Paleogene and Neogene. Galatheaidea typically exhibit a strong cervical groove, an inflated carapace, and a wide rostrum (ROBINS & others, 2016) (FIG. 3.7). Extant forms prefer rough substrates, including corals, from the intertidal down to 1200 m (POORE & AHYONG, 2023). As is typical in this group, fossil forms are predominantly found in coral limestones, with a few in clays, sands, and lithographic limestones. The oldest

forms are known from Europe, where the family was well-established from the Cretaceous through the Pliocene. Cretaceous

occurrences are from Japan and the Western Interior Seaway of North America. Extant forms are cosmopolitan but more common

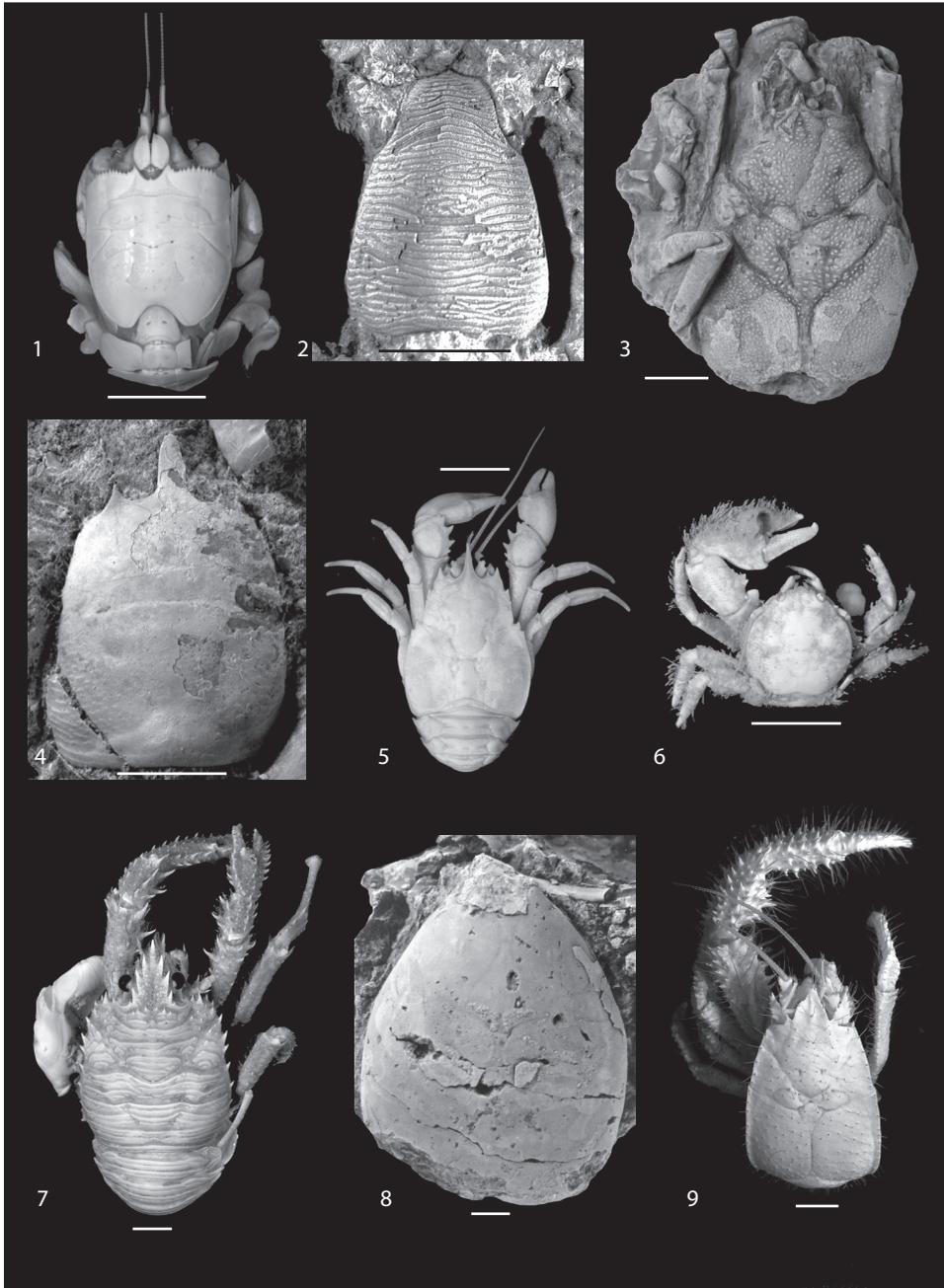


FIG. 3. Representative non-paguroid anomurans. 1, Albuneidae; 2, Paragalatheidae; 3, Eocarcinidae; 4, Munidopsidae; 5, Aeglididae; 6, Porcellanidae; 7, Galatheidae; 8, Retrorsichelidae; 9, Kiwaidae. All figures from SCHWEITZER and others (2023). Scale bars 1 cm.

in temperate latitudes (POORE & AHYONG, 2023). The extant *Galathea* FABRICIUS, 1793, has an extensive fossil record and is the only extant genus known from fossils.

Like Galatheidae, Munididae is a diverse extant group appearing in the Late Jurassic (Tithonian). However, the family diversified later, reaching its maximum diversity in the fossil record in the late Eocene, and all but two referred genera are Cenozoic. Fossil species are referred to the family based on their strong transverse ornamentation and trifid frontal margin, with a rostrum and supraorbital spines (ROBINS & others, 2016). Predictably, the Jurassic and later European forms are reported from coral limestone, but occurrences outside Europe are in siliciclastics. Paleogene North American occurrences are in mixed siliciclastics, and South American occurrences are in shales. Extant munidids tend to inhabit offshore continental shelf and slope settings but can be found in the intertidal (POORE & AHYONG, 2023); the family is cosmopolitan (OBIS, 2023). The shift from coral reefs to offshore settings seems to have begun outside Europe as early as the Eocene on Pacific coastal North America (SCHWEITZER & FELDMANN, 2000). Several extant genera have fossil records, *Agononida* BABA & DE SAINT LAURENT, 1996; *Munida* LEACH, 1821; *Raymunida* MACPHERSON & MACHORDOM, 2000; and *Sadayoshia* BABA, 1969, all from Eocene or younger rocks and mostly Oligocene or younger. The Paleogene records accord with the proposed explosive diversification of the group at that time, as suggested by molecular analyses (MACHORDOM & others, 2022).

The extinct Paragalatheidae is confined almost entirely to the Late Jurassic (one Early Cretaceous occurrence) (FIG. 3.2), central Europe, and limestone reefal habitats. This family seems to have radiated quickly but also rapidly disappeared (ROBINS & others, 2016). Their distinctive morphology includes a very inflated carapace with a wide rostrum and uniform, dense ornamentation overall (ROBINS & others, 2016).

Rather different in habitat and body form from other galatheoids are the Porcellanidae (FIG. 3.6). They exhibit strong carcinization, with a flattened cephalothorax and pleon held against the ventral surface of the thoracic somites. They are specialized in habitat, primarily inhabiting reefs at shelf depths (POORE & AHYONG, 2023). Like Munididae, they originated in the Tithonian but did not diversify until the Eocene. Similar to other galatheoids, early occurrences are almost exclusively in coral limestones, with only a few exceptions. Almost every Cenozoic fossil occurrence is in coral-associated limestones; thus, it appears they have not changed in environmental preferences since their time of origin.

Porcellanidae was established by the Late Jurassic, at about the same time as the other non-carcinized galatheoid families appeared. Only two galatheoid occurrences predate the porcellanids, both of which are Middle Jurassic munidopsids. A phylogenomic analysis recovered Porcellanidae as sister to all other galatheoids in a basal position, which indicates an early appearance of the porcellanid body form (PALERO & others, 2019). Thus, it is difficult to suggest which body form appeared earliest because the fossil records of galatheoid families, as well as molecular evidence, are equivocal. Carcinization appears to have been a specialization for reef dwelling and hiding in small crevices, although nearly all Jurassic occurrences of Galatheoidea, not just porcellanids, are in coral limestones. Extant porcellanids generally inhabit corals or rocky intertidal areas, but a few may be found associated with sponges or soft corals (OSAWA & CHAN, 2010). Today, the carcinized Porcellanidae remain the main denizens of reefs in Galatheoidea. The other galatheoid families largely have moved into different habitats. Munididae moved into primarily siliciclastic and offshore habitats in the Eocene and in the Paleogene in Munidopsidae. Galatheidae has maintained a variable habitat since the Cretaceous, including, but not limited to, coral reefs.

