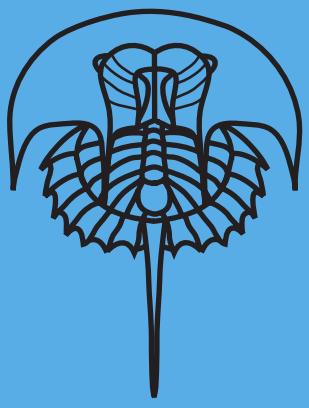

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Part R Revised, Volume 1, Evolutionary History of Decapod Groups: Brachyura (Sections Dromiacea, Homoloida, Callichimaeroida, Torynommoida, Etyoida, Raninoida, Dakoticancroida, Cyclodorippoida)

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PART R, REVISED, VOLUME 1, TREATISE ONLINE 196:

EVOLUTIONARY HISTORY OF DECAPOD GROUPS: BRACHYURA (SECTIONS DROMIACEA, HOMOLOIDA, CALLICHIMAEROIDA, TORYNOMMOIDA, ETYOIDA, RANINOIDA, DAKOTICANCROIDA, CYCLODORIPPOIDA)

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INTRODUCTION AND OVERVIEW

The eight sections of podotrematous crabs comprise a heterogeneous, non-monophyletic group of brachyurans, all possessing female gonopores on the coxae of pereiopods 3 and male gonopores on the coxae of pereiopods 5. They differ from the other true crabs, Eubrachyura, in which the placement of the female gonopore is on the sixth thoracic sternite. Much ink has been spilled on whether or not podotrematous crabs are monophyletic (summarized in Schweitzer & others, 2025b), but nearly all molecular, phylogenomic, and morphological phylogenetic analyses find that they are not. Who are they? In modern oceans, podotremes are generally less common members of the brachyuran fauna. They include Dromiacea, or sponge crabs; Homoloida, or carrier crabs; Raninoida, spanner or frog crabs; and Cyclodorippoida. The podotreme fossil record includes four additional extinct sections, Callichimaeroida, Torynommoida, Etyoida, and Dakoticancroida. Here, the podotrematous brachyurans are treated in a single chapter for convenience and because they constitute a distinct evolutionary fauna, dominating the decapod record in the Late Jurassic through the Cretaceous (Schweitzer & Feldmann, 2015). All geological stage names are taken from the International Chronostratigraphic Chart v.2023/09 (Cohen & others, 2013).

The eight sections into which podotrematous crabs are arranged have been determined phylogenetically and are treated herein from most basal to most derived (Schweitzer & others, 2025b) (Fig. 1). Dromiacea is recovered as either the basal-most section in Brachyura (Karasawa & others, 2011; Luque & others, 2019) or as sister to Homoloida in a clade sister to all other Brachyura (Wolfe & others, 2024). Callichimaeroida, Torynommoida, and Etyoida are each distinct clades and form a series of sequential sister groups to the remainder of Brachyura. Raninoida is sister to Dakoticancroida + (Cyclodorippoida + Eubrachyura) (Karasawa & others, 2011; Luque & others, 2019) or Cyclodorippoida + Eubrachyura (Wolfe & others, 2024). Cyclodorippoida is thus phylogenetically recovered as the most derived of the podotrematous sections.

The podotrematous brachyuran sections are morphologically variable, each with distinct synapomorphies and evolutionary and natural histories (Fig. 2-4). These crabs range from longer than wide, with deep grooves and well-developed regions, to wider than long with more subdued regions. Reports of fossil occurrences increase by the year, but there are variable records for each family. Dromiaceans are common and well-recognized as fossils, whereas some homoloid

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families have sparse fossil records. The ability to carry other organisms as camouflage has appeared several times among these sections, involving modifications of the pleon, sternum, and pereiopods but resulting in differing carrying positions, seen across Dromiacea, Homoloida, and Cyclodorippoida. Burrowing adaptations occur in Raninoida and Cyclodorippoida, and Callichimaeroida are adapted for swimming. Podotrematous crabs are paraphyletic, constituting a grade (rather like lobsters), sharing some plesiomorphic similarities, such as the position of the female sexual openings, but each with their own evolutionary history and not forming a natural group, unlike Eubrachyura.

The origin of Brachyura as a clade, and of each section of the podotrematous crabs, remains somewhat obscure. Eocarcinoidea have been considered as either basal anomurans or as stem-brachyurans (Luque & others, 2024; Schweitzer & Karasawa, 2025). The earliest confirmed brachyuran crab is the Early Jurassic (Pliensbachian) *Eoprosopon klugi* Förster, 1986, with potential affinities with Homolodromioidea (Fig. 2.6). Other early dromiaceans are reported from the Middle Jurassic (Schweitzer & Feldmann, 2010a). The preponderance of evidence, then, suggests that the earliest crabs were dromiacean, based upon the fossil record and their basal position in phylogenies.

Although podotrematous crabs are not monophyletic, many sections share some morphological features. This is most likely a result of convergent evolution (within the convergent evolution of a carcinized form). Gonopores on the coxae of the pereiopods in both males and females is a symplesiomorphy of Decapoda. Podotrematous female decapods have a pouch or invagination derived from two adjacent thoracic somites, basically a split between the two plates of the intersegmental phragma 7/8, one derived from sternite 7, called a spermatheca (Guinot, 1979; Hartnoll, 1979; Guinot & others, 2013; Schweitzer & others, 2024a). The spermathecae are used for sperm storage but they do not connect directly with the ovaries (McLay

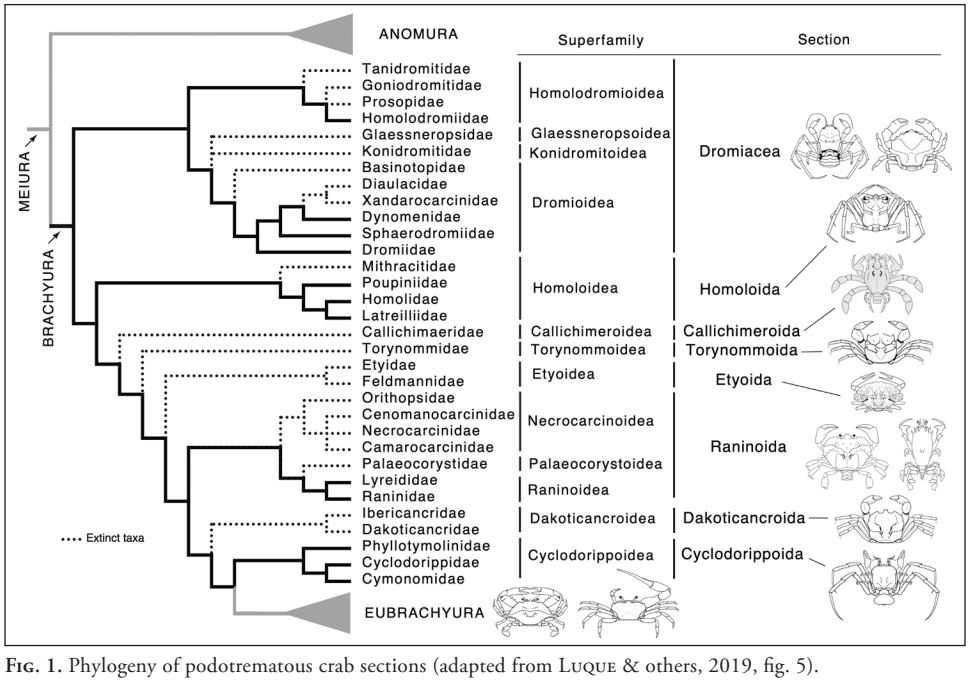

Fig. 1. Phylogeny of podotrematous crab sections (adapted from Luque & others, 2019, fig. 5).

& Becker, 2015). The possession of spermathecae in podotrematous crabs has been shown to most likely be independently derived among podotremes (Schweitzer & others, 2025b). Notably, all female decapods are podotrematous except eubrachyuran crabs, and other decapodan groups possess specialized structures for sperm storage, such as the thelycum of dendrobranch shrimp (Schweitzer & others, 2024a). Spermathecae and thelyca may be examples of independentt and convergent evolution of structures for sperm storage strategies.

GENERAL TRENDS IN PODOTREMATOUS CRAB EVOLUTION

Broad morphological trends

Each podotrematous section exhibits unique adaptations signaling the independent evolution of each lineage; these are discussed under each section. On the other hand, several morphological trends characterize the sections. A somewhat elongate, longer than wide carapace, with deep grooves, characterizes many dromiaceans and homoloidans (Fig. 2). These two sections often possess cervical groove, postcervical groove, and branchiocardiac grooves, similar to many lobsters although not known to be homologous (discussion in Schweitzer & others, 2025c). Although the cervical groove is typically seen in most podotrematous and eubrachyuran crabs, the other two grooves are not present, or in the case of the branchiocardiac groove, are present as concave grooves bounding the urogastric and cardiac regions in eubrachyurans.

Protection for the eyes independently arose several times (Schweitzer & others, 2024a, figs. 117, 118). Homolids and homolodromioids have a "plage orbitaire," or a smooth space for the eye, rather than deep, true orbits (Guinot, 1991; Guinot & Richer de Forges, 1995). Orbits, or deep areas that can hold the eyestalk and cornea, appeared several times among podotrematous crabs and indeed even within superfamilies. Within Homolodromioidea, true orbits occurred in Lecythocaridae and Longodromitidae. "Augenrests," or depressions to accommodate the cornea distinct from the orbit, are known in several dromiacean families, each with different positions and characteristics. These may be considered as early morphological "experiments" in protecting and housing the eyes, and they are discussed within the appropriate taxonomic section.

Most podotrematous crabs have a pleon that is at least partially visible in dorsal view, especially in females. This, as well as the tilted position of the posterior thoracic sternites, may allow positioning of the coxae of the fifth and sometimes fourth pereiopods in a subdorsal position, which may have facilitated the evolution of carrying behaviors for camouflage (Tavares & Franco, 2004; Guinot & Wicksten, 2015). Dakoticancroida are an exception to this pleon position, wherein the pleon is held close to the sternum as in eubrachyurans.

Some podotrematous crabs have very narrow sterna, with poorly developed episternal projections (Schweitzer & others, 2024a, fig. 122). This results in the coxae of the pereiopods being placed close together near the axis. In other sections, such as Torynommoida, Etyoida, Dakoticancroida, and Cyclodorippoida, the sternites are wide, with parallel edges, much more similar in shape and spacing of the bases of the pereiopods to those of eubrachyuran crabs. Callichimaeroida also has exceptionally wide sternites 5 and 6 for a podotrematous crab, yet its sternal configuration is unique among brachyurans (Luque & others, 2019)

A wider than long carapace, superficially convergent with eubrachyuran crabs like Xanthoidea sensu lato, appears many times among the podotrematous clades. Some Dromioidea, Etyoida, Dakoticancroida, and Torynommoida display rectangular or hexagonal, wider than long carapaces. This shape seems to co-occur with a wide sternum.

Overall podotrematous diversity

Podotrematous sections were much more diverse in the past than today (Schweitzer & Feldmann, 2015) (Fig. 5). Podotremes first appeared in the Early to Middle Jurassic (Pliensbachian–Bathonian) (Schweitzer & Feldmann, 2010a) and had radiated considerably by the Late Jurassic (Tithonian) (Schweitzer & others, 2012a) (Fig. 2). The podotremes as an evolutionary grade reached their maximum diversity in the Early Cretaceous (Albian), represented by 60 genera in 22 families, and the Campanian, with 52 genera in 23 families present (Fig. 5). For comparison, lobsters reached peak diversities in the Late Jurassic (Tithonian) when 29 genera in 16 families were present and the Late Cretaceous (Cenomanian) during which 11 families with 26 genera have been recorded (Schweitzer & Feldmann, 2014).

After reaching peaks in the Early and Late Cretaceous, podotreme diversity diminished dramatically during the Paleocene only to peak again in the early Eocene (Ypresian), with 12 families and over 40 genera recorded. Over one-third of the Eocene genera belonged to Raninoida (Fig. 5). After this third diversity peak, podotreme diversity decreased to its current level of about 6% of the Holocene decapod fauna (Schweitzer & Feldmann, 2015). The podotrematous crabs are part of the decapod turnover fauna, replacing the clawed lobsters in highest overall decapod diversity beginning in the Early Cretaceous, only to be replaced themselves by the heterotrematous crabs in the Cenozoic (Schweitzer & Feldmann, 2015).

Podotrematous crabs occupied the highest percentage of the decapod fauna during the Late Cretaceous, when they accounted for between 30%–40% of all known decapods. Their percentage was also rather high in the Late Jurassic and Early Cretaceous, between 20% and 30% of the decapod fauna (Schweitzer & Feldmann, 2015).

Extinction patterns

Podotrematous crabs experienced a sharp decline throughout the Late Cretaceous. Half of the decapod families that became extinct at the end of the Cretaceous were podotremes. A similarly large number of podotreme genera became extinct as well, with Dromiacea, Raninoida, and Homoloida particularly hard hit (Schweitzer & Feldmann, 2023). Podotremes that survived the end-Cretaceous extinction preferentially occurred in the North Atlantic, particularly in European reef habitats (Schweitzer & Feldmann, 2023). However, this paleobiogeographic pattern might be apparent due to the poorly sampled tropics, with new findings starting to challenge these views (Luque & others, 2019). Several possibilities may explain the preferential extinction of podotremes. In podotrematous crabs, the sperm is stored in a secondary opening, called a spermatheca, and fertilization is external, whereas in eubrachyurans, the sperm is inserted directly into the gonopore (McLay, 2019). Thus, their reproductive strategies may be less efficient than those of eubrachyurans (McLay & Becker, 2015; Schweitzer & Feldmann, 2023).

Podotrematous crabs comprise eight of the nine brachyuran sections, and they evolved unique body forms independently several times. The carcinized body form appears to have facilitated radiation of podotremes in the Jurassic and Cretaceous, but the podotrematous condition is apparently outcompeted by the heterotrematous condition, as that group has dominated the entire decapod fauna since the Eocene.

