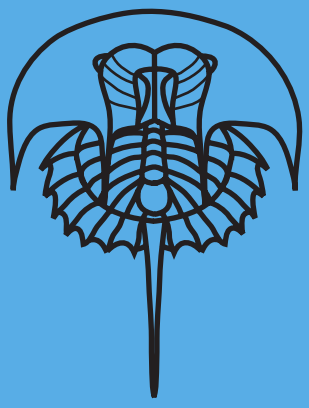

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Carrie E. Schweitzer and Frederick R. Schram

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PART R, REVISED, VOLUME 1, TREATISE ONLINE 195:

EVOLUTIONARY HISTORY OF DECAPOD GROUPS: ORIGINS OF DECAPODA

Carrie E. Schweitzer[1] and Frederick R. Schram[2]

[1]Department of Earth Sciences, Kent State University, cschweit@kent.edu;
[2]Burke Museum, University of Washington, Seattle, fschram@whidbey.com]

INTRODUCTION

Decapoda is part of the large and diverse Pancrustacea. Commonly known as shrimps, lobsters and crabs, but also including hermit crabs, ghost shrimp, and other lesser-known forms, decapods are themselves diverse components of the modern ecosystem with over 17,000 known species (De Grave & others, 2023). The fossil record is much less speciose but includes over 4,500 extinct species of decapods. Because of their commercial and ecological importance as members of most marine and many freshwater food webs, crustaceans have received considerable monographic attention in recent decades (volumes in the *Traité de Zoologie,* F.R. Schram, M. Charmantier-Daures, & J.C. von Vaupel Klein, eds., 2004–2015; *The Natural History of the Crustacea,* M. Thiel, ed., 2015–2020; *Evolution and Phylogeny of Pancrustacea* Schram & Koenemann, 2021; *Marine Decapod Crustacea* Poore & Ahyong, 2023; *Treatise Online, Revision Part R, Decapoda*, Schweitzer & Feldmann, eds., 2012-2025). It is a good time to summarize and consider origins of Decapoda.

The number of species within the numerous higher taxa of pancrustaceans varies depending on the authority and is highly variable within and among the higher taxa. For example, the Allotriocarida include about 1,200 extant species, exclusive of insects, which alone comprise perhaps more than two million living species (Schram & Koenemann, 2021). Malacostraca fall somewhere in between, with about 40,000 extant species (Schram & Koenemann, 2021).

WHAT IS A CRUSTACEAN?

Crustacea embraces those arthropods with segmented bodies and two pairs of antennae associated with the first two cephalic somites (Poore & Ahyong, 2023). Crustacea had been considered as a subphylum of Arthropoda, parallel to the subphyla Hexapoda (insects), Trilobitomorpha (trilobites and relatives), Myriapoda (millipedes and centipedes) and Chelicerata (spiders, scorpions, horseshoe crabs) (Brusca & Brusca, 2003). However, recent work suggests that insects form a monophyletic group with what were traditionally regarded as crustaceans. The names Pancrustacea (Zrzavý & Štys, 1997) and Tetraconata (Dohle, 2001) have been proposed for this clade, with Pancrustacea receiving widespread usage (Ahyong, 2020; Hegna, Luque, & Wolfe, 2020; Schram & Koenemann, 2021). Crustacea is still used for those taxa traditionally considered as crustaceans (excluding insects) because of its familiarity (Poore & Ahyong, 2023), but this usage does not conform strictly to a monophyletic group in recent analyses. A detailed and exhaustive discussion of the range of variation among Pancrustacea can be found elsewhere (Schram & Koenemann, 2021). The typical features of Crustacea include a cephalon composed of five somites, each with a pair of appendages which from

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anterior to posterior correspond to antennules, antennae, mandibles, first maxillae, and second maxillae; a body composed of three regions designated as cephalon, thorax or pereon, and pleon or abdomen; multiramous appendages (often secondarily uniramous); and development through larval stages (Schram & Koenemann, 2021). All of these features are symplesiomorphic for Decapoda.

Within Pancrustacea, most phylogenetic analyses recover three major groupings (Fig. 1; Table 1). Usually recovered as basal within Pancrustacea is Oligostraca, composed of ostracodes, branchiurans, and mystacocarids (Regier & others, 2010; Oakley & others, 2012; Schwentner & others, 2018; Bernot & others, 2023). Oligostracans are generally characterized by overall small size, a short thorax, gonopores typically on the fourth thoracomere, and usually a short abdomen, which is congruent with some of the earliest Cambrian crustacean forms (Ahyong, 2020; Schram & Koenemann, 2021). A second clade, Allotriocarida, embraces remipedes, branchiopods, and hexapods (Regier & others, 2010, Oakley & others, 2012; Schwentner & others, 2018) and sometimes includes copepods (Bernot & others, 2023). This clade has widely divergent morphology, ranging from the well-known insect body form to the remipedes, which have a long body of many somites and lack tagmatization (Ahyong, 2020). Most importantly for this volume, the third clade within Pancrustacea, Multicrustacea, embraces Cirripedia, sometimes Copepoda, and Malacostraca (Regier & others, 2010, Oakley & others, 2012; Schwentner & others, 2018; Hegna, Luque, & Wolfe, 2020; Bernot & others, 2023). Malacostraca, and specifically Decapoda, will be discussed in detail.

