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# EVOLUTIONARY HISTORY OF DECAPOD GROUPS: LOBSTERS (PALAEOPALAEEMONIDA, POLYCHELIDA, ACHELATA, GLYPHEIDEA, MARINE ASTACIDEA)

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## INTRODUCTION

The evolution of lobsters has received considerable attention because of their economic importance, iconic recognizability, and robust fossil record (KARASAWA, SCHWEITZER, & FELDMANN, 2013; BRACKEN-GRISOM & others, 2014; SCHWEITZER & FELDMANN, 2014). Lobsters are those decapods that have an elongate pleon held nearly straight and posteriorly from the cephalothorax, rarely partially curled ventrally, with a flattened telson (HAUG & HAUG, 2021); strong pereopods that may be chelate, achelate, or pseudochelate; and a carapace with a complex pattern of multiple carapace grooves. Lobster forms comprise the earliest peak in the sequential faunal turnover in Decapoda, peaking in the Jurassic, and replaced by podotrematous and heterotrematous crabs (SCHWEITZER & FELDMANN, 2015). Here, we summarize the evolutionary history of the decapod lobster groups at the infraorder level (FIG. 1; Table 1).

## PALAEOPALAEEMONIDA

Palaeopalaemonida comprises one family, genus, and species, *Palaeopalaemon newberryi* WHITFIELD, 1880. It is notable for being one of the oldest Decapoda and the oldest to exhibit a lobster-like, or macruran, body form. Palaeopalaemonida is found

to be basal among lobster-like decapods (KARASAWA, SCHWEITZER, & FELDMANN, 2013; JONES & others, 2018) (FIG. 2.1). The lobster-like body form is demonstrated by the elongate dorsal carapace ornamented with typical decapodan grooves, a pleon extending posteriorly, and chelae or pseudo-chelae on the first of five pairs of pereopods (FIG. 5.1).

*Palaeopalaemon* is known from Late Devonian to Early Mississippian marine deposits of Ohio, Iowa, Kentucky, and New York (SCHRAM, FELDMANN, & COPELAND, 1978). Fossils were recovered from concretions in black shales, which suggests an offshore habitat. *Palaeopalaemon* was most likely benthic, as suggested by its robust pereopods and possible trace fossils associated with the body fossils (JONES & others, 2018).

## POLYCHELIDA

Polychelida are unique among Decapoda in possessing a fourth chelate pereopod, and thus four, and sometimes five, pairs of chelate pereopods. Chelae and fingers generally are elongate, and the fingers are sometimes equipped with spines on the occlusal surfaces. Other diagnostic features include a dorsoventrally compressed cephalothorax, reduced rostrum, and in some forms, reduced eyes (AUDO, CHARBON-

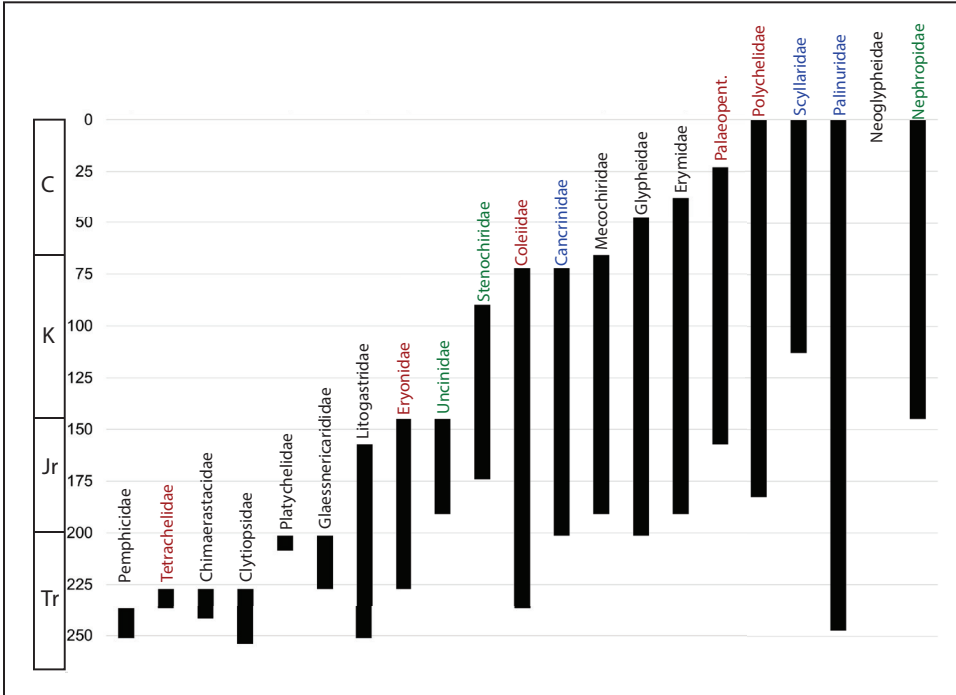


FIG. 1. Geologic range of families of decapod lobsters, in millions of years before present; *C*, Cenozoic; *K*, Cretaceous; *Jr*, Jurassic; *Tr*, Triassic; *black*, Glypheidea; *blue*, Achelata; *red*, Polychelida; *green*, Astacida; *Palaeopent.*, Palaeopentachelidae. Neoglypheidae is extant only.

NIER, & KROBICKI, 2017). The telson is narrow and pointed (CHAN, 1998) (FIG. 5.4; 5.7). In extant species, the giant eryoneicus balloon-shaped larvae are another notable diagnostic feature.

The early evolutionary history of Polychelida is shrouded in darkness. Like other ancient lineages of decapods, Polychelida probably diverged from other lineages around the middle of the Paleozoic. For instance, WOLFE and others (2019) suggested a divergence from Astacidea (clawed lobsters) in the Devonian. Yet the exact affinities of Polychelida are debated: historically, some were considered allied to shrimps, whereas others were considered more closely allied to lobsters, notably slipper lobsters (H. MILNE EDWARDS, 1837; PICTET, 1854). Because of their reduced rostrum and characteristics of the epistome and mouthparts, they were, for a long time, considered closely allied to slipper lobsters and spiny lobsters (BORRADAILE, 1907;

BURKENROAD, 1981). More recently, they often have been considered as a sister group to all other non-shrimp decapods (SCHOLTZ & RICHTER 1995; KARASAWA, SCHWEITZER, & FELDMANN, 2013; BRACKEN-GRISSOM & others, 2014), or within non-shrimp decapods, sister to Achelata (TSANG & others, 2008), Astacidea (WOLFE & others, 2019) or Glypheidea (TAN & others, 2018; WANG & others, 2021) (FIG. 2).

The polychelid fossil record is known almost completely from fossil Lagerstätten (AUDO & others, 2013). Maximum generic diversity (nine) occurred in the Middle Jurassic (Callovian), making Polychelida a typical group in Jurassic deposits (AUDO & others, 2013, 2014; SCHWEITZER & FELDMANN, 2014; AUDO, SCHWEIGERT, & CHARBONNIER, 2020) (FIG. 1; FIG. 3.1; FIG. 6). The earliest confirmed fossil record for the group is Late Triassic (FIG. 1). The monotypic Tetrachelidae occurred only in the Carnian, and the Coleiidae originated then.

These Carnian Polychelida already had a wide biogeographic distribution, from Japan to Europe, and featured species living in rather deep water and shallow water (KARASAWA & others, 2003; AUDO, CHARBONNIER, & KROBICKI, 2018; GAŠPARIČ & others, 2020; AUDO, BARRIEL, & CHARBONNIER, 2021).

The Early and Middle Jurassic were times of increasing polychelidan biodiversity. Coleiidae never was particularly diverse and reached maximum generic diversity (three) in the Callovian (Middle Jurassic) and became extinct in the Campanian (Late Cretaceous). Eryonidae was the most diverse polychelid family, with ten referred genera, and diversity peaked in the Middle and Late Jurassic, with five genera, when it became extinct in the Tithonian. Palaeopentachelidae originated in the Kimmeridgian and may have become extinct then (AUDO, BARRIEL, & CHARBONNIER, 2021). An alternative hypothesis is that it became extinct in the Oligocene (KARASAWA, SCHWEITZER, & FELDMANN, 2013). During the latest part of the Jurassic, the development of wide shallow-water lagoonal environments, and the greater fossilization potential offered inside the lagoons themselves, documents this massive diversification of polychelidan lobsters in Europe. Several monotypic genera appeared at this time but became extinct following sea-level variations, perhaps coupled with the emergence of Brachyura (AUDO, BARRIEL, & CHARBONNIER, 2021).

The extant Polychelidae first appeared in the Toarcian and has a long ghost range, from the Early Cretaceous (Valanginian) until the Holocene, where it makes up part of the modern lobster fauna and is represented by eight genera (SCHWEITZER & FELDMANN, 2014). Polychelida exhibited its highest percentage of the decapod fauna during the Triassic and Early Jurassic but was reduced to less than 5% of the decapod fauna by the Early Cretaceous (SCHWEITZER & FELDMANN, 2015).