Some podotremes may have been susceptible to environmental or climatic change, suggested by the constriction in range of Raninoida to more tropical regions through the Cenozoic (Hartzell & others, 2022). Some of the podotreme groups that survived the end-Cretaceous extinction shifted environmental preferences. Homoloidans and homolodromioids appear to have migrated to deeper water conditions in the Cenozoic, having been associated with shallow water

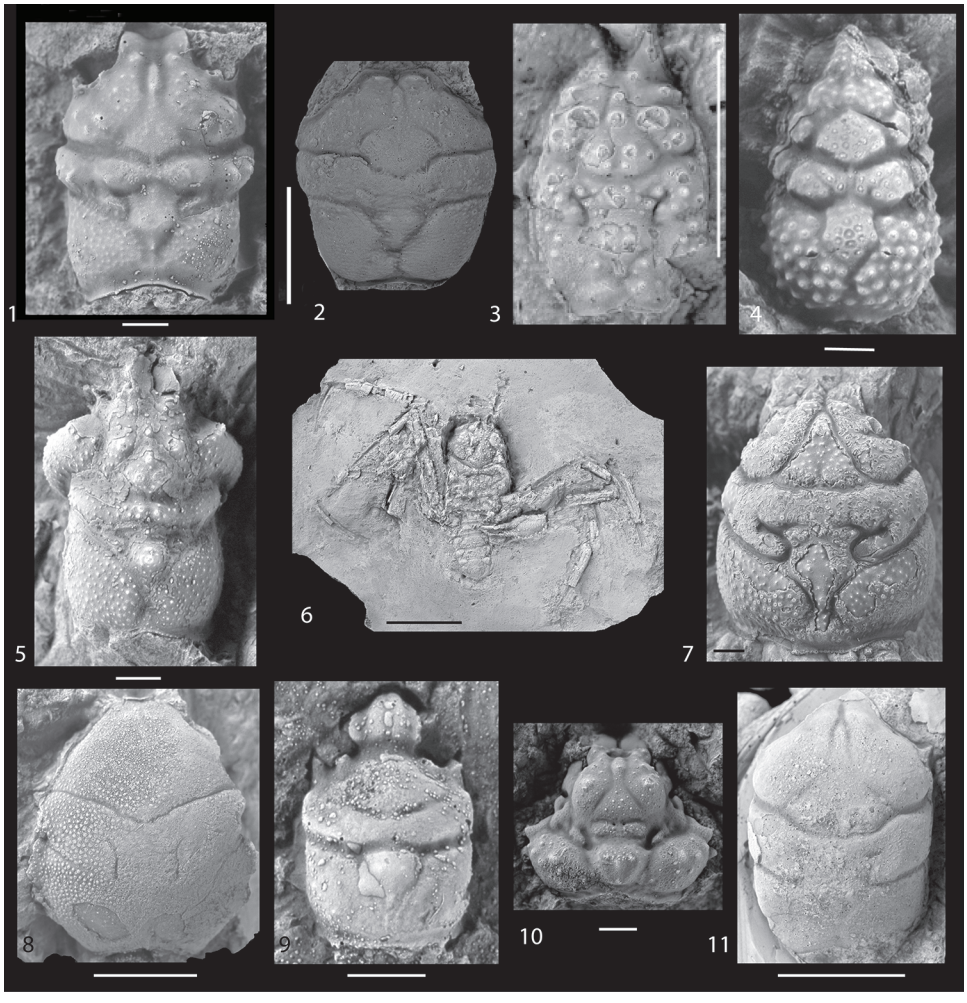

Fig. 2. Representative Jurassic podotrematous crabs. *1, Abyssophthalmus spinosus* (von Meyer, 1842) (Dromiacea, Longodromitidae) (Schweitzer & others, 2012b, fig. 9.1). *2, Goniodromites polyodon* Reuss, 1858 (Dromiacea, Goniodromitidae) (Schweitzer & others, 2012b, fig. 3.1b). *3, Doerflesia ornata* Feldmann & Schweitzer, 2009 (Homoloida, Homolidae) (Feldmann & others, 2012, fig. 1.4). *4, Verrucarcinus torosus* (Von Meyer, 1857) (Dromiacea, Glaessneropsidae) (Schweitzer & others, 2012b, fig. 14.2). *5, Bucculentum bachmayeri* Schweitzer & Feldmann, 2009 (Dromiacea, Bucculentidae) (Schweitzer & others, 2012b, fig. 2.1b). *6, Eoprosopon klugi* Förster, 1986 (Dromiacea, Homolodromioidea) (Schweitzer & others, 2012b, fig. 1.7). *7, Europrosopon aculeatum* (Von Meyer, 1857) (Dromiacea, Prosopidae) (Schweitzer & Feldmann, 2024, fig. 2.2). *8, Konidromites gibbus* (Reuss, 1858) (Dromiacea, Konidromitidae) (Schweitzer & others, 2012b, fig. 1a). *9, Glaessneropsis heraldica* (Patrulius, 1959) (Dromiacea, Glaessneropsidae) (Schweitzer & others, 2012b, fig. 13.1a). *10, Lecythocaris paradoxa* (Von Meyer, 1858) (Dromiacea, Lecythocaridae) (Schweitzer & Feldmann, 2009, fig. 6.4). *11, Tanidromites richardsoni* (Woodward, 1907) (Dromiacea, Tanidromitidae) (Schweitzer & others, 2012b, fig. 11.1c). Scale bars 1, 4, 5, 9, 10 = 1 mm. Scale bar 8 = 5 mm. Scale bars 2, 3, 6, 7, 11 = 1 cm.

environments, including coral reefs in the Jurassic and Cretaceous (Schweitzer & others, 2004).

Those podotreme clades that survived the extinction generally exhibit specializations, either for carrying camouflage or burying (Schweitzer & Feldmann, 2023). Almost all extant raninoids have a streamlined body adapted for burying (Hartzell & others, 2022). Many extant homoloidans and most extant dromiaceans exhibit carrying behavior for camouflage (Guinot & Wicksten,

2015). Cyclodorippoidans either burrow or carry camouflage (Guinot & Wicksten, 2015). Those more generalist podotremes appear to have experienced higher end-Cretaceous and early Cenozoic extinctions

A pattern that requires further investigation is the apparent convergent carapace morphology among extinct podotremes and heterotrematous clades that preferentially survived (Schweitzer & Feldmann, 2023). The apparently convergent carapace features should be quantified and analyzed. For example, the convergence in dorsal carapace morphology between Dynomenidae and Xanthidae has long been observed (Wright & Collins, 1972; Glaessner, 1980; McLay, 1999). Analyzing environmental preferences would also be necessary here, to determine if convergent morphologies replaced one another in similar environments.

Faunal turnover within podotrematous Brachyura

By section.—Dromiacea appeared first within Brachyura and has maintained a marine presence since the Early Jurassic (Schweitzer & others, 2012b; Luque & others, 2019, 2021) (Fig. 6). Dromiacea achieved highest generic diversity in the Tithonian and Albian, with a secondary peak in the Eocene (Ypresian). Dromiacea comprised most families of podotrematous crabs until the late Early Cretaceous, when Raninoida approached the generic diversity and then eclipsed that of Dromiacea beginning in the Late Cretaceous (Fig. 5). So, Dromiacea and Raninoida exhibited successive turnovers in terms of diversity. Their high diversity in terms of numbers of genera as well as disparity in body form may have made them broadly adapted to maintain a strong presence in modern oceans. Homoloida is a consistent component of the podotrematous brachyuran groups, with peaks in the Albian and Maastrichtian, but otherwise maintaining a consistent generic diversity since its appearance in the Tithonian and into the present. Etyoida, Dakoticancroida, Torynommoida, and Callichimaeroida composed the Cretaceous podotrematous crabs, with only Etyoida persisting into the Eocene. Cyclodorippoida radiated latest of all of the podotrematous groups, with a diversity peak in the Eocene, and is still present in modern oceans. The Late Cretaceous was the most diverse time in terms of sections, with all present in the Late Cretaceous.

By superfamily.—The largest podotrematous sections include superfamilies that, within their embraced families, demonstrate successive faunal turnover. Homolodromioidea embraces six families and dominated the early podotrematous fauna until the late Early Cretaceous (Aptian). Also occurring early and forming a dominant component of the early podotreme fauna was the Glaessneropsoidea, consisting of four families. These two dromiacean superfamilies comprise the Jurassic Fauna; only three Jurassic brachyuran genera do not belong to those two superfamilies. Within Dromiacea, these two superfamilies yielded in diversity to Dromioidea in the Cenozoic. Diversity patterns in Raninoida also show successive turnover in superfamilies. In the Cretaceous, Palaeocorystoidea and Necrocarcinoidea dominated the fauna, to be replaced by Raninoidea in the Cenozoic.

The Cretaceous was a time of high diversity for the podotrematous crabs. Dominating the fauna during the Cretaceous were homolodromioids, which exhibited a long diversity tail from the Jurassic into the Cretaceous and Cenozoic. Necrocarcinoidea and the related raninoidan Palaeocorystidae, together with Etyoida, Dakoticancroida, and the minor group Torynommoida, round out the podotreme Cretaceous Fauna. To date, Callichimaeroida sensu stricto remains monotypic and restricted to the early Late Cretaceous (Luque & others, 2019). Nearly every podotrematous family present today originated during the Cretaceous, exceptions being Homolodromiidae and Homolidae (Jurassic) and Cymonomidae (Eocene).

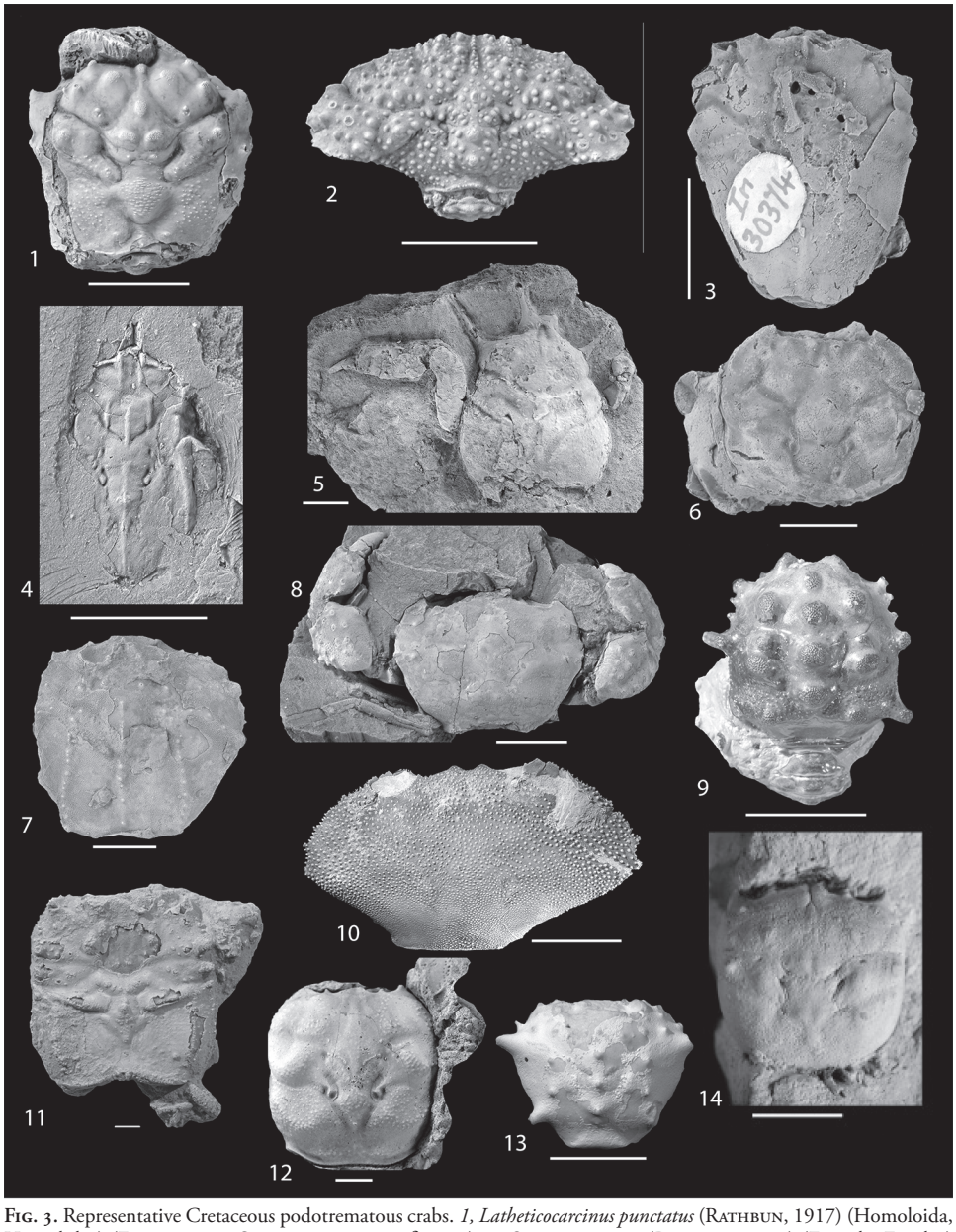

Fig. 3. Representative Cretaceous podotrematous crabs. *1, Latheticocarcinus punctatus* (Rathbun, 1917) (Homoloida, Homolidae) (Feldmann & Schweitzer, 2015, fig. 3.1). *2, Steorrosia aspera* (Rathbun, 1935) (Etyoida, Etyidae) (Schweitzer & others, fig. 2.4a). *3, Joeranina broderipi* (Mantell, 1844) (Raninoida, Palaeocorystidae) (Schweitzer & others, 2018, fig. 9.2a). *4, Callichimaera perplexa* Luque & others, 2019 (Callichimaeroida, Callichimaeridae) (Luque & others, 2023, fig. 1a). *5, Rhinopoupinia bicornis* Feldmann, Tshudy & Thomson, 1993 (Homoloida, Poupiniidae) (Feldmann & others, 2012, fig. 5). *6, Dakoticancer overanus* Rathbun, 1917 (Dakoticancroida, Dakoticancridae) (Feldmann & others, 2017, fig. 1.1a). *7, Cenomanocarcinus vanstraeleni* Stenzel, 1945 (Raninoida, Cenomanocarcinidae) (Schweitzer & others, 2018, fig. 3.1a). *8, Xandarocarcinus sternbergi* (Rathbun, 1926) (Dromiacea, Xandarocarcinidae) (Schweitzer & others, 2012b, fig. 23.1a). *9, Kierionopsis nodosa* Davidson, 1966 (Dromiacea, Dynomenidae) (Schweitzer & others, 2012b, fig. 21.3a). *10, Feldmannia wintoni* (Rathbun, 1935) (Etyoida, Feldmanniidae) (Schweitzer & others, 2017c, fig. 3.4a). *11, Quadratoplanus primitivus* Franţescu, 2014) (Cyclodorippoida, Quadratoplanidae) (Schweitzer & others, 2017b, fig. 3a).

Fig. 3 Caption is continued on the top of the next page . . .

12, Tetracarcinus subquadratus Weller, 1905 (Dakoticancroida, Dakoticancridae) (Schweitzer & others, 2025a, fig. 1.2). *13, Arcticocarcinus insignis* (Segerberg, 1900) (Raninoida, Necrocarcinidae) (Schweitzer & others, 2018, fig. 4.2). *14, Torynomma quadrata* Woods, 1953 (Torynommoida, Torynommidae) (Schweitzer & others, 2017a, fig. 1.1). Scale bars 10, 12 = 5 mm. Scale bar 11 = 1 mm. All others = 1 cm.