THE POSITION OF DECAPODA AMONG PANCRUSTACEA

Decapoda is a member of Malacostraca, considered the most diverse group within Crustacea (Ahyong, 2020). Malacostraca includes Phyllocarida and Eumalacostraca (Wolfe & others, 2016), differentiated by the number of pleonal somites (generally seven in phyllocarids, six in eumalacostracans) (Schram & Koenemann, 2021) (Fig. 1, Table 1). Among the Malacostraca, Phyllocarida are considered basal and have a long fossil record extending into the Cambrian (Schram & Koenemann, 2021). They are distinctive in exhibiting a bivalved carapace with a seven-segmented pleon, yielding the superficial appearance of a clam with a tail, and have a robust fossil record (Hegna & others, 2020).

Eumalacostraca comprises a diverse group including Peracarida (isopods, amphipods, mysids, and others), Hoplocarida (stomatopods and relatives), Bathynellacea, Anaspidacea, and Eucarida (Regier & others, 2010; Wolfe & others, 2016), in addition to the extinct Thylacocephala (Schram & Koenemann, 2021). A recent analysis found crown Eumalacostraca as paraphyletic and instead recognized three groups: Leptostraca, Peracarida, and a large clade, Stomatocarida (Bernot & others, 2023). Eumalacostracans are united in possessing characters in Table 1.

An additional subgroup, Caridoida, has been used by some authors and embraces Eucarida, Peracarida, Bathynellacea, and Anaspidacea as a subset of Eumalacostraca (Schram & Koenemann, 2021). Caridoida was based upon one of the first conceptions of the body plan for early decapods and their relatives (Calman, 1904, 1909; Hessler, 1983). Calman conceived of the caridoid facies, which included a carapace covering the thorax, stalked eyes, biramous first antennae, a scale-like exopod of the second antenna, swimming exopods on the thoracopods, and an elongate pleon with uropods and telson forming a tail fan (Hessler, 1983). This morphology was attributed to taxa that now comprise most Eumalacostraca (Table 1) and includes the characters considered as basal in most eumalacostracans (Hessler, 1983; Schram & Koenemann, 2021). Caridoida is not monophyletic in recent analyses.

The closest relatives of Decapoda are among the Eumalacostraca, and a brief differentiation of the groups usually included in Eumalacostraca follows (Fig. 1, Table 1). Hoplocarida is composed of stomatopods and relatives, the mantis shrimp. Widely known to the general public for their smashing and stabbing predatory abilities,

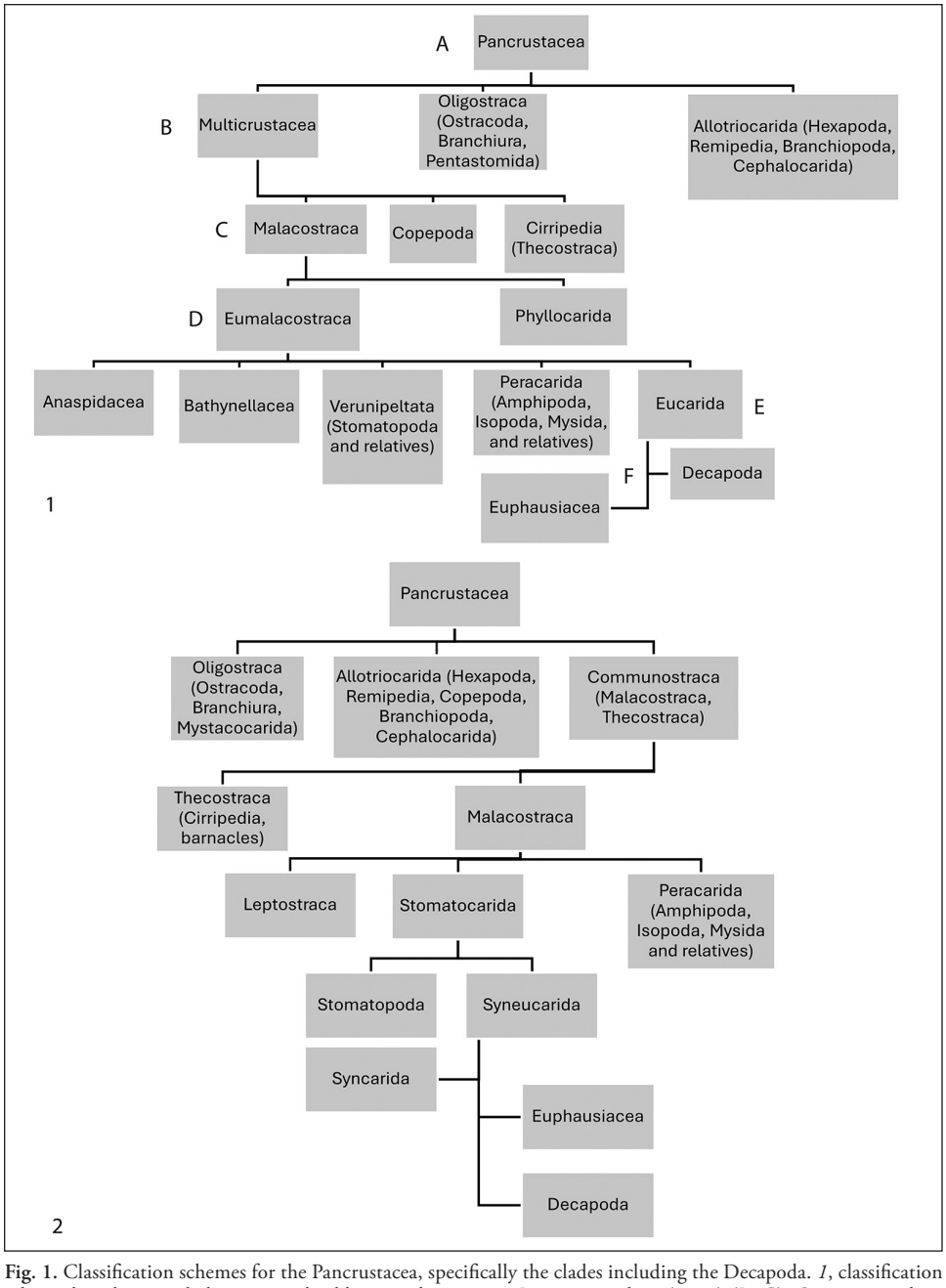

Fig. 1. Classification schemes for the Pancrustacea, specifically the clades including the Decapoda. *1*, classification scheme based upon phylogenies and calibration diagrams in Regier & others (2010) (B, C), Oakley & others (2012) (A, B, C), and Wolfe & others (2016) (A–F). *2*, classification scheme based upon phylogeny of Bernot & others (2023).