## CHIROSTYLOIDEA

Like galatheoids, Chirostyloidea commonly are called squat lobsters, because they exhibit convergent morphology but are not in a monophyletic group with Galatheoidea. The included extant families form a monophyletic group (Chirostylidae, Kiwaidae, Eumunididae, Sternostylidae) (AHYONG, SCHNABEL, & MAAS, 2009; TSANG & others, 2011; BRACKEN-GRISSOM & others, 2013; TAN & others, 2018; WANG & others, 2023) (FIG. 1). Chirostyloidea often is recovered as sister to a clade comprised of Aeglidae and Lomisidae (AHYONG, SCHNABEL, & MAAS, 2009; TSANG & others, 2011; BRACKEN-GRISSOM & others, 2013; TAN & others, 2018). The fossil record of Chirostyloidea is poor, with only four recognized species. Fossils have been reported from the Late Cretaceous of Lebanon and the Eocene of Italy, apparently in quite different environments from those inhabited by modern forms. The lithographic occurrence in Lebanon and the Italian occurrence in shallow water limestones suggest a shallow origin for the group, but extant shallow species are uncommon and sometimes coral-associated (POORE & AHYONG, 2023). Most extant chirostyloids inhabit deep water and form associations with corals and crinoids (POORE & AHYONG, 2023), habitats unlikely to be fossilized.

The extinct *Pristinaspinidae* was recognized to be similar to, and possibly an ancestor of, *Kiwaidae* (AHYONG & ROTERMAN, 2014), the latter of which inhabit hydrothermal vents today (MACPHERSON, JONES, & SEGONZAC, 2005) (FIG. 3.9). *Pristinaspina* SCHWEITZER & FELDMANN, 2000, was recovered from siliciclastics of Late Cretaceous age in northern North America, which is quite different from modern habitats for most chirostyloids and kiwaidae, in particular (ROTERMAN & others, 2018). The inflated branchial regions of *Pristinaspina* as compared with other chirostyloids were suggested as a possible preadaptation

to low oxygen environments favored by modern *Kiwaidae* (AHYONG & ROTERMAN, 2014).

## AEGLOIDEA AND LOMISOIDEA

The monotypic Aegloidea has an odd history. Two Cretaceous occurrences are known, both from marine deposits. The older is from the Early Cretaceous of Mexico, with a later occurrence from the Late Cretaceous (Maastrichtian) of New Zealand (FELDMANN, 1984; FELDMANN & others, 1998). Extant forms exclusively inhabit freshwater locations in South America (MARTIN & ABELE, 1988). The distinctive carapace groove pattern in aeglids, present in the New Zealand fossil, leave little doubt that the fossils are related to extant forms (FIG. 3.5). The events leading to this disjunct dispersal in habitat and time are murky, but phylogenetic and biogeographic evidence suggests that aeglids originated in marine habitats with subsequent invasion of South America from the South Pacific (ORTMANN, 1902; FELDMANN, 1986; BOND-BUCKUP & others, 2008). Lomisidae have no fossil record and occur today in Australia (POORE & AHYONG, 2023). Lomisids appear to be specialized, carcinized forms related to chirostyloids. Interestingly, they often are recovered as sister to (TSANG & others, 2011), or at least phylogenetically close to, Aeglidae (AHYONG, SCHNABEL, & MAAS, 2009; BRACKEN-GRISSOM & others, 2013; TAN & others, 2018). Lomisids and aeglids have superficially similar carapaces that broaden posteriorly, and their spermatozoal architecture is more similar to one another than to any other anomuran (WOLF & others, 2023). The forms appear to be closely related phylogenetically and, based on their geographic occurrences, may now be relicts in two different parts of the Southern Hemisphere, possibly as a result of the breakup of Pangea (WOLF & others, 2023).

## RETRORSICHELIDAE

The extinct Retrorsichelidae currently is unplaced at the superfamily level. This Late Cretaceous family is monotypic and has an unusual morphology. The carapace is smooth and ovate, widening posteriorly, and the chelae appear to be held under the body against the mouthparts (FIG. 3.8). FELDMANN, TSHUDY, and THOMSON (1993) suggested a burrowing habit for *Retrorsichela* FELDMANN, TSHUDY, and THOMSON, 1993, similar to that of hippoids. LUQUE and others (2019) proposed an affinity with the brachyuran Callichimaeridae, but the vastly different carapace and chela shapes of *Callichimaera* LUQUE & others, 2019, and *Retrorsichela* suggest it is best retained in a monotypic anomuran family, for now.

## HERMIT CRABS

The terms “hermit crab,” “pagurid” and “paguroid” have been used for what are now recognized to be several distinct clades, most of which use gastropod shells for protection. They usually have a reduced, asymmetrical pleon, but some cases of symmetrical pleons occur. In addition, in rare cases, the paguroid does not carry any protection, and organisms other than gastropod shells can be used for protection, such as corals, sea anemones, and even found human-made objects (POORE & AHYONG, 2023; JAGIELLO, DYLEWSKI, & SZULKIN, 2024). In this volume, 15 families of hermit crab are recognized, of which three are extinct. In compilations of systematics and taxonomy, paguroids usually are treated together for convenience, even though the group likely is not monophyletic (POORE & AHYONG, 2023; SCHWEITZER, FELDMANN, & FRAAIJE, 2023).

Most phylogenies for the hermit crab families have been conducted thus far only on the basis of genetic information (FIG. 1.2). One exception is BRACKEN-GRISOM and others (2013), in which both a molecular phylogeny and a molecular + morphologic phylogeny were produced (FIG. 1.1). Most analyses have found that

some paguroid families, such as Pylochelidae, are polyphyletic and that paguroids as a group are not monophyletic. One exception was the morphology + molecular phylogeny of BRACKEN-GRISOM & others (2013) which found paguroids to be monophyletic, although in the same paper, a molecular-only analysis found polyphyletic Paguroidea.

Various analyses have found different relationships between and among paguroid families. AHYONG, SCHNABEL, and MAAS (2009) found Lithodidae and Hapalogastridae embedded within Paguridae, Pylochelidae as polyphyletic, and Parapaguridae as sister to one clade of Pylochelidae. TSANG and others (2011) also found Pylochelidae as polyphyletic, and their analysis found Parapaguridae associated with Lomisidae, Aeglidae, and Chirostyloidea. Diogenidae and Coenobitidae were sister groups, and Lithodidae was embedded in Paguridae. BRACKEN-GRISOM and others (2013) produced a molecular-only phylogeny with Pylochelidae as polyphyletic, one clade associated with Galattheoidea and another associated with Aeglidae + Lomisidae + Chirostyloidea. Diogenidae was paraphyletic and contained Coenobitidae, and Paguridae contained Lithodidae and Hapalogastridae. Their analysis combining morphology and molecular data found a monophyletic Paguroidea (BRACKEN-GRISOM & others, 2013).

The consensus of these studies indicates that Pylochelidae is not monophyletic, with one clade associated with Chirostyloidea + Lomisidae + Aeglidae, and one associated with Galattheoidea. Coenobitidae appears embedded within Diogenidae, at least as these families currently are construed. Lithodids are clearly derived pagurids. As yet, no phylogeny has included the three extinct paguroid families, nor have Pylojaquesidae, Probebeidae, or Xylopaguridae been examined. Compounding the problem of paraphyletic families, some genera like *Pagurus* FABRICIUS, 1775, are also paraphyletic (SCHRAM & KOENEMANN, 2021). This suggests that a massive sampling effort of extant paguroids is necessary to resolve the

superfamily, family, and generic placements of taxa within this group.

Most fossil paguroids are referred to Diogenidae or Paguridae. Consequently, each has an extensive fossil record, mostly based on claws, but sometimes on the carapace only. Fossil chelae, probably the most abundant hermit crab remains in the fossil record, are usually placed in Paguridae if the right chela is larger and Diogenidae if the left chela is larger. There are obvious shortcomings to this, but in the absence of other information, these are the most parsimonious placements for the material. More recently, some carapace-only fossils have been referred to these two families, but this has the disadvantage that family-level synapomorphies of carapace morphology have not been hypothesized, let alone diagnosed.

Only recently have extinct paguroid families been recognized. The work of FRAAIJE and colleagues (summary in FRAAIJE & others, 2022), which recognized preserved paguroid carapaces and sixth pleonal somites in the fossil record, has revolutionized our understanding of hermit crab diversity and evolution.

### Pylochelidae

Pylochelidae as currently construed appears to be polyphyletic, as discussed above, and appears in two different clades in several recent phylogenies. Extant genera referred to Pylochelidae have a straight, not coiled, pleon that usually is symmetrical and well-calcified (POORE & AHYONG, 2023), with symmetrical chelae on the first pereopods (TUDGE, ASAKURA, & AHYONG, 2012). Their straight, well-calcified pleon may be a synapomorphy, which allies them more closely to squat lobsters than other hermit crabs (POORE & AHYONG, 2023). Their recovery in two different clades, each associated with squat lobsters, supports this hypothesis in a general sense. All extinct genera referred to Pylochelidae are known from only the carapace or only the sixth

pleonal somite, from Mesozoic rocks of Europe (FIG. 4.5). Thus, it is very difficult to make comparisons between the fossils and extant forms. More work is needed to ensure that the composition of this family including both extant and extinct forms is monophyletic.