By family.—Jurassic brachyuran faunas are dominated by Goniodromitidae, Prosopidae, and Longodromitidae. Goniodromitidae [Dromiacea] dominated until the Late Cretaceous, when Lyreididae and Raninidae [Raninoida] and Dromiidae [Dromiacea] became the most abundant and diverse families. Other key Cretaceous families include Dakoticancridae, Etyidae, Feldmanniidae, and all of the extinct Raninoida families.

Some families were long ranging but never diverse, such as Konidromitidae with never more than two genera per stage but ranging from Oxfordian to Campanian. Similar long ranging but low diversity families (never more than two genera per stage) are Tanidromitidae (Bajocian–Valanginian) and Glaessneropsidae (Toarcian–Maastrichtian).

Except for the monotypic Callichimaeroida, each section of podotrematous crab is characterized by both short and long ranging families (Fig. 6). Forms appeared and evolved at varying rates, with some lineages becoming extinct quickly. The Late Jurassic was clearly a time of rapid appearance and extinction, with four short-lived families appearing then (Lecythocaridae, Nodoprosopidae, Jurellanidae, Tithonohomolidae). Late Cretaceous time also saw rapid appearance and extinction, with five short-lived families then (Callichimaeridae, Dakoticancridae, Xandarocarcinidae, Camarocarcinidae, Ibericancridae). These short-lived families often originated at about the same time as other families within their superfamily. Thus, the Late Jurassic and Late Cretaceous were times of rapid evolution and body plan experimentation in podotremes.

Late Jurassic radiation has been tied to reef development (Klompmaker & others, 2013). The presence of reefs seems to have facilitated the radiation of podotrematous crabs, especially in the Jurassic. Comparison of habitats for podotremes compared to clawed lobsters, for example, shows that in the Jurassic, podotremes inhabited coral environments in high numbers, whereas lobsters did not (Schweitzer & Feldmann, 2015). Of other decapod groups, other than eubrachyurans, only anomurans inhabited coral reefs in any substantial numbers across the fossil record (Schweitzer & Feldmann, 2015).

SYSTEMATIC ACCOUNTS

DROMIACEA

Overview

The earliest brachyurans, based on the known fossil record, are Dromiacea. The group originated during the Early Jurassic (Pliensbachian) and diversified extensively in the Late Jurassic, late Early Cretaceous, Late Cretaceous, and early Eocene (Fig. 5). Nearly all of the earliest occurring podotreme families known are dromiacean, but note that families appeared over the course of 180 million years, and four are extant. This suggests broad adaptability as a trend in the evolution of the section but paralleled by specialization, with some very short ranging families interspersed with the long ranging ones. Family diversity exhibited faunal turnover, with different families diversifying at different times and potentially being replaced in various habitats. Jurassic dromiaceans were primarily reef dwellers, but most of those families were either extinct by the mid-Cretaceous or had moved into siliciclastic environments. Dromioidea were the primary reef-associated dromiaceans during post-Cretaceous time.

Dromiacea, as construed in this volume, has been found to be monophyletic in two large analyses, including extinct and extant forms (Karasawa & others, 2011; Luque & others, 2019), and is composed of mostly extinct families and genera. Of the 18 families, 14 are extinct, and of the 138 genera, 89 are extinct (Table 1).

Table 1. Dromiacea superfamilies and constituent families, age ranges, and number of genera extinct and extant. Systematics of Dromiacea are found in Schweitzer & others (2012b) and Schweitzer & Feldmann (2024).

Taxon	Range	Extinct (†), Extant only (*), and Both
Homolodromioidea Alcock, 1900a		
Homolodromiidae Alcock, 1900a	Lower Jurassic (Pliensbachian)–Holocene	6†; 1*, 1
Bucculentidae Schweitzer & Feldmann, 2009	Oxfordian–Cenomanian	2†
Goniodromitidae Beurlen, 1932	Oxfordian–Ypresian	16†
Prosopidae Von Meyer, 1860	Bathonian–Albian	8†
Tanidromitidae Schweitzer & Feldmann, 2008	Bajocian–Hauterivian	2†
Longodromitidae Schweitzer & Feldmann, 2009	Bajocian–Eocene	15†
Jurellanidae Klompmaker & Robins in Robins & Klompmaker, 2019	Tithonian	2†
Glaessneropsoidea Patrulius, 1959	Oxfordian–Maastrichtian	
Glaessneropsidae Patrulius, 1959	Oxfordian–Maastrichtian	8†
Lecythocaridae Schweitzer & Feldmann, 2009	Oxfordian–Tithonian	2†
Nodoprosopidae Schweitzer & Feldmann, 2009	Kimmeridgian–Tithonian	1†
Viaiidae Artal & others, 2012	Albian–Cenomanian	4†
Konidromitoidea Schweitzer & Feldmann, 2010b	Oxfordian–Campanian	
Konidromitidae Schweitzer & Feldmann, 2010b	Oxfordian–Campanian	2†
Dromioidea De Haan, 1833	Aptian–Holocene	
Basinotopidae Karasawa & others, 2011	Ypresian–Serravallian	4†
Dromiidae De Haan, 1833	Aptian–Holocene	6†, 33*, 6
Sphaerodromiidae Guinot & Tavares, 2003	Campanian–Holocene	3†, 3*, 0
Dynomenidae Ortmann, 1892	Albian–Holocene	5†, 1*, 4
Diaulacidae Wright & Collins, 1972	Albian–Eocene	1†
Xandarocarcinidae Karasawa & others, 2011	Upper Cretaceous (Santonian–Maastrichtian)	2†

Dromiaceans are characterized by a generally longer than wide or an as long as wide carapace with some exceptions; orbits often with an augenrest, a secondary concavity to house the eyeball; well-defined cervical, postcervical, and branchiocardiac grooves; subhepatic regions; pereiopod 5 reduced and usually subdorsal as well as commonly pereiopod 4. Because it is such a large group, morphology varies but usually these features obtain. For specific defining characters for each family, please consult Schweitzer &

others (2012b), Schweitzer & Feldmann (2024), and Table 1, which includes superfamilies and constituent families, numbers of genera, and their geologic ranges.

Homolodromioidea

Homolodromioidea is composed of seven families, all of which are extinct except Homolodromiidae (Table 1). The superfamily originated in the Early Jurassic, peaking in both diversity and numbers of genera in the Tithonian. Many of the individual families are found preferentially in carbonate environments; those with the longest ranges generally inhabited a broader range of environments. Constituent families experienced extinction by the end of the Jurassic in a first wave and in the Cretaceous in a second wave.

Among homolodromioids, an array of structures arose to house the eye. A depression to house the eyestalk and cornea is absent in Homolodromiidae, whereas other families have orbits to house these structures or orbits plus an augenrest to protect the eye.

Goniodromitidae.—Goniodromitidae first appeared in the Middle Jurassic (Bathonian), and peaked in diversity during the Late Jurassic (Tithonian) (Fig. 2.2). Several of the constituent genera are quite speciose, with more than five species. Almost all occurrences are in carbonates, either coral reef, sponge reef, or nonframework carbonates. The sole instance in which pereiopods are known to be preserved shows that pereiopod 5 was small and carried subdorsally (Feldmann & others, 2016). Goniodromitidae is typified by an augenrest that lies directly adjacent to the orbit and is separated from it by a transverse ridge. The group shifted its preference to mixed and low energy siliciclastics in the Late Cretaceous. Although most species within the family occurred in Europe, the group is also known from east coastal North and South America, West Coastal North America, Gulf Coastal North America and Caribbean, Japan, and Antarctica. The family survived into the early Eocene in Italy, a known refuge for reef carbonate dwellers (Artal & others, 2022; Schweitzer & Feldmann, 2023). Its long geologic range may be attributed to its broad geographic range and apparent ability to move into different habitats as documented by rock type.

Prosopidae.—Prosopidae had a similar early history to Goniodromitidae, appearing in the Middle Jurassic (Bathonian) but becoming extinct earlier in the Late Cretaceous (Cenomanian) (Fig. 2.7). Prosopids exhibit an unusual morphology for protecting the eye in which the augenrest is formed between an inflated suborbital and supraorbital swelling, not contiguous with the position from which the eyestalk extends. Its occurrences are predominantly in coral limestone with many fossils found in high energy siliciclastics, suggesting that in general, this group favored higher energy environments overall. Almost all of the occurrences are European, with one exception from Japan.

Tanidromitidae, Bucculentidae, Jurellanidae.—Tanidromitidae exhibited very restricted environmental preferences, essentially only carbonate settings, usually associated with sponges and algae or bedded limestones (Schweitzer & Feldmann, 2008; Starzyk, 2016). Their shallow augenrests, a concave depression adjacent to the orbit, would not have afforded much protection for the eyes, and their large branchial regions may have been an adaptation to low oxygen levels (Schweitzer & Feldmann, 2008) (Fig. 2.11). In addition, only one species was found outside of Europe, in east Africa (Tanzania). The geologic range of the family extended from the Middle Jurassic (Bajocian) to the Early Cretaceous (Hauterivian).

Bucculentidae have very unusual morphological aspects. One is an augenrest placed dorsally on the hepatic region of the carapace (Fig. 2.5). It is a concave, smooth depression bounded by tiny spines, proposed to be the location of placement of the cornea

(Schweitzer & Feldmann, 2009). In addition, members of the family have an extremely laterally inflated hepatic region, possibly an adaptation for feeding (Schweitzer & Feldmann, 2009). Perhaps because of this unusual morphology, the family is known from only two genera and was geographically restricted, occurring only in Europe, from the Late Jurassic (Oxfordian) through Late Cretaceous (Cenomanian). Jurellanidae are smooth crabs, with simple ornamentation, and have a carapace morphology convergent with the anomuran group Porcellanidae. Jurellanidae is very restricted in time and place, known only from Tithonian rocks of central and Eastern Europe.

Longodromitidae.— Longodromitidae have true orbits, a single, deeply excavated depression to house the eyes (Fig. 2.1). This family exhibits one of the broadest ranges of environmental preferences of the entire Dromiacea, was nearly cosmopolitan in occurrences, and had one of the longest geologic ranges. Longodromitids are known from carbonate and siliciclastic settings of all types and ranged from the Middle Jurassic (Bathonian) to the early Eocene (Ypresian). Unlike other families, occurrences in siliciclastic and carbonate settings are common among members of Longodromitidae, and perhaps this apparent eurytypic adaptation contributed to the long range of the family. Although its geographic occurrences are broad as a family, genera exhibit restricted geographic ranges. Some genera are known only from Europe, whereas others occurred in Antarctica, Australia, Russia, or Japan. A few genera were restricted to North America.

Homolodromiidae.—This family has a limited but long fossil record, originating in the Early Jurassic (Pliensbachian) but represented by only two extant genera (Fig. 4.7). It has been recovered from a variety of settings, including siliciclastic and carbonate; however, Cretaceous and Cenozoic occurrences are all siliciclastic. Its geographic occurrences are antitropical, in Northern Europe and North America and Antarctica and New Zealand. Extant members inhabit outer shelf and slope habitats. Carrying behavior has been observed only a few times, and in each case, the animal carried a glass sponge on the dorsal carapace, fitted to it in a similar manner to that of dromiids (Ng & Naruse, 2007). The family originated in the Jurassic, a time of sponge and coral reefs, and the related Jurassic Goniodromitidae are known to have subdorsal pereiopods 5. This is suggestive of the carrying habit being ancient, but no actual fossil evidence is available to demonstrate that Homolodromiidae have always been carriers of camouflage.

Glaessneropsoidea

This superfamily is composed of four constituent families, all of which contain between one and four genera. Nearly all inhabited carbonates.

Glaessneropsidae.—This is the most speciose and generically rich family in the group, ranging from the Late Jurassic (Oxfordian) to the Late Cretaceous (Maastrichtian). Like other dromiaceans, most occurrences are European, with exceptions in Russia and the Western Interior Seaway and Gulf Coastal North America. With their oldest fossils known from reef carbonate facies, Glaessneropsidae shifted into siliciclastic settings in the Late Cretaceous (Campanian-Maastrichtian).

Glaessneropsidae had true orbits (Fig. 2.4, 2.9). Notable among them is preservation of eyes in *Ekalakia* Bishop, 1976. The eyes are extremely large compared with the size of the orbits, such that the eyes were not completely protected. This was proposed to be an adaptation to low light levels in cryptic, offshore settings (Feldmann & others, 2008).

Lecythocaridae and Nodoprosopidae.—These small families have only European, Late Jurassic occurrences in carbonates. Each have highly ornamented, nodose carapaces that may have been specialized for reef

carbonate environments. Lecythocaridae are typified by well-developed, small orbits that are directed forward, in addition to the complex carapace, all of which suggested adaptation to benthic, perhaps cryptic, lifestyles in reefs (Schweitzer & Feldmann, 2009) (Fig. 2.10). Nodoprosopidae have very long rostral spines, which are distinctive and diagnostic for the family.

Viaiidae.—These unusual forms have a deep excavation on the lateral margin that is ovate and lies posterior to the orbit, at about the position of the intersection of the cervical groove with the lateral margin. It is a diagnostic feature, but no functions have yet been proposed. All taxa are known from European carbonates of Cretaceous age, suggesting that like Lecythocaridae and Nodoprosopidae, they were quite specialized for a reef environment.

Konidromitoidea

Konidromitoidea embraces only the nominal family and two genera. Despite its low diversity, taxa are known from both Late Jurassic and Early Cretaceous coral limestones of Europe and Late Cretaceous siliciclastics of the Western Interior Seaway. The distinct, ovate shape and corrugated lateral margins with depressions to accommodate the pereiopods diagnose the family (Schweitzer & Feldmann, 2010b) (Fig. 2.8).

Dromioidea

The oldest fossil record of Dromioidea is much younger than that of Homolodromioidea, in the late Early Cretaceous (Fig. 6). The comprising families never reached the generic or species level diversity of some homolodromioid families, but this could be due to faunal turnover patterns beginning in the Late Cretaceous that favored survival and radiation of eubrachyuran crabs (Schweitzer & Feldmann, 2015, 2023) (Fig. 5). Peak family and generic diversity, prior to the Holocene, occurred in the Eocene. Unlike Homolodromioidea, which are preferentially found in carbonates, two of the extinct families, Diaulacidae and Xandarocarcinidae, inhabited primarily siliciclastic habitats, whereas Basinotopidae was associated with carbonates and volcaniclastics. Extant groups inhabit siliciclastic, carbonate, or both types of environments.