Table 1. Definitions of taxonomic groups to which Decapoda belongs from highest level to lowest level. Defining characteristics of each clade extracted from cited works. All except caridoid facies and Caridoida are as proposed in the phylogenetic analyses cited in column two.

Taxon/Clade	Analysis and composition	Characteristics
Pancrustacea	Oakley & others (2012): Multicrustacea, Oligostraca, Allotriocarida Bernot & others (2023): Communostraca, Oligostraca, Allotriocarida	Mostly defined by genes; one shared feature is tetrapartite crystalline cones in compound eyes. Note that not all pancrustaceans have compound eyes and some lack eyes altogether (Schram & Koenemann, 2021)
Multicrustacea	Oakley & others (2012): Malacostraca, Copepoda, Cirripedia	Mostly defined by genes; possess gonopores on either thoracic somites six and eight or on thoracomere seven (Schram & Koenemann, 2021)
Communostraca	Bernot & others (2023): Malacostraca, Cirripedia (their Thecostraca)	Male and female gonopores located on different thoracic somites (Bernot & others, 2023)
Malacostraca	Oakley & others (2012): Eumalacostraca, Phyllocarida Bernot & others (2023): Phyllocarida (their Leptostraca), Stomatocarida, Peracarida	Gonopores on thoracic somites six and eight; posterior pleon with a nerve cord and usually with pleopods; pleonal somites variable in number, usually six or seven (Schram & Koenemann, 2021)
Eumalacostraca	Wolfe & others (2016): Anaspidacea +Bathynellacea (formerly Syncarida), Verunipeltata (= Hoplocarida), Peracarida, Eucarida	Six pleonal somites (Schram & Koenemann, 2021); 19 body somites (five cephalic, eight thoracic, six pleonal); five cephalic appendages; three thoracic somites fused to head, five thoracic somites for feeding and locomotion; six pleonal somites (Poore & Ahyong, 2023)
Stomatocarida	Bernot & others (2023): Stomatopoda, Syneucarida	Six pleonal somites; telson and uropods (Schram & Koenemann, 2021)
Caridoid facies *sensu* Calman, 1904	Euphausiacea, Mysidacea, some Decapoda, most Stomatopoda, most Leptostraca	Carapace, movable eyes, exopod of the antenna, elongated pleon and tailfan (Calman, 1904, p. 147)
Caridoid facies *sensu* Calman, 1909	Euphausiacea, Mysidacea, some Decapoda, most Stomatopoda, Syncarida	Carapace covering thorax, movable, stalked eyes, biramous antennules, exopod of the antenna, natatory appendage on thorax; elongated pleon and tailfan (Calman, 1909, p. 144)
Caridoida *sensu* Hessler, 1983	Eocarida, Syncarida, Peracarida, Eucarida, Pancarida	Pleonal musculature facilitating the caridoid escape response (Hessler, 1983, p. 147); epipods of pleopods lost; movable rostrum or cephalon absent; antennal scale with one segment; mandible with bristles between incisor and molar processes (Hessler, 1983, p. 158)
Caridoida *sensu* Schram & Koenemann (2021)	Eucarida, Peracarida, Bathynellacea, Anaspidacea	Nineteen body somites (five cephalic, eight thoracic, six pleonal); carapace covering all thoracomeres if present (Schram & Koenemann, 2021)

Table 1. *Continued*

Taxon/Clade	Analysis and composition	Characteristics
Eucarida	Oakley & others (2012): Decapoda, Euphausiacea	Carapace fused to thoracomeres; telson and uropods (Schram & Koenemann, 2021); carapace covering all thoracomeres; eyes on movable stalks (Poore & Ahyong, 2023)
Syneucarida	Bernot & others (2023): Bathynellacea, Anaspidacea, Decapoda, Euphausiacea	Six pleonal somites; telson and uropods (Schram & Koenemann, 2021)
Decapoda	Oakley & others (2012), Bernot & others (2023): Dendrobranchiata and Pleocyemata	Carapace fused to and covering thoracomeres; gonopores on thoracic somites six and eight; six pleonal somites with pleopods, telson and uropods forming termination; three pairs of maxillipeds as specialized thoracopods (Schram & Koenemann, 2021)

mantis shrimp have highly modified second maxillipeds and excellent vision (Ahyong, 2020). Their fossil record extends into the Devonian (Ahyong, 2020; Schram & Koenemann, 2021). Anaspidacea and Bathynellacea, formerly Syncarida, exhibit some odd features compared to other eumalacostracans, most notably lack of a carapace (Ahyong, 2020; Schram & Koenemann, 2021). They are recovered as two separate clades within Eumalacostraca (Wolfe & others, 2016) or Syneucarida (Bernot & others, 2023). Anaspidacea has a fossil record extending into the Mississippian (Schram & Koenemann, 2021). Bathynellacea have no fossil record (Schram & Koenemann, 2021). Peracarida includes Amphipoda, Isopoda, Lophogastrida, and Mysida, along with several other less speciose groups (Schram & Koenemann, 2021). They are characterized by a cephalon, pereon, and pleon and a brood chamber formed by oöstegites in females (Ahyong, 2020). Isopods, commonly known as pill-bugs or roly-polies, have a modest fossil record (Maguire & others, 2018), and notable extant forms include the giant deep-water isopod *Bathynomus* A. Milne-Edwards, 1879. Mysidaceans, small shrimp-like forms, also have a modest fossil record (Feldmann & others, 2016). The oldest peracarids in the fossil record are Devonian (Hegna & others, 2020; Robin & others, 2021).

