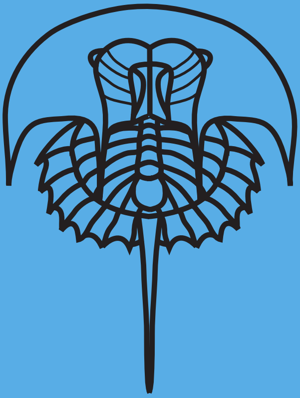

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PART R, REVISED, VOLUME 1: TREATISE ONLINE 179

GENERALIZED EXTERNAL ADULT DECAPODA MORPHOLOGY

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Decapoda are members of Eumalacostraca, characterized by possession of three basic body regions, the cephalon, thorax, and pleon, comprised of five, eight, and six somites respectively (Fig. 1). Like most crustaceans they possess two pairs of antennae. The cephalon and thorax are fused to form what is typically termed the cephalothorax, and this structure is covered by a dorsal carapace (also called the shield), a continuous plate of cuticle covering and fused to the 13 somites of the cephalon and thorax. In Decapoda, thoracic somites 1 through 3 along with their respective appendages are fused to the head and are modified to function as mouthparts, leaving five pairs of thoracic appendages resulting in the name of the group. This chapter deals primarily with adult morphology. Larvae and juveniles will be discussed in more detail in a separate chapter; included here is generalized morphology for those larvae known from the fossil record.

Across Decapoda, there is considerable variation in the shape and nature of the carapace, pleon, and appendages (Fig. 2). A general description of the morphology of Decapoda precedes more specific descriptions for each group. General morphological discussions are based on several works as well as personal observations (Glaessner, 1969; McLaughlin, 1980; Bauer, 2004; Gherardi & others, 2010; Goy, 2010; Lavalli & Spanier, 2010; Tavares & Martin, 2010; Wicksten, 2010; Dworschak, Felder, & Tudge, 2012; Tudge, Asakura, & Ahyong, 2012; Wahle & others, 2012; Davie, Guinot, & Ng, 2015; Schram & Koenemann, 2021).

ANATOMICAL TERMS OF LOCATION

In the morphology of all animals, specific terminology is used to express direction and location on the body (Fig. 3, Fig. 4). Anterior refers to locations toward the head, or front, whereas posterior refers to the opposite location toward the rear, or tail end. The dorsal surface is the back or upper surface,

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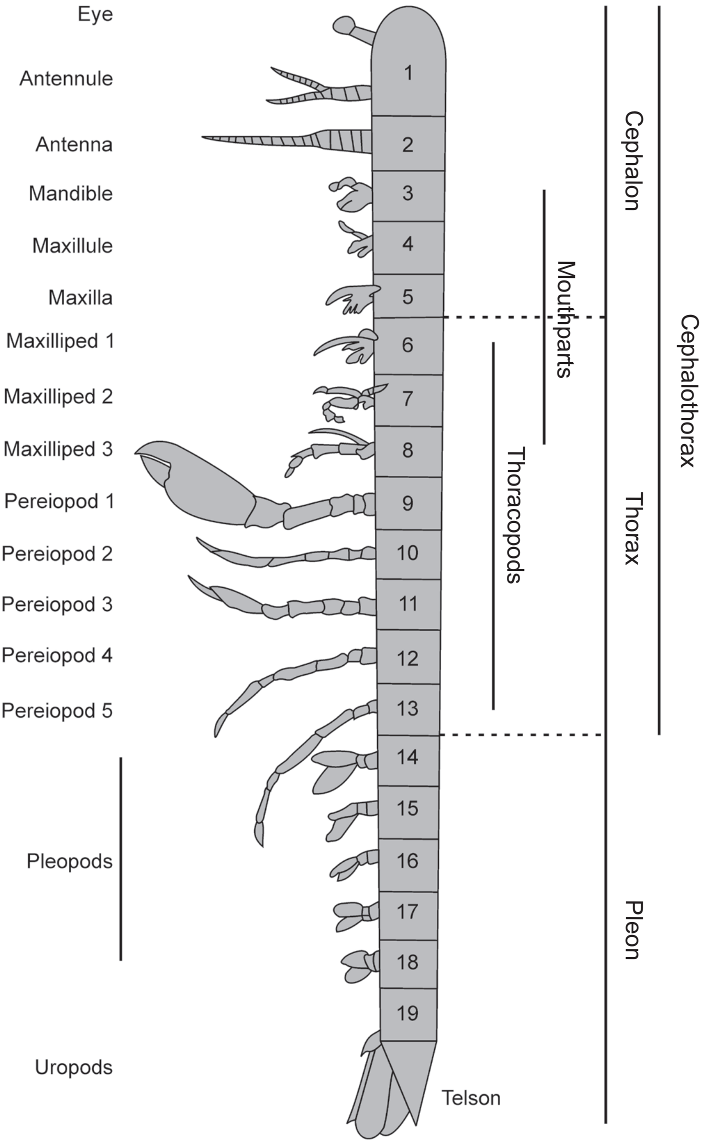


