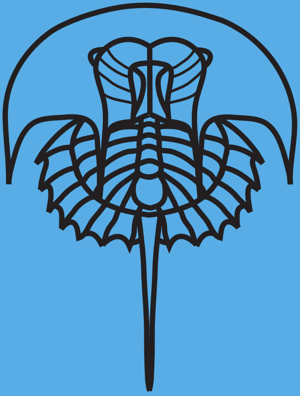

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EVOLUTIONARY HISTORY OF DECAPOD GROUPS: SHRIMP-LIKE (NATANT) DECAPODS

Carrie E. Schweitzer,[1] Sylvain Charbonnier,[2]
Rodney M. Feldmann,[3] and Günter Schweigert[4]

[[1]Department of Earth Sciences, Kent State University at Stark, cschweit@kent.edu; [2]Muséum national d'Histoire naturelle, Paris, sylvain.charbonnier@mnhn.fr; [3]Department of Earth Sciences, Kent State University (deceased); [4]Staatliches Museum für Naturkunde, Stuttgart, Germany, guenter.schweigert@smns-bw.de]

SHRIMP OVERVIEW

The fossil record for all types of decapod shrimp, among suborder Dendrobranchiata and infraorders Procaridea, Caridea, and Stenopodea, is sparse compared with decapods with more sclerotized and/or calcified cuticle. All decapod shrimp combined are represented by 448 genera in the modern oceans, whereas the highest number of genera in any given geological stage is 29 (as of March, 2023, Fig. 1). This being said, dendrobranch and stenopodid shrimp are among the oldest known lineages of decapods, extending into the Late Devonian (Feldmann & Schweitzer, 2010) and Early Mississippian (Jones & others, 2014), respectively (Fig. 1, Fig. 2, Fig. 3). Molecular phylogenies predicted the origin of the groups in the Silurian (Wolfe & others, 2019). Shrimp of all kinds comprised a significant percentage of the Triassic and Jurassic decapod fauna, as high as 40% of all decapod occurrences in these two periods, but their fossils are scarce after the Cenomanian (Late Cretaceous) (Schweitzer & Feldmann, 2015) (Fig. 1, Fig. 2). In the modern fauna, shrimp comprise about 20% of the known decapod genera, so the Cenozoic appears to be an interval of largely missing record (Schweitzer & Feldmann, 2015). Because shrimp have softer and less calcified cuticle than other decapods (Amato & others, 2008), their record is unsurprisingly dominated by Konservat-lagerstätten, most notably the Solnhofen-type limestones of Germany and the Cenomanian and Santonian plattenkalks of Lebanon. Indeed, most fossil occurrences of shrimp are in lithographic limestones and laminated shales. Much has been made of the importance of lagerstätten in the fossil record of Malacostraca (Sepkoski, 2000), but this seems to be most critical for shrimp and Polychelida (a type of lobster) among the Decapoda. Other decapod groups are not preferentially preserved in such deposits because of hostile sea floor conditions unfavorable for benthic decapods.

Shrimp exhibit several distinct patterns in terms of preservation. They are almost always preserved in lateral aspect, so that the sides of the carapace and pleon as well as appendages are visible (Fig. 4). Rarely are shrimp fossils preserved in ventral or dorsal aspect, but when they are, details of the scaphocerites, telson, and uropods often are observed (Schweitzer & others, 2014). Because the fossils are usually strongly compressed, it can be difficult to determine which pereiopod is being observed because counting them from first to fifth and differentiating left and right can be difficult. The tiny claws associated with penaeoid and caridean shrimp often are not observed. They do not fossilize well, are lost during molting and thus not preserved in exuviae, or are lost during preparation of the sample slabs. Placement of fossil taxa within shrimp families is strongly hampered by lack of preservation of the softer parts

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of the shrimp, as well as the reliance on tiny and/or soft parts for classification of extant members of the group. Mouthparts other than the third maxillipeds are almost never preserved. These preservational issues constrain classification of shrimp fossils and interpretation of the evolutionary history of specific shrimp lineages.

Despite their sparse fossil record, shrimps have some of the longest family ranges among the decapods (Decapoda mean = 70.3 million years [my]) (Schweitzer & Feldmann, 2023). They also exhibit little extinction at the family level over geologic time (Fig. 3). Stenopodidae is by far the longest ranging family, extending