Modern polychelids, represented by eight genera, inhabit extremely deep-water

environments and because they have no commercial value, they are less well studied than most other lobster groups (HOLTHUIS, 1991; CHANG, AHYONG, & TSANG, 2024). Extant members inhabit primarily bathyal environments, with some even ranging to abyssal depths (GALIL, 2000; LAVALLI & SPANIER, 2010). A recent observation of an individual of *Pentacheles laevis* BATE, 1878, actively swimming was suggested to support its basal position within Decapoda based on perceived similarity with the 'Natantia' (swimming shrimp) (ARNÉS-URGELLÉS & others, 2020). Polychelidan families had diverged in environmental occurrences by the Jurassic (SCHWEITZER & FELDMANN, 2014; AUDO, BARRIEL, & CHARBONNIER, 2021; CHANG, AHYONG, & TSANG, 2024). Extant specimens of the polychelidan *Willemoesia* spp. were collected with siliceous sponges. Coleiids are found most commonly in carbonates, some sponge-bearing, and eryonids tend to be recovered from plattenkalks and other low-energy deposits (SCHWEITZER & FELDMANN, 2014). Thus, the sponge association may be ancient (GORE, 1984). Some Early to Middle Jurassic polychelidans possessed well-developed eyes, suggesting a preference for shallow water, at least in the photic zone (AHYONG, 2009; AUDO & others, 2016). Other Early Jurassic polychelidans exhibited reduced ocular incisions, which suggests they were adapted to deeper, dysphotic environments (AUDO, CHARBONNIER, & KROBICKI, 2017). Thus, polychelidans inhabited both shallow photic depths as well as dysphotic habitats (up to 1000 m) by the Late Triassic. This broad diversification in environmental preferences across the group may indicate that their lineage is much older than Triassic (AUDO, BARRIEL, & CHARBONNIER, 2021). The colonization of deep-water habitats may have occurred early in the evolution of the group because the most derived extant genera inhabit the deepest environments, which suggests long periods of evolution in that environment (CHANG, AHYONG, & TSANG, 2024).

**Table 1.** Geologic ranges for decapod lobster infraorders, superfamilies, and families.

Taxon	Geologic Range
IO Palaeopalaemonida Schram & Dixon, 2004	Late Devonian–Mississippian
Palaeopalaemonidae Brooks, 1962	Late Devonian–Mississippian
IO Polychelida Scholtz & Richter, 1995	Late Triassic (Carnian)–Holocene
Coleiidae Van Straelen, 1925*	Late Triassic (Carnian)–Late Cretaceous (Campanian)
Eryonidae De Haan, 1841*	Late Triassic (Norian)–Late Jurassic (Tithonian)
Palaeopentachelidae Ahyong, 2009*	Late Jurassic (Kimmeridgian)–Oligocene
Polychelidae Wood-Mason, 1875	Early Jurassic (Toarcian)–Holocene
Tetrachelidae Beurlen, 1930*	Late Triassic (Carnian)
IO Achelata Scholtz & Richter, 1995	Middle Triassic (Anisian)–Holocene
Cancrinidae Beurlen, 1930*	? Early Jurassic (Hettangian–Sinemurian), Late Jurassic (Tithonian)–Late Cretaceous (Cenomanian)
Palinuridae Latreille, 1802	Middle Triassic (Anisian)–Holocene
Scyllaridae Latreille, 1825	Early Cretaceous (Albian)–Holocene
IO Glypheidea Winckler, 1882	Permian–Holocene
Superfamily Erymoidea Van Straelen, 1925	Early Triassic (Olenekian)–Holocene
Erymidae Van Straelen, 1925*	Middle Triassic (Anisian)–Eocene (Bartonian)
Pemphicidae Van Straelen, 1928*	Early Triassic (Olenekian)–Middle Triassic (Ladinian)
Superfamily Glaessnericaroida Karasawa, Schewitzer, & Feldmann, 2013	Late Triassic (Norian)
Glaessnericarididae Karasawa, Schewitzer, & Feldmann, 2013*	Late Triassic (Norian)
Superfamily Glypheoidea Winckler, 1882	Permian–Holocene
Chimaerastacidae Amati, Feldmann, & Zonneveld, 2004*	Middle Triassic (Ladinian)–Late Triassic (Carnian)
Clytiopsidae Beurlen, 1927*	Permian–Late Triassic (Carnian)
Glypheidae Winckler, 1882*	Early Jurassic (Hettangian)–Eocene (Ypresian)
Litogastroidae Karasawa, Schewitzer, & Feldmann, 2013*	Early Triassic (Olenekian)–Late Jurassic (Oxfordian)
Mecochiridae Van Straelen, 1925*	Early Jurassic (Pliensbachian)–Late Cretaceous (Maastrichtian)
Neoglypheidae Karasawa, Schewitzer, & Feldmann, 2013	Holocene
Platychelidae Glaessner, 1969*	Late Triassic
IO Astacidea Latreille, 1802	Lower Jurassic (Pliensbachian)–Holocene
Section Homarida Scholtz & Richter, 1995	Lower Jurassic (Pliensbachian)–Holocene
Superfamily Enoplometopoidea de Saint Laurent, 1988	Lower Jurassic (Pliensbachian)–Holocene
Enoplometopidae de Saint Laurent, 1988	Holocene
Uncinidae Beurlen, 1930*	Lower Jurassic (Pliensbachian)–Upper Jurassic (Tithonian)
Superfamily Stenochiroidea Beurlen, 1928	Early Jurassic (Sinemurian)–Upper Cretaceous (Cenomanian–Turonian)
Stenochiridae Beurlen, 1928*	Early Jurassic (Sinemurian)–Upper Cretaceous (Cenomanian–Turonian)
Superfamily Nephropoidea Dana, 1852	Lower Cretaceous (Berriasian)–Holocene
Nephropidae Dana, 1852	Lower Cretaceous (Berriasian)–Holocene

\* Indicates extinct families. IO = infraorder.

AHYONG (2009) hypothesized that Polychelida became adapted to a burrowing or burying habit through time; AUDO, BARRIEL, and CHARBONNIER (2021) suggested that extinct and extant forms may have acquired the burrowing habit independently. Extant forms exhibit shallow burying behavior (GORE, 1984). The antennular stylocerites in extant taxa assist with respiration, and the carapace is narrower in extant forms, both of which are adaptations for shallow burying (AHYONG, 2009). A video from the National Oceanic and Atmospheric Administration (NOAA) shows an individual identified as *Pentacheles laevis* bursting from what appears to be mud, then swimming backward with its first pereopods outstretched. It then swims away with its anterior forward and pereopods folded alongside the body, using very large pleopods (NOAA, 2017). In addition to the typical caridoid escape response, *P. laevis* was observed swimming forward with its pleopods. This swimming style was probably retained in Polychelids, although it disappeared for other non-shrimp decapods (ARNÉS-URGELLÉS & others, 2020). Images of extant polychelidans resting in their native habitat show them holding their first pereopods parallel to the body, with the articles extending back to the second or third pleomere (NOAA, n.d.). Among fossil forms, some coleiid and *Palaepentacheles* are preserved with their pereopods in this position, parallel to the body and extending to the pleon. It is not known if the carrying position of the pereopods has any correlation with swimming or burying. The extant swimming polychelidan referenced above exhibits very large pleopods; in fossil species, pleopods are rarely preserved. Those that are, however, seem shorter than those of modern polychelids.

Geographically, most fossil occurrences are in Triassic and Jurassic rocks of Europe, with a few found in Antarctica, Western North America, India, and Japan. Extant forms are mostly in the Indian, southwestern Pacific, and Atlantic oceans, with few in the eastern Pacific (OBIS, 2023), in tropical to temperate

latitudes (LAVALLI & SPANIER, 2012). Extant polychelidans were posited to have originated in the Atlantic during the Late Jurassic, with subsequent global dispersal (CHANG, AHYONG, & TSANG, 2024). The paucity of fossils post-Jurassic makes testing geographic range changes over time difficult.

Aside from the reduction in eyes in some extinct and all extant forms, a few other morphological trends have been identified. In some extinct forms, the carapace covers the bases of the antennules and antennae, whereas in extant forms, these are visible dorsally (AHYONG, 2009). The width between the orbits was reduced over time, and chelipeds are generally more slender in extant forms (AHYONG, 2009). These morphological changes may be associated with a move from shallow, benthic habitats to deeper habitats (AHYONG, 2009).