Phylogeny of Dromioidea.—Phylogenetic analyses based on morphology indicate that among Dromioidea, Basinotopidae is sister to a clade formed by the remaining dromioid families. Dromiidae is basal and sister to the remaining families (Fig. 1). Sphaerodromiidae is then basal and sister to a clade with Dynomenidae, and the extinct Xandarocarcinidae and Diaulacidae (Karasawa & others, 2011; Luque & others, 2019). In molecular phylogenies, Dynomenidae has been recovered either as sister to Dromiidae or derived from Dromiidae (Ahyong & others 2007; Wolfe & others, 2024), a hypothesis followed by other taxonomic studies (Guinot, 2008; Poore & Ahyong, 2023; Luque & others, 2024). Sphaerodromiidae has been recovered as sister to a clade containing both Dromiidae and Dynomenidae, although taxon sampling was not high for these families (Wolfe & others, 2024), or as sister to Dynomenidae, more derived than Dromiidae (Luque & others, 2021). The fossil record and timing of appearance of each family tell a different story. Basinotopidae first appeared in the fossil record in the early Eocene, yet it is recovered as most basal phylogenetically (Fig. 1). Sphaerodromiidae has been hypothesized as being a basal group in Dromioidea, but it is known from younger fossils than either Dromiidae or Dynomenidae, in the Late Cretaceous. Both Dromiidae and Dynomenidae have first occurrences in the Early Cretaceous, with Dynomenidae earlier (Barremian vs. Aptian), suggesting that the lineages are both basal in Dromioidea. Clearly, more work is needed on these groups, both genetically and morphologically, to resolve these issues.

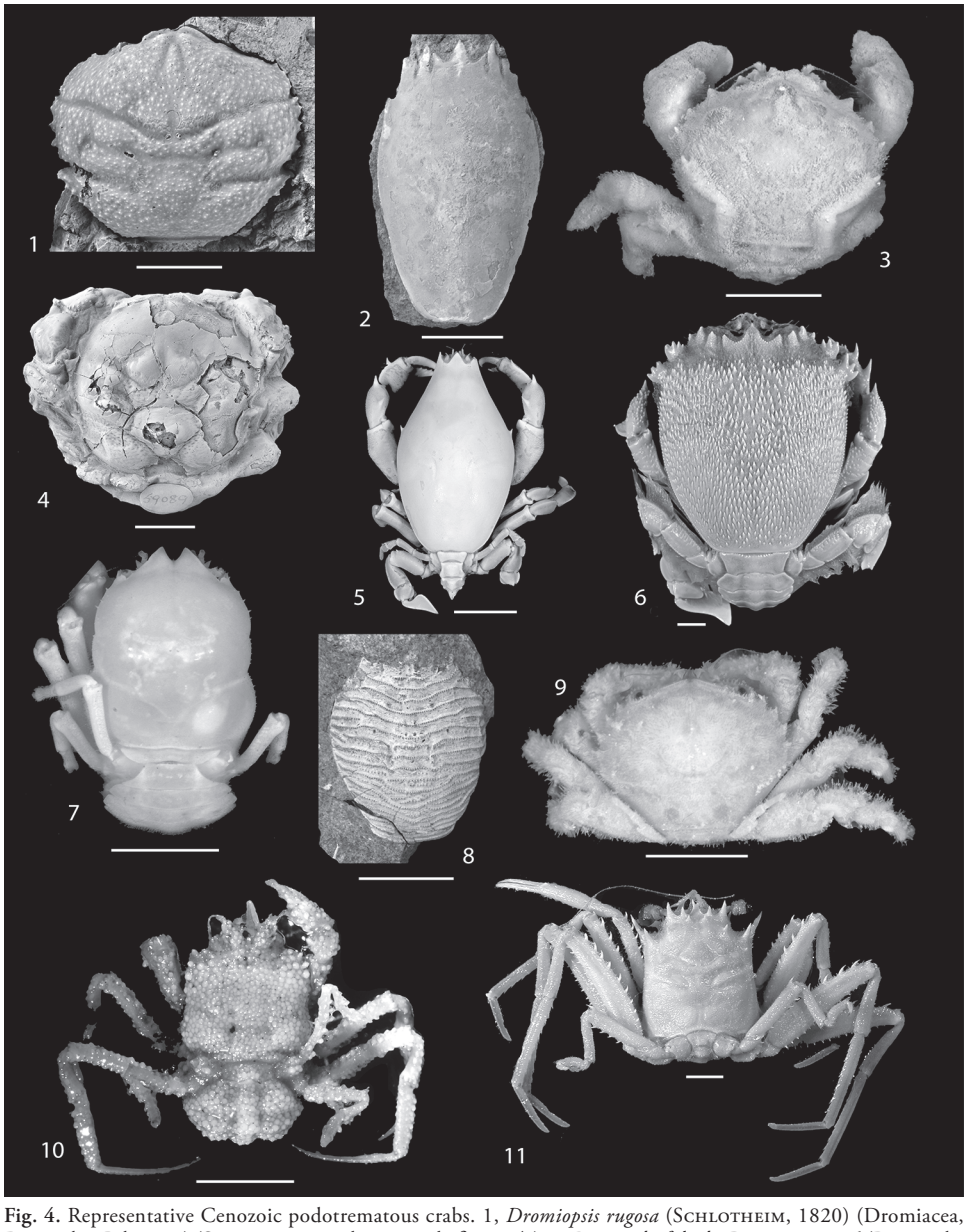

Fig. 4. Representative Cenozoic podotrematous crabs. 1, *Dromiopsis rugosa* (Schlotheim, 1820) (Dromiacea, Dromiidae, Paleocene) (Schweitzer & others, 2012b, fig. 19.4a). 2, *Raninoides fulgidus* Rathbun, 1926 (Raninoida, Raninidae, Eocene) (Schweitzer & others, 2018, fig. 18.1a). 3, *Dromia personata* (Linnaeus, 1758) (Dromiacea, Dromiidae, Holocene) (Schweitzer & others, 2012b, fig. 19.1a). 4, *Dromilites bucklandi* H. Milne Edwards, 1837 [in 1834-1840] (Dromiacea, Sphaerodromiidae, Eocene) (Schweitzer & Feldmann, 2010c, fig. 2A). 5, *Lyreidus tridentatus* De Haan, 1841 (Raninoida, Lyreididae, Holocene) (Schweitzer & others, 2018, fig. 10.2a). 6, *Ranina ranina* (Linnaeus, 1758) (Raninoida, Raninidae, Holocene) (Feldmann & Schweitzer, 2007, fig. 1C). 7, *Dicranodromia ovata* A. Milne-Edwards, 1880 (Dromiacea, Homolodromiidae, Holocene) (Schweitzer & others, 2012b, fig. 6.3a). 8, *Lophoranina bittneri* (Lőrenthey, 1902) (Raninoida, Raninidae, Eocene) (Schweitzer & others, 2018, fig. 17.2). 9, *Dynomene hispida* (Latreille, 1812) (Dromiacea, Dynomenidae, Holocene) (Schweitzer & others, 2012b, fig. 21.1a). 10, *Cymonomus curvirostris* Sakai, 1965 (Cyclodorippoida, Cymonomidae, Holocene) (Schweitzer & others, 2017b, fig. 2.1a). 11, *Homola ranunculus* Guinot & Richer de Forges, 1995 (Homoloida, Homolidae, Holocene) (Feldmann & others, 2012, fig. 1.1a). Scale bar 10 = 3 mm. All other scales = 1 cm.

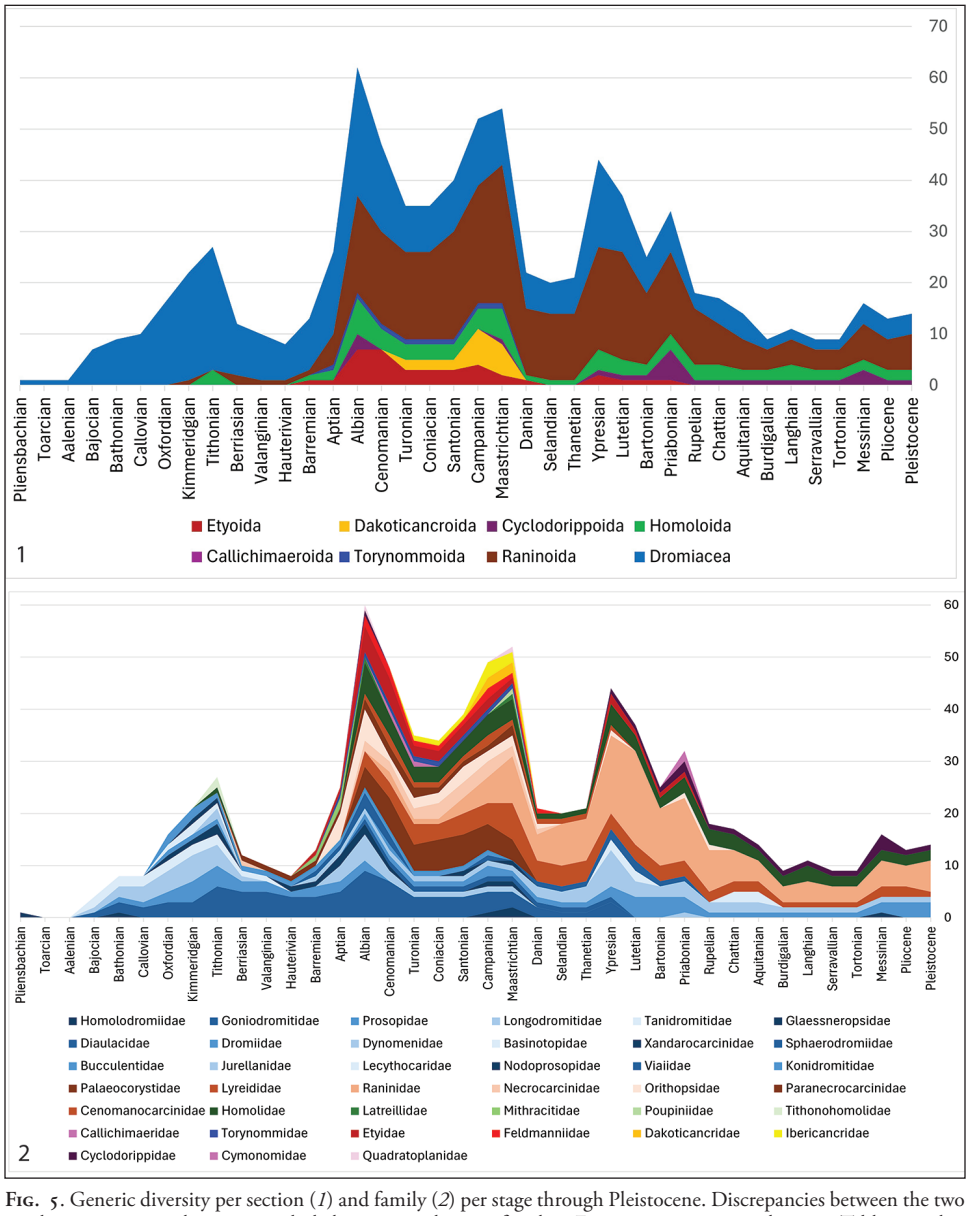

Fig. 5. Generic diversity per section (*1*) and family (*2*) per stage through Pleistocene. Discrepancies between the two are due to incertae sedis genera included in sections but not families. For extant generic numbers, see Tables 1 and 2.

Dromiidae.—Dromiidae is first recorded from the Early Cretaceous (Fig. 6) and is typified by carapaces that are about as wide as long with exceptions and with variable ornamentation (Fig. 4.1, 4.3). Like other extant families, members inhabited an array of environments through time of both siliciclastic and carbonate types. Most occurrences are in Europe, with some in North America and Neogene fossils from Japan. Extant taxa, for which at least 41 genera are known (Decanet, 2025), usually inhabit tropical to subtropical environments in subtidal to outer shelf environments.

Dromiidae are notable in possessing pereiopods 4 and 5 held subdorsally and

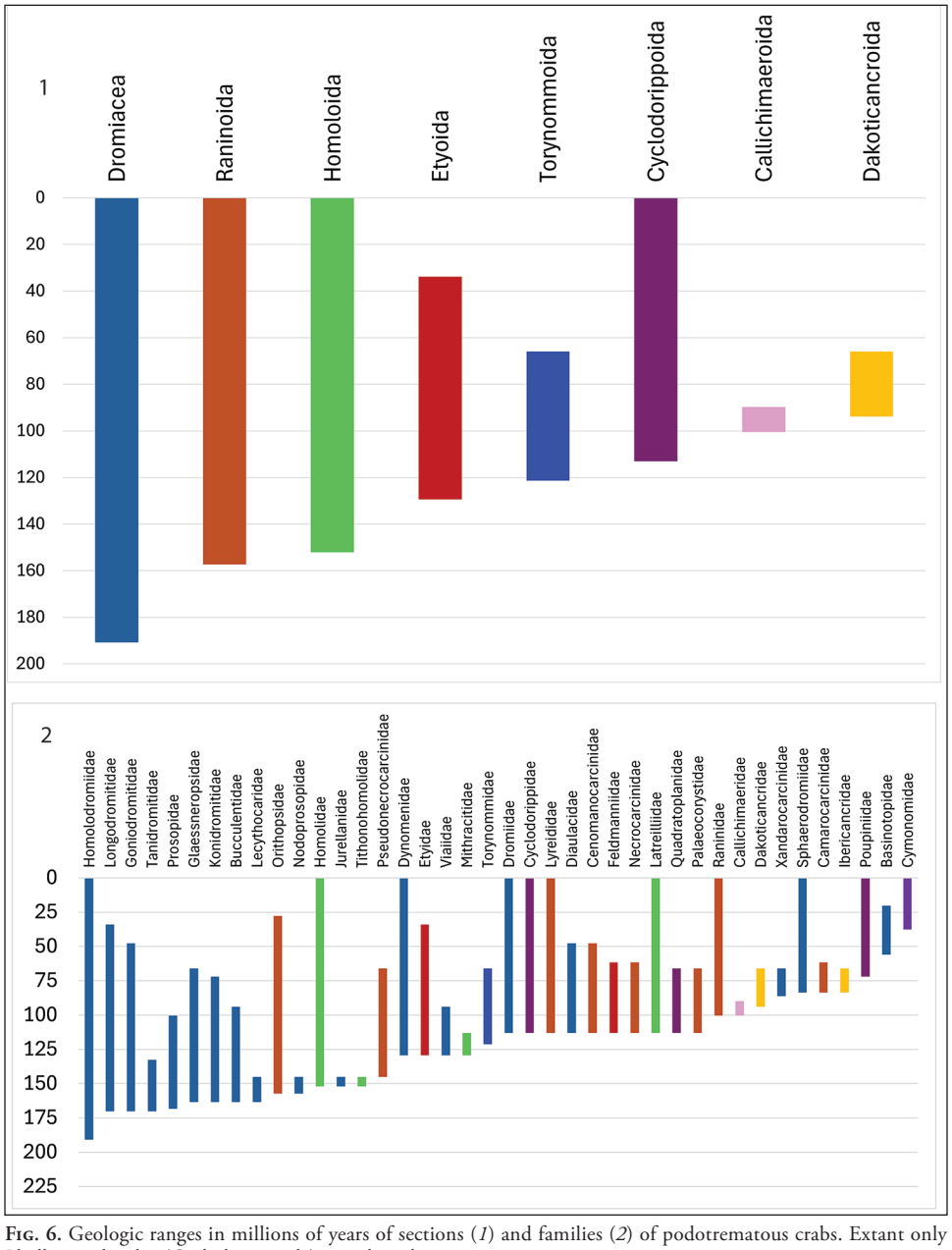

Fig. 6. Geologic ranges in millions of years of sections (*1*) and families (*2*) of podotrematous crabs. Extant only Phyllotymolinidae (Cyclodorippoida) not plotted.