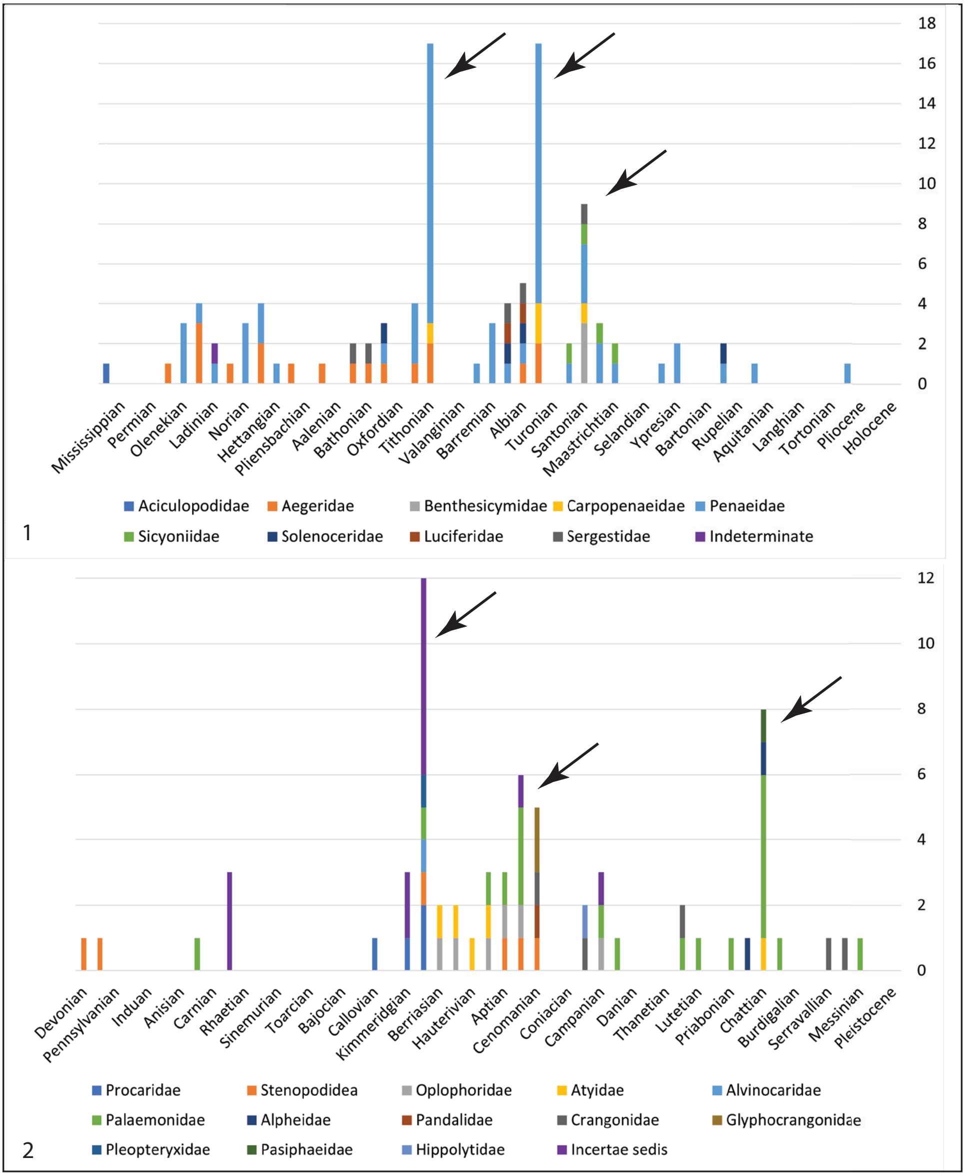

Fig. 1. Number of genera per unit time for *1*, dendrobranch shrimp, and *2*, caridean shrimp. Arrows indicate times of important lagerstätten for shrimp.

358 my (Schweitzer & Feldmann, 2023). Dendrobranchiata average about 125 my for families, Procaridea about 166 my, and Caridea about 93 my (Schweitzer & Feldmann, 2023). Generic ranges are shorter for shrimps compared with other decapods: from about 27 my in dendrobranchs to 20.5 my in the stenopodid, caridean, and procaridean shrimps. This was suggested to be a result of rapid evolution within the group, perhaps because of broad morphological diversity (Schram & Koenemann, 2021; Schweitzer & Feldmann, 2023), and could explain their low family-level extinction rates.

In the fossil record of decapod crustaceans, the shrimps are not well-represented (Schweitzer & others, 2010): about 100–150 species of dendrobranchiates (*ca* 540 extant species; De Grave & others, 2023), about 3–4 stenopodidean species (*ca* 100 extant species; De Grave & others, 2023), and about 60–70 caridean species (*ca* 3825 extant species; De Grave & others, 2023). Thus, since the Devonian, the fossil record of shrimps is particularly sparse, and the present-day biodiversity is relatively difficult to explain. The taxonomic richness of shrimps is driven by the heterogeneity of the fossil record and/or sampling effort, and shrimp alpha diversity is obviously underestimated, especially in the Cenozoic. This is intimately linked to the depositional paleoenvironments: Numerous fossil shrimps are found in Konservat-Lagerstätten deposits, known for the exceptional preservation of fossilized organisms or traces. It is not universal, but it is very often the case. Several Mesozoic Lagerstätten are particularly important for their contribution to the knowledge of shrimp faunas: the Early Triassic Paris Biota in Idaho and Nevada, USA (Smith & others, 2022), the Late Triassic alpine outcrops in Italy (e.g., Udine, Bergamo; Garassino & Teruzzi 1993; Garassino, Teruzzi, & Dalla Vecchia, 1996), the Early Jurassic Osteno Lagerstätte in Italy (Pinna, 1985; Garassino & Teruzzi, 1990), the Middle Jurassic La Voulte-sur-Rhône in France (Jauvion, Charbonnier, & Bernard, 2017), the Late Jurassic lithographic limestones from Germany (e.g., Solnhofen, Eichstätt, Nusplingen; Schweigert & others, 2016), and the Late Cretaceous lithographic limestones (Cenomanian of Hadjoula, Hakel) and chalky limestones (Santonian of Sahel Alma) from Lebanon (Audo & Charbonnier, 2013; Charbonnier & others, 2017). These Lagerstätten correspond to marine depositional palaeoenvironments, including shallow epicontinental settings (from lagoons to distal platforms) to deep-water settings (from slope-basin transition to bathyal zone). The shallow carbonate environments are frequent and the lithographic limestones, also called plattenkalks, are particularly favorable to shrimp fossilization. In the case of the world-famous Solnhofen plattenkalks, the sediments were deposited in relatively deep lethal lagoons, where the seafloor was dominated by microbial mats, and the burial setting does not correspond exactly to the original living environment of shrimps. Numerous fossil shrimps from Solnhofen are not corpses but exuviae swept into the lagoons from more or less distant neighboring environments (Schweigert, 2011). The introduction of still-living shrimps into the adverse lagoonal conditions also might have triggered their molting process. This also is the case of the Lebanese plattenkalks that recorded mass mortality events of organisms originally living in well-oxygenated waters, around the depositional settings (Charbonnier & others, 2017). The La Voulte Lagerstätte is an exception because it corresponds to a unique deep-water (bathyal) setting including hydrothermal activity (Charbonnier, 2009). In this case, shrimps often are three-dimensionally preserved in carbonate concretions with their soft parts (Wilby, Briggs, & Riou, 1996). This fauna is composed of juvenile and adult specimens, which is in agreement with an *in situ* burial (Charbonnier & others, 2010).