Polychelidan lobsters have a surprisingly robust fossil record of larvae, and even eggs are known from fossils. Extant polychelids exhibit an eryoneicus larva, which is large, spiny, and balloon-shaped, and adapted to planktonic strategies in deep-sea environments (MARTIN, OLESEN, & HØEG, 2014; HAUG & others, 2015). Larval forms resembling an eryoneicus larva have been found in Cenomanian rocks, and larval forms that appear more similar to the corresponding polychelid adult are known from older, Bajocian-Bathonian (BRAVI & others, 2014) and Tithonian rocks (EILER & HAUG, 2016). The transition from the adult-like larval form to the eryoneicus-type larvae occurred by paedomorphosis and was suggested to be an adaptation to deeper water (EILER & HAUG, 2016). A Callovian polychelidan was preserved with a small number of large eggs, similar to egg clutches in extant polychelidans; thus, whereas the larval forms changed through time, egg size and number in each clutch apparently did not (JAUVION & others, 2020). The development of a well-adapted, planktonic, eryoneicus larva may have compensated for the small number of eggs in each brood so that brood size did not change (JAUVION & others, 2020).



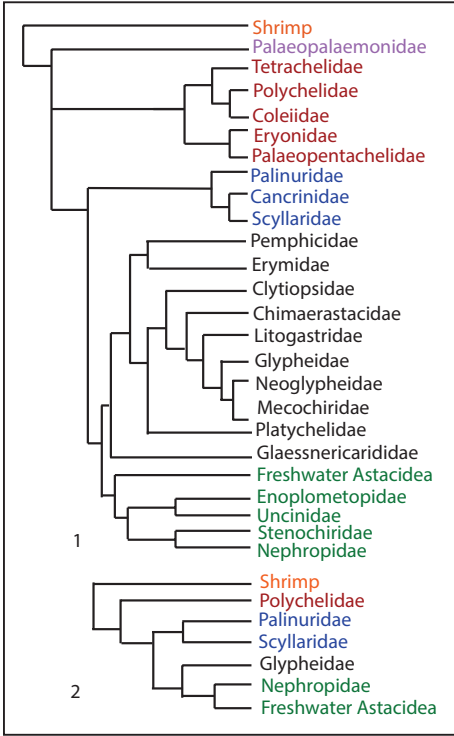


FIG. 2. Simplified phylogenies for decapod lobsters; 1, tree including all fossil and extant families (adapted from Karasawa & others, 2013); 2, tree including extant families (adapted from Bracken-Grissom & others, 2014); *black*, Glypheidae; *blue*, Achelata; *green*, Astacida; *purple*, Palaeopalaemonidae; *orange*, outgroup; *red*, Polychelida.

Thus, although never speciose, Polychelida has maintained a low-level presence as part of the decapod fauna since the Triassic. Its long-term success may be attributable to its acquisition of a planktonic larval form concomitant with the move to, or change in, preference to deeper water environments.

## ACHELATA

Achelata is comprised of lobster-like decapods, characterized by a generally dorsoventrally flattened, strongly ornamented or sclerotized body, and strongly developed antennae (Fig. 5.3, 5.8). They are unique in lacking chelate appendages, except for the rare fifth pereopod and the occasional pseudochelate first pereopod. The group appeared early in the history of Decapoda and has

maintained a significant presence in modern oceans (FIG. 1). Placement of Achelata, with respect to other decapod clades, is variable within recent phylogenies (FIG. 2). KARASAWA, SCHWEITZER, and FELDMANN (2013) and BRACKEN-GRISSOM and others (2014) both found Achelata sister to Glypheidea + Astacidea. TSANG and others (2008) recovered Achelata as sister to Polychelida in a clade sister to Astacidea + Axiidea. WOLFE and others (2019) and WANG and others (2021) differed and found Achelata as basal to all non-shrimp decapods. Thus, evolutionary relationships of Achelata with other Decapoda remain unresolved. Within Achelata, Palinuridae was recovered sister to Scyllaridae (BRACKEN-GRISSOM & others, 2014) or sister to a clade of Cancrinidae + Scyllaridae (KARASAWA, SCHWEITZER, & FELDMANN, 2013).

Molecular analyses predicted appearance of Achelata in the Devonian or earliest Mississippian, with divergence between the two extant families, Palinuridae and Scyllaridae, during the Permian or Triassic (BRACKEN-GRISSOM & others, 2014; WOLFE & others, 2019). Palinuridae was the earliest family to appear, based on fossil occurrences in the Middle and Late Triassic. The family radiated in the Late Jurassic and the Early Cretaceous, has maintained a moderate fossil record since then, and is an important component of the modern lobster fauna (SCHWEITZER & FELDMANN, 2014) (FIG. 3.2; FIG. 6). One extinct family, Cancrinidae, has a questionable occurrence in the Early Jurassic (Hettangian-Sinemurian), with confirmed occurrences in the Late Jurassic (Tithonian), and was extinct by the early Late Cretaceous (SCHWEITZER & others, 2015). Scyllaridae appeared in the Early Cretaceous and have never been speciose in the fossil record (AUDO & CHARBONNIER, 2012). They are, however, a robust component of the modern lobster fauna (SCHWEITZER & FELDMANN, 2014) (Fig. 6). Achelata has maintained a relatively consistent percentage of the decapod fauna in any given geologic stage, ranging from 2% to 7% of the total decapod fauna (SCHWEITZER &



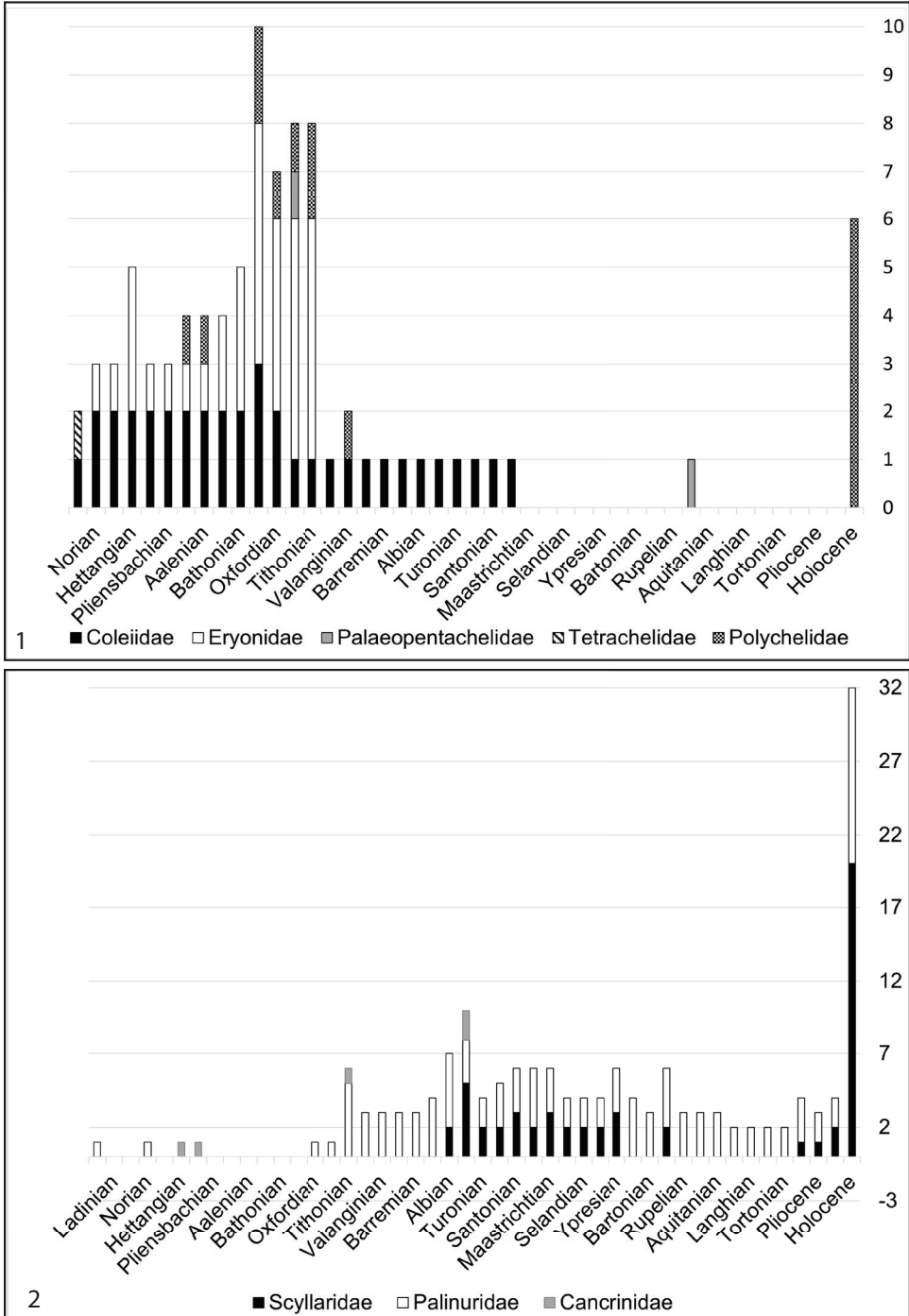


FIG. 3. Number of genera per unit time in families of 1, Polychelida, and 2, Achelata.