FIG 1. Generalized decapod morpology: 1–5 are cephalic somites, 6–13 are thoracomeres, and 14–19 are pleonal somites (adapted from Holthuis, 1991, fig. 2).

in decapods referring to the carapace and terga of the pleon, and the ventral surface is the lower or underside, in decapods referring to the surface including the sternum and the insertions of the pereiopods. Axial locations are along the midline of the body, whereas lateral locations are positioned away from the axis or midline. Proximal refers to locations at the base of a structure, such as an appendage or positions close to the axis. Distal structures are situated away from the midline or furthest from the base of a structure, such as an appendage.

DECAPOD CARAPACE

All Decapoda possess a carapace, the dorsal cephalothorax (Fig. 2). This cuticular structure extends from the anterior end of the head and covers all 13 somites of the cephalon and thorax, folding laterally to form a chamber for the gills (Oleson, 2013). A notable exception occurs in Achelata, in which the antennular somite is not covered by the carapace (Holthuis, 1991). The carapace ranges from being a ventrally open cylindrical structure in shrimp and some lobsters to an ovate, dorsally flattened, platelike structure in most crabs. The carapace protects the cephalothorax and is fused to the cephalic and thoracic somites dorsally (Warner, 1977). It provides a site of attachment for muscles and can contribute to hydrodynamics or the ability to burrow (Oleson, 2013). In a few taxa, such as palinurid lobsters, the carapace is used for sound production (Henninger & Watson, 2005).

The decapod carapace is characterized by several general features (Fig. 5). Anteriorly, a rostrum or frontal area extends between the orbital regions, which are usually at least somewhat concave or notched and house the eyes. The lateral margins of the carapace can be smooth or spinose. Dorsally, an array of grooves, spines, tubercles, keels, or other structures may be present, and the carapace is divided into various regions that may or may not reflect internal anatomy.

The branchiostegite is the lateral and ventral folding of the carapace (tergal in nature) around the gills, forming the outer wall enclosing of the branchial chamber (Fig. 6.1, 6.4). The pterygostome is a cuticular plate bounding the buccal frame in crabs and other flattened decapods, which, in Brachyura, is separated from the carapace by the *linea brachyura* (Davie, Guinot, & Ng, 2015) (Fig. 6.4). The proepistome (interantennular septum) and the epistome are located anteriorly (Fig. 6.1–3). The proepistome is small and is the ventral portion of the cephalic somite bearing the antennules (Davie, Guinot, & Ng, 2015). The epistome forms a plate between the bases of the antennae (Davie, Guinot, & Ng, 2015).

Considerable attention is directed to the carapace margins and dorsolateral carapace regions, because these are most commonly used in identification of fossil decapods. The dorsolateral carapace is commonly the only, or the most completely preserved, part of the fossil organism, exclusive of isolated cheliped elements. A complicated nomenclature of grooves, spines, and keels has been developed to characterize the carapace of decapods (Fig. 5). Terminology for grooves, especially the major grooves such as the cervical and branchiocardiac, is applied across Decapoda, although whether these grooves are truly homologous has not been determined. Glaessner (1960) and Secrétan (1982) considered that some grooves were dorsal expressions of internal segmentation, whereas Albrecht (1981) and Tshudy and Babcock (1997) interpreted grooves as muscle attachment sites. Spines and keels are less universally named across Decapoda. Discussion of spines, keels, and grooves specific to each decapod appear herein under the relevant group.

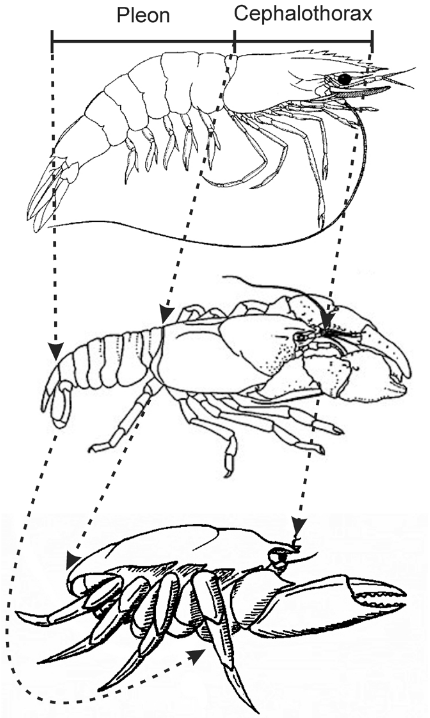


Fig 2. Generalized decapod body plan in shrimp, lobsters, and crabs, top to bottom (adapted from Glaessner, 1969, fig. 217).