Extant pylochelids inhabit wood, rocks, sponges, bamboo, or scaphopod shells, usually at outer shelf or slope depths (POORE & AHYONG, 2023) in tropical to temperate latitudes (OBIS, 2023). Nearly all the extinct forms were recovered from reefal limestones.

### Coenobitidae

Coenobitidae has a limited fossil record in Pliocene and younger occurrences in the tropics (FIG. 4.2). They are popularly called “land hermit crabs” or “coconut crabs” and “robber crabs,” and many videos of their antics, including climbing trees, can be found. There are only two genera, each exhibiting a terrestrial or semiterrestrial habitat (POORE & AHYONG, 2023). They carry a gastropod shell, at least as juveniles, and the left cheliped is larger than the right. Fossils of both extant genera have been reported from the Pliocene to Holocene in the same geographic area and habitat, which suggests that they recently are specialized to the terrestrial habitat.

### Diogenidae and Calcinidae

Diogenidae includes left-handed hermit crabs, in which the left cheliped is larger than the right or in which they are isochealous, and the pleon is coiled and reduced. As noted, the family is likely not monophyletic. We follow POORE & AHYONG (2023) in the generic composition of the family, with the exception of *Calcinus* DANA, 1851, which we recognize in a monotypic Calcinidae. The oldest fossils referred to Diogenidae are Late Jurassic, and the family has been diverse since the early Eocene. Diogenidae includes two especially speciose genera in the fossil record, *Paguristes* DANA, 1851, with 27 extinct and 122 extant species, and

*Dardanus* PAUL'SON, 1875, with 23 extinct and 44 extant species. Extant diogenids are cosmopolitan, excluding polar areas, and with more occurrences in the Northern Hemisphere (OBIS, 2023). Only one fossil species of diogenid, referred to *Paguristes*, is known from the Southern Hemisphere, from Late Cretaceous rocks of Antarctica (FELDMANN, TSHUDY, & THOMSON, 1993). Thus, the primarily Northern Hemisphere distribution seems to be ancient.

Calcinidae originally was defined as embracing several genera (FRAAIJE, VAN BAKEL, & JAGT, 2017). In this volume, we recognize it as monotypic, with *Calcinus* as the sole representative (FIG. 4.7). The other proposed rearrangements of genera from Diogenidae to Calcinidae remain to be tested phylogenetically (POORE & AHYONG, 2023).

### Paguridae, Lithodidae, and Hapalogastridae

Paguridae has an extensive fossil record, mostly based on claws, sometimes the carapace only, and with one species represented by both claws and a carapace. Paguridae embraces the oldest hermit crabs known, Early Jurassic in age, and has maintained moderate diversity since the Jurassic. Both *Pagurus* and *Palaeopagurus* VAN STRAELEN, 1925, include dozens of extinct species and may be “form” or “waste-basket” genera for right-handed fossil paguroids. Paguridae is cosmopolitan today but more abundant in northern temperate to polar regions (OBIS, 2023) (FIG. 4.8, 4.9). Paguridae includes only one fossil occurrence in the Southern Hemisphere, from the Miocene of New Zealand (HYDEN & FOREST, 1980). Clearly, the paguroid fossil record is strongly skewed toward the Northern Hemisphere, particularly to Europe.

Lithodidae have a fossil record extending into the Miocene, and they are strongly carcinized (FIG. 4.1). Commonly called king crabs, they are a cosmopolitan family, mostly inhabiting deep water, and are especially common in temperate to polar regions

(AHYONG, MACPHERSON, & CHAN, 2010). Many species are economically important fisheries (AHYONG, MACPHERSON, & CHAN, 2010). Lithodids carry their pleon against the sternum and do not inhabit shells. They are readily identified by their carcinized body; four pairs of pereopods, usually the right cheliped larger than the left; and an asymmetrical pleon in females. The two fossil records are of extant genera, *Paralomis* WHITE, 1856, and *Paralithodes* BRANDT, 1848, and recovered from Miocene rocks within their modern biogeographic zones in New Zealand and Japan, respectively (FELDMANN, 1998; KARASAWA & others, 2017). Therefore, as far as is known, lithodids have been conservative in terms of morphology and distribution since the Miocene. Hapalogastridae has a minimal fossil record, with the extant *Hapalogaster Brandt*, 1850, collected from lower Pleistocene rocks of Japan (KATO & others, 2017).

The nesting of Lithodidae within Paguridae in all recent phylogenies strongly supports the “hermit to king” hypothesis, in which the free-living lithodid crabs were derived from a paguroid ancestor, secondarily losing the carrying habit (summarized by BRACKEN-GRISSOM & others, 2013; POORE & AHYONG, 2023). In fact, some recent works eliminate Lithodoidea and place Lithodidae within Paguroidea (POORE & AHYONG, 2023), whereas others retain Lithodoidea (DECANET, 2024). In addition to secondary loss of the carrying of a shell, lithodids represent a distinctly carcinized lineage in Anomura.

### Parapaguridae, Pylojacquesidae, and Xylopaguridae

Parapaguridae is recovered as a distinct clade of hermit crabs in most analyses (TSANG & others, 2011; BRACKEN-GRISSOM & others, 2013). They are right-handed hermit crabs, with the right cheliped larger than the left, and have a small carapace. No fossils currently are referred to taxa within this family. Extant forms live in deep water

regions, from the continental shelf to more than 5000 m, mostly between 200 and 3000 m (TUDGE, ASAKURA, & AHYONG, 2012; POORE & AHYONG, 2023). They use gastropod shells, sea anemones, or other

cnidarians for protection, with one form even using a clam shell (POORE & AHYONG, 2023). In modern oceans, Parapaguridae is cosmopolitan (OBIS, 2023). Pylojacquesidae is unknown in the fossil record, has

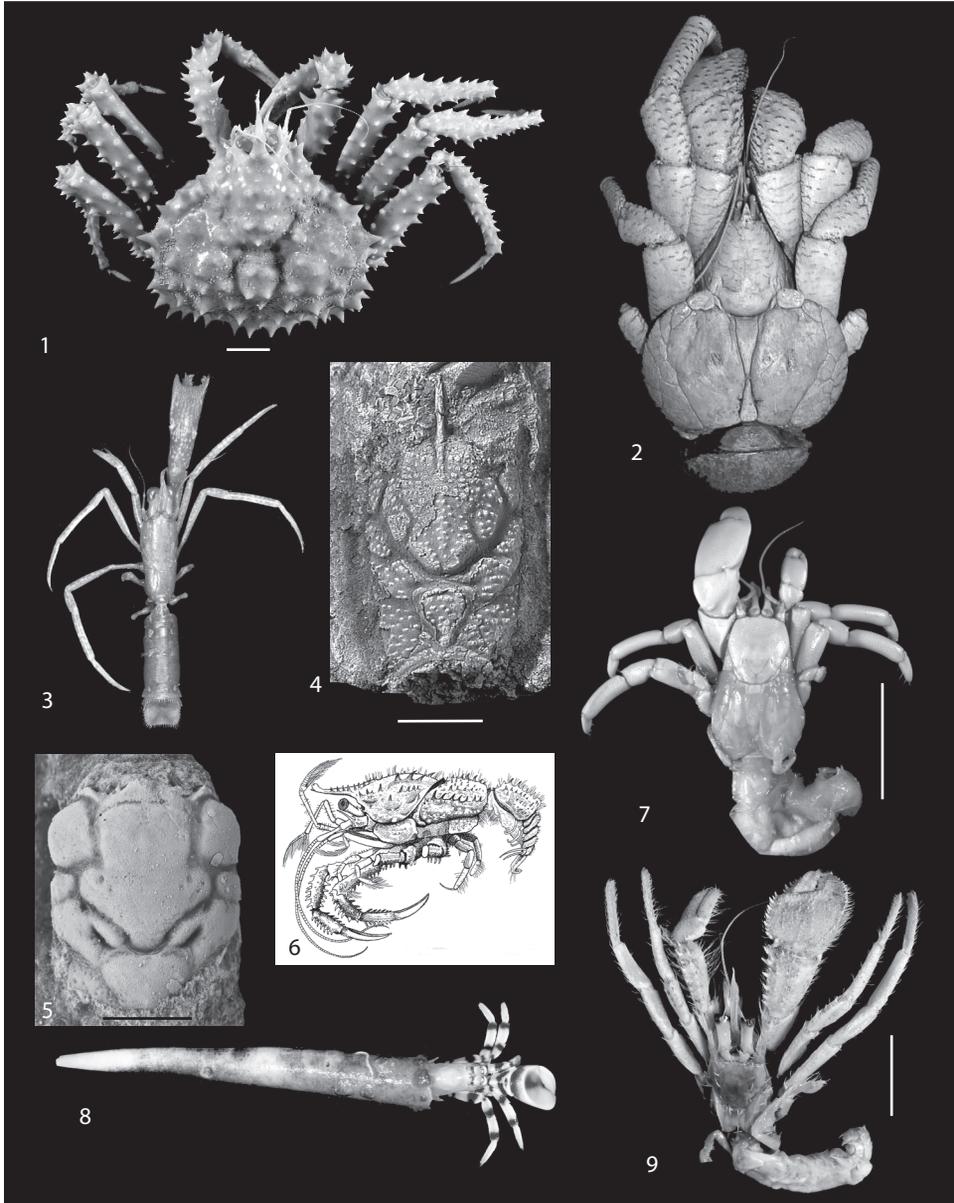


FIG. 4. Representative paguroids. 1, Lithodidae; 2, Coenobitidae; 3, Xylopaguridae; 4, Gastrodoridae; 5, Pylochelidae; 6, Probeebeidae; 7, Calcinidae; 8, Paguridae; 9, Paguridae. All figures from SCHWEITZER, FELDMANN, and FRAAIJE (2023). Scale bars 1cm.