FELDMANN, 2015). The achelates exhibited little extinction, only one genus, at the end of the Cretaceous, perhaps because of the relatively long mean genus range within the group of approximately 41 million years, and the long family range of over 100 million years (SCHWEITZER & FELDMANN, 2023).

Antennal structure is unusual within Achelata compared with other decapods. Palinuridae are characterized by long, robust antennae, unique among Decapoda. Cancrinidae have elongated, ovate antennal structures composed of over a dozen articles (HAUG & others, 2016). HAUG and others (2016) showed that antennae within Achelata evolved from a robust multisegmented structure to the derived, flattened, shovel-like structures seen in Scyllaridae. They found intermediate morphologies between and among the antennae of Cancrinidae, Palinuridae, and Scyllaridae (SCHWEITZER & others, 2024). Thus, evolution of antennal shape is a key feature of Achelata.

Achelatans are unique among decapods in that they are almost entirely lacking chelae. The group is old, extending back to the Middle Triassic. Lack of chelae does not seem to have impeded their survival because the earliest appearing group, Palinuridae, is abundant in modern oceans. Achelatans use their blade-like dactyls of the pereopods to wedge open clams (SCHWEITZER & FELDMANN, 2010).

Unusual in the decapod fossil record is the abundance of preserved achelatan larvae. Palinurid lobsters exhibit a leaf-like phyllosoma larva that transitions to a more lobster-like puerulus form, and in scyllarids, the phyllosoma is followed by a nisto larva (MARTIN, OLESEN, & HØEG, 2014). Fossil achelatan larvae show a broad range of morphologies similar to, but not the same as, extant forms (HAUG & HAUG, 2016). Achelatan evolution has been suggested to include several heterochronic events during larval development that resulted in different larval morphologies, some of which are no longer extant, and possibly lead to the modern crown group morphologies (HAUG & others, 2013).

## Palinuridae

Palinuridae includes the spiny lobsters, sometimes called rock lobsters, that are characterized by a rectangular cross-section of the cephalothorax, a dorsoventrally flattened tail, and long, robust, spinose antennae (FIG. 5.3). They are an important group for lobster fisheries (HOLTHUIS, 1991).

GEORGE and MAIN (1967) hypothesized that the Palinuridae could be divided into two tribes, the Silentes and Stridentes, with different evolutionary histories. The two lineages were hypothesized to have diverged in the early Mesozoic (BRACKEN-GRISSOM & others, 2014). Stridulating, or noise producing, structures are present in the Stridentes and absent in Silentes, and each group is phylogenetically distinct (PALERO & others, 2009; BRACKEN-GRISSOM & others, 2014). Most fossil forms belong to the Stridentes and, indeed, sometimes have preserved stridulating structures (FELDMANN & SCHWEITZER, 2022). Confirmed occurrences of genera known to belong to Stridentes, *Linuparus* WHITE, 1847, and *Palinurus* WEBER, 1795, are recorded from the Late Jurassic (Tithonian) and are well known from the Cretaceous (SCHWEITZER & others, 2015). The oldest fossil taxa considered to belong to the Silentes, based on their similarity with the extant *Jasus*, are two species of *Archaeocarabus* M'COY, 1849, from the Eocene of England and Alabama, USA (GEORGE & MAIN, 1967; SCHWEITZER & others, 2015). Genera referred to Stridentes have a much more robust fossil record than Silentes, echoing the modern differential diversity of the two groups. This was hypothesized to be a result of the ability of Stridentes to escape predation and communicate using sound (BRACKEN-GRISSOM & others, 2014). Additionally, Stridentes have reproductive adaptations considered to allow more flexibility in mating as compared with Silentes, which also may explain their comparative abundance and diversity (LAVALLI & SPANIER, 2010). Many palinurid fossils from the Triassic and Jurassic are not yet placed

in genera regarded as either *Silentes* or *Stridentes*; more work will be needed to determine the earliest appearance of each of these lineages. For now, the earliest fossil occurrence of *Palinuridae* is Middle Triassic (FELDMANN & others, 2012); the earliest *Stridentes* is Tithonian, and the earliest *Silentes* is Eocene.

Among palinurids, a move from deeper to shallower water through time has been suggested (GEORGE & MAIN, 1967), and facies analysis of fossil members supports this for some lineages. *Palinurids* shifted from primarily low energy siliciclastic, possibly deeper water environments, in the Mesozoic to coral reef and higher energy siliciclastic environments in the Cenozoic (SCHWEITZER & FELDMANN, 2014). *Linuparus* generally inhabits deeper water environments today than as recorded in the fossil record, from depths of 200–300 m on muddy or sandy bottoms (HOLTHUIS, 1991). Fossils are found in siliciclastic sediments of all grain sizes as well as lithographic limestones, which suggests a range of depths from shallow subtidal across the slope (SCHWEITZER & FELDMANN, 2014). *Palinurus* fossils are found in nearly every type of sediment, including clay, sand, oolitic limestone, coral reefs, and lithographic limestones, which suggests broad environmental adaptability (SCHWEITZER & FELDMANN, 2014). Extant members generally live between 50 and 300 m, sometimes deeper, on rocky substrates (HOLTHUIS, 1991). *Palinurids* in general prefer habitats in which caves, crevices, or other protective structures are present (LAVALLI & SPANIER, 2010). Thus, the changes in environmental preferences from onshore to offshore, or vice versa, as well as substrate preference, are quite complex (PALERO & others, 2009), and based on the known fossil record, may have occurred multiple times.

The two palinurid groups have different geographic ranges in modern oceans. Extant *Silentes* inhabit mid-latitudes of 30–40 degrees, and fossil *Silentes* are not found in locations lower than 30 degrees latitude.

Extant *Stridentes* inhabit lower latitudes of 0–30 degrees (LAVALLI & SPANIER, 2010). The fossil record of both groups is largely in the 30–50 degree latitudinal range, mostly in Europe and North America. Only a few *Stridentes* fossil occurrences are between 0 and 30 degrees, including some Late Cretaceous and Danian species of *Linuparus*. *Yunnanopalinura* FELDMANN & others, 2012, from the Middle Triassic of China is the only other low-latitude occurrence, but it is unplaced as either *Stridentes* or *Silentes*. Thus, *Stridentes* must have become limited to lower latitudes as a more recent phenomenon, based on confirmed fossil occurrences at middle latitudes during the Oligocene (SCHWEITZER & others, 2015).

Within *Palinuridae*, *Linuparus*, *Palinurus*, and *Panulirus* WHITE, 1847, are all extant and have fossil records, for which the former two genera are quite extensive. Modern occurrences of *Linuparus* and *Palinurus* are limited and suggested to be relicts of much broader distributions in Cretaceous and Paleogene time, primarily in middle latitudes (PATEK & others, 2006). *Panulirus* has a limited fossil record but is widespread in tropical and subtropical modern oceans (PATEK & others, 2006). In general, the overall geographic distribution of fossil palinurids overlaps that of modern occurrences. Exceptions are in the Indian Ocean, coastal Africa, and the central Pacific Ocean, which lack fossils but have robust modern occurrences (HOLTHUIS, 1991). Africa lacks rocks of the appropriate age, for the most part, and Indian fossil decapods are poorly known. The central Pacific Ocean has little area available for fossilization; thus, any discrepancies in the fossil and modern distribution may be because of biases in the fossil record. Potentially relevant to the fossil record is that extant palinurid genera usually do not occur together in a geographic area, and when they do, they exhibit niche partitioning (LAVALLI & SPANIER, 2010).

*Palinurids* are known for a distinctive behavior, in which they form lines of up to 50 individuals, with the pleon of one indi-

vidual in contact with the antenna of the following individual (LAVALLI & SPANIER, 2010). This behavior can be very complex and apparently confers benefit in being part of a group (LAVALLI & SPANIER, 2010). Although the behavior cannot be seen in fossils, it might be possible to find groups of palinurids fossilized together, as a result of their association.

### **Cancrinidae**

Cancrinidae is a small family, comprising only two genera. They have very distinctive ovate, inflated antennae. So far they are known only with certainty from lithographic limestones of the Tithonian and Late Cretaceous, in Germany and Lebanon (SCHWEITZER & others, 2015). A questionable occurrence has been reported from Early Jurassic (Hettangian-Sinemurian) deposits of the UK. HAUG and others (2016) described an evolutionary transition from the long antennae of palinurids, through the shorter, ovate antennae of cancrinids, to the flattened antennae of scyllarids. Cancrinids lacked diversity but seemed to occupy an intermediate morphological position between two important lobster lineages that are still extant.