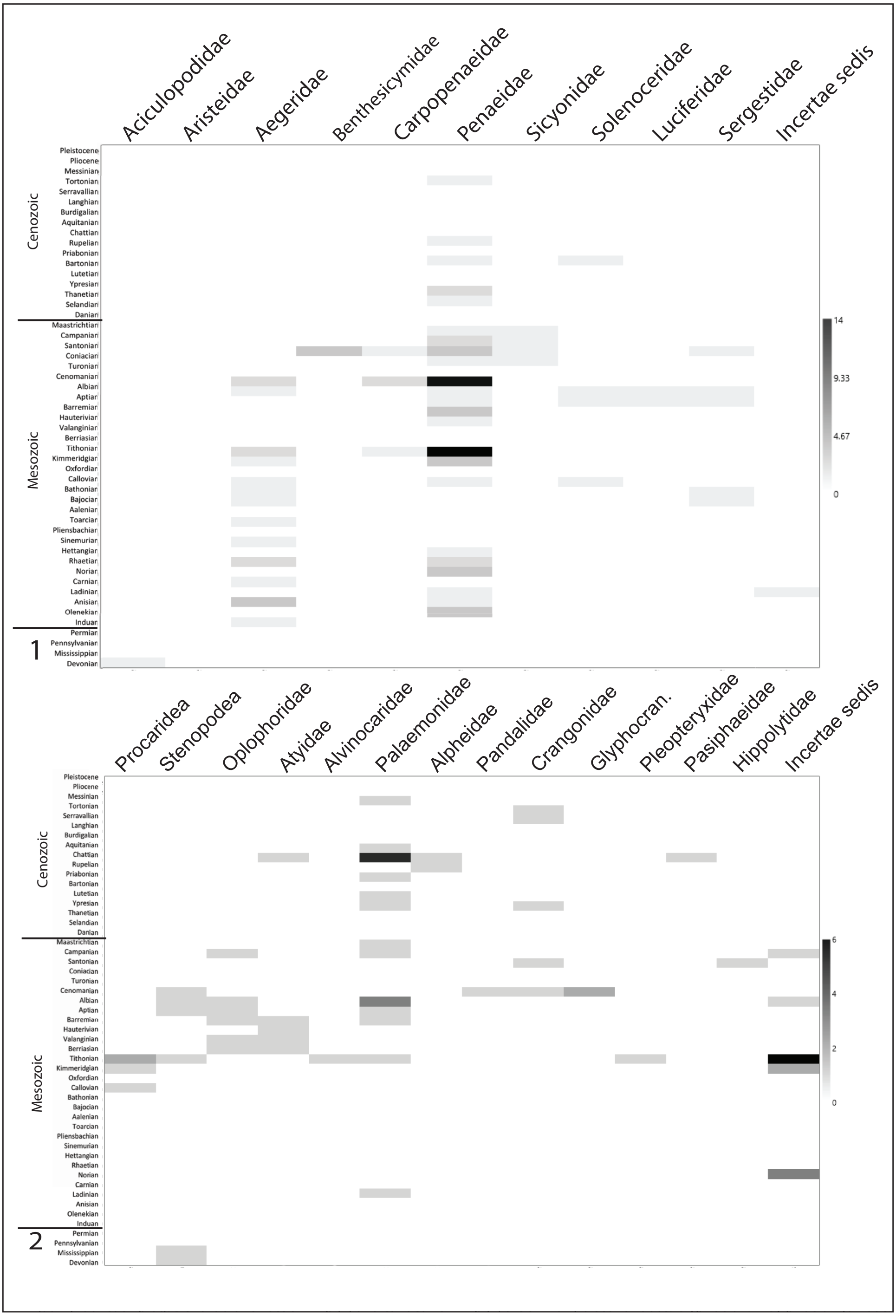

Fig. 2. Matrix plots (PAST 4.08) showing discontinuous fossil record for most shrimp families. Gray tones shaded to number of genera (at right of each plot). Dendrobranchiate shrimp (1) and caridean shrimp (2) are similarly discontinuous. Glyphocran. = Glyphocrangonidae.

DENDROBRANCHIATA

Dendrobranchiata are recognized in the fossil record by their shrimp-like facies and pleonal somite two not overlapping pleonal somite one (Fig. 4.6). Extant taxa usually have three pairs of chelae. Most dendrobranch shrimp in modern oceans are marine, with a few exceptions among Sergestidae (Tavares & Martin, 2010). Nearly all recent phylogenies place Dendrobranchiata as the earliest diverging lineage within Decapoda and sister to the remainder of the Decapoda, the Pleocyemata Burkenroad, 1963 (Tsang & others, 2008; Tan & others, 2018, 2019; Wolfe & others, 2019) (Fig. 5). Among the dendrobranchs, Sergestoidea (Sergestidae + Luciferidae) were recovered as sister to Penaeoidea, which includes all other dendrobranch shrimp families (Wolfe & others, 2019) (Table 1). Robalino and others (2016) divided the Penaeoidea into a deep-water clade, Phorcysida, including Solenoceridae, Aristeidae, and Benthesicymidae, and a shallow-water clade, including Penaeidae.

Statistical methods recovered a Paleozoic origin for the dendrobranchs (Ma & others, 2009; Wolfe & others, 2019), with crown dendrobranchs inferred to diverge from other decapods in the Late Devonian. The earliest known dendrobranch shrimp fossil was Late Devonian (Famennian), assigned to the monotypic Aciculopodidae within Penaeoidea (Feldmann & Schweitzer, 2010) (Table 1; Fig. 1, Fig. 4.1). Spines on the merus of preserved appendages suggested affinities with Aegeridae, another extinct dendrobranch family well known from the Triassic and Jurassic (summarized by Schweitzer & others, 2014) (Fig. 4.6). Shrimp clearly assignable to Dendrobranchiata were reasonably abundant by Late Triassic time (two Triassic families and 11 Triassic genera) (Smith & others, 2022), and all the extant families except Aristeidae have a fossil record extending at least into the Late Cretaceous, and often much earlier (Fig. 3). Aristeidae are thus far unknown in the fossil record. There are three extinct dendrobranch families: Aciculopodidae, Aegeridae, and Carpopenaeidae.

Early Triassic members of Penaeidae have been reported from Madagascar (Van Straelen, 1933; Garassino & Teruzzi, 1995; Garassino & Pasini, 2002), and this family has a robust fossil record (for shrimp). Within Penaeidae there are some "wastebasket" genera. *Antrimpos*, previously including more than a dozen species, recently was reevaluated, and the number of included

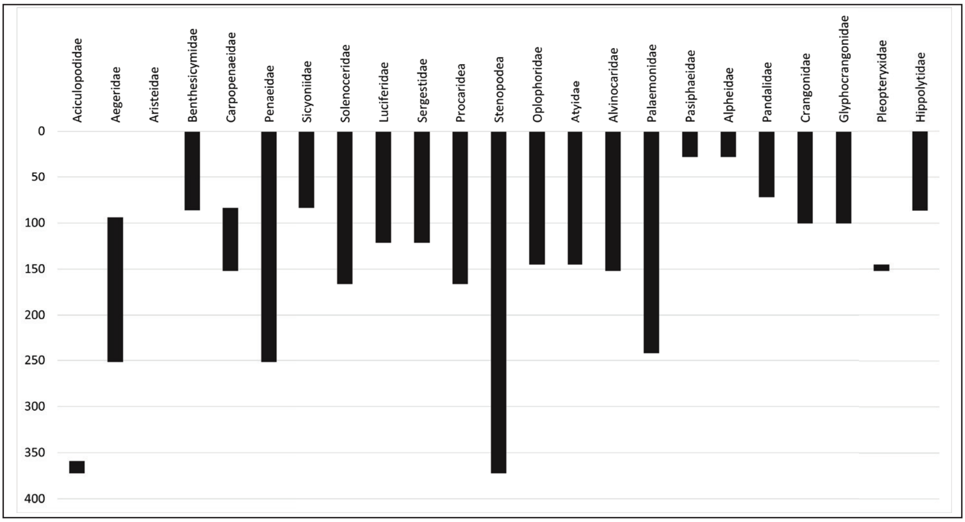

Fig. 3. Geologic range, in millions of years, of shrimp families. Only those caridean shrimp with a fossil record are included.

species was reduced by about half (Garassino & others, 2023). Robalino and others (2016) considered that Late Jurassic shrimps of *Antrimpos* were clearly related to extant penaeoids; however, many extinct penaeoids possess a diaresis not seen, or at least not mentioned, in modern taxa (Schweitzer & others, 2014). *Penaeus* includes many more fossil species than other shrimp genera (Schram & Koenemann, 2021) and is likely a form genus for Cretaceous and Cenozoic occurrences. Fossil taxa referred to Penaeoidea may need to be reevaluated to determine their placement. In modern oceans, penaeid shrimp typically are found in shallow, tropical to subtropical environments (Tavares & Martin, 2010). Nearly all fossil penaeids are recovered from shale or lithographic limestone, deposited in quiet conditions, so interpretation of paleoenvironments is hampered by preservational bias.