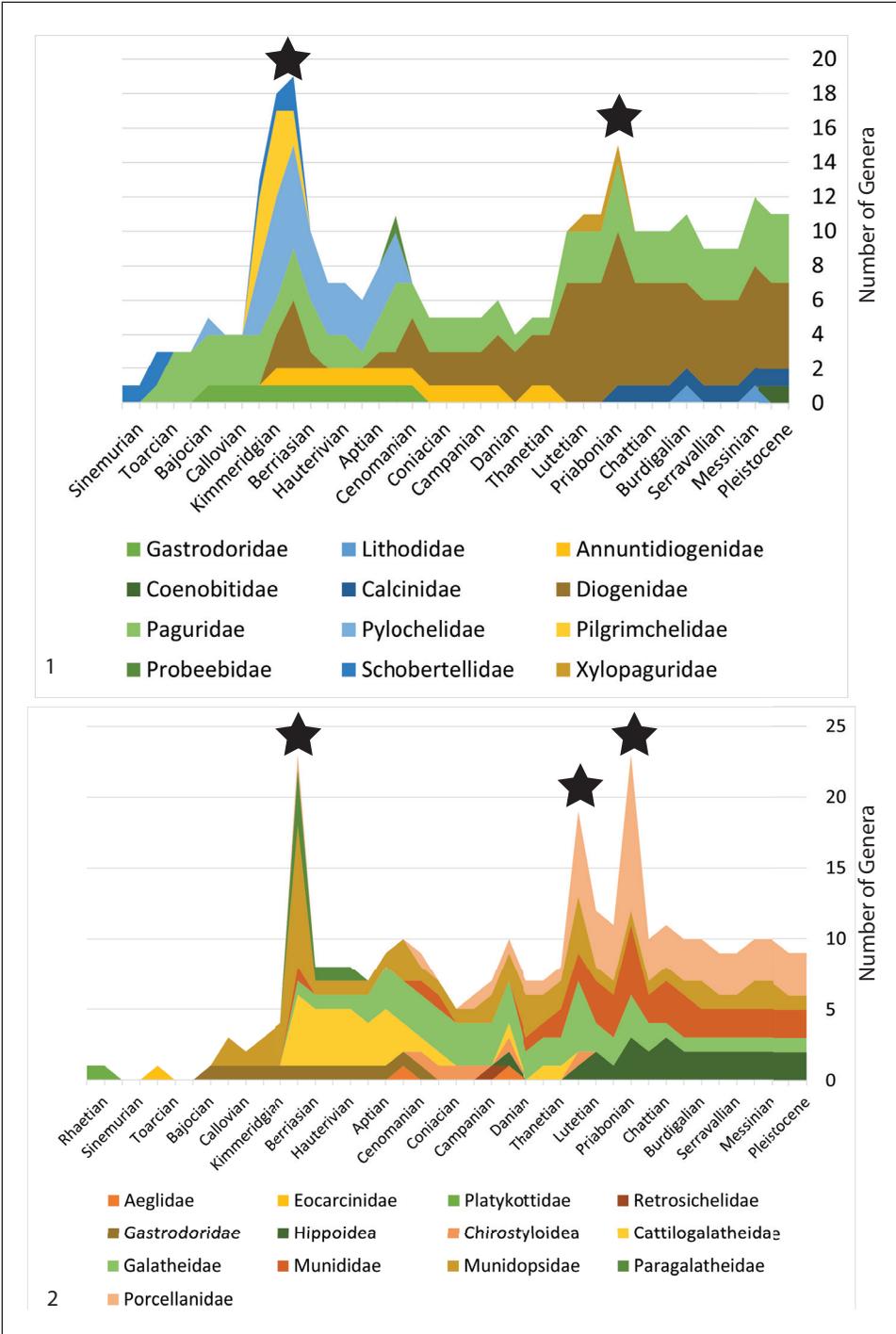


FIG. 5. Generic diversity through the Pleistocene. 1, hermit crabs, with peaks in Tithonian and Priabonian. 2, non-hermit anomurans, with same peaks plus Ypresian.

a distinct sternal morphology, and inhabits outer shelf and slope habitats (POORE & AHYONG, 2023). Only two extant genera are referred to the family, and both are reported to inhabit tubes of serpulid worms (McLAUGHLIN & LEMAITRE, 2001).

Xylopaguridae is represented from two fossil taxa, only represented by a right chela and a sixth pleonal somite, respectively, from Europe (GAŠPARIČ & others, 2016; SCHWEITZER, FELDMANN, & FRAAIJE, 2023) (FIG. 4.3). Extant forms inhabit the Americas and the eastern Pacific in wood or bamboo, ranging from the intertidal to the continental slope (POORE & AHYONG, 2023). They are characterized by a long pleon, a well-calcified carapace, and a sixth pleonal somite forming an operculum over the opening of the object it carries (POORE & AHYONG, 2023).

### Probebeidae

This unusual family had been synonymized with Parapaguridae (DE SAINT LAURENT, 1972), but recovery of a fossil very similar to the type genus, *Probebe* BOONE, 1926, led to its resurrection (FRAAIJE & others, 2024). Probebeids are unusual in having a strongly calcified carapace with posteriorly strong carapace ornamentation and grooves and a well-calcified pleon (FIG. 4.6). Extant members are known from the eastern Pacific off the coast of northern South and Central America, in deep water between 3000 and 4800 m (OBIS, 2023). They are abundant in some abyssal areas and often carry sea anemones (CUVELIER & others, 2023). The sole fossil representative was collected from siliciclastic sediments deposited in shallow conditions, from the Early Cretaceous (Albian) of Central Russia (FRAAIJE & others, 2024).

### Annuntidiogenidae, Pilgrimchelidae, and Schobertellidae

Annuntidiogenidae currently is recognized from Late Jurassic to Paleocene rocks in Europe, mostly reef limestones (YOST,

FELDMANN, & SCHWEITZER, 2023). They are known only from the dorsal carapace, which is characterized by well-developed grooves and regions. Pilgrimchelidae and Schobertellidae are small extinct families reported from the Mesozoic of Europe (SCHWEIGERT & others, 2013; FRAAIJE, 2014). Pilgrimchelidae is characterized by a well-calcified carapace with a distinct rostrum. Chelae of Pilgrimchelidae are unknown, and its occurrences range from Late Jurassic (Oxfordian) to Early Cretaceous (Albian) of Central Europe. Schobertellidae is represented by both carapaces and claws, with carapaces that are well-ornamented and well-calcified posterior to the cervical groove. Schobertellids range nearly throughout the Jurassic in clays and reef limestones. Schobertellids yield insight into teratologies, with a claw deformation recorded from the Early Jurassic that is seen in extant decapods (SCHWEIGERT & others, 2013; FELDMANN & SCHWEITZER, 2024).

### Evolution in hermit crabs

Recognition of extinct paguroid taxa and their generic and family placement is made problematic by several factors. Convergent evolution is common and recurring in Anomura, which is demonstrated by the recurrence of the squat lobster form in at least three superfamilies (Chirostyloidea, Eocarcinoidea, Galatheoidea) and carcinization in another three (Galatheoidea, Lithoidea, Lomisoidea) (BRACKEN-GRISSOM & others, 2013). Phylogenetic analysis indicates that at least one extant paguroid family is polyphyletic (Pylochelidae) (TSANG & others, 2011). The asymmetrical pleon in hermit crabs appears to have arisen twice (TSANG & others, 2011; BRACKEN-GRISSOM & others, 2013, molecular-only analysis). The carrying habit in hermit crabs occurs in at least three different lineages that are distinct phylogenetically (TSANG & others, 2011; BRACKEN-GRISSOM & others, 2013, molecular-only analysis). Thus, claw shape, carapace shape, and shape of other

preserved remains in the fossil record, such as sixth pleonal somites, also might exhibit convergent or parallel evolution. No analysis based on a large dataset of morphological characters has yet been conducted on fossil and extant hermit crabs; thus, there are no hypotheses on phylogeny, convergence and homoplasy, or character polarization in chelae, carapace, or pleonal features for this group.