### **Scyllaridae**

Scyllaridae are known commonly as slipper lobsters and are characterized by a dorsoventrally flattened cephalothorax and pleon, and very wide, flattened, short antennae (FIG. 5.8). By the Late Cretaceous, fossils clearly attributable to Scyllaridae had appeared, which suggests the family was well-differentiated from the other achelatan lineages by that time (WEBBER & BOOTH, 2007). Modern scyllarids are placed within four subfamilies, Arctidinae, Ibacinae, Scyllarinae, and Theninae. AUDO and CHARBONNIER (2012) reported a juvenile arctidine scyllarid from the Cenomanian; thus, that subfamily had diverged by at least the Late Cretaceous. One extinct genus has been placed within Ibacinae, from the early Eocene (Ypresian) (AUDO, 2019), but

other extinct genera have not been placed reliably within subfamilies. Furthermore, some generic placements of extinct species in extant genera are not confirmed. Thus, timing of radiation of the various subfamilies within Scyllaridae is poorly constrained.

Scyllarid genera often coinhabit the same region today, which suggests niche partitioning in the lineage (WEBBER & BOOTH, 2007). A tendency toward cryptic lifestyles, with camouflage and a flattened body form, has been suggested for the group, which today is found mostly in warmer waters (WEBBER & BOOTH, 2007), up to 45 degrees latitude (LAVALLI & SPANIER, 2010). Scyllarid genera usually prefer a particular type of substrate, either a hard surface like rocks or reefs in genera with more ornamented and vaulted bodies, or soft, muddy or sandy areas in flattened forms that may bury (LAVALLI & SPANIER, 2010; POORE & AHYONG, 2023).

In terms of depth, Scyllaridae was found to have invaded deep-water habitats (defined as >200 m) fifteen times (YANG & others, 2012). The extant Arctidinae inhabit shallow water, whereas the most recently branching clade within Scyllaridae, Scyllarinae, are deeper-water taxa (YANG & others, 2012). Both Arctidinae and Scyllarinae have less dorsoventrally compressed carapaces than other subfamilies and inhabit rocks and corals (POORE & AHYONG, 2023). The Ibacinae and Theninae have more flattened cephalothoraxes and burrow into soft sediments (POORE & AHYONG, 2023). Extinct scyllarid species are recovered from fine siliciclastics and lithographic limestones, interpreted as quiet and/or deeper-water environments, whereas extant species inhabit coarse siliciclastics, carbonates, and reefal environments, interpreted as shelf environments (SCHWEITZER & FELDMANN, 2014). Thus, it seems clear that a shift in habitats occurred over time, but the poor fossil record of Scyllaridae makes it difficult to test timing of such shifts and the number of times they occurred.

## GLYPHEIDEA

Glypheidea, which encompasses glypheoid and erymoid lobsters, was a great Mesozoic success story (SCHWEITZER & FELDMANN, 2014). With only two extant genera, this group flourished early in the history of decapods. The infraorder embraces two large superfamilies, Glypheoidea (Chimae-rastacidae, Clytiopsidae, Glypheidae, Lito-gastroidea, Mecochiridae, Neoglypheidae, Platychelidae) and Erymoidea (Erymidae, Pemphicidae) as well as the monotypic Glaess-nericaridoidea sensu KARASAWA, SCHWEITZER, and FELDMANN (2013) (Table 1). Erymoid and glypheoid lobsters each have a distinctive appearance (FIG. 5.2, 5.5). Erymidae are clawed lobsters, generally with a short but robust pleon and large chelae with slender fingers. Glypheoids have chelate or pseudo-chelate pereiopods and a slender pleon. Both have strongly developed carapace groove patterns.

KARASAWA, SCHWEITZER, and FELDMANN (2013) recovered Erymoidea (Erymidae + Pemphicidae) as sister to Glypheoidea + Glaessnericaridoidea. All three are part of a clade sister to Astacidea (FIG. 2). BRACKEN-GRISOM and others (2014) recovered extant glypheids as sister to the Astacidea, whereas TAN and others (2018) recovered a clade consisting of Polychelida + Glypheidea as sister to Astacidea. CHARBONNIER and others (2014) considered Pemphicidae as part of Glypheidea, which they recovered as a clade among unresolved clades of homarids, erymids, and other lobsters. DEVILLEZ, CHARBONNIER, and BARRIEL (2019) recovered Erymidae as sister to Homarida, together in a clade sister to several glypheoid lineages. Thus, Glypheoidea and Erymidae sensu KARASAWA, SCHWEITZER, and FELDMANN (2013) always are recovered as monophyletic, with Pemphicidae in variable placement. We follow KARASAWA, SCHWEITZER, and FELDMANN (2013) because, their findings are congruent with those of BRACKEN-GRISOM and others (2014) using molecular data and because KARASAWA, SCHWEITZER, and FELDMANN (2013) used members of

every lobster group, extinct and extant, within their phylogeny, which makes it the most complete to date. Despite alternative placements of glypheidean families at higher taxonomic levels, the composition of families and genera is remarkably consistent across these works. Thus, lobster classification is moving toward consensus.

Erymoidea embraces two families. Erymidae are characterized by possession of a strong cervical groove, well-developed parallel or subparallel postcervical and branchiocardiac grooves, an intercalated plate, and a well-developed, chelate first pereiopod. Pemphicidae bear a well-developed cervical groove and a branchiocardiac groove that intercepts the postcervical groove. Pemphicids have a strong, subchelate first pereiopod. The monotypic Glaessnericaridoidea have four pairs of chelate appendages in addition to well-developed cervical, postcervical, and branchiocardiac grooves. Glypheoidea possess a branchiocardiac groove that typically is parallel to the postcervical groove and converges toward the cervical groove. The families among Glypheoidea are differentiated based on the nature of the pereiopod terminations, which are chelate or pseudochelate on the first pereiopod and pseudo- or achelate on the second through fifth pereiopods. A well-developed demarcation between pleural terga and pleura is present in glypheoids.

Erymoidea ranged from the Middle Triassic to the early Eocene and reached their greatest diversity in the Jurassic (FIG. 1; FIG. 4.1). Glypheoidea are known from the late Permian to the Holocene (FELDMANN & others, 2015). Glypheoidea, embracing six extinct families, flourished through the Jurassic and Cretaceous. Although they are not among the earliest branching clades within Decapoda, some of the earliest known fossil decapods are glypheidean lobsters. Nearly all of the families within the infraorder originated in the Triassic, and maximum generic diversity was reached in the Late Jurassic and extended into the Early and middle Cretaceous (FIG. 1; FIG. 4.1). This has been described as an explosive radia-

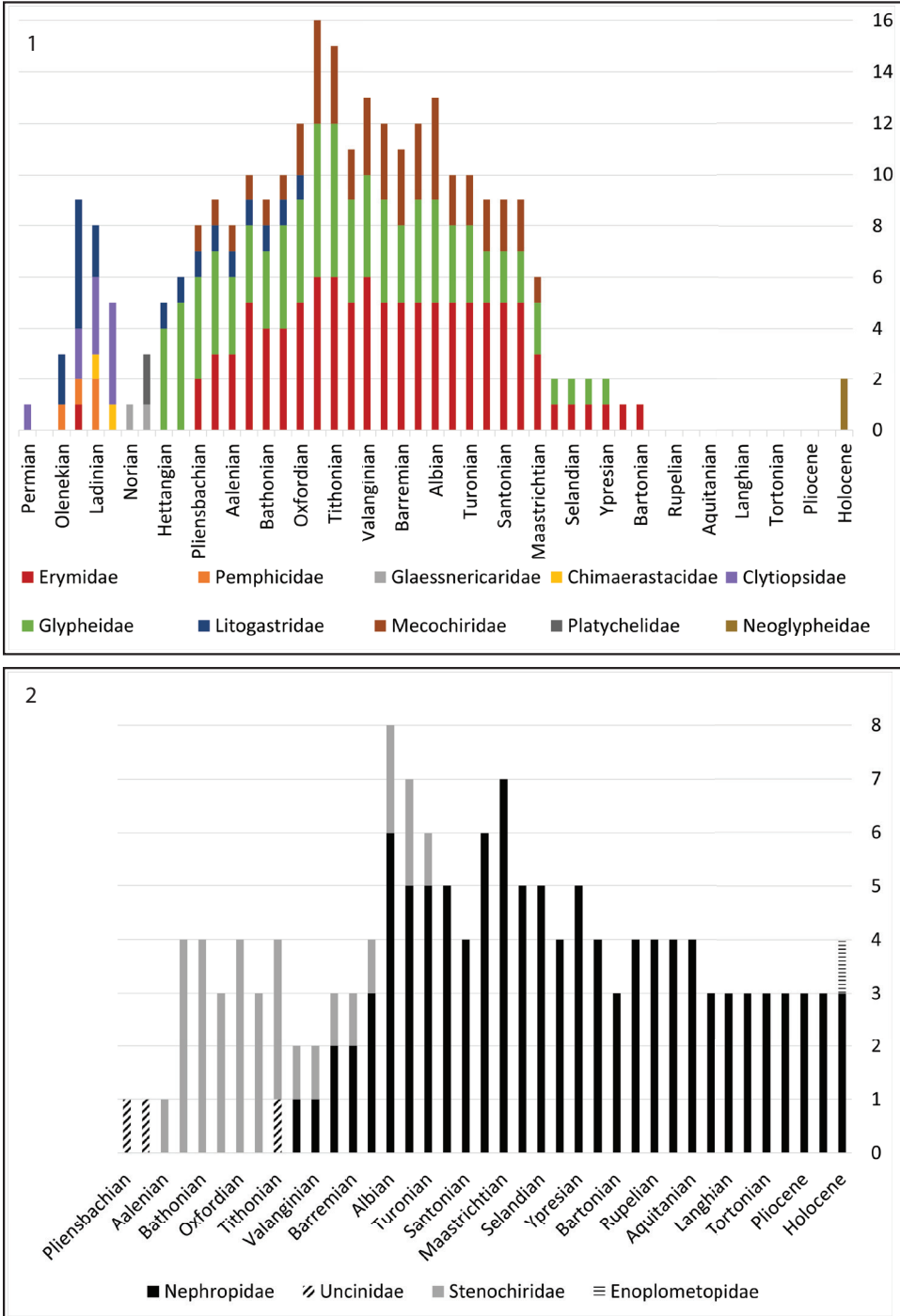


Fig. 4. Number of genera per unit time in families of 1, Glypheidea, and 2, Homarida.