Aegeridae appeared in the Early Triassic of the Western USA (Smith & others, 2022) and the Middle Triassic in China and Europe, and the family was extinct by the Late Cretaceous (Santonian) (Schweitzer & others, 2014) (Fig. 1, Fig. 2, Fig. 3, Fig. 4.6). The extinct Carpopenaeidae ranged from Late Jurassic (Tithonian) to Late Cretaceous (Santonian) (Charbonnier & others, 2017). Sicyonidae have an unverified record from the Late Cretaceous (von der Marck, 1858) but no other fossil occurrences; extant members are benthic and range from the intertidal to the continental slope (Poore & Ahyong, 2023). Solenoceridae first appeared in the Middle Jurassic (Callovian), with a few subsequent occurrences (Carriol &

Table 1. Dendrobranchiata family classification and ranges.

Taxon	Range
Suborder **Dendrobranchiata** Bate, 1888	Late Devonian (Famennian) – Holocene
Superfamily **Penaeoidea** Rafinesque, 1815	Late Devonian (Famennian) – Holocene
†**Aciculopodidae** Feldmann & Schweitzer, 2010	Late Devonian (Famennian)
†**Aegeridae** Burkenroad, 1963	Early Triassic (Olenekian) – Late Cretaceous (Santonian)
***Aristeidae** Wood-Mason *in* Wood-Mason & Alcock, 1891	Holocene
Benthesicymidae Wood-Mason *in* Wood-Mason & Alcock, 1891	Late Cretaceous (Santonian) – Holocene
†**Carpopenaeidae** Garassino, 1994	Late Jurassic (Tithonian) – Late Cretaceous (Santonian)
Penaeidae Rafinesque, 1815	Early Triassic (Induan/Olenekian) – Holocene
Sicyoniidae Ortmann, 1898	Late Cretaceous – Holocene
Solenoceridae Wood-Mason *in* Wood-Mason & Alcock, 1891	Middle Jurassic (Callovian) – Holocene
Superfamily **Sergestoidea** Dana, 1852	Early Cretaceous (Aptian-Albian) – Holocene
Luciferidae De Haan, 1849	Early Cretaceous (Aptian-Albian) – Holocene
Sergestidae Dana, 1852	Early Cretaceous (Aptian-Albian) – Holocene

† extinct, * extant only

Riou, 1991; Garassino & others, 2014; Alcencar & others, 2018); the earliest extinct forms and the extant forms inhabit deep, offshore environments (Charbonnier & others, 2010; Tavares & Martin, 2010). The Luciferidae, only known from three total genera, have a fossil record extending into the late Early Cretaceous of Brazil (Saraiva & others, 2018). Luciferidae are specialized, planktonic forms in modern oceans (Tavares & Martin, 2010) that, despite their unusual form, are cosmopolitan and locally abundant (Poore & Ahyong, 2023). Sergestidae first appeared in the Middle Jurassic (Bravi & others, 2014) and are known from a few Cretaceous occurrences (Maisey & De Carvalho, 1995; Garassino & Schweigert, 2006). Both Luciferidae and Sergestidae were hypothesized to have diverged from one another in the Carboniferous (Wolfe & others, 2019); however, fossils do not yet support this early divergence. Extant sergestid shrimps are pelagic in offshore environments (Poore & Ahyong, 2023). Thus, Dendrobranchiata, although not abundant as fossils, has an established record for both extinct and extant groups throughout the Mesozoic and Cenozoic. It is notable that extant forms often inhabit environments that are not readily fossilizable, such as outer shelf, slope, and abyssal areas (Poore & Ahyong, 2023).

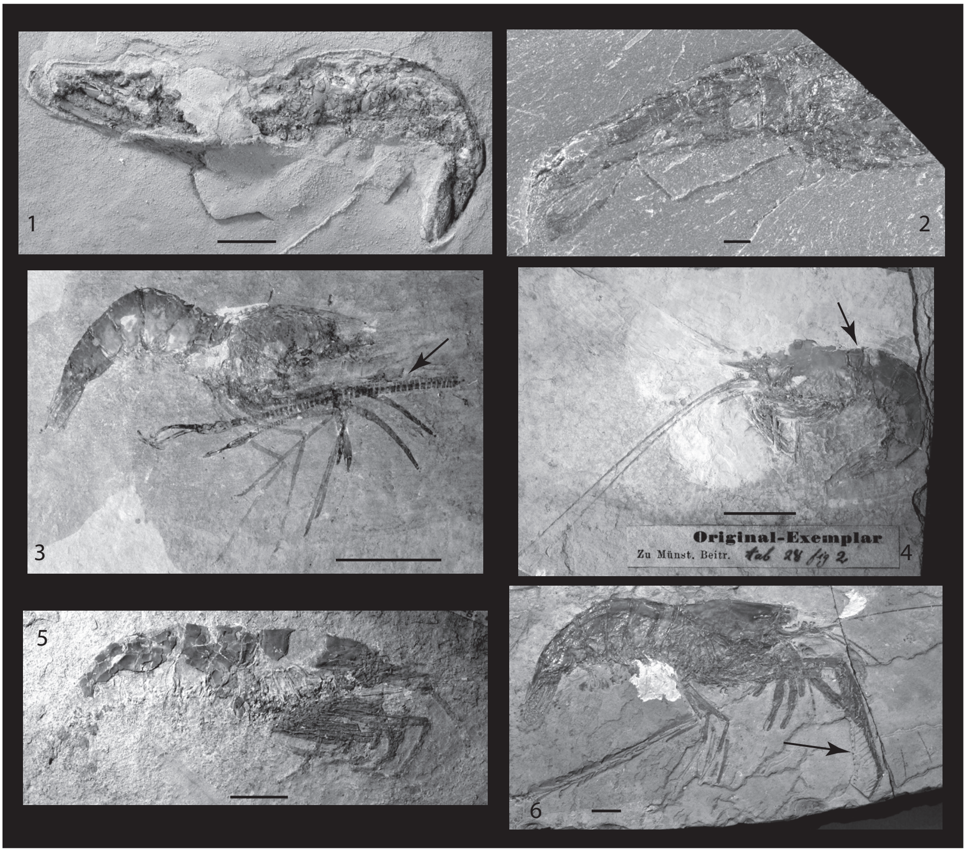

Fig. 4. *1, Aciculopoda mapesi* Feldmann & Schweitzer, 2010, holotype USNM 540766; *2, Devonostenopus pennsylvaniensis* Jones & others, 2014, CM 39653; *3, Blaculla sieboldi* Oppel, 1862, BSPG AS 1973, arrow indicates multiarticulate carpus of first pereiopod; *4, Hefriga serrata* Münster, 1839, BSPG AS VII 722, arrow indicates caridean second pleonite; *5, Udora brevispina* Münster, 1839, holotype BSPG AS VII 725; *6, Aeger insignis* Oppel, 1862, BSPG AS 1960, arrow indicates spinose third maxilliped. Scale bar for 2 = 1 mm, all others = 1 cm.