Eucarida includes the euphausiaceans (krill) and Decapoda (Oakley & others, 2012; Ahyong, 2020). Euphausiids are known since at least the Jurassic, possibly even from the Carboniferous (Schram & Koenemann, 2021), and a major feature differentiating them from decapods is that they possess no maxillipeds, whereas decapods possess three pairs. Euphausiaceans include krill, a major component of the modern marine food web. An additional extinct group, Angustidontida, was included in Eucarida (Gueriau & others, 2014; Wolfe & others 2016; Schram & Koenemann, 2021). Angustidontids are characterized by one or two pairs of well-developed maxillipeds which can be spinose, and they might exhibit an overall shrimp-like morphology with the carapace fused to the thorax (Schram & Koenemann, 2021; Gueriau & others, 2014). Angustidontans have been collected from both marine and freshwater deposits of Devonian and Mississippian age (Gueriau & others, 2014).

POSSIBLE STEM DECAPODS AND EARLY RELATIVES OF DECAPODS

Despite their highly variable body plans, all Decapoda are part of a monophyletic group (Wolfe & others, 2019; Bernot & others, 2023), and their ancestry lies among

the extinct eumalacostracans. Crown taxa are defined as monophyletic groups formed by the most recent common ancestor of all the living forms within that group and all of its descendants (Budd & Mann, 2020). Thus, a crown decapod would be expected to possess most of the synapomorphies of the group, which include a carapace fused to the thoracomeres; a pleon with six somites, pleopods on each somite, and a telson with uropods; gonopores on thoracic somites six or eight; and three pairs of maxillipeds which are specialized thoracopods (Table 1). Stem groups are those extinct taxa most closely related to, but not part of, a crown group (Budd & Mann, 2020). Stem taxa have been defined as those with plesiomorphic body forms, composed of characters considered as "primitive" but are those characters that appeared first and are shared across groups as the basal body plan (Schram & Koenemann, 2021). As of now, only crown decapods, and no stem decapods, are formally recognized (Wolfe & others, 2016; Hegna, Luque, & Wolfe, 2020).

What might the first decapod have looked like? Of the major defining features of decapods, some are regularly observable in fossils. Decapods have three pairs of maxillipeds, which are specialized thoracic appendages and for which the corresponding somites are fused to the cephalic somites. Many decapod fossils exhibit the third maxillipeds, easily recognized as such by comparison with extant forms (Schweitzer & others, 2024). Angustidontans, extinct eucaridan forms, have one or two pairs of maxillipeds (Schram & Koenemann, 2021). Thus, maxillipeds are preservable and recognizable morphological features and could be predicted to be both present and preserved in the earliest decapod as well as potentially in a stem decapod.

All three of the earliest known forms currently referred to crown Decapoda have an elongate pleon held posteriorly from the cephalothorax; consequently, a shrimp-like form might be hypothesized for a stem decapod (references and discussion below). In addition, a shrimp-like or lobster-like body form is seen in all early eumalacostracans known thus far, and indeed, the shrimp-like body form has long been considered the basal form among Decapoda (Glaessner, 1969). Burkenroad (1963, p. 15) predicted that a stem decapod would be shrimp-like and possess a branchiocardiac groove, strong but achelate pereiopods, reduced endopods on the first three thoracic appendages, and unspecialized walking legs. All decapods plesiomorphically have a telson with uropods, a feature exhibiting high preservation potential, and which is seen in many eucarid and decapod fossils (Schram & Koenemann, 2021; Treatise Online Systematics Chapters Part R Revised). This suggests that the earliest crown decapod must have exhibited a shrimp-like pleon with telson and uropods, as is probable for a stem decapod.

Fusion of the carapace to the thoracomeres is determinable in some fossil forms (Schram & Koenemann, 2021). The nature of the fusion, however, is unknown for some of the earliest eumalacostracans and is a difficult character to determine with certainty in fossils (Jones & others, 2018). The position of the gonopores has yet to be seen in extinct Paleozoic eucarideans but is known from many decapod fossils (Schweitzer & others, 2024). This feature is preservable in fossils but not particularly common.

What other features might be expected in a stem decapod or in the earliest crown decapod? Stem groups have their own specializations and apomorphies which may not persist in crown groups; thus, a stem decapod could differ substantially in some ways from crown decapods (Schram & Koenemann, 2021). Pereiopod terminations in a stem decapod are difficult to predict. One of the earliest crown decapods, *Palaeopalaemon* Whitfield, 1880, has claw-like terminations on the first pereiopods. The other Devonian decapods lack preserved appendages but are referred to chelate groups. Most other early eumalacostracans are achelate, so this may suggest achelate

terminations as ancestral and potentially present in a stem decapod and the earliest crown decapods. We note that it is probable that pseudochelae and chelae evolved more than once, and achelate appendages may result from loss of the chelate form. Pseudochelae are widely known across decapod groups (some Achelata, Gebiidea, Glypheidea, even some brachyurans), supporting their independent evolution multiple times. As there are very few crown decapods with achelate-first pereiopods (most Achelata, Procaridea), this might be a secondarily derived characteristic among crown decapods.