tion, followed by stasis, with a subsequent decline in diversity (SCHWEITZER & FELDMANN, 2014). Chimaerastacidae, Clytiopsideae, Glaessnericaridae, Pemphicidae, and Platychelidae appeared and became extinct during the Triassic. Glypheidae and Litogastroidae originated in the Triassic. Litogastroidae originated in the Early Triassic and was most diverse generically in the Middle Triassic (SMITH & others, 2022), whereas Glypheidae reached peak generic diversity in the Late Jurassic. Mecochiridae originated in the Early Jurassic and became extinct by the end of the Cretaceous and reached peaks in diversity in the Kimmeridgian and Albian. Erymidae have a questionable occurrence during the Triassic but are confirmed from the Early Jurassic, peak in the Late Jurassic and Early Cretaceous, and finally become extinct in the Eocene (DEVILLEZ & CHARBONNIER, 2022).

The Triassic decapod fauna was characterized by a radiation of glypheidean lobsters that extended into the Jurassic and may have been promoted by habitat partitioning (SCHWEITZER & FELDMANN, 2014) (FIG. 6). Mecochiridae and Litogastroidae are found most frequently in carbonate habitats, often low energy, and low-energy siliciclastics. Members of Chimaerastacidae, Clytiopsideae, and Platychelidae most commonly are found in non-reefal carbonates and high-energy siliciclastics. Glypheidae is present in a broad range of habitats (SCHWEITZER & FELDMANN, 2014). Jurassic and Cretaceous Glypheidae and Mecochiridae were more generalized and preferred a variety of habitats. Erymoid lobsters inhabited nearly every type of fossilized marine environment in the Jurassic and Early Cretaceous but disappeared from siliciclastic environments by the Late Cretaceous (SCHWEITZER & FELDMANN, 2014). Extinct families do not appear to have shifted into deeper water as seen in some other lobster groups; however, the extant neoglypheids range into somewhat deeper water than predicted from fossil occurrences, from outer shelf to upper slope depths, 187–536 m (OBIS, 2023).

Within Glypheoidea, Erymidae and Glypheidae are by far the most species-rich families, and perhaps predictably, each family exhibited a wide range of inhabited environments.

Within Erymidae, the pattern of environmental preference is complicated. In the Jurassic, *Stenodactylina* BEURLIN, 1928, was concentrated in European sites and expressed a strong preference for soft carbonate substrates (SCHWEITZER & FELDMANN, 2014). Following a reduction in numbers of taxa in the Early Cretaceous, *Eryma* VON MEYER, 1840, and *Enoploclytia* M'COY, 1849, were dominant taxa in the Lower Cretaceous. Presence of those taxa are known from low and high energy environments in carbonate and siliciclastic substrates.

Biogeographically, the record of glypheidean lobsters is strongly skewed toward Europe and North America, but with notable Southern Hemisphere occurrences. Extant forms are known only from the Indo-Pacific, which suggests that it may be a refugium for this lineage. During the Late Cretaceous, erymid diversity shifted from predominantly European to mostly North American occurrences (DEVILLEZ & CHARBONNIER, 2022).

Regardless of the interpreted relationships between them, the glypheoids and erymoids were the dominant lobster-like body form during the Triassic and into the Jurassic (FIG. 6). As other decapod groups appeared, the proportion of glypheoids and erymoids diminished. Erymoids remained a significant proportion of the lobster fauna into the Cretaceous, but glypheideans continued to diminish over time until the extinction of all lineages except one: the extant Neoglypheidae, embracing two genera, remains in modern oceans (SCHWEITZER & FELDMANN, 2014). Among the two major superfamilies, Glypheoidea comprised upward of 50% of the decapod fauna in the Early Triassic but diminished to less than 15% by the Middle Jurassic and less than 5% by the Late Cretaceous. Erymoidea comprised between 7% and 14% of genera during the Triassic and



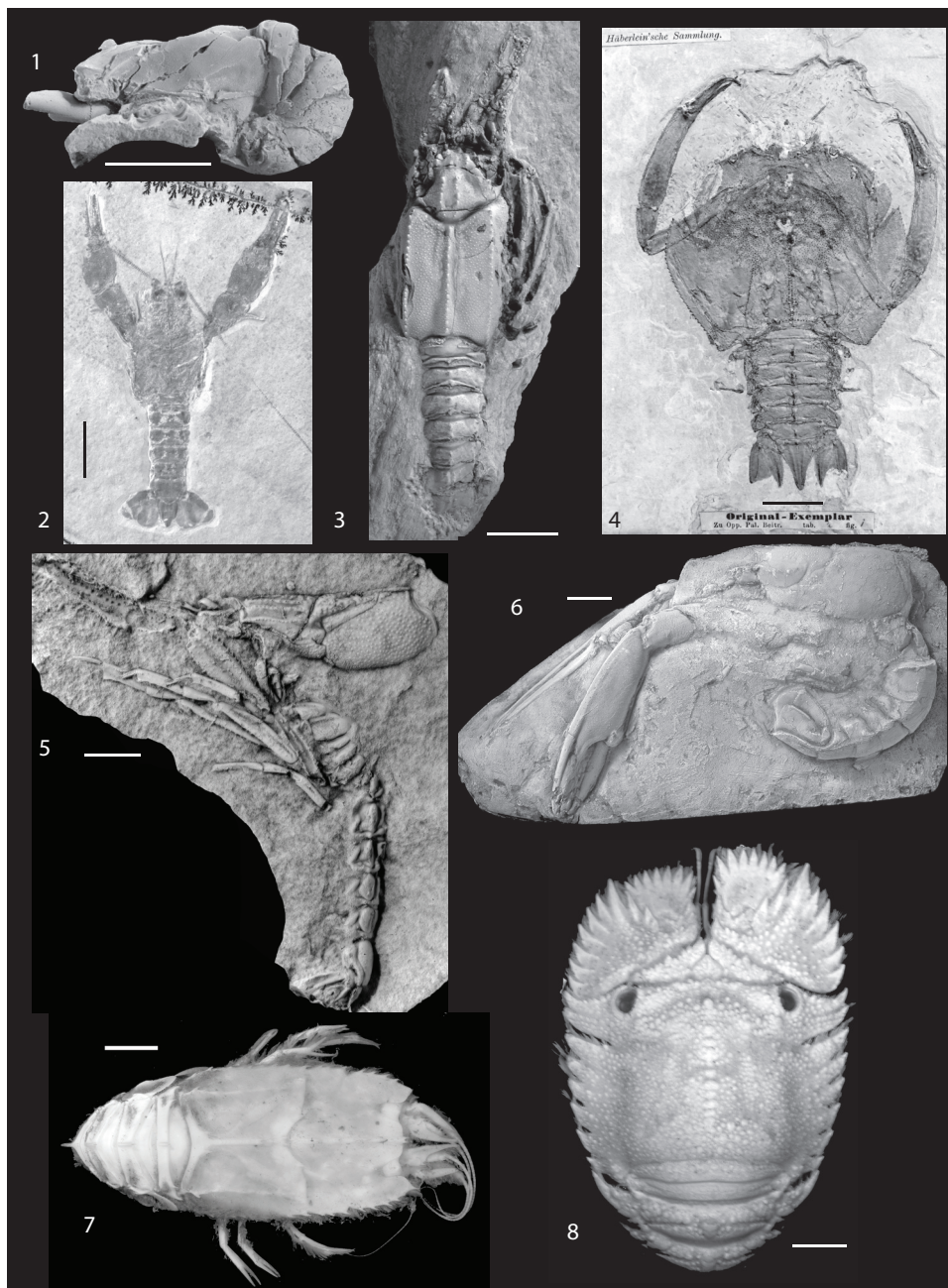


FIG. 5. Representative lobsters. 1, Palaeopalaemonida, *Palaeopalaemon newberryi* (TO 59); 2, Glypheidea, *Eryma modestiforme* (TO 68); 3, Achelata, *Linuparus grimmeri* (TO 67); 4, Polychelida, *Cycleryon propinquus* (TO 60); 5, Glypheidea, *Trachysoma rostrata* (TO 68); 6, Astacida, *Hoploparia longimana* (TO 74); 7, Polychelida, *Polycheles typhos* (Schweitzer & Feldmann, 2010, fig. 3E); 8, Achelata, *Parribacus antarcticus* (TO 67). TO indicates Treatise Online issue from which the image was taken.