The early appearance of the dendrobranch lineage was considered important in the evolution of large-bodied shrimp that are farmed for food in modern oceans because it is an ancient lineage apparently adapted to cooler waters in a warming world (Robalino & others, 2016). Vereshchaka (2017) speculated that colonization of dysphotic and aphotic environments by deep-sea shrimp probably occurred in the Cenozoic. However, the environments of the Callovian La Voulte, as well as the Santonian Sahel Alma locations, were at least dimly lit, if not aphotic; thus, the fossil record suggests such adaptations by at least the Middle Jurassic (Charbonnier, 2009; Charbonnier & others, 2017). Sergestidae inhabit outer shelf to slope habitats up to about 1400 m (OBIS, 2023b) or are planktonic (Tavares & Martin, 2010), but their fossils are known from coastal environments (Saraiva & others, 2018). Thus, the timing of the colonization of deeper environments by dendrobranch families requires further investigation.

Vereshchaka, Kulagin, and Lunina (2021) reported that Benthesicymidae demonstrated coevolution of characters related to reproduction, such as the petasma, rarely to fossilized (see Audo & Charbonnier, 2013), and of potentially fossilizable characters of the carapace and pereiopods related to feeding. Extant members are deep benthic or planktonic (Tavares & Martin, 2010; Poore & Ahyong, 2023), which are environments not readily fossilizable. Thus, as the fossil record improves, it might be possible to test the timing of this coevolution using the fossil record.

A remarkable case study for dendrobranch shrimp is the Solnhofen fauna. These fossils are widely known and incredibly diverse, including more genera and species of dendrobranch shrimp than any other

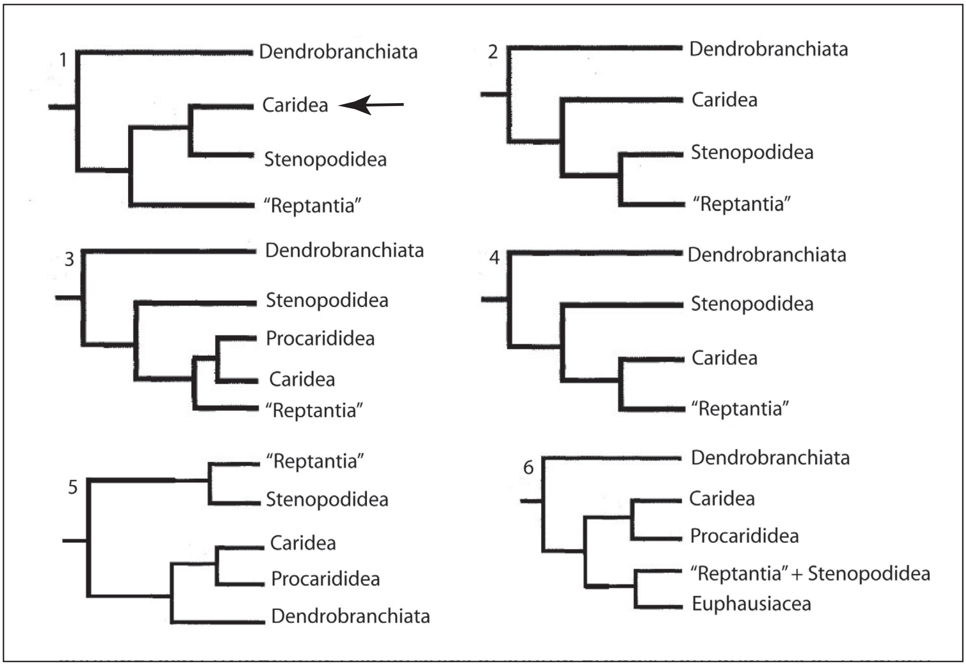

Fig. 5. Phylogenetic relationships of shrimp groups, from *1*, Burkenroad (1963); *2*, Abele & Felgenhauer (1986), Schram and Dixon (2004) and Dixon, Ahyong, and Schram (2003); *3*, Christofferson (1998); *4*, Porter, Pérez-Losada, and Crandall (2005); *5*, Bracken, De Grave, and Felder (2009); *6*, Bracken & others (2009). Wolfe & others (2019) recovered similar topology to *1* except with Caridea + Procaridea on branch indicated with arrow. Adapted from Fransen & De Grave (2009, fig. 2).

location. In a similarly diverse occurrence, the lagerstätten of the Late Cretaceous of Lebanon have yielded numerous genera and species. These two sets of deposits make up a very large proportion of the dendrobranch fossil record, and each will be discussed in subsequent articles planned for publication as part of Treatise Volume R. These two sets of lagerstätten document significant radiations among dendrobranch shrimp in the Late Jurassic and Late Cretaceous (Fig. 1).

STENOPODEA

This infraorder, composed of 13 extant genera, has a sparse fossil record (Table 2; Fig. 1, Fig. 2, Fig. 3). Stenopodea has been recovered as sister to the caridean shrimp, in a clade sister to all other decapods (Tsang & others, 2008; Wolfe & others, 2019) or as the sister group to all nonshrimp decapods (Tan & others, 2018; Wang & others, 2021) (Fig. 5). Stenopodea includes one of the oldest known decapods, from the Mississippian of Pennsylvania, as well as a Late Jurassic Solnhofen genus and Late Cretaceous occurrences in China and Lebanon (Schram & others 2000; Garassino, 2001; Jones & others, 2014; Winkler & others, 2021) (Fig. 2, Fig. 4.2). There are only three genera known from the fossil record. Thus, little can be said for the evolutionary history of the group, based on fossils, other than that the infraorder is one of the earliest appearing in the fossil record. Extant members inhabit rocky or muddy sea floors, often in reefs, on rubble, or in caves, and may exhibit mutualistic or commensal habits (Goy, 2010). Some are cleaners for fishes, and commensal relationships with siliceous sponges are common (Goy, 2010). Some members of the group inhabit glass sponges in deep water, and another group lives in anchialine caves (Poore & Ahyong, 2023), which are environments not likely to fossilize. Fossil occurrences are all in shales or lithographic limestones, so direct comparison of extinct habitats with those of extant members remains difficult.