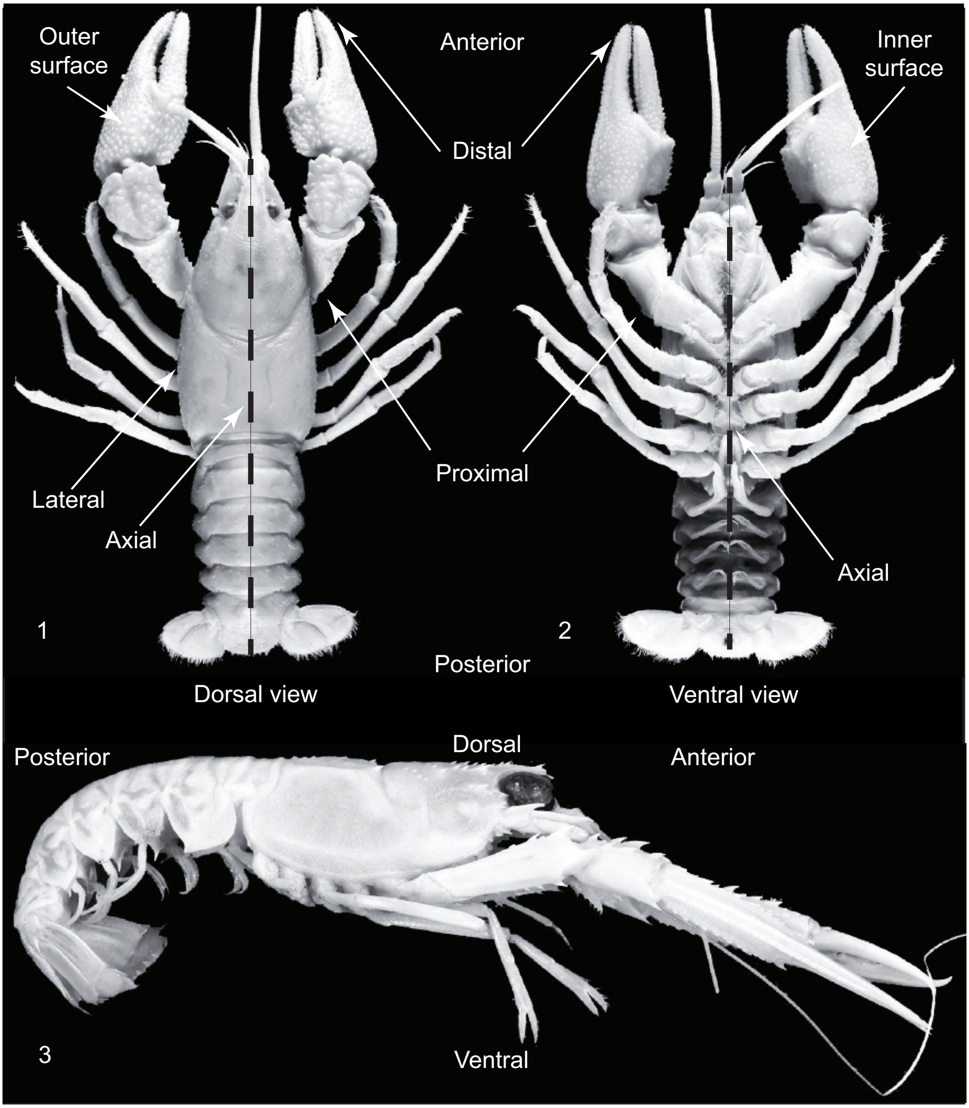


Fig. 3. Anatomical terms of location for decapods: *1,* dorsal, and *2,* ventral views of a freshwater crayfish SMF-13096; *3,* right lateral view of nephropid lobster (Feldmann, Schweitzer, & Karasawa, 2016, fig. *1–2* and 20,*1*; images *1–2,* photos by Sven Tänkner; *3,* photo by R. Feldmann)