Similarly, much has been made of the transition of decapods from a heavily ornamented carapace with distinctive, stereotyped groove patterns to a nearly smooth carapace with reduction of grooves (summarized by Glaessner, 1969). *Palaeopalaemon* has been interpreted as possessing cervical, post-cervical, and branchiocardiac grooves (Jones & others, 2018). Does this mean that all early decapods possessed such grooves? This is unknown, as axiideans, dendrobranch shrimp, and stenopodid shrimp, the groups to which other Paleozoic decapods have been referred, generally possess only the cervical groove of these three (Schweitzer & others, 2024). Indeed, it has not yet been determined if these grooves, which can occur across Decapoda, are homologous (Glaessner, 1960; Secretan, 1960a, b; Schweitzer & others, 2025). A stem decapod may have possessed none, some, or all of these grooves. All the earliest decapods known had at least the cervical groove.

Predicting the body plan for a stem decapod or early crown decapod is complicated by the rampant convergence within Decapoda and other crustaceans. Convergence may exist from the smallest details of carapace grooves and spines to the overall body plan. Recent attention has been directed at carcinization, or acquisition of a crab-like body form (Keiler & others, 2017; Wolfe & others, 2021). Many decapod groups have a lobster-like facies: Polychelida, Achelata, Glypheidea, and Astacidea, as well as mud shrimp and stenopodid shrimp. Schram & Koenemann (2021) discussed Belotelsonidea as so-called lobsteroids due to their lobster- or crayfish-like appearance. *Mamayocaris* Brooks, 1962, and related pygocephalans are superficially lobster-like as well (Hotton & others, 2002; Irham & others, 2010). The convergence of the lobster-like body form across Hoplocarida, Decapoda, and Peracarida was well documented, and the process of reptantization was described as a series of morphological changes from a shrimp-like form, promoting a benthic lifestyle (Haug & Haug, 2021). Like carcinization, reptantization proceeds from a shrimp-like body form and is therefore unlikely in a stem decapod, although the early crown decapod *Palaeopalaemon* is considered lobster-like.

Candidates for Stem Decapoda

Early stem decapod candidates include members of Angustidontida, Anthracophausiidae, Essoidiidae, Belotelsonidea, Waterstonellidea, *Palaemysis* Peach, 1908, and *Archangeliphausia* Dzik & others, 2004 (Schram & Koenemann, 2021) as well as *Hohensteiniella* Haug & others, 2017 (Table 2). Each of these early eumalacostracans could be a stem decapod (Schram & Koenemann, 2021). *Archangeliphausia* exhibits a shrimp-like facies with uropods and telson (Dzik & others, 2004). Whether or not the carapace is fused to the thoracomeres is currently not known (Schram & Koenemann, 2021). Essoidiidae and *Waterstonella* Schram, 1979, are little-known shrimp-like organisms with indeterminate affinities other than as probable eumalacostracans (Schram & Koenemann, 2021). Essoidiids have a shrimp-like pleon. *Palaemysis* and *Waterstonella* are also shrimp-like with poorly known or unusual thoracopods containing multisegmented terminations (Clark, 1991). Belotelsonids lack maxillipeds, and so are most similar to euphausiids, a sister group to decapods. An interesting fossil from the early Devonian

Table 2. Possible stem decapod taxa or early decapod relatives. List adapted from Schram & Koenemann (2021, chapter 20). Characters and ages from original article naming the taxon or from the cited reference.

Taxon	Age	Characters
Angustidontida Gueriau, Charbonnier & Clément, 2014	Late Devonian, Mississippian, North America and Europe	One or two pairs of maxillipeds; caridoid facies
Anthracophausiidae Brooks, 1962	Pennsylvanian (Moscovian-Kasimovian), Illinois, Alabama, USA	Lacking carapace grooves; no apparent differentiation of thoracopods (Vohs, Feldmann & Schweitzer, 2023)
Archangeliphausia Dzik, Ivantsov & Deulin, 2004	Early Devonian (Lochkovian), northwest Russia	Caridoid facies; uropods and telson; fusion of carapace to thoracomeres unknown
Belotelsonidea Schram, 1981	Carboniferous (Mississippian and Pennsylvanian) of Europe and USA	No maxillipeds
Essoidiidae Schram, 1974	Middle Pennsylvanian (Moscovian), USA	Caridoid facies with bent pleon; no apparent maxillipeds
Hohensteiniella Haug & others, 2017	Early Devonian (Emsian), Germany	Carapace not covering all thoracomeres
Palaemysis Peach, 1908	Carboniferous (Late Mississippian, Serpukhovian) (Bearsden), Scotland	Possibly one pair of maxillipeds; caridoid facies
Waterstonella Schram, 1979	Carboniferous (Mississippian), Scotland	Carapace not fused to thoracomeres; no maxillipeds; caridoid facies

Hunsrück Slate, *Hohensteiniella engeli* Haug & others, 2017, has eumalacostracan affinities including a biflagellate antennule, an antenna, a small carapace not covering all of the eight thoracomeres, six pleomeres, and several thoracic appendages (Haug & others, 2017). Angustidontids, with one or two pairs of maxillipeds, appear to be the most likely candidate at this time for a stem decapod morphology, based on the characters discussed above. Placement of *Tealliocaris* Peach, 1908, as a decapod has been much debated, summarized in detail (Clark, 2013; Jones and others, 2016; Schram & Koenemann, 2021), and is therefore not considered as a decapod here. In conclusion, there are many eucarid/eumalacostracan forms in the fossil record that present a morphology that might be typical of a stem decapod. To sort out the relationships between and among these animals with respect to decapods, a comprehensive phylogeny based upon morphological characters and using all of these taxa, plus representatives of decapods, euphausiids, syncarids, and other sister groups, will be necessary.