modified with chelae or subchelae to carry objects on their dorsal carapace for camouflage (Fig. 4.3, Fig. 7.3, arrows). Most are known to carry sponges, ascidians, anemones, or pelecypods (Rathbun, 1937; Sakai, 1976; Williams, 1984; McLay, 1993) (Fig. 7.1, 7.3-7.7). Sakai (1976) reported taxa collected from a range of substrates, including siliciclastics of all sizes, with many on rocky bottoms. Studies show that some species of dromiid inhabit sponge substrates, using the same sponge species to create caps

that they hold for camouflage (McLay, 1983). Dromiids may even be responsible for distribution and dispersal of species of sponges or ascidians they carry and discard (McLay, 1983). Overall, higher energy environments seem to be preferred, with an abundance of rocky substrates and crushed shell sea floors reported for dromiids. Fossil dromiids are common in coral and carbonate environments; thus, the association with sponges or other organisms may be ancient. Only one fossil dromiid has been reported associated with camouflage, a bivalve shell (Robin & others, 2017). However, because the crabs carry their cap with the pereiopods, it is likely that the cap is lost soon after death of the organism so that an association in the fossil record is not likely.

Dynomenidae.—Dynomenidae first occurred in the Early Cretaceous (Barremian), earlier than the first dromiids (Albian), and have maintained low, but consistent, diversity through time. They have inhabited primarily carbonate and coral reef habitats since their appearance. The five known extant genera inhabit tropical reef environments (Sakai, 1976; Poore, 2004). There are no records of Dynomenidae as carriers of camouflage in the biological literature. In fact, the fifth pereiopod in the group is reduced and often the articles are fused, so that in males it bears the gonopores and otherwise may be vestigial (McLay, 1999) (Fig. 4.9).

Referral of extinct genera to Dynomenidae has varied considerably. Many of the genera considered by Glaessner (1969) and McLay (1999) to belong to the family have been moved to Goniodromitidae or Dromiidae (Schweitzer & others, 2012a). Those extinct taxa currently referred to the family are most similar to *Dynomene* Desmarest, 1823, and *Metadynomene* McLay, 1999, or to *Acanthodromia* A. Milne-Edwards, 1880. McLay (1999) considered their small carapace size to be a feature of the family, but that remains to be defined (what is small?) and tested.

The reduced fifth pereiopod cannot be used for carrying, and this may be a secondary loss, with ancestral forms retaining the carrying habit (Poore & Ahyong, 2023) (Fig. 7.2, arrows). Tiny fifth pereiopods are known in fossil dynomenids from at least the early Late Cretaceous (Cenomanian), so the feature appeared early in their fossil record (Van Bakel & others, 2012a).

Extant dynomenids inhabit both dead and live corals or rocky or sandy bottoms, ranging down to about 500 m (McLay, 1999; Poore & Ahyong, 2023). Dromiids inhabit a similar range of environments, whereas homolodromiids and homolids generally inhabit deeper water of the continental slopes (McLay, 1999). It was proposed that all of these groups originated from a deep-water ancestor because Homolodromiidae is the most ancient lineage in the group and inhabits deep water in modern environments (McLay, 1993). However, early homolodromiids are found in sediments, suggesting shallow environments, including coral reefs, as are Homolidae, so it is more likely that the radiation into deeper water happened later in all three families (Schweitzer & others, 2004).

Dynomenid crabs are rather restricted biogeographically in modern oceans (OBIS, 2024). They are most abundant in the Indo-Pacific and central Pacific, with a few Central American and Caribbean and Indian Ocean occurrences. Fossil dynomenids, like most dromiaceans, are primarily reported from Europe but with a significant number from Gulf Coastal and Caribbean North America (Fig. 3.9), as well as Neogene Pacific occurrences in Fiji and Japan. The Indo-Pacific occurrences may stem from ancestral Tethyan forms.

Sphaerodromiidae.—This is a small family, composed of only three extinct and three extant genera (Fig. 4.4). Members of the three extant genera inhabit shelly, sandy, or muddy substrates in middle to outer shelf environments, and some carry ascidians or sponges (Sakai, 1976; McLay, 1993; Guinot & Tavares, 2003). Extinct

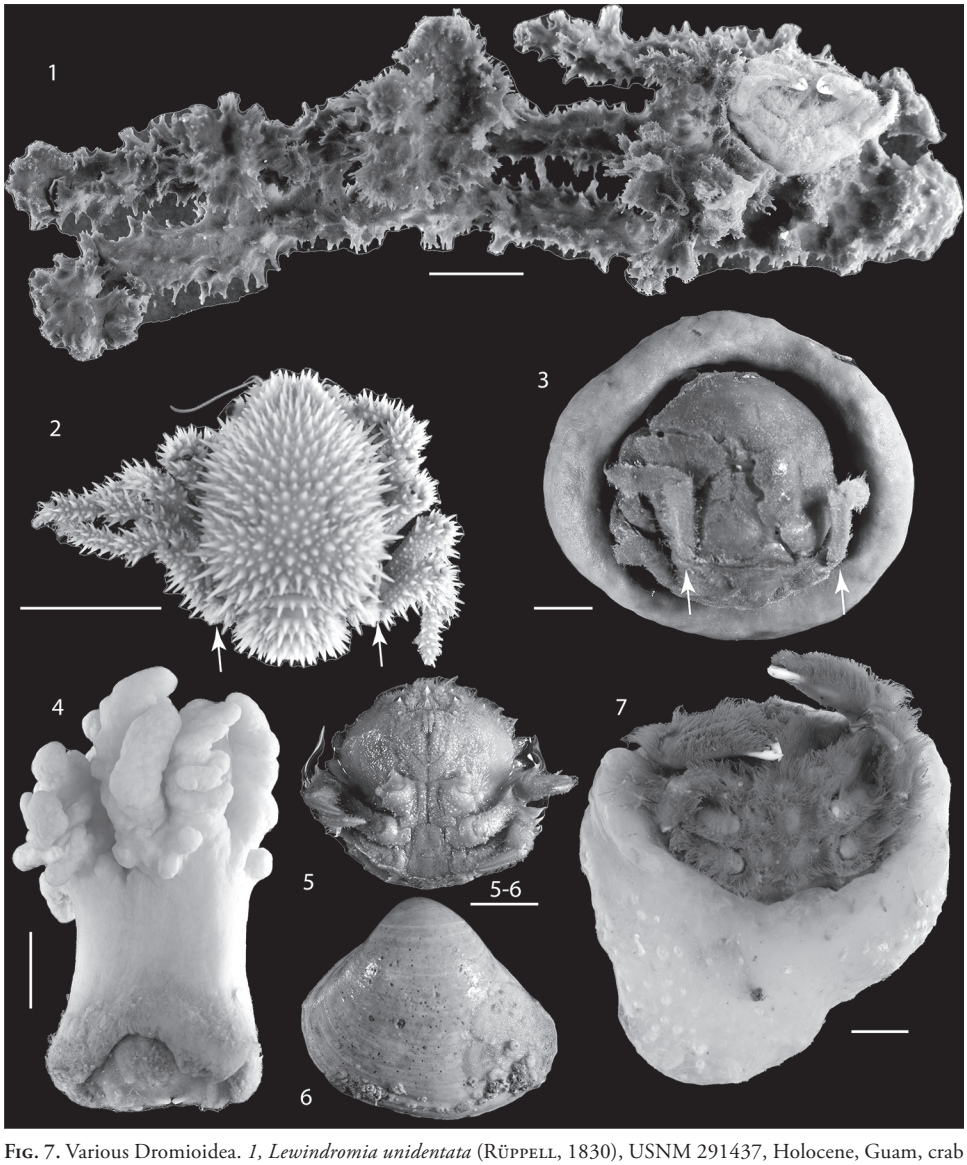

Fig. 7. Various Dromioidea. *1, Lewindromia unidentata* (Rüppell, 1830), USNM 291437, Holocene, Guam, crab with long sponge. *2, Acanthodromia erinacea* A. Milne-Edwards, 1880, Holocene, Caribbean Sea, arrows indicate tiny legs not adapted for carrying. *3, Moreiradromia antillensis* (Stimpson, 1859), USNM 66335, Holocene, Gulf of Mexico, crab flipped over in sponge cap to show dorsally carried fifth pereiopods. *4, Lewindromia unidentata* (Rüppell, 1830), USNM 291439, Holocene, Guam, crab with ascidian cap. *5, 6, Hypoconcha lowei* Rathbun, 1933, USNM 1447101, crab (*5*) and clam cap (*6*). *7, Lamarckdromia globosa* (Lamarck, 1818), USNM 98890, Holocene, Australia, crab with sponge cap in place. Scale bars = 1 cm. Arrows in *2* and *3* indicate fifth pereiopods. Photos by R. M. Feldmann.

genera inhabit primarily low to high energy siliciclastic environments, consistent with their extant descendants, and are restricted to Europe and Gulf Coastal and Western Interior North America. Sphaerodromiidae has been considered as the most basal form among Dromioidea, based on its possession of a smooth carapace, podobranchs, and vestigial pleopods in males, and spines on the pereiopods opposing the dactyli on

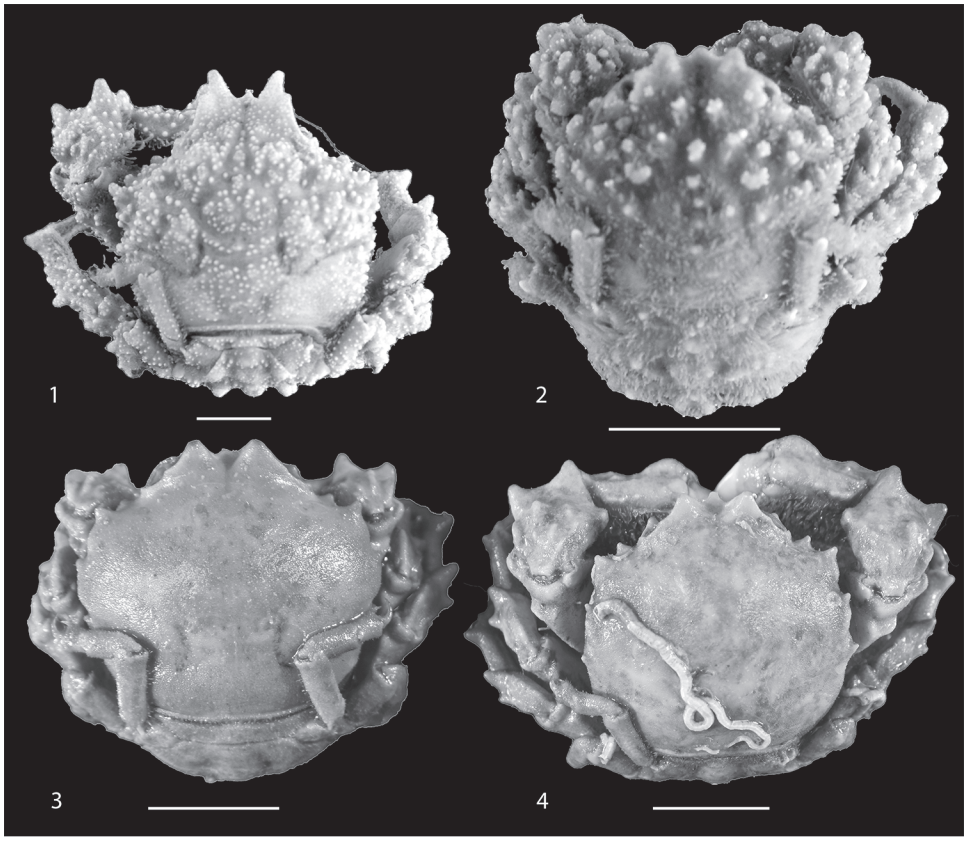

Fig. 8. Sexual dimorphism in Dromiidae. *1, 2, Epigodromia sculpta* (Haswell, 1882), USNM 17056, Holocene, Australia, female (*1*) and male (*2*). *3, 4, Stimdromia lateralis* (Gray, 1831), USNM 17048, Holocene, Australia, female (*3*) and male (*4*). Scale bars 1, 2 = 5 mm. Scale bars 3, 4 = 1 cm. Photos by R. M. Feldmann.

pereiopods one through four that could facilitate carrying objects (McLay, 1993; Guinot & Wicksten, 2015). The hypothesized more derived condition would be one in which only pereiopods 4 and 5 retained such structures (McLay, 1993). Molecular analysis found *Sphaerodromia* to be basal to other dromiids, although a limited number of genera were sampled (Wolfe & others, 2024), and it appeared in the fossil record later than other extant dromioid families. McLay (1993) reported that species of extant *Sphaerodromia* carry sponges and range in depth from 200 to 400 m (OBIS, 2024).

This family is often compared with Dynomenidae because both have a more posterior position of the spermathecal openings rather than displaced anteriorly, as in Dromiidae, as well as other presumably basal features (McLay, 1993; Poore & Ahyong, 2023).