FRAAIJE and others (2022) suggested several trends in paguroid evolution. Because no phylogenetic analysis for the group including extinct members yet exists, it is not possible at this time to test these hypotheses. Many of their proposed patterns of evolution among hermit crabs are contingent on Gastrodoroidea being a hermit crab lineage, but its systematic position lacks consensus. An example is reduction in rostrum length as an evolutionary trend among hermit crabs; however, this is contingent on gastrodoroids belonging to the group (FRAAIJE & others, 2022). Platykottidae was proposed to be the earliest hermit crab form, based on its possession of rimmed orbits (FRAAIJE & others, 2022). The original placement of Platykottidae was within Anomura, unrelated to hermit crabs, which is a position that was later supported because of its elongate carapace, squat lobster body form, and broad, triangular sternum (CHABLAIS, FELDMANN, & SCHWEITZER, 2011; WOLFE, LUQUE, & BRACKEN-GRISSEM, 2021). “Branchial condensation” (FRAAIJE & others, 2022) was hypothesized to have arisen from the fusion of the branchial and cervical grooves in hermit crabs. Fusion of grooves currently is not known among decapods; loss of grooves in decapods, or at least reduction in their expression, is well documented across both lobsters and crabs (GLAESSNER, 1960, 1969). Changes in carapace ornamentation over time, such as the presence of ridges or granules, the expression of the mesogastric region, and calcification of the carapace, potentially are homoplastic and require phylogenetic testing. Isochely was considered as a basal character among

hermit crabs (FRAAIJE & others, 2022), but it may be polyphyletic, as in the Pylochelidae discussed above. A phylogeny demonstrating basal groups versus derived groups among paguroids would facilitate testing these hypotheses.

### Hermit crabs as carriers of shells or other protective animals or objects

Hermit crabs that are preserved in or near a shell appear rarely in the fossil record. The Hauterivian *Palaeopagurus vandenengeli* FRAAIJE, 2003, was preserved in an ammonite. Hermit crab claws closely associated with gastropod shells were recovered from Campanian and Santonian-Campanian rocks of Antarctica, respectively (AGUIRRE-URRETA & OLIVERO, 1992; FELDMANN, TSHUDY, & THOMSON, 1993). A Late Cretaceous (Maastrichtian) hermit crab preserved in a gastropod has been reported from Belgium (JAGT & others, 2006). Thus, Paguroidea appears to have inhabited coiled shells since at least the Early Cretaceous (Hauterivian) (FRAAIJE, 2003).

Various paguroids have been reported in, or closely associated with, gastropod shells throughout the Cenozoic. Paguroids have been reported *in situ* in a gastropod shell from Eocene (Ypresian–Lutetian) rocks of Denmark (COLLINS & JAKOBSEN, 2003), Russia (Lutetian) (JAGT & others, 2006), and Italy (Ypresian) (GARASSINO, DE ANGELI, & PASINI, 2009). Oligocene occurrences of Paguridae s. l. in a gastropod shell are reported from Japan (KARASAWA, 2002) and Washington, USA (PASINI & others, 2020). Miocene occurrences in shells are more common. Two Miocene species were recovered in gastropod shells in Maryland (USA), one a diogenid and one a pagurid (WALLAARD & others, 2023). Early (Burdigalian) and late Miocene (Tortonian–Messinian) pagurids in shells were collected in New Zealand (HYDEN & FOREST, 1980; FELDMANN & KEYES, 1992). An early Miocene pagurid in a gastropod shell has been reported from Taiwan (HU & TAO, 1996) and a middle

Miocene specimen from The Netherlands (JAGT & others, 2006). Pleistocene occurrences of Diogenidae within gastropod shells were discovered in Costa Rica (TODD & COLLINS, 2005). Thus, the association of Paguridae and Diogenidae with coiled shells seems to have been established in the Cretaceous and has been documented across the Cenozoic.

Some occurrences of paguroids may indicate sheltering in, but not carrying of, the shell. An Early Jurassic ammonite has been reported with hermit crab chelae preserved inside, but it is not clear whether the hermit crab was carrying the shell or taking shelter within it (JAGT & others, 2006). Similarly, a Late Jurassic hermit crab was described as recovered from the body chamber of an ammonoid (VAN BAKEL & others, 2008). A Late Jurassic (Kimmeridgian-Tithonian) specimen interpreted to be a symmetrical hermit crab is preserved fully within an ammonite shell, but not in a position to carry it (MIRONENKO, 2020). Symmetrical hermit crabs today inhabit non-molluscan objects like wood, bamboo, and stone. Epibionts associated with gastropod shells and hermit crabs have been discussed elsewhere (FELDMANN & SCHWEITZER, 2024).

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## REFERENCES

- Aguirre-Urreta, M. B., & E. B. Olivero. 1992. A Cretaceous hermit crab from Antarctica: predatory activities and bryozoan symbiosis. *Antarctic Science* 4:207–214. [DOI:10.1017/S0954102092000324].
- Ahyong, S. T., Nikos Andreakis, & Joanne Taylor. 2011. Mitochondrial phylogeny of the deep-sea squat lobsters, Munidopsidae (Galatheaidea). *Zoologischer Anzeiger* 250:367–377. [DOI:10.1016/j.jcz.2011.06.005].
- Ahyong, S. T., Enrique Macpherson, & Tin-Yam Chan. 2010. Part II. Lithoidea (King crabs). *In* Tin-Yam Chan, ed., *Crustacean Fauna of Taiwan: Crab-like anomurans (Hippoidea, Lithoidea and Porcellanidae)*. National Taiwan Ocean University. Keelung, Taiwan. p. 42–66.
- Ahyong, S. T., & C. N. Roterman. 2014. Pristinaspiniidae, a new family of Cretaceous kiwaiform stem-lineage squat lobster (Anomura, Chirostyloidea). *Scripta Geologica* 147:125–131.
- Ahyong, S. T., K. E. Schnabel, & E. W. Maas. 2009. Anomuran phylogeny: new insights from molecular data. *In* J. W. Martin, K. A. Crandall, & D. L. Felder, eds., *Decapod Crustacean Phylogenetics*. CRC Press. New York. p. 399–414.
- Ahyong, S. T., K. E. Schnabel, & Enrique Macpherson. 2011. Phylogeny and fossil record of marine squat lobsters. *In* G. C. B. Poore, S. T. Ahyong, & Joanne Taylor, eds., *The Biology of Squat Lobsters*. *Crustacean Issues*, 20. CSIRO Publishing. Collingwood, Victoria, Australia. p. 73–104.
- Baba, Keiji. 1969. Four new genera with their representatives and six new species of the Galatheaidea in the collection of the Zoological Laboratory, Kyushu University, with redefinition of the genus *Galathea*. Ohmu. Occasional Papers of the Zoological Laboratory, Faculty of Agriculture, Kyushu University. 2:1–32.
- Baba, Keiji, & Michele de Saint Laurent. 1996. Crustacea Decapoda: revision of the genus *Bathymunida* Balss, 1914, and description of six new related genera (Galatheaidea). *In* A. Crosnier, ed., *Résultats des Campagnes MUSORSTOM 15. Mémoires du Muséum national d'Histoire naturelle (Série A)* *Zoologie* 168:433–502.
- Baba, Keiji, & A. B. Williams. 1998. New Galatheaidea (Crustacea, Decapoda, Anomura) from hydrothermal systems in the west Pacific Ocean: Bismarck Archipelago and Okinawa Trough. *Zoosystema* 20:143–156.
- Benedict, J. E. 1904. A new genus and two new species of crustaceans of the family Albuneidae from the Pacific Ocean; with remarks on the probable use of the antennule in *Albunea* and *Lepidopa*. *Proceedings of the United States National Museum* 27(1367):621–625.
- Bond-Buckup, Georgina, C. G. Jara, Marcos Pérez-Losada, Ludwig Buckup, & K. A. Crandall. 2008. Global diversity of crabs (Aeglidae: Anomura: Decapoda) in freshwater Hydrobiologia 595:267–273. [DOI:10.1007/978-1-4020-8259-7\_29].
- Boone, Lee. 1926. A new family of Crustacea. Preliminary technical description. *New York Zoological Society Bulletin* 29:1–73.
- Boyko, C. B., & Alan Harvey. 2009. Phylogenetic systematics and biogeography of the sand crab families Albuneidae and Blepharipodidae (Crustacea: Anomura: Hippoidea). *Invertebrate Systematics* 23(1):1–18 [DOI:10.1071/IS06053].
- Bracken-Grissom, H. D., M. E. Cannon, Patricia Cabezas, R. M. Feldmann, C. E. Schweitzer, S. T. Ahyong, D. L. Felder, Rafael Lemaitre, & K. A. Crandall. 2013. A comprehensive and integrative reconstruction of evolutionary history for Anomura (Crustacea: Decapoda). *BMC Evolutionary Biology* 13:128. [DOI:10.1186/1471-2148-13-128].