WHEN DID DECAPODA ARISE?

All of this is to say that the identity of stem Decapoda and the timing of origin of crown Decapoda is not yet known. Schram (2009) summarized the state of knowledge about decapod origins, and little has changed since then (Ahyong, 2020; Hegna & others, 2020). Schram (2009) suggested

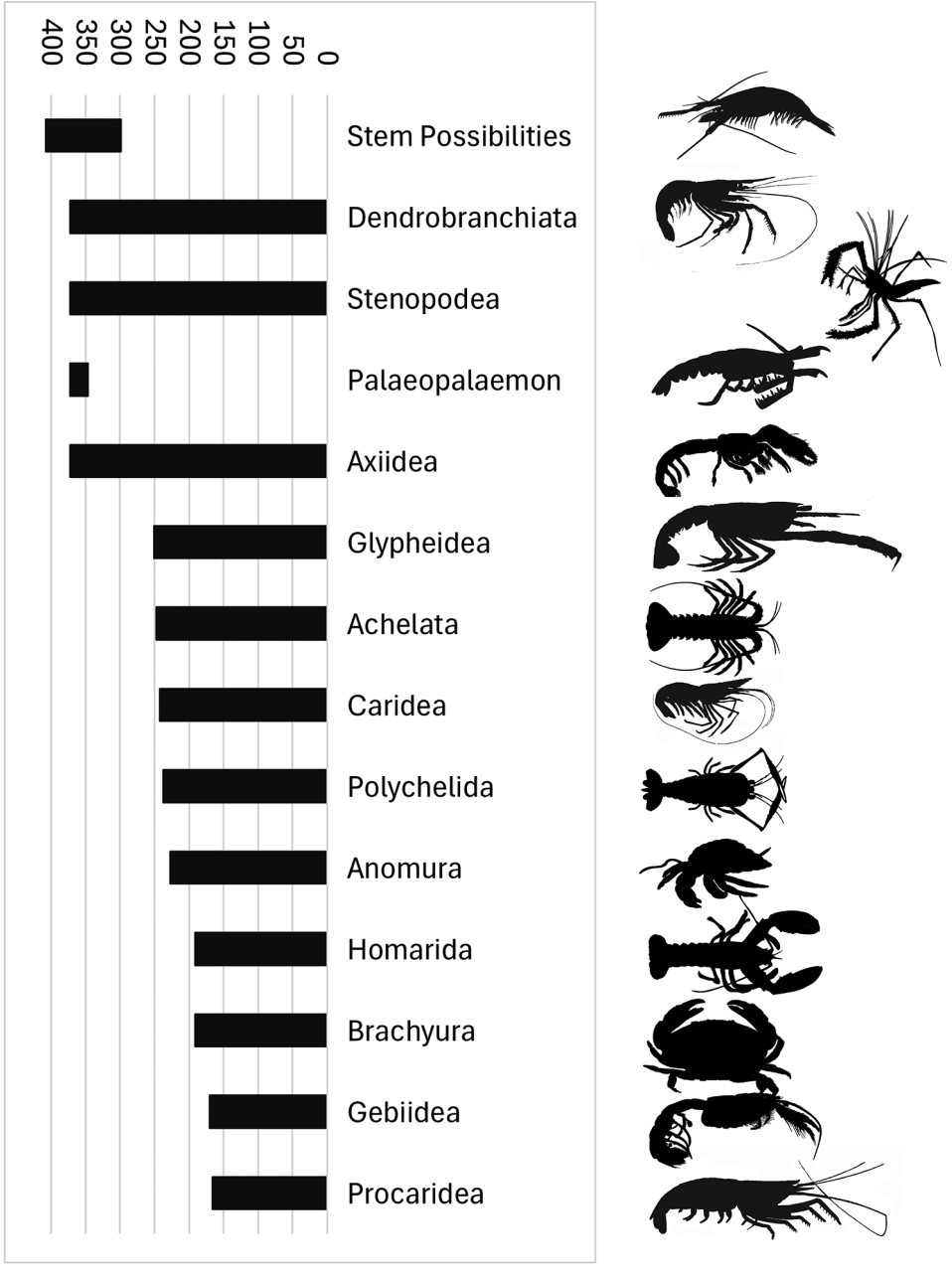

Fig. 2. Geologic ranges (in millions of years) for Decapoda infraorders and possible stem Decapoda. Silhouettes from Phylopic or new. Silhouette for stem decapod modified from Qohelet12, Wikipedia, under CC BY-SA 4.0.

that confounding issues related to determining the origins of Decapoda lay in four major areas: 1) lack of consensus on the sister-group to Decapoda, 2) crown-group status of Paleozoic forms, 3) lack of pre-Devonian occurrences of decapods and the generally restricted known biogeography of Paleozoic decapods (nearly all from North America), and 4) possible erroneous hypotheses on the morphological appearance of an

ancestral form. Euphausiaceans have been recovered as sister to the Decapoda (Wolfe & others, 2019; Bernot & others, 2023), but they are crown-group malacostracans and are most likely younger than other decapods in terms of fossil occurrences (Schram & Koenemann, 2021). Thus, they do not shed much light on decapod origins. Additional Paleozoic decapods have been recognized after 2009 (see below), but they are all crown-group members and North American in origin, adding no resolution to Schram's (2009) points two and three. Most hypotheses suggest a shrimp-like ancestor for Decapoda, as some of the earliest forms are shrimp and the shrimp-like body form is recurrent among Crustacea (Burkenroad, 1963, 1981; Bauer, 2004). However, fossils do not yet support this hypothesis, as the earliest decapods exhibit three different body forms (shrimp, ghost shrimp, lobster). As noted by several previous workers, we await more fossils that could illuminate the origin of Decapoda (Schram, 2009; Ahyong, 2020; Hegna & others, 2020).