MAJOR CARAPACE GROOVES

Holthuis (1974) is followed, unless otherwise attributed. The letter designations for the grooves follow Van Straelen (1925) and Glaessner (1969) each following Boas (1880), the latter of whom originated these designations. Although the letter system is obscure, it has remained in use. Charbonnier and others (2013) also provided a detailed set of terms for the body regions and grooves on the carapace of glypheidean lobsters, the body regions being more-or-less specific to glypheids, and the grooves following closely the general nomenclature derived from Van Straelen (1925) and subsequent works such as Holthuis (1974). The cervical, postcervical, and branchiocardiac grooves are most widespread across

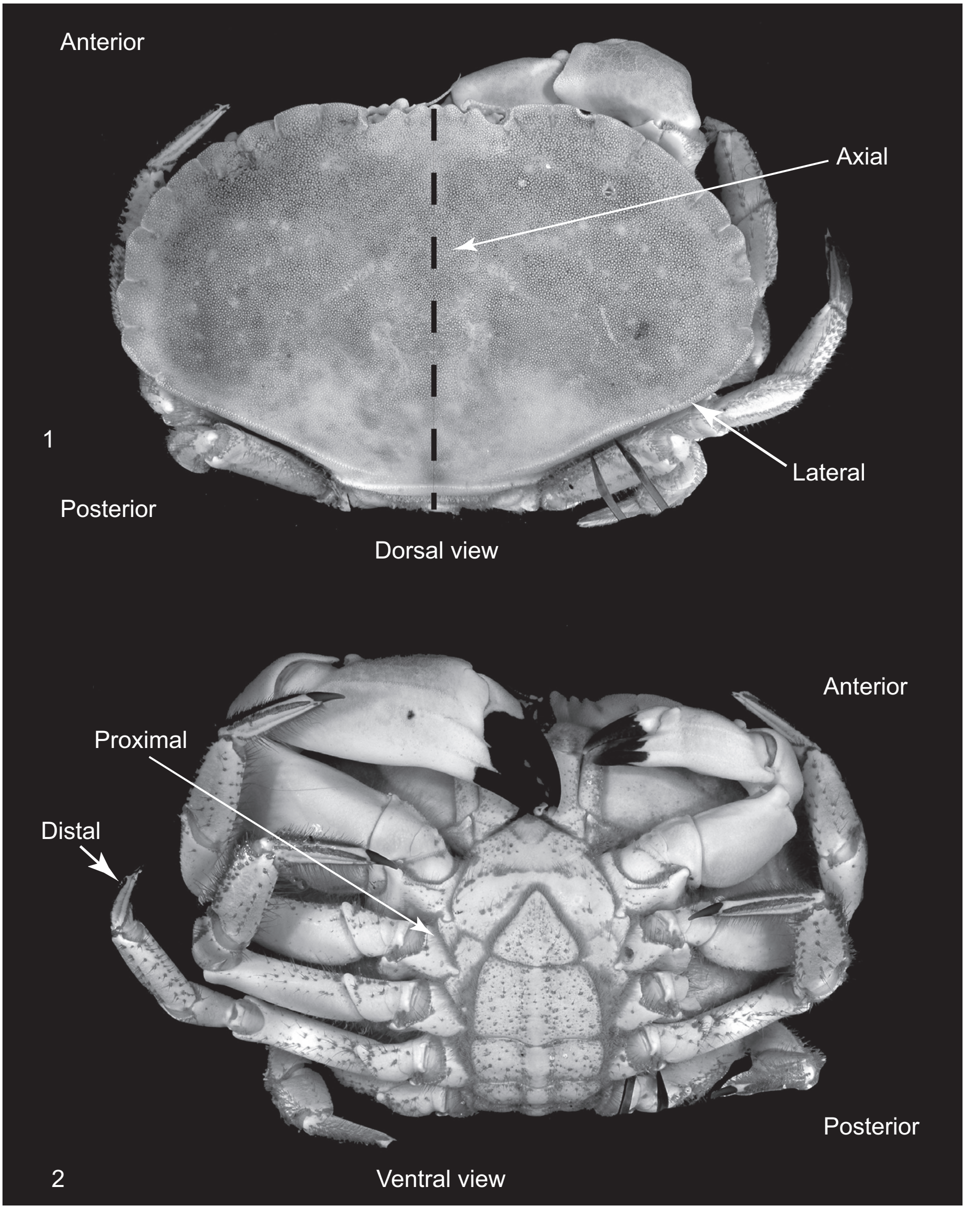


Fig. 4. Anatomical terms of location for decapods: *1,* dorsal, and *2,* ventral view of cancrid brachyuran (Schweitzer & Feldmann, 2019b, fig. 2,*1a–b*; photo by R. Feldmann).

Decapoda, although homology has not yet been demonstrated. Groove patterns of a generalized lobster are illustrated in Figure 5.

Some grooves are recognized only in specific decapod groups, and those are described and illustrated for their appropriate taxa.