- Brandt, J. F. 1848. Die Gattung *Lithodes* Latreille nebst vier neuer ihr verwandten von Wosnessenski entdeckten, als Typen einer besondern Unterabtheilung (Tribus Lithodea) der Edward'shen Anomuren. Bulletin de la Classe physico-mathématique de l'Académie Impériale des Sciences de Saint-Petersbourg 7:171–176.
- Brandt, J. F. 1850. Vorläufige bemerkungen über eine neue aus zwei noch unbeschriebenen Gattungen und Arten gebildete Unterabtheilung (Hapalogastrica) der Tribus Lithodina, begleitet von einer Charakteristik der eben genannten Tribus der Anomuren. Bulletin de la Classe Physico-Mathématique de l'Académie Impériale des Sciences de Saint-Petersbourg 8:266–269.
- Chablais, Jérôme, R. M. Feldmann, & C. E. Schweitzer. 2011. A new Triassic decapoda, *Platykotta akaina*, from the Arabian shelf of the northern United Arab Emirates: earliest occurrence of the Anomura. Paläontologische Zeitschrift 85:93–102. [DOI:10.1007/s12542-010-0080-y].
- Collins J. S. H., & S. L. Jakobsen. 2003. New crabs (Crustacea, Decapoda) from the Eocene (Ypresian/Lutetian) Lillebaelt Clay Formation of Jutland, Denmark. Bulletin of the Mizunami Fossil Museum 30:63–96.
- Cuvelier, Daphne, Mathilde Vigneron, Ana Colaço, & Jens Greinert. 2023. Delayed response of hermit crabs carrying anemones to a benthic impact experiment at the deep-sea nodule fields of the Peru Basin? Marine Environmental Research 185:105899 [DOI:10.1016/j.marenvres.2023.105899].
- Dana, J. D. 1851. Paguridae. Conspectus Crustaceorum quae in Orbis Terrarum circumnavigatione, Carolo Wilkes e Classe Reipublicae Foederatae Duce, lexit et descripsit. Proceedings of the Academy of Natural Sciences of Philadelphia 5:267–272.
- Davis, K. E., Sammy De Grave, Cyrille Delmer, A. R. D. Payne, Steve Mitchell, & M. A. Wills. 2022. Ecological transitions and the shape of the decapod tree of life. Integrative and Comparative Biology 62:332–344. [DOI:10.1093/icb/icac052].
- DecaNet eds. 2024. DecaNet. [DOI:10.14284/600].
- de Saint Laurent, Michèle. 1972. Sur la famille des Parapaguridae Smith, 1882. Description de *Typhlopagurus foresti* gen. nov., sp. nov., et de quinze espèces ou sous-espèces Nouvelles de *Parapagurus* Smith (Crustacea, Decapoda). Bijdragen tot de dierkunde, 42:97–123.
- Fabricius, J. C. 1775. Systema entomologiae, sistens insectorum classes, ordines, genera, species, adiectis synonymis, locis, descriptionibus, observationibus. 832 p.
- Fabricius, J. C. 1793. Entomologia Systematica Emendata et Aucta. Secundum Classes, Ordines, Genera, Species Adiectis Synonymis, Locis, Observationibus, Descriptionibus. Christian Gottlob Prof. Hafniae 2:i–viii + 1–519.
- Feldmann, R. M. 1984. *Haumuriaegla glaessneri* n. gen. and sp. (Decapoda; Anomura; Aeglididae) from Haumurian (Late Cretaceous) rocks near Cheviot, New Zealand. New Zealand Journal of Geology and Geophysics 27:379–385. [DOI:10.1080/00288306.1984.10422305].
- Feldmann, R. M. 1986. Paleobiogeography of two decapod crustacean taxa in the Southern Hemisphere: global conclusions from sparse data. Crustacean Issues 4:5–19.
- Feldmann, R. M. 1998. *Paralomis debodeorum*, a new species of decapod crustacean from the Miocene of New Zealand: first notice of the Lithodidae in the fossil record. New Zealand Journal of Geology and Geophysics 41:35–38. [DOI:10.1080/00288306.1998.9514788].
- Feldmann, R. M., & I. W. Keyes. 1992. Systematic and stratigraphic review with catalogue and locality index of the Mesozoic and Cenozoic decapod Crustacea of New Zealand. New Zealand Geological Survey Record 45. 73 p.
- Feldmann, R. M., & C. E. Schweitzer. 2009. Revision of Jurassic Homoloidea de Haan, 1839, from the Ernstbrunn and Štramberk limestones, Austria and the Czech Republic. Annalen des Naturhistorischen Museums in Wien (Serie A) 111:183–206.
- Feldmann, R. M., & C. E. Schweitzer. 2010. Is *Eocarcinus* the earliest brachyuran? Journal of Crustacean Biology 30:241–250. [DOI:10.1651/09-3230.1].
- Feldmann, R. M., & C. E. Schweitzer. 2024. Part R, Revised, Volume 1, Biotic interactions. Treatise Online 178:1–17, 14 fig. [DOI:10.17161/to.vi.22368].
- Feldmann, R. M., D. M. Tshudy, & M. R. A. Thomson. 1993. Late Cretaceous and Paleocene decapod crustaceans from James Ross Basin, Antarctica Peninsula. The Paleontological Society Memoir 28. 41 p.
- Feldmann, R. M., F. J. Vega, S. P. Applegate, & G. A. Bishop. 1998. Early Cretaceous arthropods from the Tlayúa Formation at Tepexi de Rodríguez, Puebla, Mexico. Journal of Paleontology 72(1):79–90. [DOI:10.1017/S0022336000024033].
- Fraaije, R. H. B. 2002. The first record of albuneid crabs (Crustacea, Decapoda) from the Cretaceous. Bulletin of the Mizunami Fossil Museum 29:69–72.
- Fraaije, R. H. B. 2003. The oldest in situ hermit crab from the Lower Cretaceous of Speeton, UK. Palaeontology 46:53–57. [DOI:10.1111/1475-4983.00286].
- Fraaije, R. H. B. 2014. Diverse Late Jurassic anomuran assemblages from the Swabian Alb and evolutionary history of paguroids based on carapace morphology. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 273:121–145. [DOI:10.1127/0077-7749/2014/0419].
- Fraaije, R. H. B., E. V. Mychko, L. S. Barsukov, & J. W. M. Jagt. 2024. A new mid-Cretaceous hermit crab (Crustacea, Anomura) from Central Russia sheds new light on paguroid evolution. Cretaceous Research 154:05749. [DOI:10.1016/j.cretres.2023.105749].
- Fraaije, R. H. B., B. W. M. van Bakel, & J. W. M. Jagt. 2017. A new paguroid from the type Maastrichtian (upper Cretaceous, the Netherlands) and erection of a new family. BSGF Earth Sciences Bulletin 188(17):1–4. [DOI:10.1051/bsgf/2017185].
- Fraaije, R. H. B., B. W. M. van Bakel, J. W. M. Jagt, Sylvain Charbonnier, Guenter Schweigert, Géraldine Garcia, & Xavier Valentin. 2022. The evolution of hermit crabs (Crustacea, Decapoda, Anomura, Paguroidea) on the basis of carapace morphology:

- a state-of-the-art-report. *Geodiversitas*, 44: 1-16. [DOI:10.5252/geodiversitas2022v44a1].
- Franțescu, O. D. 2014. Fossil decapods from the Cretaceous (late Albian) of Tarrant County, Texas. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 273(3):22–239. [DOI:10.1127/0077-7749/2014/0427].
- Garassino, Alessandro, Antonio De Angeli, & Giovanni Pasini. 2009. *In situ* hermit crab (Crustacea, Anomura, Paguroidea) from the Early Eocene (Ypresian) of NE Italy. *Atti della Società italiana di Scienze Naturali e del Museo civico di Storia naturale in Milano* 150:229–238.
- Garassino, Alessandro, Antonio De Angeli, & Giovanni Pasini. 2014. A new porcellanid genus (Crustacea, Decapoda) to accommodate the Late Cretaceous *Paragalathea africana* Garassino, De Angeli & Pasini, 2008 from southeast Morocco. *Scripta Geologica* 147:117–124.
- Gašparič, Rok, R. H. B. Fraaije, Ninon Robin, & Antonio De Angeli. 2016. The first record of paguroids from the Eocene of Istria (Croatia) and further phylogenetic refinement of the Paguroidea (Crustacea, Anomura). *Bulletin of Geosciences* 91:467–480. [DOI:10.3140/bull.geosci.1616].
- Glaessner, M. F. 1960. The fossil decapod Crustacea of New Zealand and the evolution of the order Decapoda. *New Zealand Geological Survey Paleontological Bulletin* 31:3–63, pl. 1–7.
- Glaessner, M. F. 1969. Decapoda. *In* R. C. Moore, ed., *Treatise on Invertebrate Paleontology, Part R, Arthropoda* 4, Vol. 2. The Geological Society of America & The University of Kansas Press. Boulder & Lawrence. p. 400–533, 626–628.
- Hu, C.-H., & H.-J. Tao. 1996. Crustacean fossils of Taiwan. *Ta-Jen Printers*. Taipei, Taiwan, Republic of China. 228 p., 28 pl.
- Hyden, F. M., & Jacques Forest. 1980. An *in situ* hermit crab from the early Miocene of Southern New Zealand. *Palaeontology* 23:471–474.
- Jagiello, Zuzanna, Łukasz Dylewski, & Marta Szulkin. 2024. The plastic homes of hermit crabs in the Anthropocene. *Science of the Total Environment* 913:168959. [DOI:10.1016/j.scitotenv.2023.168959].
- Jagt, J. W. M., B. W. M. van Bakel, R. H. B. Fraaije, & Christian Newmann. 2006. *In situ* hermit crabs (Paguroidea) from northwest Europe and Russia. Preliminary data on new records. *Revista Mexicana de Ciencias Geológicas* 23:364–369.
- Karasawa, Hiroaki. 2002. Fossil uncinidean and anomalan Decapoda (Crustacea) in the Kitakyushu Museum and Institute of Natural History. *Bulletin Kitakyushu Museum of Natural History* 21:13–16.
- Karasawa, Hiroaki, Yoshiaki Mizuno, Kiichiro Hachiya, & Yusuke Ando. 2017. Reappraisal of anomuran and brachyuran decapods from the lower Miocene Morozaki Group, Japan, collected by the Tokai Fossil Society. *Bulletin of the Mizunami Fossil Museum* 43:47–69.
- Kato, Hisayoshi, Shinji Isaji, Akihiro Koizumi, & Susumu Tomida. 2017. Additions to the fossil decapod Crustacea from the Miura and Kazusa groups of the Boso Peninsula, Japan. *Journal of the Natural History Museum and Institute, Chiba, Special Issue* 10:51–60.
- Klompemaker, A. A., Pedro Artal, R. H. B. Fraaije, & J. W. M. Jagt. 2011. Revision of the family *Gastrodoridae* (Crustacea, Decapoda), with description of the first species from the Cretaceous. *Journal of Paleontology* 85:226–233. [DOI:10.1666/10-028.1].
- Klompemaker, A. A., C. E. Schweitzer, R. M. Feldmann, & Michał Kowalewski. 2013. The influence of reefs on the rise of the Mesozoic marine crustaceans. *Geology* 41:1179–1182. [DOI:10.1130/G34768.1].
- Leach, W. E. 1821. *Galatæadées, Galatæadæ. (Crust.)*. *In* F. Cuvier, ed., *Dictionnaire des Sciences Naturelles, dans lequel on trait Méthodiquement des Différens êtres de la Nature, considérés soit en eux-mêmes, d'après l'état actuel de nos connoissances, soit relativement a l'utilité qu'en peuvent retirer la Médecine, l'Agriculture, le Commerce et les Arts. Suivi d'une biographie des plus Célèbres Naturalistes. Ouvrage destiné aux médecins, aux agriculteurs, aux commerçans, aux artistes, aux manufacturiers, et à tous ceux qui ont intérêt à connoître les productions de la nature, leurs caractères génériques et spécifiques, leur lieu natal, leurs propriétés et leurs usages*. Vol. 18. F. G. Levrault et Le Normant, Strasbourg et Paris. p. 49–56.
- Luque, J., R. M. Feldmann, O. Vernygora, C. E. Schweitzer, C. B. Cameron, K. A. Kerr, F. J. Vega, A. Duque, Michael Strange, A. R. Palmer, & Carlos Jaramillo. 2019. Exceptional preservation of mid-Cretaceous marine arthropods and the evolution of novel forms via heterochrony. *Science Advances* 5:eaav3875. [DOI:10.1126/sciadv.aav3875].
- Machordom, Annie, S. T. Ahyong, Nikos Andreakis, Keiji Baba, David Buckley, Ricardo Garcia-Jiménez, A. W. McCallum, P. C. Rodríguez-Flores, & Enrique Macpherson. 2022. Deconstructing the crustacean squat lobster genus *Munida* to reconstruct the evolutionary history and systematics of the family Muniidae (Decapoda, Anomura, Galatheoidea). *Invertebrate Systematics* 36:926–970. [DOI:10.1071/IS22013].
- Macpherson, Enrique, W. J. Jones, & Michel 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.
- Macpherson, Enrique, & Annie Machordom. 2000. *Raymunida*, new genus (Decapoda: Anomura: Galatheidae) from the Indian and Pacific Oceans. *Journal of Crustacean Biology* 20:253–258. [DOI:10.1163/1937240X-90000027].
- Martin, J. W., & L. G. Abele. 1988. External morphology of the genus *Aegla* (Crustacea, Anomura, Aeglidæ). *Smithsonian Contributions to Zoology* 453:46 p.
- McLaughlin, P. A., & Rafael Lemaitre. 2001. 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. [DOI:10.1163/20021975-99990198].