Statistical models estimated the origin of Decapoda in the Ordovician (Wolfe & others, 2019), whereas the earliest known fossils referred to as Decapoda, of four different crown groups, are in the latest Devonian and earliest Mississippian (Feldmann & others, 2013; Schweitzer & others, 2023a, b, c) (Fig. 2). Such discrepancies between molecular estimates and the actual fossil record were explored and suggested to be a result of rapid diversification of major groups over a short period of time, which previous models had not captured (Budd & Mann, 2020). The timing of appearance of Decapoda is not well-constrained, either statistically or by the fossil record, which shows four crown groups appearing more-or-less simultaneously.

EARLY CONFIRMED DECAPODA

The earliest Paleozoic crown decapod to be recognized was *Palaeopalaemon* (Schram & others, 1978; Feldmann & others, 2013; Jones & others, 2018) (Fig. 2, 3.1). This lineage is interpreted as being allied with lobster-like decapods, recovered as sister to Polychelida (Jones & others, 2018) and is reported from Upper Devonian to Lower Mississippian rocks (Feldmann & others, 2013). *Palaeopalaemon* is a crown decapod based upon possession of a third maxilliped and five pereiopods, the first of which is pseudochelate; a carapace fused to the thoracomeres; a pleon with six somites, a telson, and uropods; and a complex carapace groove pattern typical of glypheidean and polychelidan lobsters (Jones & others, 2018).

Feldmann & Schweitzer (2010a) and Jones & others (2014) recognized Paleozoic members of two different groups of shrimp, Dendrobranchiata and Stenopodea, respectively. The Late Devonian (Famennian) *Aciculopoda* Feldmann & Schweitzer, 2010a, was referred to the dendrobranch superfamily Penaeoidea, based upon its possession of a carapace covering all thoracic somites and fused to the thorax; a pleon with six somites, a telson, and uropods; and a spinose anterior thoracopod (Fig. 3.4). The Late Devonian to Early Mississippian *Devonostenopus* Jones & others, 2014, was referred to Stenopodidae, due to its six pleonal somites with one and two reduced, a telson and uropods, and tiny spines on the ventral margin of the carapace (Fig. 3.2). Late Devonian rocks of Ohio have also yielded an axiidean, *Devonoaxius garlandi* Feldmann & Schweitzer, 2019, referred to Axiidae based upon its short bifid rostrum, a well-developed carapace with dorsal oval, and pleon with six somites (Fig. 3.5). The features of the carapace in particular are apomorphies for axiidean shrimp.

Other Paleozoic taxa referred to as Decapoda have been questioned as to their age or membership in the order. As mentioned, placement of *Tealliocaris* has been questioned and discussed (Schram & Koenemann, 2021). The Permian lobster *Protoclytiopsis* Birshtein, 1958, is clearly a member of Clytiopsidae Beurlen, 1927, of