PROCARIDEA

Procaridea sensu stricto has no fossil record (Table 2; Fig. 1). Procaridea is predicted to have diverged from its sister taxon Caridea in the Carboniferous (Tsang & others, 2008; Wolfe & others, 2019; Wang & others, 2021). A key diagnostic feature of Procaridea is the lack of chelae on all pereiopods; thus, those extinct shrimp genera appearing to lack chelae are currently referred to this infraorder (Felgenhauer & Abele, 1983; Fransen & De Grave, 2009). *Udora* Münster, 1839, apparently lacks chelae, is currently referred to Procaridea, and is known from Middle and Late Jurassic rocks of Europe (Schweitzer & others, 2023) (Fig. 2, Fig. 4.5). Members of Udorellidae Van Straelen, 1925, also appear to lack chelae, based on examination of material in BSP, Munich; thus, this monotypic family is referred to Procaridea. All the fossil occurrences are in marine sediments. Extant members of the family inhabit anchialine environments globally (Bruce & Davie, 2006). It is unknown as to when this shift in habitat occurred, nor is it known whether the lack of chelae is a convergent character, so that the fossil groups are not actually related to Procaridea at all. Compounding interpretation of procarids in the fossil record is Pleopteryxidae, a monotypic family currently referred to Caridea but that lacks chelae entirely or only has pereiopod one as chelate (Schweigert & Garassino, 2006; Schram & Koenemann, 2021), depending on interpretation of material. Is it a procarid? Preservation of the material is not sufficient at this time to determine.

CARIDEA

Caridean shrimp have a sparser fossil record than Dendrobranchiata, with about half the number of genera. They are nearly always recognized by having a shrimp-like facies with pleonal somite two overlapping both somites one and three (Fig. 4.4). A sizable proportion of extant forms inhabit reefs (Davis & others, 2018), and many are freshwater inhabitants (Wicksten, 2010; De Grave & others, 2015b). Neither of these environments is conducive to fossilization of weakly sclerotized organisms. In addition to the small number of caridean fossils, an outsize proportion of the fossil genera are assigned to Caridea incertae sedis or Palaemonidae (Schweitzer & others, 2023) (Fig. 1, Fig. 2). Because morphological characters defining caridean families often are based on mouthparts, antennal features, fusion of pereiopod segments, and development of multiarticulate appendages, they are difficult to observe in fossils, probably because of poor preservation potential.

Caridea and Procaridea were recovered as diverging in the Pennsylvanian, with crown carideans appearing by the Late Triassic (Wolfe & others, 2019). Varying times of origin for caridean shrimp lineages

Table 2. Procaridean, stenopodean, and caridean shrimp and their ranges.

Taxon	Range
Infraorder **Stenopodea** Claus, 1872	Devonian-Mississippian - Holocene
Stenopodidae (=Spongicolidae, Macromaxillocaridae)	Devonian-Mississippian - Holocene
Infraorder **Procaridea** Chace & Manning, 1972	Late Jurassic (Kimmeridgian) - Holocene
***Procarididae** Chace & Manning, 1972	Holocene
†**Udorellidae** Van Straelen, 1925	Late Jurassic (Kimmeridgian)
Infraorder **Caridea** Dana, 1852	Late Triassic (Norian) - Holocene
Superfamily **Alpheoidea** Rafinesque, 1815	Late Cretaceous (Santonian) – Holocene
Alpheidae Rafinesque, 1815	Oligocene (Chattian) – Holocene
***Barbouriidae** Christofferson, 1987	Holocene
***Bythocarididae** Christofferson, 1987	Holocene
Hippolytidae Bate, 1888	Late Cretaceous (Santonian) – Holocene
***Lysmatidae** Christofferson, 1987	Holocene
***Merguiidae** Christofferson, 1990	Holocene
***Ogyrididae** Hay & Shore, 1918	Holocene
***Thoridae** Kingsley, 1878	Holocene
*Superfamily **Campylonotoidea** Sollaud, 1913	Holocene
***Bathypalaemonellidae** de Saint Laurent, 1985	Holocene
***Campylonotidae** Sollaud, 1913	Holocene
Superfamily **Crangonoidea** Haworth, 1825	Late Cretaceous (Cenomanian) – Holocene
Crangonidae Haworth, 1825	Late Cretaceous (Cenomanian) – Holocene
Glyphocrangonidae Smith, 1884	Late Cretaceous (Cenomanian) – Holocene
Superfamily **Oplophoroidea** Dana, 1852	Early Cretaceous (Berriasian-Valanginian) - Holocene
***Acanthephyridae** Bate, 1888	Holocene
Oplophoridae Dana, 1852	Early Cretaceous (Berriasian-Valanginian) - Holocene

have been predicted based on molecular and Bayesian methods. All extant families have been predicted to have arisen by the Late Jurassic (Davis & others, 2018), and diversification of caridean shrimp was inferred to have begun in the Triassic (Davis & others, 2018; Wolfe & others 2019). Nearly all recognized extant families have been recovered as monophyletic (Davis & others, 2018).

The oldest confirmed caridean shrimp are from the Triassic; these are mostly unplaced at the family level (Pinna, 1974) (Fig. 1, Fig. 2, Fig. 3). A few families are known from Tithonian Solnhofen-type limestones, including Alvinocarididae and Palaemonidae (Schweitzer & others, 2023). Davis and others (2018) predicted a timing of origin for these two families in the Triassic and Jurassic, respectively. Alvinocarids are

Table 2. Procaridean, stenopodean, and caridean shrimp and their ranges. *(Cont'd)*

Taxon	Range
*Superfamily **Bresilioidea** Calman, 1896	Holocene
***Agostocarididae** Hart & Manning, 1986	Holocene
***Alvinocarididae** Christofferson, 1986	Holocene
***Bresiliidae** Calman, 1896	Holocene
***Disciadidae** Rathbun, 1902	Holocene
***Pseudochelidae** De Grave & Moosa, 2004	Holocene
*Superfamily **Nematocarcinoidea** Smith, 1884	Holocene
***Eugonatonotidae** Chace, 1937	Holocene
***Lipkiidae** Burukovsky, 2012	Holocene
***Nematocarcinidae** Smith, 1884	Holocene
***Rhynchocinetidae** Ortmann, 1890	Holocene
***Xiphocarididae** Ortmann, 1895	Holocene
Superfamily **Palaemonoidea** Rafinesque, 1815	Late Jurassic (Tithonian) – Holocene
***Desmocarididae** Borradaile, 1915	Holocene
***Euryrhynchidae** Holthuis, 1950	Holocene
Palaemonidae Rafinesque, 1815	Late Jurassic (Tithonian) – Holocene
***Typhlocarididae** Annandale & Kemp, 1913	Holocene
Superfamily **Pandaloidea** Haworth, 1825	Late Cretaceous (Cenomanian) - Holocene
***Chlorotocellidae** Komai & others, 2019	Holocene
Pandalidae Haworth, 1825	Late Cretaceous (Cenomanian) - Holocene
Unplaced in superfamily or monotypic superfamily	
Atyidae De Haan, 1849	Early Cretaceous – Holocene
Pasiphaeidae Dana, 1852	Oligocene - Holocene
***Physetocarididae** Chace, 1940	Holocene
†**Pleopteryxidae** Schweigert & Garassino, 2006	Late Jurassic (Tithonian)
***Processidae** Ortmann, 1896	Holocene
***Psalidopodidae** Wood-Mason & Alcock, 1892	Holocene
***Stylodactylidae** Bate, 1888	Holocene