- Mironenko, Aleksandr. 2020. A hermit crab preserved inside an ammonite shell from the Upper Jurassic of central Russia: implications to ammonoid palaeoecology. *Palaeogeography, Palaeoclimatology, Palaeoecology* 537:109397. [DOI:10.1016/j.palaeo.2019.109397].
- Müller, Pál. 1978. Decapoda (Crustacea) fauna a Budapesti miocénből (5). Faune de Décapodes (Crustacés) dans le Miocène de Budapest. *Földtani Közlöny* 108:272–312, pl. 1–23.
- Nyborg, Torrey, & F. J. Vega. 2008. Three new fossil species of *Lophomastix* (Decapoda: Blepharipodidae) from the Cenozoic of Washington. *Journal of Crustacean Biology* 28:361–369. [DOI:10.1163/20021975-99990381].
- Ocean Biodiversity Information System (OBIS). 2023. OBIS. Intergovernmental Oceanographic Commission of UNESCO. Accessed February 19, 2025. <https://www.obis.org>.
- Ortmann, A. E. 1902. The geographical distribution of freshwater decapods and its bearing upon ancient geography. *Proceedings of the American Philosophical Society, Philadelphia*, 41:267–400. [DOI:10.5962/bhl.title.16020].
- Osawa, Masayuki & Tin-Yam Chan. 2010. Part III. Porcellainidae (Porcelain crabs). In Tin-Yam Chan, ed., *Crustacean Fauna of Taiwan: Crab-like anomurans (Hippoidea, Lithoidea and Porcellanidae)*. National Taiwan Ocean University. Keelung, Taiwan. p. 67–181.
- Palero, Ferran, Aymee Robainas-Barcia, Laure Corbari, & Enrique Macpherson. 2017. Phylogeny and evolution of shallow-water squat lobsters (Decapoda, Galatheoidea) from the Indo-Pacific. *Zoologica Scripta* 46:584–595. [DOI:10.1111/zsc.12230].
- Palero, Ferran, P. C. Rodrigues-Flores, Patricia Cabezas, Annie Machordom, Enrique Macpherson, & Laure Corbari. 2019. Evolution of squat lobsters (Crustacea: Galatheoidea): mitogenomic data suggest an early divergent Porcellanidae. *Hydrobiologia* 833:173–184. [DOI:10.1007/s10750-019-3898-7].
- Pasini, Giovanni, Alessandro Garassino, Torrey Nyborg, S. G. Dunbar, & R. H. B. Fraaije. 2020. *In situ* hermit crab (Anomura, Paguroidea) from the Oligocene Pysht Formation, Washington, USA. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 295:17–22. [DOI:10.1127/njgpa/2020/0865].
- Paul'son, Otton. 1875. Studies on the Crustacea of the Red Sea with notes regarding other seas. Part 1. Podophthalmata and Edriophthalmata (Cumacea). S. V. Kul'zhenko. Kiev. [Translation published for The National Science Foundation, Washington, D. C. and Smithsonian Institution, U.S.A., by the Israel Program for Scientific Translations, 1961.] p. 1–164, 21 pl.
- Perrin, Christine. 2002. Tertiary: the emergence of modern reef ecosystems. In Wolfgang Kiessling, Erik Flügel, & Jan Golonka, eds., *Phanerozoic Reef Patterns*. SEPM Special Publication 72. p. 587–621. [DOI:10.2110/pec.02.72.0587].
- Poore, G. C. B., & S. T. Ah Yong. 2023. *Marine Decapod Crustacea: a guide to families and genera of the world*. CRC Press. Boca Raton, FL. 916 p.
- Robins, C. M., R. M. Feldmann, & C. E. Schweitzer. 2013. Nine new genera and 24 new species of the Muniopsidae (Decapoda: Anomura: Galatheoidea) from the Jurassic Ernstbrunn Limestone of Austria, and notes on fossil muniopsid classification. *Annalen des Naturhistorischen Museums in Wien (Serie A)*. 115:167–251.
- Robins, C., R. M. Feldmann, C. E. Schweitzer, & Aubrey Bonde. 2016. New families Paragalatheidae and Catillogalatheidae (Decapoda: Anomura: Galatheoidea) from the Mesozoic, restriction of the genus *Paragalathea*, and establishment of 6 new genera and 20 new species. *Annalen des Naturhistorischen Museums in Wien (Serie A)* 118:65–113.
- Rodríguez-Flores, P. C., Enrique Macpherson, K. E. Schnabel, S. T. Ah Yong, Laure Corbari, & Annie Machordom. 2022. Depth as a driver of evolution and diversification of ancient squat lobsters (Decapoda, Galatheoidea, *Phylladorhynchus*). *Molecular Phylogenetics and Evolution* 171:107467. [DOI:10.1016/j.ympev.2022.107467].
- Rodríguez-Flores, P. C., C. A. Seid, G. W. Rouse, & Gonzalo Giribet. 2023. Cosmopolitan abyssal lineages? A systematic study of East Pacific deep-sea squat lobsters (Decapoda: Galatheoidea: Muniopsidae). *Invertebrate Systematics* 37:14–60. [DOI:10.1071/IS22030].
- Roterman, C. N., W.-K. Lee, Xinming Liu, Rongcheng Lin, Xinzhen Li & Y.-J. Won. 2018. A new yeti crab phylogeny: vent origins with indications of regional extinction in the East Pacific. *PLoS One*, 13(3): e0194696. [DOI:10.1371/journal.pone.0194696].
- Scholtz, Gerhard. 2020. *Eocarcinus praecursor* Withers, 1932 (Malacostraca, Decapoda, Meiura) is a stem group brachyuran. *Arthropod Structure & Development* 59:100991 [DOI:10.1016/j.asd.2020.100991].
- Schram, F. R., & Stefan Koenemann. 2021. *Evolution and Phylogeny of Crustacea*. Oxford University Press. Oxford, UK. 872 p.
- Schweigert, Günter, René Fraaije, Philippe Havlik, & Alexander Nützel. 2013. New early Jurassic hermit crabs from Germany and France. *Journal of Crustacean Biology* 33:802–817. [DOI:10.1163/1937240X-00002191].
- Schweitzer, C. E., & R. M. Feldmann. 2000. First notice of the Chirostylidae (Decapoda) in the fossil record and new Tertiary Galatheidae (Decapoda) from the Americas. *Bulletin of the Mizunami Fossil Museum* 27:147–165.
- Schweitzer, C. E., & R. M. Feldmann. 2008. New Eocene hydrocarbon seep decapod crustacean (Anomura: Galatheidae: Shinkaiinae) and its paleobiological implications. *Journal of Paleontology* 82:1021–1029. [DOI:10.1666/08-007.1].
- Schweitzer, C. E., & R. M. Feldmann. 2015. Faunal turnover and niche stability in marine Decapoda in the Phanerozoic. *Journal of Crustacean Biology* 35:633–649. [DOI:10.1163/1937240X-00002359].
- Schweitzer, C. E., & R. M. Feldmann. 2023. Selective extinction at the end-Cretaceous and appearance of the modern Decapoda. *Journal of Crustacean Biology* 43:ruad018. [DOI:10.1093/jcbiol/ruad018].

- Schweitzer, C. E., R. M. Feldmann, & R. H. B. Fraaije. 2023. Part R, Revised, Volume 1, Systematic descriptions: Anomura (Gastrodoroidea, Lithodoidea, Lomisoidea, Paguroidea). *Treatise Online* 173:1–26, 10 fig. [DOI:10.17161/to.vi.21517].
- Schweitzer, C. E., R. M. Feldmann, Hiroaki Karasawa, A. A. Klompmaker, & C. M. Robins. 2023. Part R, Revised, Volume 1, Chapter 8T22: Systematic descriptions: Infraorder Anomura (exclusive of Lithodoidea, Lomisoidea, and Paguroidea). *Treatise Online* 168:1–31, 13 fig. [DOI:10.17161/to.vi.21021].
- Tan, M. H., H. M. Gan, Y. P. Lee, Stuart Linton, Frederic Grandjean, M. L. Bartholomei-Santos, A. D. Miller, & C. M. Austin. 2018. ORDER within the chaos: insights into phylogenetic relationships within the Anomura (Crustacea: Decapoda) from mitochondrial sequences and gene order rearrangements. *Molecular Phylogenetics and Evolution* 127:320–331. [DOI:10.1016/j.ympev.2018.05.015].
- Todd, J. A., & J. S. H. Collins, 2005. Neogene and Quaternary crabs (Crustacea, Decapoda) collected from Costa Rica and Panama by members of the Panama Paleontology Project. *Bulletin of the Mizunami Fossil Museum* 32:53–85, pl. 1–4.
- Tsang, L. M., T.-Y. Chan, S. T. Ahyong, & K. H. Chu. 2011. Hermit to king, or hermit to all: multiple transitions to crab-like forms from hermit crab ancestors. *Systematic Biology* 60:616–629. [DOI:10.1093/sysbio/syr063].
- Tudge, C. C., Akira Asakura, & S. T. Ahyong. 2012. Infraorder Anomura MacLeay, 1838. *In* F. R. Schram, & J. C. von Vaupel Klein, eds., *The Crustacea*, Vol. 9, Part B. Brill. Leiden. p. 221–333.
- van Bakel, B. W. M., R. H. B. Fraaije, J. W. M. Jagt, & Pedro Artal. 2008. An unexpected diversity of Late Jurassic hermit crabs (Crustacea, Decapoda, Anomura) in Central Europe. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 250:137–156.
- Van Straelen, Victor. 1925. Contribution à l'étude des Crustacés Décapodes de la période jurassique. *Mémoires d'Académie Royale de Belgique, Science (série 2)* 4(7):1–462, pl. 1–10.
- Via Boada, Luis. 1981. Les Crustacés Décapodes du Cénomaniens de Navarre (Espagne): premiers resultats de l'étude des Galatheidae. *Géobios* 14(2):247–251.
- Wallaard, J. J. W., R. H. B. Fraaije, B. W. M. van Bakel, J. R. Nance, Adam Lindholm, & J. W. M. Jagt. 2023. New hermit crab species (Anomura, Paguroidea) from the upper Miocene St. Marys Formation of Maryland (USA), preserved in their host shells. *Zootaxa* 5227(3):389–397. [DOI:10.11646/zootaxa.5227.3.7].
- Wang, Zhengfei, Xinyi Xu, Yuqing Zheng, Jie Wang, Qian Yu, & Bo Liu. 2023. Taxonomic status and phylogenetic relationship of Anomura (Crustacea: Decapoda) based on mitochondrial sequences and gene order rearrangements. *Gene* 851:14702.
- White, Adam. 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* 24:132–135, pl. 42.
- Whiteaves, J. F. 1874. On recent deep-sea dredging operations in the Gulf of St. Lawrence. *American Journal of Science* 3(7):210–219.
- Withers, T. H. 1932. A Liassic crab, and the origin of the Brachyura. *Annals and Magazine of Natural History (series 9)* 3:13–323, pl. 9–10.
- Wolf, M. R., C. C. Tudge, S. L. S. Bueno, F. J. Zara, & A. L. Castilho. 2023. The ultrastructure of spermatozoa of two species of *Aegla* (*A. parana* and *A. quilombola*) (Crustacea, Decapoda) endemic to Brazil. *Arthropod Structure & Development* 74:101265. [DOI:10.1016/j.asd.2023.101265].
- Wolfe, J. M., Javier Luque, & H. D. Bracken-Grissom. 2021. How to become a crab: phenotypic constraints on a recurring body plan. *BioEssays* 43:2100020. [DOI:10.1002/bies.202100020].
- Wolfe, J. M., J. W. Breinholt, K. A. Crandall, A. R. Lemmon, E. M. Lemmon, L. E. Timm, M. E. Siddall, & H. D. Bracken-Grissom. 2019. A phylogenetic framework, evolutionary timeline and genomic resources for comparative studies of decapod crustaceans. *Proceedings of the Royal Society B* 286:20190079. [DOI:10.1098/rspb.2019.0079].
- Yost, S. L., R. M. Feldmann, & C. E. Schweitzer. 2023. New Anomura (Decapoda) from the Kambühel Formation, Austria. *Annalen des Naturhistorischen Museums in Wien (Serie A)* 124:149–166.