Jurassic but diminished to less than 6% during the Cretaceous. Extant Neoglypheidae are morphologically similar to extinct forms that are hundreds of millions of years older; however, the two extant lineages are proposed to have diverged during the Oligocene (BRACKEN-GRISSOM & others, 2014).

### Glypheidean morphology

Among Glypheidea, several notable morphological trends are unique to the group, including variable chela terminations, complex carapace groove patterns, and an intercalated carapace plate in Erymidae (KARASAWA, SCHWEITZER, & FELDMANN, 2013; CHARBONNIER & others, 2014; DEVILLEZ, CHARBONNIER, & BARRIEL, 2019). Among glypheoids, notable evolutionary patterns include an explosive early radiation in the Triassic. Groove patterns in the group are complex. The constituent families display an array of appendage termination patterns, from fully chelate first pereiopods in Chimaerastacidae and Mecochiridae to pseudochelate first pereiopods in Glypheidae.

In Glypheidea, two main morphotypes of lobsters appeared, those with chelate and those with pseudochelate pereiopods. Glypheoidea includes taxa with pseudochelate or chelate first pereiopods, with pseudochelate being the more common. Pseudochelae, because the occlusion of their dactylus with the manus is only partial, must function differently than a true chela in which the two fingers occlude along a long surface. Pseudochelate terminations of pereiopods are most common among Glypheoidea but are known to occur in some Gebiidea and Achelata and occasionally among pereiopods 2–5 of brachyurans. Of the earliest glypheideans, both pseudochelate and chelate terminations are known. There is no polarity of this character to determine if one chela form was derived from another or whether the two different chela termination types appeared multiple times independently. We suspect the latter.

A key feature of all glypheidean lobsters is possession of numerous well-developed, dorsal carapace grooves. The three key transverse grooves, the cervical, postcervical, and branchiocardiac, are nearly always present in glypheideans, and there may be a variety of other shorter grooves in various orientations (SCHWEITZER & others, 2024). Many workers have tried to advance a progression scheme of development and loss of grooves between and among decapod lineages, generally from older to younger forms (GLAESSNER, 1969, fig. 227). Grooves have been interpreted as remnants of segmentation, and the reduction of grooves to be a result of increased fusion of somites (GLAESSNER, 1969; SECRETAN, 1960a, b). However, GLAESSNER (1960) and SECRETAN (1960a, b) did not agree on which somite boundaries corresponded with which groove—an issue never resolved (GLAESSNER, 1969). As a result, homology of the three transverse grooves across all decapods has never been established.

Application of this proposed morphological progression to the interpretation of the evolution of lobsters, and decapods generally, is hampered by several issues. The groove terminology currently in use is based primarily on the position of the grooves on the carapace. The cervical groove, out of all of the grooves, appears to have anatomical significance, separating the anterior gastric regions from the branchial regions in all decapods (GLAESSNER, 1969). The other two major grooves, the postcervical and branchiocardiac, as well as the more minor grooves, are not found in some decapods; thus, they cannot be compared across groups. Perhaps because of this, the morphological progression of groove patterns usually depicts only lobster-like forms and sometimes podotrematous crabs. A transition is shown from the complex groove pattern of glypheideans to the reduced groove ornamentation of nephropid lobsters (modern clawed lobsters), which have a well-developed cervical groove but in which the other

grooves are reduced. Contrarily, many podotrematous brachyurans possess cervical, postcervical, and branchiocardiac grooves that are much better developed than those of nephropids. Shrimps, gebiids, and axiideans usually have a cervical groove but lack the other two or have different types of grooves altogether.

Thus, an evolutionary progression of development of carapace grooves cannot be developed reliably. The earliest known decapod, *Palaeopalaemon* WHITFIELD, 1880, possesses all three grooves. Possession of the three may be ancestral, and reduction of groove development in the decapod carapace may have evolved independently numerous times. The two other confirmed Paleozoic decapods, *Aciculopoda* FELDMANN & SCHWEITZER, 2010, and *Devonostenopus* JONES & others, 2014, both shrimps, lack preserved carapaces, and so their groove patterns are unknown. Whereas a progressive development of grooves cannot be posited, decapod families are internally consistent at the family level in their expression of the various grooves.

Erymid lobsters are unique in possession of an intercalated plate on the dorsal carapace that is positioned just posterior to the rostrum on the dorsal axis and possibly is related to molting (GLAESSNER, 1969). Extant Enoplometopidae (Astacidea) possess a pair of grooves delimiting a narrow structure hypothesized to be homologous to the intercalated plate (SCHRAM & DIXON, 2004). However, this structure is not the same because the narrow structure in Enoplometopidae is not a separate plate and was thus interpreted to not be homologous (DEVILLEZ, CHARBONNIER, & BARRIEL, 2019).

Glypheidean lobsters have no fossil record of larvae, and only eggs are known in Late Cretaceous Mecochiridae. CHARBONNIER and others (2023) reported large eggs in *Mecochirus* GERMAR, 1827, for which size and number suggest an ontogenetic development similar to the extant decapod crustaceans with short larval stage.

## ASTACIDEA (MARINE LOBSTERS)

Astacidea comprises two major lineages, the freshwater crayfish (Astacidea) and the marine clawed lobsters (Homarida). Both are characterized by a cylindrical cephalothorax, with a reduced groove pattern compared with other lobsters, and strongly chelate first pereopods (FIG. 5.6). The marine nephropid lobster *Homarus* WEBER, 1795, is iconic as the classic lobster form.

KARASAWA, SCHWEITZER, and FELDMANN (2013) and BRACKEN-GRISSOM and others (2014) recovered Astacidea and Homarida as sister lineages, in a clade sister to Glypheidea (FIG. 2). Other works have recovered Astacidea as sister to Achelata + Polychelida (TSANG & others, 2008), Polychelida (WOLFE & others, 2019), and Polychelida + Glypheidea (TAN & others, 2019). Thus, although Astacidea is monophyletic, its position among Decapoda is unresolved. The evolutionary history of freshwater astacideans is treated in a separate chapter that will be published in the future.

Homarida has a very good fossil record, ranging from the Early Jurassic (Pliensbachian) to the Holocene (FIG. 1; FIG. 4.1). Enoplometopoidea has a significantly disjunct geologic distribution with one extant only family, Enoplometopidae, and the extinct Uncinidae that ranges from Early Jurassic to Late Jurassic (Pliensbachian to Tithonian). The phylogenetic relationship recovered for these two families may have resulted from a long history in deep water environments that are not well sampled in the fossil record. Alternatively, their association on morphological grounds may not represent actual biological relationships. Uncinids are typified by unusual chelae, in which the manus is quite long, and the fingers very robust, often with a strongly convex lower margin of the fixed finger and upper margin of the movable finger (BOGAN & others, 2023). The family exhibits a Northern Hemisphere distribution, in Europe, North America, and Japan. Their

unusual morphology may represent an early specialization in the lineage that did not survive the Jurassic.

Stenochiroidea, with one included family, ranges from the Early Jurassic (Sinemurian) to the Late Cretaceous (Turonian) and is sister to Nephropidae within Nephropoidea. Stenochirids are characterized by first pereopods with chelae bearing long slender fingers and a more complex groove pattern than is seen in Nephropoidea. The family has a much broader geographic distribution than Uncinidae, known from both the northern and southern Hemisphere.

The largest group of marine Astacidea, the Nephropidae, originated in the Early Cretaceous. Their highest generic diversity in the fossil record occurred during the Late Cretaceous. The group is an important part of the modern lobster fauna, both in terms of number of species and economically (SCHWEITZER & FELDMANN, 2014) (FIG. 6). Nephropidae comprised approximately 5% of the decapod fauna from the Jurassic through the Paleocene, after which they diminished as a component (SCHWEITZER & FELDMANN, 2014, 2105). SCHRAM and KOENEMANN (2021) suggested that homarid lobsters represented a relict fauna, as the number of extinct members is as high as the number of extant forms. This echoes the finding that nephropids are part of the first decapod turnover fauna of clawed lobsters (SCHWEITZER & FELDMANN, 2015).