Extinct dromioids.—Several families within Dromioidea are now extinct. These were small families generally composed of one to three genera, each with a unique geographic distribution. Basinotopidae has been recovered from volcaniclastics associated with carbonates, carbonates, and fine siliciclastics, all from Europe, ranging from early Eocene (Ypresian) through the Miocene. Diaulacidae and Xandarocarcinidae are primarily associated with siliciclastics and became extinct in the Eocene and Maastrichtian respectively (Fig. 3.8). Their carapace morphology may be convergent with Xanthidae, as seen in Dynomenidae. Each is characterized by

distinct morphological features. Diaulacidae exhibit very large spermatheca situated posteriorly along sternal suture 7/8 (Schweitzer & others, 2012a, fig. 18b). Diaulacidae exhibits an unusual distribution, known from Europe, South America, and Japan, all from a single genus. Xandarocarcinidae possess female gonopores situated obliquely and distally on coxae 3, apparently a unique apomorphy (Schweitzer & others, 2012a, p. 35). Xandarocarcinidae is restricted to west coastal North America (Schweitzer & others, 2012a).

Trends in Dromioidea.—McLay (1993) proposed that evolutionary trends in Dromiidae were the loss of the tendency to carry camouflage, reduction in size of pereiopods 4 and 5, and development of a strongly ornamented carapace. The first two are difficult to test, as the pereiopods are not frequently preserved. Dromiids have been well-ornamented since their appearance in the Cretaceous. Extinct sphaerodromiids have deep grooves and moderately developed regions, opposite to the relatively smooth extant *Sphaerodromia*. More data will be necessary to adequately test these hypotheses.

McLay (1993) envisioned a recent tropical radiation of Dromiidae in the Indo-Pacific region along with the persistence of more basal forms like *Sphaerodromia* there. Of note is that many dromiid lineages originated in the Tethys, apparently migrating to the Indo-Pacific sometime before its closure, which could account for the presence of ancient lineages and more recent radiations there (Harzhauser & others, 2007; Renema & others, 2008; Liu & others, 2018). McLay (1993) considered that the dromiid faunas of Australia and South Africa were each unique and possibly composed of older lineages, and that the Atlantic fauna was similarly old, tied to the opening of the Atlantic. The high diversity of Dromiidae in the Paleocene and Eocene in the North Atlantic could support this hypothesis (Schweitzer & Feldmann, 2023), but the scanty fossil record for Southern Hemisphere dromiids makes the other two hypotheses difficult to test with fossils.

Notable in extant Dromiidae but not observed in Dynomenidae is sexual dimorphism in the ornamentation and shape of the carapace, unusual among brachyurans. Species of *Epigodromia* McLay, 1993, show clear distinctions in which the males have larger swellings and larger tubercles on the carapace, whereas females have more subdued ornamentation (Fig. 8.1, 8.2). *Stimdromia* McLay, 1993, has smaller, shorter spines in females as compared to males (Fig. 8.3, 8.4). Males of *Exodromidia* Stebbing, 1905, have a much better developed crispate flange on the posterolateral margin as well as more inflated carapace regions, as compared to females (USNM 231224). Large male *Hypoconcha* Guérin-Méneville, 1854, have tiny spines on the orbital margin in males, which are lacking in females and small males (USNM 1447110). Specimens of species of Dynomenidae do not exhibit differences in the carapace between males and females (USNM 125582, 41046, 48964, 49224). These observations are relevant to fossil species recognition, wherein differences in carapace morphology are often the only factor in defining a new species. Noting that males and females have slightly different ornamentation may help to recognize separate species that are actually male–female pairs in the fossil record.

HOMOLOIDA

Homoloida are characterized by elongate carapaces, often, but not always, with a *linea homolica*, a suture line along the lateral edge of the carapace that facilitates molting. Many extinct members of Homolidae are known only from the portion of the carapace located between the *lineae*, presumably a postmolt fragment of the carapace. Homoloids lack a true orbit, instead with a "plaige orbitaire," or concave area to house the ocular peduncle (Guinot, 1991; Guinot & Richer de Forges, 1995). Latreilliidae have long supraocular spines that may

protect the eye, but the eyestalks are long and not housed in an orbit (Williams, 1982; Castro & others, 2003).

The section has maintained relatively low but consistent diversity in the fossil record since the middle Cretaceous and is known from several extant genera (Fig. 5). The overwhelming majority of fossil occurrences are Homolidae, but other small families have limited fossil records (Table 2). Two families are extinct, and as a section, the group inhabited a broad range of environments. Their wide geographic range and broad environmental tolerance may explain the persistence of the group over geological time.

Homolidae.—Homolidae appeared in the Tithonian and has had a more or less continuous fossil record since (Fig. 2.3, 3.1, 4.11). Peaks in diversity in the Albian, Maastrichtian, and Ypresian parallel that for most podotrematous groups, and fourteen extant genera, are currently known (DecaNet, 2025). The family inhabited nearly every type of environment in the fossil record, but predominantly carbonates and fine siliciclastic environments (Shaffer & Schweitzer, 2024). Extant taxa inhabit shelf to slope environments with substrates of rocks, sand, broken shells, and mud (Sakai, 1976; Guinot & Richer de Forges, 1995). The lack of fossil specimens in the Cenozoic suggests that the family originated in shallower water environments and subsequently moved into deeper water environments over time (Schweitzer & others, 2004). Extant forms are carriers, bearing sponges or cnidarians (Wicksten, 1985), and instead of fitting the object to the carapace, they hold it above or behind the carapace (Guinot & Richer de Forges, 1995). Perhaps this is because of the development of the *linea homolica,* which would need to be clear of objects during molting of the exoskeleton. Because the process of collection causes the crabs to lose the objects they are carrying, it is not known if homolids always carry objects, but it has been suggested that they do (Guinot & Richer de Forges, 1995).

Geographically, Homolidae is more varied than dromioid families, with many fossil occurrences in Europe, but also Antarctica; Australia; Japan; Western Interior Seaway, West Coastal, East Coastal, and Gulf Coastal North America; and Argentina (South America). Homoloids tend to inhabit deeper water, so they may exhibit a broader range of tolerance to temperature ranges than Dromioidea, which inhabit shallower, tropical areas (Shaffer & Schweitzer, 2024).

Other families.—Latreilliidae are diagnosed by their anterior carapace extended into an elongate neck, rostral horns, a reduced subchelate fifth pereiopod, and lack of *lineae homolicae*. Extant Latreilliidae inhabit middle to outer shelf environments on rocky, sandy, and muddy substrates and are only represented by two genera, with temperate to subtropical occurrences in both hemispheres. The two fossil genera were collected from the Cretaceous of Gulf Coastal North America from siliciclastics and exhibit the characteristic anterior neck of latreilliids. Some extant latreilliids have been observed to carry objects with their fifth pereiopods, including seaweeds and hydrozoans; however, the scant knowledge of this behavior cannot be attributed across the family (Castro & others, 2003).

Poupiniidae occupy a morphology considered intermediate between Latreilliidae and Homolidae (Williams & Moffitt, 1991). Poupiniids lack a *linea homolica* and have achelate fifth pereiopods of similar size to the other pereiopods, but still carried subdorsally. Resemblance of the extant form with fossil homolids was noted at the time the family was recognized (Guinot, 1991), and a fossil poupiniid was soon reported from the Cretaceous of Antarctica (Feldmann & others, 1993) (Fig. 3.5). The sole extant member of Poupiniidae inhabits deep water of the Indo-Pacific, whereas the fossil was collected in medium grained siliciclastics of Maastrichtian rocks.

Extinct homoloids include the Mithracitidae, collected from Cretaceous siliciclastics

in Europe and Colombia, and the Tithonohomolidae, known only from Jurassic (Tithonian) coral limestones of Europe. Tithonohomolidae exhibit odd preservation in only being preserved from the intralineal portions of the carapace (Feldmann & Schweitzer, 2009). Thus, we do not yet know what the entire carapace looked like. Mithracitidae look much like some other Cretaceous homoloids, such as *Lignihomola* Collins, 1997, but lacking the *linea*. The presence of all three extant families, as well as two extinct families by the Cretaceous, suggests that Homoloida radiated and diversified early, like other podotrematous groups, with a small but significant presence in modern oceans.

CALLICHIMAEROIDA

This enigmatic section is monotypic but evolutionarily important. The sole genus, *Callichimaera* Luque & others, 2019, is typified by an elongate body, very broad fifth and sixth sternites, paddle-like second and third pereiopods, and large eyes lacking orbits or any protective orbital structure, proposed to be a result of heterochrony (Luque & others, 2019) (Fig. 3.4). The adult *Callichimaera* retains some features of larval stages but is clearly an adult, as seen in the dissimilar body sizes between juvenile (~5 mm) and adult (>20 mm) individuals, and the presence of well-developed reproductive organs such as male gonopods in larger specimens (Luque & others, 2019). The elongate body form with a wide sternum is proposed to be a result of decarcinization, or secondary loss of the crab-like body form, which has occurred at least five times (Luque & others, 2019). Phylogenetically, Callichimaeroida is recovered in an intermediate position between the least inclusive podotrematous sections (Dromiacea and Homoloida) and the more inclusive podotrematous groups (Torynommoida, Etyoida, Raninoida, Cyclodorippoida, and Dakoticancroida), so its evolutionary origins are still unclear (Luque & others, 2019). Callichimaeroida was a short-lived section, ranging from the Cenomanian–Turonian, occurring in Colombia and Wyoming, USA (Fig. 6). Thus, *Callichimaera* is an example of the unique podotrematous morphologies that characterized both podotrematous and eubrachyuran crabs during their Cretaceous radiation (Luque & others, 2019; Schweitzer & Feldmann, 2023).

TORYNOMMOIDA

Torynommoida embraces a single family and two genera, characterized by rectangular carapaces, very wide orbits, complex carapace regional development, and wide sterna (Fig. 3.14). It is limited to Cretaceous taxa in siliciclastic environments but with an antitropical distribution. One genus is known from Early (Albian) to Late (Cenomanian–Maastrichtian) Cretaceous rocks of Australia and New Zealand, whereas the other occurrence is in Early Cretaceous (Aptian) rocks of England. Glaessner (1980) considered the group to be closely related to what is now recognized as Cyclodorippoidea, whereas phylogenetic analysis of podotrematous crabs found the section as basal in a clade constituted by several podotrematous sections and the Eubrachyura (Karasawa & others, 2011; Luque & others, 2019). Its rectangular carapace and broad sternum suggest convergence with the eubrachyuran morphology.

ETYOIDA

Section Etyoida and superfamily Etyoidea embrace two families (Table 2). Etyoids differ from other podotremes in being distinctly wider than long, with well-developed carapace regions in some taxa and lacking the postcervical and branchiocardiac grooves in all taxa (Guinot & Tavares, 2001; Karasawa & others, 2011). Their morphology is superficially convergent with Dynomenidae or xanthoid crabs, reflected in their placement with those groups in older publications (Glaessner, 1969, and Wright & Collins, 1972, respectively).

However, their sterna are more like other podotrematous crabs in their long lateral sternal projections but lack of episternites. The spermatheca are in somewhat different positions than in other podotrematous crabs, in that they lie completely on sternite 7 and are not associated with sternal suture 7/8. This supports the findings that podotreme crabs evolved more than once and under different conditions.

Etyoid crabs are unusual in having sternites 1–4 positioned at a very high angle to the remainder of the sternites (Schweitzer & others, 2012a, fig. 10.4, 5). This makes it highly unlikely that etyoids were swimming crabs (Fraaye, 1996) due to the resulting vertically high lateral profile (Schweitzer & others, 2012b). The lateral profile of the crabs seems potentially more adapted to burrowing or resting in a position with the body directed upward, as seen in calappid or aethrid crabs. Etyoida were likely not carriers of camouflage due to the arrangement of the pereiopods with respect to the dorsal carapace and the carapace ornamentation, according to Guinot & Tavares (2001). One genus in Feldmanniidae, *Caloxanthus* A. Milne-Edwards, 1864, retains dorsally held pereiopods 5 (Schweitzer & others, 2012b, fig. 11.1, 11.3), and in all etyoids with sterna and coxae preserved, coxae 1 and 2 are visible in ventral view and coxae 3–5 are visible in posterior view (Schweitzer & others, 2012b). These features are more suggestive of a carrying ability. The unusual form of the sternum and the arrangement of the pereiopod coxae have no modern analog, so at this time, it is inconclusive as to whether etyoids were carriers.

The two constituent families have slightly differing carapace morphologies (Schweitzer & others, 2012b). Etyidae have more ornamented carapaces and deeper grooves (Fig. 3.2), whereas Feldmanniidae have poorly defined grooves and regions and generally have densely granular ornamentation (Fig. 3.10). The sterna differ in the angle of sternites 5–8 with the other sternites, being much higher in Feldmanniidae.

Members of each family predominantly inhabited siliciclastic environments, with a sizable occurrence in carbonates but few associated with reefs. Specimens can be very abundant, notably at the Cretaceous localities in Texas (Schweitzer Hopkins & others, 1999; Schweitzer & others, 2012b). Like many Cretaceous podotrematous groups, Etyidae is known mostly from European occurrences, with some in Japan, Gulf coastal, east coastal and Western Interior North America, and one in Madagascar. Feldmanniidae is also predominantly European, with a few occurrences in Gulf Coastal North America and one in Madagascar. Both families survived the end-Cretaceous extinction, ranging into the Paleocene (Feldmanniidae) and Eocene (Etyidae) in Europe (Fig. 6).

RANINOIDA

This large section is composed of three superfamilies (Table 2). The section displays a wide range of carapace morphologies, but the group is united by having generally poorly defined carapace regions; orbital spines; mouthparts and buccal cavity converging anteriorly; lack of a sterno-pleonal cavity; and narrow sternites, sometimes very reduced (Luque, 2015; Schweitzer & others, 2018; Poore & Ahyong, 2023). Extant forms have an elongate carapace and dactyls of some of the pereiopods modified for digging and are colloquially called "frog crabs." Extinct forms can vary considerably from this carapace shape.

Raninoida has been recovered as a monophyletic group among the podotrematous crabs in molecular (Ahyong & others, 2007; Wolfe & others, 2024) and morphological (Karasawa & others, 2011; Karasawa & others, 2014; Luque, 2015; Luque & others, 2019, 2021) analyses of phylogeny. Three superfamilies are also monophyletic (Karasawa & others, 2011; Karasawa & others, 2014; Schweitzer & others, 2016): Necrocarcinoidea, Palaeocorystoidea, and Raninoidea. Raninoida is documented from

Early Cretaceous through Holocene rocks, with complex patterns of diversity, extinction, and radiation within each superfamily.

Because of its extensive fossil record and perhaps because of the clear similarity between extinct and extant forms, Raninoida has received considerable attention in both the biological and paleontological literature (Bourne, 1922; Goeke, 1985; Guinot, 1993; Van Bakel & others, 2012b; Karasawa & others, 2014; Schweitzer & others, 2016; Schweitzer & others, 2018; Hartzell & others, 2022). Thus, the evolutionary history of the group is well-considered based on the fossil record as now known.