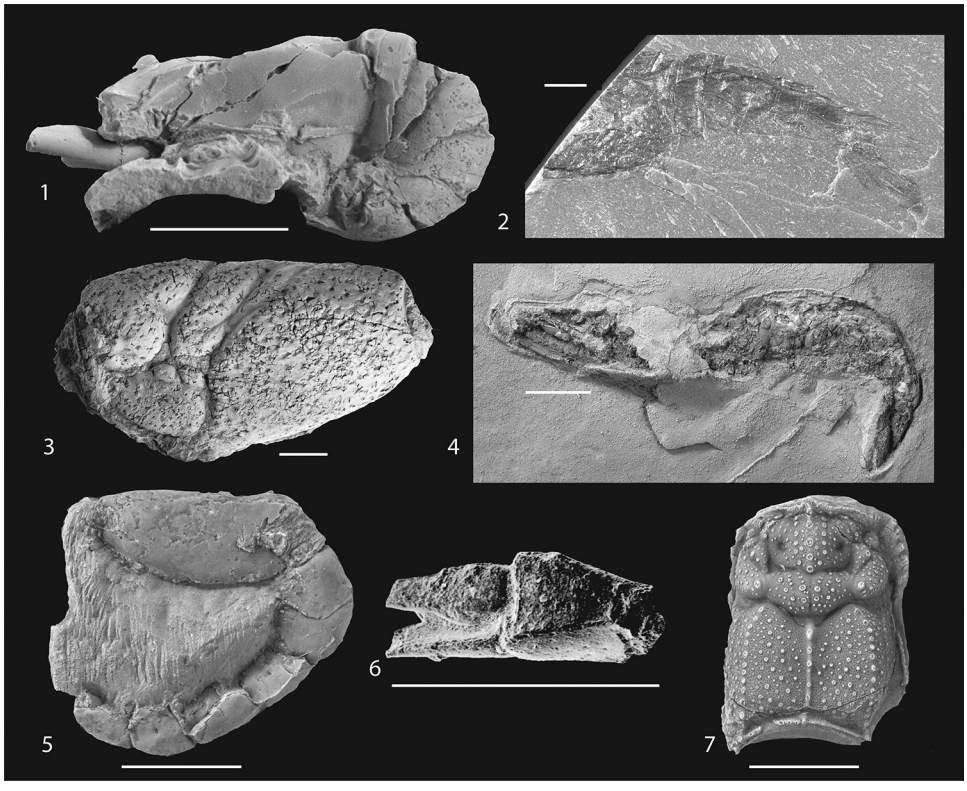

Fig. 3. Paleozoic Decapoda and other crustaceans. *1*, *Palaeopalaemon newberryi* Whitfield, 1880, UI 10752; *2*, *Devonostenopus pennsylvaniensis* Jones & others, 2014, holotype CM 39653; *3*, *Protoclytiopsis antiqua* Birshtein, 1958, holotype PIN 1453; *4*, *Aciculopoda mapesi* Feldmann & Schweitzer, 2010, holotype USNM PAL 540766; *5*, *Devonoaxius garlandi* Feldmann & Schweitzer, 2019, holotype USNM PAL 726800; *6*, *Eryma hoerstgenensis* (Bachmayer & Malzahn, 1983), holotype NHMW 1982/0106/0000; *7*, *Imocaris tuberculata* Schram & Mapes, 1984, SDSNH 25139. Scale bars = 1 cm, except *2* = 1 mm and *7* = 5 mm. *1* and *3* by Schram; *6* from Bachmayer & Malzahn (1983, pl. 1, fig. 1); remainder by R. M. Feldmann.

Glypheoidea (Karasawa & others, 2013), but in actuality may have been recovered from younger, Triassic strata (E. Mychko, personal commun. 2024) (Fig. 3.3). *Imocaris* Schram & Mapes, 1984, has been considered as a decapod (Schram & Mapes, 1984, Schram, 2009), a peracarid (Racheboeuf & Villarroel, 2003), or a non-decapod crustacean (Schweitzer & Feldmann, 2005) (Fig. 3.7). Most recently, it has been argued to be a brachyuran (Schram & Koenemann, 2021). Currently, placement of *Imocaris* remains enigmatic. We note that the arrangement of carapace regions is unlike that of any brachyurans, notably in the lack of any differentiated axial regions such as mesogastric, urogastric, and cardiac, which are generally at least weakly developed in all brachyurans. The keeled branchial regions are much like those seen in many types of lobsters, including Polychelida, Erymoidea, and Glypheidea, and exhibit no evidence of lineae. The carapace presents no aspects of a rostrum, orbits, or augenrest as seen in early brachyurans within Dromiacea.

The Triassic *Rioarribia* Rinehart & others, 2003, originally described as a eubrachyuran with affinities with Raninoida or Eocarcinidae, is difficult to interpret. Raninoida are podotrematous brachyurans, whereas Eubrachyura are defined as the more derived crabs and are heterotrematous or thoracotrematous (Ng & others, 2008; De Grave & others, 2009). Eocar-

cinidae is interpreted as either a member of Anomura (Feldmann & Schweitzer, 2010b) or as a stem-brachyuran (Scholtz, 2020), forms clearly outside Eubrachyura. So, whereas *Riarribia* was heralded as the "earliest eubrachyuran," it was compared with taxa that do not belong within that group, compounding efforts to understand its placement. *Rioarribia* appears to have an elongate body, with evenly spaced, short appendages with unknown terminations along its length; carapace, sternites, and pleon are not known. The genus should be reexamined and described to place it more satisfactorily among Pancrustacea (Schram & Koenemann, 2021), but herein, we do not consider it as a decapod because of its lack of preserved apomorphies of the group. The late Permian *Eryma hoerstgenensis* Bachmayer & Malzahn, 1983, was examined and considered not to be a member of *Eryma* von Meyer, 1840 (Karasawa & others, 2013; Devillez & Charbonnier, 2017) (Fig. 3.6). However, it does appear to be a chela, but of unknown affinity. Clearly, confirmed Paleozoic decapods are scarce.

Why did Decapoda appear in the middle Paleozoic? Schram (2009) noted the abundance of arthropods, and a few crustaceans, predating their appearance. The radiation of eumalacostracan forms (Fig. 2, Table 2) in the late Devonian through Pennsylvanian documents the rapid evolution of this body plan at that time (Schram & Koenemann, 2021) so it is not surprising that a radiation of crown Decapoda began concomitant with it. This rapid diversification of stem groups and resulting crown groups was predicted by modeling using a birth-death model (Budd & Mann, 2020). However, even in the later Paleozoic, other crustacean groups like Phyllocarida, Hoplocarida, Syncarida, Peracarida, and Cyclida outnumbered the Decapoda in terms of known taxa and fossil occurrences (Schram, 2009; Schweitzer & others, 2020; Schram & Koenemann, 2021; Paleobiology Database occurrence data, October 4, 2024). Based on the record as it exists now, decapods appeared during the Devonian but maintained low levels of diversity until their more explosive radiation in the Triassic.

While there is not enough information as yet to support hypotheses on the timing of origin of stem Decapoda and the morphology of the first crown decapod, this means there is much left to discover about this group.

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INSTITUTIONAL ABBREVIATIONS

CM	Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA.
NHMW	Naturhistorisches Museum Wien (Natural History Museum), Vienna, Austria.
PIN	Paleontological Institute, Russian Academy of Sciences, Moscow, Russia.
SDSNH	San Diego Museum of Natural History, San Diego, California, USA.
UI	University of Iowa Paleontology Repository, Iowa City, Iowa, USA.
USNM	United States National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA

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ABOUT THE AUTHORS

Carrie E. Schweitzer got a B.A. in biology from Hiram College and an M.S. and Ph.D. in geology from Kent State University. She has been a professor in the Department of Earth Sciences since 2000, teaching a variety of courses in geology, paleontology, and sedimentary geology. Her research has focused on the systematics, evolution, and paleobiology of decapod crustaceans and relatives of all geological ages.

Picture and biographical information for author **Frederick R. Schram** was unavailable at time of publishing.