The nephropid genera *Hoploparia* M'Coy, 1849, and *Homarus* have been quite conservative morphologically. *Hoploparia* has been studied many times with the intent to separate the included species into multiple genera, but this has never achieved success (TSHUDY & SORHANNUS, 2003; FELDMANN & others, 2007). *Hoploparia* is one of the most speciose decapod genera in the fossil record, united by several distinctive features of the cephalothorax and chelae (FELDMANN & others, 2007). Fossil and extant species of *Homarus* also are remarkably similar as are fossil and extant *Metanephrops* JENKINS, 1972. A distinctive morphology within

some genera of Nephropidae is possession of first pereopods with long slender fingers equipped with needle-like spines (SCHRAM & KOENEMANN, 2021). Genera with this type of chela have a record extending into the Cretaceous and are found in extant oceans; this appears to be a conservative feature of Nephropidae as well.

Like most decapod groups, the fossil record of homarid lobsters is most robust in North America and Europe (SCHWEITZER & FELDMANN, 2014). Notable exceptions are nephropids in the Late Cretaceous of Antarctica, some of which belong to extant genera (FELDMANN, TSHUDY, & THOMSON, 1993; FELDMANN & SCHWEITZER, 2006). Extant nephropids primarily inhabit the Atlantic Ocean with many occurrences in the Indo-Pacific; they are more rare in the eastern Pacific (OBIS, 2024). Enoplometopidae is cosmopolitan in tropical latitudes (OBIS, 2024).

Homaridans are associated with fine to medium-coarse siliciclastic rocks as well as carbonates, ranging from coarse to fine-grained and lithographic limestones (SCHWEITZER & FELDMANN, 2014). Although the majority of fossils are known from shallow, generally photic, environments, some range into deeper environments. In the Enoplometopidae, the Jurassic genera in Uncinidae are known from fine clastic sediments (BOGAN & others, 2023), whereas the present-day representative of the clade, *Enoplometopus* A. MILNE-EDWARDS, 1862, occupies coral and carbonate rock reef sites in relatively shallow water (CHAN, 1998). Stenochiroidea, sister to Nephropoidea, are preserved in fine-grained carbonate rocks, interpreted as low energy shelf/slope deposits. Extinct nephropid lobsters are recovered from a wide variety of siliciclastic sediments, ranging from low to high energy as well as carbonates, mostly from shallow settings (WAHLE & others, 2012). Extant nephropids, for example, are represented by only two or three shallow-water genera compared to ten or more deep-water genera (WAHLE & others, 2012; SCHWEITZER &



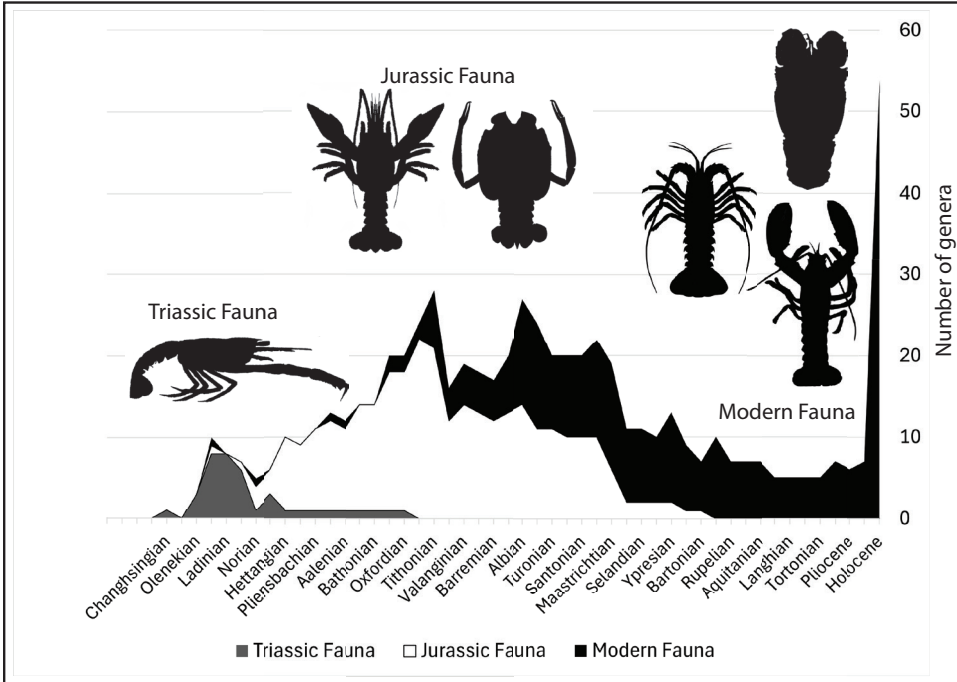


FIG. 6. Three lobster evolutionary faunas. Most common body forms in each fauna illustrated by silhouettes. Palinurid and homarid silhouette from Phylopic. Modified after Schweitzer & Feldmann (2014, fig. 14).

FELDMANN, 2014). Although some of the taxa known only from deep-water settings are characterized by having long delicate chelae bearing needle-like denticles, others have chelae comparable to those common forms from shallow-water settings. Additional morphologic characteristics that may be present in deep-water taxa are less strongly calcified cuticle and reduced pleura on the pleons. The sparsity of nephropid records through the Cenozoic may be a result of migration to deeper water settings as a sort of refugium (WAHLE & others, 2012; SCHWEITZER & FELDMANN, 2014). Extant species of nephropids, *Homarus americanus* H. MILNE EDWARDS, 1837, in the northwestern Atlantic Basin, and *Nephrops norvegicus* (LINNAEUS, 1758) in the northeastern Atlantic Basin, have each exhibited changes in migration patterns and ranges suggested as having been caused by climate change (RHEUBAN, KAVANAUGH, & DONEY, 2017; MCGEADY, LORDAN, & POWER, 2019). Their evolution continues.

## OVERALL PATTERNS IN LOBSTER EVOLUTION

Lobsters likely responded to the Mesozoic Marine Revolution through development of fully chelate first pereiopods in nephropids, including cutter and crusher claws (SCHWEITZER & FELDMANN, 2010, 2014). Predation on molluscs and other organisms by lobsters also is achieved by use of pereiopods in Achelata to wedge open shells (SCHWEITZER & FELDMANN, 2010).

Lobster families appeared rapidly in their early evolution, experienced successive extinctions during the Mesozoic, followed by stasis at the family level by the Late Cretaceous. The end-Cretaceous mass extinction did not severely affect lobster families, with only one end-Cretaceous extinction, Meco-chiridae (SCHWEITZER & FELDMANN, 2014, 2023). Clawed lobster families exhibited lower extinction rates than crabs at the end-Cretaceous, with no polychelidans and nearly one-third of nephropid lobsters

becoming extinct. Glypheidea was already in decline and experienced 75% generic extinction. Achelatan lobsters, which have comprised a consistent percentage of the decapod fauna since their appearance, experienced low levels of extinction at the end-Cretaceous, with only 13% of genera becoming extinct (SCHWEITZER & FELDMANN, 2023).

Clawed lobster families exhibit moderately long family ranges as compared with other decapods, and Achelata has some of the longest family ranges in the group; clawed lobsters are part of the decapod turnover faunas and would be expected to exist for shorter durations (SCHWEITZER & FELDMANN, 2015, 2023). Generic ranges for most lobsters are rather long as compared with other decapods (~40 my) with the exception of polychelidan genera (~17 my) (SCHWEITZER & FELDMANN, 2023).

Clawed lobsters including the Glypheidea, Polychelida, and marine Astacidea, were the first of the three decapod turnover faunas to dominate the marine realm (SCHWEITZER & FELDMANN, 2015). They composed at least 40% of the decapod fauna until the Late Jurassic, after which they were replaced in abundance by podotrematous crabs (SCHWEITZER & FELDMANN, 2015). Lobsters exhibit clear diversity and abundance patterns by time (SCHWEITZER & FELDMANN, 2014) (FIG. 6). The Triassic fauna is comprised of mostly glypheidean families, Chimaerastacidae, Clytiopsidae, Glassnericarididae, Litogastroidae, Pemphicidae, and Platychelidae, and one polychelidan, Tetrachelidae. The Jurassic lobster fauna is comprised of glypheideans (Erymidae, Glypheidae, Mecochiridae) and polychelidans (Coleiidae, Eryonidae). The modern lobster fauna is comprised of achelatan (Palinuridae, Scyllaridae), Nephropidae, and Polychelidae.

In addition to being divided into distinct faunas, the number of body plans increased through time (SCHWEITZER & FELDMANN, 2014). Differences in lobster body plan were defined by the nature of pereiopod

terminations as chelate, pseudochelate, or achelate and a flattened or cylindrical cephalothorax. The increase in number of body plans over time, even while families arose and became extinct, was suggested to be a result of environmental specialization among lobsters over time. Although clawed nephropid lobsters are iconic, in fact, there are many more achelate lobster genera extant today compared with chelate forms. This is perhaps a result of competition with crabs (SCHWEITZER & FELDMANN, 2014, 2015).

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