Raninoida is composed of mostly extinct families and genera. Necrocarcinoidea embraces crabs with carapace forms about as wide as long, with some regional development and moderate carapace ornamentation; all are extinct. The extinct Palaeocorystoidea and extant Raninoidea are dominated by elongate, possibly burrowing forms. All families within these three superfamilies were present during the Late Cretaceous.

Necrocarcinoidea

Necrocarcinoidea are united by carapaces that are about as wide as long and usually heavily ornamented, as well as a sternum

Table 2. Other podotrematous sections, superfamilies, and constituent families, age ranges, and number of genera extinct and extant *(continued on next page)*.

Taxon	Range	Extinct (†), Extant only (*), and Both
Homoloida De Haan, 1839 Tithonian–Holocene Feldmann & others (2012) and Schweitzer & others (2024b)		
Homoloidea De Haan, 1839	Tithonian–Holocene	
Homolidae De Haan, 1839	Tithonian–Holocene	13†, 11*, 3
Latreilliidae Stimpson, 1858a	Albian–Holocene	2†, 2*, 0
Mithracitidae Števčić, 2005	Barremian–Aptian	2†
Poupiniidae Guinot, 1991	Maastrichtian–Holocene	1†, 1*, 0
Tithonohomolidae Feldmann & Schweitzer, 2009	Tithonian	2†
Callichimaeroida Luque & others, 2019 Cenomanian–Turonian Luque & others (2023)		
Callichimaeroidea Luque & others, 2019	Cenomanian–Turonian	
Callichimaeridae Luque & others, 2019	Cenomanian–Turonian	1†
Torynommoida Glaessner, 1980 Aptian–Maastrichtian Schweitzer & others (2017a)		
Torynommoidea Glaessner, 1980	Aptian–Maastrichtian	
Torynommidae Glaessner, 1980	Aptian-Maastrichtian	2†
Etyoida Guinot & Tavares, 2001 Aptian–Priabonian Schweitzer & others (2017c)		
Etyoidea Guinot & Tavares, 2001	Aptian–Priabonian	
Etyidae Guinot & Tavares, 2001	Aptian–Priabonian	9†, 0, 0
Feldmanniidae Schweitzer & others, 2012b	Albian–Thanetian	4†, 0, 0

Table 2. *Continued . . .*

Taxon	Range	Extinct (†), Extant only (*), and Both
Raninoida Ahyong & others, 2007 Berriasian–Holocene Schweitzer & others (2018) and Schweitzer & others (2024b)		
Necrocarcinoidea Förster, 1968	Berriasian–Rupelian	
Camarocarcinidae Feldmann & others, 2007	Campanian–Thanetian	2†
Cenomanocarcinidae Guinot & others, 2008	Albian–Priabonian	4†
Necrocarcinidae Förster, 1968	Aptian–Danian	4†
Paranecrocarcinidae Fraaije & others, 2008	Berriasian–Maastrichtian	4†
Orithopsidae Schweitzer & others, 2003	Aptian–Rupelian	16†
Palaeocorystoidea Lőrenthey *in* Lőrenthey & Beurlen, 1929	Aptian–Maastrichtian	
Palaeocorystidae Lőrenthey *in* Lőrenthey & Beurlen, 1929	Aptian–Maastrichtian	10†
Raninoidea De Haan, 1839	Albian–Holocene	
Lyreididae Guinot, 1993	Albian–Holocene	15†, 1*, 1
Raninidae De Haan, 1839	Cenomanian–Holocene	30†, 2*, 8
Symethidae Goeke, 1981	Maastrichtian–Holocene	2†, 2*, 0
Dakoticancroida Rathbun, 1917 Turonian–Maastrichtian Feldmann & others (2017) and Schweitzer & others (2024b)		
Dakoticancroidea Rathbun, 1917	Turonian–Maastrichtian	
Dakoticancridae Rathbun, 1917	Campanian–Maastrichtian	3†, 0, 0
Ibericancridae Artal & others, 2008	Turonian–Maastrichtian	5†, 0, 0
Cyclodorippoida Ortmann, 1892b Abian–Holocene Schweitzer & others (2017b) and Schweitzer & others (2024b)		
Cyclodorippoidea Ortmann, 1892		
Cyclodorippidae Ortmann, 1892	Albian–Holocene	2†, 9*, 2
Cymonomidae Bouvier, 1897	Priabonian–Holocene	1†, 4*,1
Phyllotymolinidae Tavares, 1998	Holocene	3*
Quadratoplanidae Franțescu, 2014	Albian–Maastrichtian	2†

with a flattened axial area that can be narrow or wide (Schweitzer & others, 2018). The superfamily was most diverse during the Cenomanian and a few taxa survived into the Cenozoic. The individual families include only two to four genera, except Orithopsidae, which has sixteen. As a superfamily, members inhabited a broad array of environments, including both siliciclastic and carbonate, as well as having a broad geographic range (Hartzell & others, 2022).

Camarocarcinidae.—This small family contains only two genera with few species, but with very distinctive dorsal carapace morphology (Schweitzer & others, 2018). They have spinose anterolateral and postero-

lateral margins with well-defined cervical and branchiocardiac grooves, unusual in the section. The cuticle of the dorsal carapace is typified by distinctive pillars yielding a tessellated appearance (Feldmann & others, 2007). The family exhibits a Northern Hemisphere distribution, with occurrences in the northern Western Interior Seaway of North America and the North Atlantic. Notably, this family survived the end-Cretaceous extinction events although constituent genera did not, perhaps due to its occurrences in the North Atlantic, which may have been protected or a refugium (Schweitzer & Feldmann, 2023). Similarities between species of *Necrocarcinus* Bell, 1863, and *Camarocarcinus* Holland & Cvancara, 1958, suggest that Camarocarcinidae may have been derived from within Necrocarcinidae (Veselská & others, 2024).

Cenomanocarcinidae.—This family has only four genera but one, *Cenomanocarcinus*, Van Straelen, 1936, is quite speciose, with nineteen species (Fig. 3.7). The other genera are composed of only one or two species. Cenomanocarcinids are typified by a wider than long, flattened carapace with transverse and/or longitudinal ridges bearing tubercles and a somewhat flattened sternum (Schweitzer & others, 2018).

Diversity in the family peaked in the Cenomanian (Hartzell & others, 2022). The family survived the end-Cretaceous extinction, although genera did not. The geographic range for the family is primarily the temperate Northern Hemisphere, with a few equatorial occurrences in Africa and one in the Southern Hemisphere (Schweitzer & others, 2016; Hartzell & others, 2022). Cenomanocarcinid crabs are among the most abundant and geographically and stratigraphically widely distributed crabs in Colombia (Guinot & others, 2008; Luque & others, 2017). Environmental preferences for the family were for siliciclastics of all types in the Cretaceous but restricted to low energy or coral environments in the Cenozoic (Schweitzer & others, 2016).

Necrocarcinidae.—Similar to Cenomanocarcinidae, only four genera are referred to the family, each with between one and five species except *Necrocarcinus*, with ten. Necrocarcinids have a rounded, strongly vaulted, well-ornamented carapace and inhabited a wide variety of environments, both siliciclastic and carbonate (Schweitzer & others, 2018; Hartzell & others, 2022) (Fig. 3.13). Maximum diversity occurred in the Albian and Campanian, and the family survived the end-Cretaceous extinction in the North Atlantic, although no genera did (Schweitzer & others, 2018; Schweitzer & Feldmann, 2023). The family exhibited an antitropical distribution, known across the Northern Hemisphere in North American, Europe, and Asia and Antarctica in the Southern Hemisphere (Schweitzer & others, 2018).

Paranecrocarcinidae.—Paranecrocarcinidae had one speciose genus, *Pseudonecrocarcinus* Förster, 1968, with eleven species, whereas the other genera had between one and four. Diversity peaked in the Cenomanian, and the family was extinct by the Maastrichtian (Hartzell & others, 2022). Geographically, the family was predominantly found in the North Atlantic and Western Tethys, with a few occurrences in the Southern Hemisphere in Africa (Schweitzer & others, 2018). Members primarily inhabited low energy and carbonate environments (Schweitzer & others, 2016; Hartzell & others, 2022).

Some members of the family display postrostral slits on the dorsal carapace, which have been considered diagnostic for some of the species. The slits are short, longitudinal grooves that do not appear to pierce the cuticle. They are variably preserved between and among species, and currently, their function is not known (Schweitzer & others, 2016).

Orithopsidae.—Orithopsidae is a large, diverse family. They are typified by an angular carapace, often hexagonal, and with long rostral and orbital spines (Schweitzer

& others, 2018). The conception of the family has evolved since its original description, now recognized as being a monophyletic group composed of sixteen genera (Schweitzer & others, 2016). The family was diverse at the genus level, but not speciose, with no more than three species per genus and most with just one and, unlike other raninoidan families, with no particularly speciose genera. This long ranging family first appeared in the Aptian, diversity peaked in the Albian, and it became extinct in the Oligocene (Schweitzer & others, 2018). Members of the family inhabited low-energy siliciclastic and carbonate environments, mostly in the North Atlantic but with Early Cretaceous occurrences in the equatorial Americas (Schweitzer & others, 2016).

Palaeocorystoidea

This superfamily contains only the nominate family, Palaeocorystidae, and is very characteristic of latest Early Cretaceous and Late Cretaceous rocks. They are typified by a longer than wide carapace, like the extant raninoids, but unlike the extant forms, palaeocorystids are very well ornamented with tubercles, keels, and ridges. Their carapace is markedly widest across the anterior one-quarter of its length, usually with multiple, wide anterolateral spines (Schweitzer & others, 2018) (Fig. 3.3). The group was moderately generically diverse, with 10 known genera. Two of these were particularly speciose, *Eucorystes* Bell, 1863, and *Joeranina* Van Bakel & others, 2012b, with eleven and nine species, respectively. The other genera range between one and five included species. Spermatheca are known to be preserved among members and they are paired but separated from one another by a median line and cuticle, unlike the spermathecae in most Raninoidea, in which the apertures lie directly adjacent to one another (Van Bakel et al., 2012b).

Palaeocorystidae reached its maximum diversity in the Albian and was moderately diverse throughout the Cretaceous (Hartzell & others, 2022). Members of the group inhabited an array of carbonate and siliciclastic environments, becoming extinct by the end of the Cretaceous. A burying habit has been inferred for members of the family (Van Bakel & others, 2012b) but the elongated body shape, broadened anterior portion of the body, and heavy ornamentation are unlike that of other burying decapods (Hartzell & others, 2022). Palaeocorystidae occupy a morphospace intermediate between the equant, heavily ornamented Necrocarcinoidea and the elongate, less ornamented Raninoidea (Hartzell & others, 2022). Palaeocorystids inhabited a broad range of environments, including siliciclastics of all kinds and carbonates, but they also exhibited a more restricted geographic range than the Cretaceous Raninoidea, possibly contributing to their extinction (Hartzell & others, 2022).

Raninoidea

This superfamily comprised two families that ranged from the Cretaceous to the Holocene. Both families are very diverse, and each family has particularly speciose genera among those with only a few species each. Most genera within Lyreididae had between one and three species, with three exceptions, *Bournelyreidus* Van Bakel & others, 2012b (8), *Lyreidus* De Haan, 1841 (11), and *Macroacaena* Tucker, 1998 (14), each in a different subfamily. Within Raninidae, five genera are particularly speciose, with the others ranging between one and five species: *Lophoranina* Fabiani, 1910 (30); *Quasilaeviranina* Tucker, 1998 (8); *Raniliformis* Jagt & others, 1993 (8); *Ranina* Lamarck, 1801 (17 in fossil record, some fragmental); and *Raninoides* H. Milne Edwards, 1837 [in 1834–1340] (37 in fossil record alone). Both families originated in the Cretaceous but rapidly radiated in the Eocene, when diversity peaked in numbers of genera and species (Hartzell & others, 2022). The range of raninoids changed over the course

of the Cenozoic, from a more global distribution to their current locations closer to the equator (Hartzell & others, 2022).

Lyreididae—This family originated in the Early Cretaceous and peaked in generic and species diversity in the Eocene. In general, lyreidids have elongate, weakly ornamented carapaces but may have well-developed rostral, orbital, and anterolateral spines (Fig. 4.5). They ave some distinctive sternal characteristics, including a double-peg pleonal holding mechanism and a lyreidid hook on sternite five (Guinot, 1991). Lyreididae was almost completely restricted to siliciclastic environments throughout its range (Hartzell & others, 2022).

Five subfamilies have been recognized. Bicornisranininae Karasawa & others, 2014, is monotypic, with one genus and species known from the Santonian of the Pacific Northwest of North America. It is quite recognizable with its long bifid anterolateral spine and long orbital spines. Lyreidinae Guinot, 1993, ranges from the Late Cretaceous to Holocene, with a cosmopolitan distribution (Schweitzer & others, 2018; Hartzell & others, 2022). Members have a smooth, elongate carapace and a reduced number of anterolateral and orbital spines. *Lyreidus* De Haan, 1841, is the most speciose genus, with 11 fossil species recognized, and three extant ones. The other included lyreidine genera range from one to two species each. Rogueinae Karasawa & others, 2014, is monogeneric with three species. They are distinctive in having a wide front, short orbital spines, and long, bifid anterolateral spines. They are all known from the Northern Hemisphere in Paleocene or Eocene rocks. Macroacaeninae has only two genera, of which *Macroaceana* Tucker, 1998, contains all but one species, for a subfamily total of sixteen species, all known from the Northern Hemisphere in the Late Cretaceous through Miocene. They are characterized by a narrow front, one anterolateral spine, and well-developed orbital spines. Marylyreidinae Van Bakel & others, 2012b, contains four genera, the most speciose of which includes eight species. They are similar to macrocaenines but have distinct fungiform nodes on their cuticle. All but one genus is restricted to the Northern Hemisphere, the sole departure in New Zealand, and the subfamily is restricted to the Cretaceous.

Extant Lyreididae include two genera with Indo-West Pacific and Caribbean occurrences, significantly restricted from its cosmopolitan range in the past (Hartzell & others, 2022). Extant forms inhabit sandy or muddy substrates or broken shells at depths of 30–800 m (Sakai, 1976; Poore & Ahyong, 2023). The smooth, elongate carapace, as well as adaptations of the pereiopods and respiratory system of extant forms has led to the interpretation that they buried themselves in the sediment (Bellwood, 2002; Haj & Feldmann, 2002; Van Bakel & others, 2012b). *Lyreidus tridentatus* De Haan, 1841 (Lyreididae, Lyreidinae), burrows in fine muddy sand substrates, using pereiopods 2–4 to excavate sand and the chelipeds to clear sand from the respiratory structures (Leng, 1964).