† extinct, * extant only.

typical of deep marine environments (Bauer, 2004) and are usually associated with mid-ocean ridges or hydrothermal vents (Sun & others, 2018; OBIS, 2023a). The shallower water Jurassic fossils should be confirmed as members of the family. Palaemonidae has a robust record for Caridea, found throughout the Cretaceous and Cenozoic, although it must be noted that many genera are placed within this family because of their clear lack of apomorphies of the numerous extant caridean families (Schweitzer & others, 2023) (Fig. 1). About one-quarter of fossil caridean genera have been referred to Caridea incertae sedis (Schweitzer & others, 2023). Confirmation of Palaemonidae as the correct family placement for genera currently referred to it and determination of family placements for those taxa currently placed incertae sedis would greatly enhance our understanding of caridean evolution.

Only an additional handful of extant caridean families are known from the fossil record, aside from Alvinocarididae and Palaemonidae (Schweitzer & others, 2010) (Fig. 1, Fig. 2, Fig. 3). Confirmed extant families in the fossil record include Alpheidae, predicted to have originated in the Late Triassic (Davis & others, 2018). The earliest confirmed alpheid fossils are much younger, Oligocene, from claw tips recovered from both Europe and North America (Hyžný & others, 2017, 2018). Now that these fossils are recognized as alpheid claws, it seems likely that more will be reported from the fossil record (Feldmann, Schweitzer, & Phillips, 2019). Some alpheids may inhabit axiid or gebiid burrows (Bauer, 2004; Wicksten, 2010), and alpheid claw tips could be sought that are associated with burrow trace fossils. Alpheid claws and otoliths of gobiid fishes found associated in middle Miocene rocks of Poland suggest that this well-documented symbiosis between these animals had appeared by at least that time (Radwańska, 2018).

Crangonidae, Glyphocrangonidae, Hippolytidae, and Pandalidae are recorded from the Cretaceous of Lebanon (Charbonnier & others, 2017), and the clades containing each family were all predicted to have diverged during the Triassic (Davis & others, 2018). Today, Crangonidae inhabits cool temperate to Arctic benthic areas, but it also inhabits both shallow and deeper environments in lower latitude areas (Han & Keesing, 2018; Bauer, 2004). This latitudinal and temperature preference seems to have been present by early Eocene time, with occurrences in Denmark and northern Russia in the Eocene and Miocene, respectively (Garassino & Jakobsen, 2005; Garassino, Pasini, & Nazarkin, 2021).

Glyphocrangonidae is monogeneric in modern oceans, in bathyal to abyssal, benthic environments most commonly in the Indo-Pacific (Bauer, 2004). This deep environmental preference may help to explain its poor fossil record. However, its occurrence in shallow water photic to potentially dysphotic, deeper conditions in the Late Cretaceous is notable (Charbonnier & others, 2017). The timing of the change in environmental preference for Glyphocrangonidae currently is not constrained. Hipplytidae are quite diverse in habitat preference in modern oceans, mostly benthic on rocks, algae, sea grasses, or other invertebrates generally on the continental shelf (Bauer, 2004), and may not be monophyletic, as currently construed (Davis & others, 2018). The sole fossil occurrence is in dysphotic environments of the Late Cretaceous (Charbonnier & others, 2017). Pandalidae is largely boreal in distribution, and lower latitude forms inhabit deeper waters; they are benthic or pelagic, sometimes both (Bauer, 2004). The Late Cretaceous occurrence of Pandalidae is in photic shallow, equatorial waters (Charbonnier & others, 2017). Thus, it seems that many caridean families originated in environments different from those in which extant forms are found.

Only one extinct family so far has been erected for Caridea, Pleopteryxidae, from the Tithonian of Germany (Schweigert & Garassino, 2004). Other families reported as fossils include Oplophoridae and Atyidae, but these should be verified by examination of type material. They are each sporadically recorded in the fossil record (Schweitzer & others, 2023) (Fig. 1, Fig. 2).

An occurrence of caridean shrimp that is noteworthy is in the lithographic deposits of Lebanon, of Cenomanian and Santonian age, with five genera and species. Nine genera and 19 species of caridean are reported from the Solnhofen limestones. These occurrences will be discussed in subsequent articles planned for publication as part of Treatise Volume R.

Caridean shrimp are remarkable in exhibiting multiarticulate podomeres on various appendages, usually the carpus of pereiopod two (Bauer, 2004; Wicksten, 2010) (Fig. 4.3). This is not known in Decapoda outside of the shrimp, and it is recorded for only one dendrobranch family, Carpopenaeidae. The multiarticulate nature of the carpus, as well as the number of articles, is diagnostic for many families within Caridea (Wicksten, 2010). The multiarticulate carpus is distinctive in the extinct caridean genus *Blaculla* Münster, 1839, so the character has existed since at least the Late Jurassic (Fig. 4.3). The nature of the multiarticulate carpus can be quite variable, ranging from a few articles to over a dozen (Wicksten, 2010). Schram and Koenemann (2021) attributed the remarkable biodiversity of carideans to their broad variation in chela types and gastric mill structures, as well as their ambisexuality and eurytypic osmoregulatory adaptations. We wonder why this lineage is so variable, yet also monophyletic? Sadly, the poor fossil record of carideans makes testing hypotheses about their origination and evolution difficult.

Many extant caridean shrimp exhibit a symbiotic lifestyle, which evolved multiple times independently, and occurs predominantly in Alpheidae and Palaemonidae (Davis & others, 2018; Frolová, Horká, & Ďuriš, 2022). The poor fossil record of carideans precludes testing the timing of appearance of symbiosis in these lineages. However, there are some features of the dactyls of the pereiopods that might indicate a symbiotic relationship in which the shrimp is anchored to a surface. These include modifications for hooking or gripping, which might be observable in fossils (Chow, De Grave, & Tsang, 2021). A reduction in carapace ornamentation was suggested to be a marker of symbiotic palaemonids as compared to free-living relatives (Frolová, Horká, & Ďuriš, 2022). Examination of fossils with respect to these features might help constrain timing of origination of these relationships.