Raninidae.—The extant Raninidae is the most diverse and morphologically disparate family in the section and has been found in a broad array of environments, including many carbonates, throughout its geologic history, beginning in the late Early Cretaceous (Albian). Raninidae is separated into two small and three large subfamilies, which are each represented by extant and extinct forms. Raninidae are characterized by a very reduced sternum, with sternites very narrow, and evidence of sexual dimorphism in most subfamilies. Only one species, *Ranina ranina* Linnaeus, 1758, is economically important, and consequently, most ecological and developmental knowledge on the family is based upon this species.

Cyrtorhininae is a small subfamily, with two genera known in the fossil record, and two additional extant genera. This subfamily is characterized by ovate, bulbous carapaces

that are heavily granular anteriorly, but most distinctly by the spine on the upper margin of the movable finger (Poore & Ahyong, 2023). They range from the Eocene to Holocene and are found preferentially in warmer areas, close to the tropics. Fossils are primarily associated with carbonates and volcanic ash in southern Europe and southern North America (Schweitzer & others, 2018; Hartzell & others, 2022). Extant species inhabit the tropical Atlantic and the tropical Indo-Pacific oceans in subtidal to shelf and slope depths (Poore & Ahyong, 2023) and where known, from sandy or muddy substrates or from coral rubble or rocky reefs (Ng & Guinot, 2020).

Notopodinae has a rich fossil record and is known from four extant and twelve extinct genera. Of these, only the extinct *Raniliformis* and the extant *Umalia* Guinot, 1993, are particularly speciose, with eight and seven species, respectively; the other genera have between one and four species. Members of the subfamily are characterized by a wide carapace, especially anteriorly, with a deep reentrant for the antennae and heavy ornamentation anteriorly. They also have a distinctive chela, in which the manus is very high and the fingers are reduced (Schweitzer & others, 2018). This long-ranging subfamily is known from the Maastrichtian to Holocene. Cretaceous occurrences are in the Netherlands and more recent locations are generally in southern Europe and the southern United States as well as Japan. Extinct forms occur in a wide array of sediments including carbonates, siliciclastics, and volcanics. Extant notopodines are found in cosmopolitan temperate to tropical locations, from intertidal to slope depths (Poore & Ahyong, 2023). Substrates for the subfamily include coarse sand, coral sand, and shells (Davie & Short, 1989; Tavares, 2006) and less frequently, mud (Sakai, 1976).

Raninae is dominated by two highly speciose genera, *Ranina* and *Lophoranina*, as well as several other less speciose genera (Fig. 4.6, 4.8). These crabs are characterized by wide carapaces with strong ornamentation in the form of terraces, dense spines, or distinctive cuticular structures. Anterolateral and orbital spines are wide and triangular (Schweitzer & others, 2018). This long ranging subfamily, Cenomanian to Holocene, is best known for the extant *Ranina ranina*, or spanner crab, which forms an important fishery in the Indo-Pacific. Fossils are notably lacking in the Southern Hemisphere, with the possible exception of one species from the Eocene of Ivory Coast, which is equatorial (Schweitzer & others, 2018). Most extant occurrences are in the Southern Hemisphere and tropical Indo-Pacific (Poore & Ahyong, 2023), perhaps a relict Tethyan distribution. Extant *Ranina* inhabits intertidal (rarely) to shallow shelf habitats (Poore & Ahyong, 2023), preferring sandy environments (Ng, 1998). Extinct raninines inhabited a wide variety of habitats (Hartzell & others, 2022), but notably, the speciose *Lophoranina* mainly has been collected from carbonates.

Particularly speciose and instantly recognizable is *Lophoranina*. The spinose transverse terraces are distinctive, and the genus is primarily tropical to subtropical in distribution, from the Eocene through Miocene (Schweitzer & others, 2018). The spinose terraces were shown experimentally to anchor the carapace in sediment (Savazzi, 1981, 1982), and the spines may have functioned to grip algal mats or other organic debris (Feldmann & others, 1996). Other raninines possess terraces that are more or less transverse and may have served similar functions.

Raninoidinae appears to be the most numerically abundant in terms of individual occurrences among extant Raninidae (OBIS, 2024). Thirty-seven species of *Raninoides* alone have a fossil record, with eighteen extant species among three extant genera in the subfamily (Poore & Ahyong, 2023) (Fig. 4.2). The genera in this subfamily have been remarkably conservative in dorsal carapace morphology, as in *Raninoides*, which is easily recognizable from Eocene

marine rocks onward worldwide. Its fossil record is distinctly antitropical, but modern occurrences are tropical and subtropical cosmopolitan (Hartzell & others, 2022). Fossil occurrences are mostly in siliciclastic sediments (Hartzell & others, 2002). Extant forms inhabit shelf and slope habitats from 20 to 645 m (Poore & Ahyong, 2023) on gravel, sand, mud, or broken shells (Rathbun, 1937; Sakai, 1976).

Symethinae is small subfamily composed of one extant and two extinct genera. It is distinctive in having an angular carapace, a narrow, extended frontal area, and pitted depressions anteriorly on the dorsal carapace (Schweitzer & others, 2018). Extant species are found in Australia, eastern Pacific, and western Atlantic oceans (Schweitzer & others, 2018) at depths of 18–100 m (Rathbun, 1937; Poore & Ahyong, 2023). Extinct species are reported from siliciclastic Cretaceous rocks of Gulf Coastal North America and Eocene marls in Spain (Nyborg & others, 2017; Van Bakel & others, 2012b).

General observations on Raninoida

Extant biogeography.—Hartzell & others (2022) showed that Raninoida as a group experienced an overall reduction in geographic range over geologic time, from cosmopolitan in the early Cenozoic to tropical and subtropical only in modern oceans. Across extant Lyreididae and the extant members of subfamilies of Raninidae, nearly all overlap to some extent in geographic distribution (OBIS, 2024). Lyreidids are absent from Africa, and Raninidae are absent from the Americas, but otherwise, most subfamilies overlap with one another and/or Lyreididae. The overlapping geographic distribution is complemented by niche partitioning between Raninidae and Lyreididae. Lyreididae has inhabited mainly siliciclastic sediments for most of its geological record, whereas Raninidae inhabited a higher percentage of carbonate environments (Hartzell & others, 2022). Among the subfamilies of Raninidae, there may also be some degree of niche partitioning, for example, with Raninoidinae mostly occurring in siliciclastics across geologic time and Ranininae mostly occurring in carbonates, at least in the fossil record.

Burying behavior.—*Ranina ranina* (Raninidae, Ranininae), also called spanner crab or Kona crab, comprise an important Indo-Pacific fishery. Consequently, they have received at least some ecological and ethological attention. Their main habitat is sandy bottoms in shallow shelf depths of 2–200 m, and they prefer strong currents and proximity to coral reefs (Thomas & others, 2013). They scavenge and spend most of their time buried in sand, presumably for predator avoidance (Thomas & others, 2013; Van Bakel & others, 2012b). They are slow-growing and apparently susceptible to high mortality when fished (Thomas & others, 2013). *Ranina ranina* uses all of its pereiopods and the pleon when digging, and it can punt with its pereiopods across the substrate and even swim short distances (Faulkes, 2006).

Other raninoids have been observed burying. An individual of *Notopus dorsipes* (Linnaeus, 1758) (Raninidae, Notopodinae), was found in the intertidal zone, shallowly buried, and when disturbed, attempted to rebury itself (Low, 2012). *Lyreidus tridentatus* De Haan, 1841 (Lyreididae, Lyreidinae), burrows in fine muddy sand substrates, using pereiopods 2–4 to excavate sand and the chelipeds to clear sand from the respiratory structures (Leng, 1964). *Raninoides benedicti* Rathbun, 1935, has been observed to bury in soft, muddy substrates, to avoid visual detection and for ambushing soft-bodied prey (Luque & others, 2019). These species seem to be the only raninoids actually having been observed burrowing.

Van Bakel & others (2012b) proposed that the narrow sternum in raninoids was secondarily acquired as a specialization for burrowing, as it results in placement of

the coxae of the pereiopods ventral to the body instead of displaced laterally, which facilitates more efficient burrowing. The gymnopleuran condition, a specialization of Raninidae, was described as a result of reduction of the branchiostegite, which exposes the posterior sternites, and subsequent development of a channel along these plates to facilitate respiration (Bourne, 1922; Van Bakel & others, 2012b). Other morphological features present in Raninidae to facilitate burying are flattened pereiopods for digging or scooping sediment, an elongate carapace shape, and a posteriorly extended, flexible pleon that can loosen or move sediment (Van Bakel & others, 2012b).

Sexual dimorphism.—Sexual dimorphism of the pleon and gonopore position is known in most groups of crabs. Raninoidea exhibit sexual dimorphism in both of these, as well as occasionally, the shape and size of the anterolateral spines. Although the pleon of both males and females is narrow in Raninoida, it is noticeably wider in females of species of both Lyreididae and Raninidae (Feldmann & Schweitzer, 2007). More unusually among brachyurans, the shape of the anterolateral spines may be sexually dimorphic. In extant *Ranina* and extinct *Lophoranina*, males have slightly larger anterolateral spines that may also be more complex, with tiny denticles or bifid tips in males (Feldmann & Schweitzer, 2007).

Cuticle.—The monotypic *Marylyreidus* (Lyreididae) as well as species of *Cretacoranina* and *Eucorystes* (Palaeocorystidae), in two separate families, exhibit distinctive hexagonal plates that cap fungiform structures in the cuticle (Haj & Feldmann, 2002). These structures slope asymmetrically, so that the gentle slope is posterior and the steep slope is anterior, posited to allow the cuticle to grip sediment surfaces while burrowing (Haj & Feldmann, 2002). The external cuticular structures of Raninoida are quite variable and have been well described and illustrated (Waugh & others, 2009).

DAKOTICANCROIDA

Dakoticancroida embraces two families and eight genera, all predominantly in siliciclastic environments (Table 2). Only one occurrence of the section is reported outside of North America, in Spain. This section appears to have been a casualty of the events in the North Atlantic at the end Cretaceous, becoming extinct in the Maastrichtian (Schweitzer & Feldmann, 2005, 2023). The two included families have similarities in the nature of the dorsal carapace but the sterna are rather different (Karasawa & others, 2011). In Ibericancridae, the sternum is narrower and with a deeper sternopleonal cavity than seen in Dakoticancridae, in which the sternum is very wide and the sterno-pleonal cavity is wide and shallow. In both families, sternites 3–8 are parallel and rectangular in shape, with small episternal projections, which differentiates the two families from other podotremes. Pereiopods 4 and 5 are reduced in Ibericancridae, whereas only pereiopod 5 is reduced in Dakoticancridae (Karasawa & others, 2011, fig. 12). Bishop & others (1998) suggested a carrying habit for *Avitelmessus* Rathbun, 1923, and *Dakoticancer* Rathbun, 1917, based on their reduced pereiopods 5. Specimens often seem to be missing their fifth pereiopods in *Avitelmessus*, but where the coxae or entire pereiopod are visible, they appear to extend posterolaterally and not subdorsally (Kesling & Reimann, 1957). Specimens of *Dakoticancer* are similar, in that the fifth coxae are reduced but directed posterolaterally (Jones & others, 2022). Examination of hundreds of specimens of *Dakoticancer* and *Tetracarcinus* Weller, 1905, did not identify a specimen with fifth pereiopods held subdorsally (Schweitzer & others, 2025a). Thus, Dakoticancridae may exhibit a similar morphology to Dynomenidae, wherein the fifth pereiopod is reduced but not subdorsal and is largely vestigial.

Dakoticancridae differs from other podotrematous families in having a wide, flattened sternum that positions the pereiopods quite far laterally, and very distinctly

sexually dimorphic sterna (Jones & others, 2022). Carapace ornamentation changes as individuals grow, with more distinct carapace ridges in smaller individuals and more pronounced orbital ornamentation in larger individuals (Schweitzer & others, 2025a). All members of this family are North American, having been reported from Western Interior, Gulf Coastal, and East Coastal locations.

Dakoticancridae are abundant in the Western Interior and Gulf Coastal North America. Huge collections of *Dakoticancer overanus* Rathbun, 1917, from a single site in South Dakota, for example, have well-documented intersex individuals, a phenomenon that seems to be distinct to that population (Jones & others, 2022) (Fig. 3.6). Similarly large numbers of specimens of *Tetracarcinus subquadratus* Weller, 1905, have been collected from Gulf Coastal localities in Mississippi, which document ontogenetic changes in carapace shape and ornamentation but not intersex individuals (Schweitzer & others, 2025a) (Fig. 3.12).

Ibericancridae are less well-known, and taxa are not as abundant at collecting localities. The type taxon was reported from Spain, and other occurrences are all in Western Interior, Gulf Coastal, and East Coastal North America. Occurrences of both Dakoticancridae and Ibericancridae are almost exclusively in siliciclastics, with outliers in marls and chalk. The group, especially Dakoticancridae, seems to have been geographically restricted but locally abundant until their extinction at the end of the Cretaceous.

CYCLODORIPPOIDA

Cyclodorippoida are odd in possessing a sternum quite unlike other podotremes, with a wide cavity to accommodate the pleon in males and with sternites 7 and 8 positioned perpendicular to the other sternites (Tavares, 1992). They are recovered as sister to the eubrachyurans (Ahyong & others, 2007; Karasawa & others, 2011; Luque & others, 2019, 2021, 2024; Wolfe & others, 2024). They have pereiopods 4 and 5 or 5 only subchelate and held dorsally to carry camouflage (Poore & Ahyong, 2023). They are small crabs with soft cuticle, perhaps explaining their limited fossil record (Karasawa & others, 2011). The wide sterno-pleonal cavity is suggested to have evolved only once, and occurs in both Cyclodorippoida and Eubrachyura (Ahyong & others, 2007).

Four families are recognized in one superfamily. The earliest occurrences are Early Cretaceous (Albian) of Cyclodorippidae and Quadratoplanidae. The distinctive sternal features of Quadratoplanidae ensure its placement in the section and the appearance of the cyclodorippoid sternum morphotype by Albian time (Franţescu, 2014) (Fig. 3.11). Cyclodorippidae maintained low diversity through the Cenozoic, and Quadratoplanidae became extinct in the Maastrichtian. Cymonomidae have been reported from the Eocene of Europe and west coastal North America (Fig. 4.10). Most of the occurrences of the section are in siliciclastic sediments, with only a few exceptions. Extant cyclodorippids inhabit a variety of depths, whereas cymonomids and the extant only Phyllotymolinidae inhabit deeper, outer shelf to slope depths (Poore & Ahyong, 2023). The limited fossil record makes it hard to interpret the evolutionary history of the group.

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Institutional Abbreviation

USNM: United States National Museum of Natural History, Smithsonian Institution, Washington, DC, USA

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