INTERSPECIFIC ASSOCIATIONS

In the fossil record, the identification of interspecific relationships is rare, whereas competition, commensalism, mutualism, predation, and parasitism have a great influence on the evolution and coevolution of species (Robin, 2021). Present-day shrimps show very diverse epibionts such as algae (Colorni, 1989), cirripeds (Dawson, 1957), bryozoans (Giri & Wicksten, 2001), hydrozoans (Widmer, Cailliet, & Geller, 2010), bivalve mollusks and isopods (Itani, Kato, & Shirayama, 2002), bacteria and diverse unicellular organisms (Fernandez-Leborans, 2010), and also cysts of trematodes (Jayasree, Jankiram, & Madhavi, 2001).

The fossil record of dendrobranchiate shrimps has yielded only three confirmed intimate associations: epibiotic bacterial colonies on Middle Jurassic solenocerid and aegerid shrimps (Robin, Petit, & Charbonnier, 2015), swellings on Early Cretaceous penaeoidean shrimp attributed to epicaridean isopods (Lima & others, 2023), and sponge gemmules on Late Cretaceous carpopenaeid shrimp (Petit & Charbonnier, 2012). In the first case, the calcifying bacteria formed colonies nested in the cuticle of both carapace and pleon, and the relation is close to parasitism (Robin & others, 2015). This relation was first identified in the fossil record and subsequently in extant penaeids. In the second case, the epicaridean isopod was classically located in the branchial chamber, and the relation is clearly parasitism (Klompmaker & others, 2014). In the third case, the sponge gemmules were fixed on the rostrum of the shrimp, and the relation is close to phoresy: the shrimp does not appear to obtain any advantage, whereas the sponge (via gemmules) is transported, which contributes to its dispersal.

FRESHWATER SHRIMP

The vast majority of shrimp occurrences in the fossil record are marine, but up to 22% of extant caridean shrimp species are found in freshwater (De Grave & others, 2015b; Ahyong & Huang, 2020). Seven extant families of Caridea are known from freshwater, and two of these have fossil records. Palaemonidae occurs in freshwater habitats as early as the late Early Cretaceous in South America (Schweitzer & others, 2018) and China (Garassino & others, 2002). Younger fossils attributed to the family occur in the Eocene of Wyoming, USA (Feldmann & others, 1981), and Europe (de Mazancourt, Wappler, & Wedmann, 2022), and in the Oligocene of South America (Martins-Neto & Mezzalira, 1991). Atyidae appeared in Europe by the Early Cretaceous. Although some of the fossil occurrences of atyids have yet to be confirmed as members of the family, the deposits that contain them are typical of fresh water (López-Horgue & Bodego, 2017). The fossil record of freshwater shrimps is very sparse but some remarkable Cenozoic deposits yielded caridean shrimps, most of the time originally living in lacustrine paleoenvironments (e.g., Eocene of Messel, Germany; de Mazancourt, Wappler, & Wedmann, 2022). Freshwater invasions were considered to promote diversity among carideans (Davis & others, 2018); however, too little is known of the caridean fossil record to suggest timing of diversification or paleobiogeographic patterns for these freshwater invasions. One dendrobranch species was reported from freshwater deposits of Cenomanian age in Morocco (Garassino, Pasini, & Dutheil, 2006); that occurrence is currently being reevaluated. Thus, only caridean shrimp have been found as fossils in freshwater deposits at this time.

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ABBREVIATIONS

BSPG: Bayerische Staatsammlung für Paläontologie und historische Geologie München (Munich), Germany

CM: Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA

USNM: United States National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA

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 (Galatheoidea). Zoologischer Anzeiger 250:367–377. [DOI:10.1016/j.jcz.2011.06.005].

Ahyong, S. T., Enrique Macpherson, & Tin-Yam Chan. 2010. Part II. Lithodoidea (King crabs). *In* Tin-Yam Chan, ed., Crustacean Fauna of Taiwan: Crab-like anomurans (Hippoidea, Lithodoidea and Porcellanidae). National Taiwan Ocean University. Keelung, Taiwan. p. 42–66.

Ahyong, S. T., & C. N. Roterman. 2014. Pristinaspinidae, 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 Galatheidae 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 (Galatheidae). *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 Galatheoidea (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 ver wandten von Wosnessenski entdeckten, als Typen einer besondern Unter abtheilung (Tribus Lithodea) der Edward'shen Anomuren. Bulletin de la Classe physico-mathématique de l'Académie Impériale des Sciences de Saint-Pétersbourg 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-Pétersbourg 8:266–269.

Chablais, Jerôme, 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 Adjectis Synonimis, Locis, Observationibus, Descriptionibus. Christian Gottllob Proft. Hafniae 2:i–viii + 1–519.

Feldmann, R. M. 1984. *Haumuriaegla glaessneri* n. gen. and sp. (Decapoda; Anomura; Aeglidae) 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].

Franţescu, 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, & Giovani 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* fossil 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.

Klompmaker, 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].

Klompmaker, 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. Galatéadées, Galateadæ. (Crust.). *In* F. Cuvier, ed., Dictionnaire des Sciences Naturelles, dans lequel on trait Méthodiquement des Différens étres 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 spécifi ques, leur lieu natal, leurs propiétés 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 Munididae (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, Aeglidae). 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. Porcellaindae (Porcelain crabs). *In* Tin-Yam Chan, ed., Crustacean Fauna of Taiwan: Crab-like anomurans (Hippoidea, Lithodoidea 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. Rodrígues-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 Paläontology, 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. Ahyong. 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 Munidopsidae (Decapoda: Anomura: Galatheoidea) from the Jurassic Ernstbrunn Limestone of Austria, and notes on fossil munidopsid 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.

Rodrígues-Flores, P. C., Enrique Macpherson, K. E. Schnabel, S. T Ahyong, Laure Corbari, & Annie Machordom. 2022. Depth as a driver of evolution and diversification of ancient squat lobsters (Decapoda, Galatheoidea, *Phylladiorhynchus*). Molecular Phylogenetics and Evolution 171:107467. [DOI:10.1016/j.ympev.2022.107467].

Rodrígues-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: Munidopsidae). Invertebrate Systematics 37:14–60. [DOI:10.1071/IS22030].

Roterman, C. N., W.-K. Lee, Xinming Liu, Rongcheng Lin, Xinzheng 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, Philipe 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 (serié 2) 4(7):1–462, pl. 1–10.

Via Boada, Luis. 1981. Les Crustacés Décapodes du Cénomanien de Navarra (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 (Amomura, 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.