Cervical groove (*e–e′*).—The cervical groove is the most commonly identified groove among Decapoda. It is usually at least moderately developed as a transverse groove that separates the gastric and hepatic regions anteriorly from the cardiac and branchial

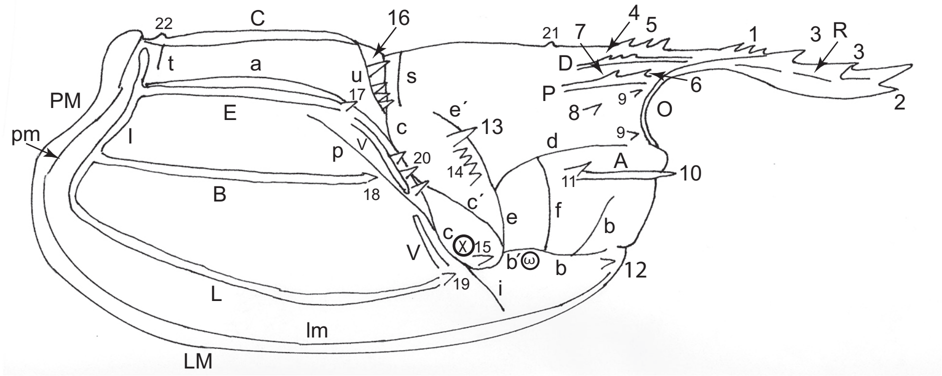


Fig. 5. Groove, spine, and carina terminology of lobsters: a=branchiocardiac groove; b=antennal groove; b´=hepatic groove; c=postcervical groove, c´=intercervical groove; d=gastro-orbital groove, e-e´=cervical groove; f=buccal groove, i=inferior groove; lm=lateromarginal groove; p=parabranchial groove; pm=postmarginal groove; s=seller groove; t=intestinal groove; u=urogastric groove; χ=attachment of musculus dorsoventralis posterior (musculus adductor testis); ω=swelling near cervical groove; A=antennal carina; B=branchial carina; C=median carina; D=subdorsal carina; E=intermediate carina; I=intestinal carina; L=lateral carina; LM=lateromarginal carina; O=orbital carina; P=supraorbital carina; PM=posteromarginal carina; R=rostral carina; V=postcervical carina; 1=suprarostral spine; 2=subrostral spine; 3=lateral rostral spine; 4=subdorsal spine; 5=medial spine; 6=supraorbital spine; 7=postsupraorbital spine; 8=postorbital spine; 9=metorbital spine; 10=antennal spine; 11=postantennal spine; 12=branchiostegal spine; 13=cervical spine; 14=cervical spinelets; 15=hepatic spine; 16=postcervical spine; 17=intermediate spine; 18=branchial spine; 19=lateral spine; 20=postcervical spinelets; 21=gastric tubercle; 22=intestinal tubercle (adapted from Holthuis, 1974, fig. 2).

regions posteriorly. It typically crosses the median line but can also be restricted to the marginal part of the carapace, as in Nephropoidea. As such, confusion may arise with the postcervical groove.

Postcervical groove (*c*´).—The postcervical groove is typically shorter than the cervical groove. It is positioned posterior to the cervical groove and more or less parallel to it and may be developed only axially, or more commonly as segments lateral to the axis.

Branchiocardiac groove (*a*).—The branchiocardiac groove separates the branchial and cardiac regions of the carapace. It more-or-less parallels the cervical and postcervical grooves at least laterally, but it arcs posteriorly as it approaches the axis. It extends from the hepatic groove, near the anterior edge of the postcervical groove, crosses the lateral margin of carapace, in dorsoventrally flattened groups, then extends through the branchial region and parallels the lateral margins of the cardiac region, if present (Audo, Hyžný, & Charbonnier, 2018).

Antennal groove (*b*).—A short groove extending anteriorly from the ventral (lateral) part of the cervical groove.

Hepatic groove (*b*´).—Extends posteriorly from the cervical groove at the level of the antennal groove and connects the cervical groove with the postcervical groove and/or the branchiocardiac groove.

Intercervical groove (*c*´).—An oblique groove connecting the lateral part of the cervical groove with the postcervical groove.

Gastro-orbital groove (*d*).—A short groove extending anteriorly from the cervical groove, at about the midlength of cervical groove.

Inferior groove (*i*).—A short groove extending ventrally (laterally) from the intersection of the hepatic and postcervical grooves.

CARAPACE REGIONS

Regional development of the carapace is best expressed in Brachyura, for which an extensive terminology has been developed. In shrimps and lobsters, regional termi-

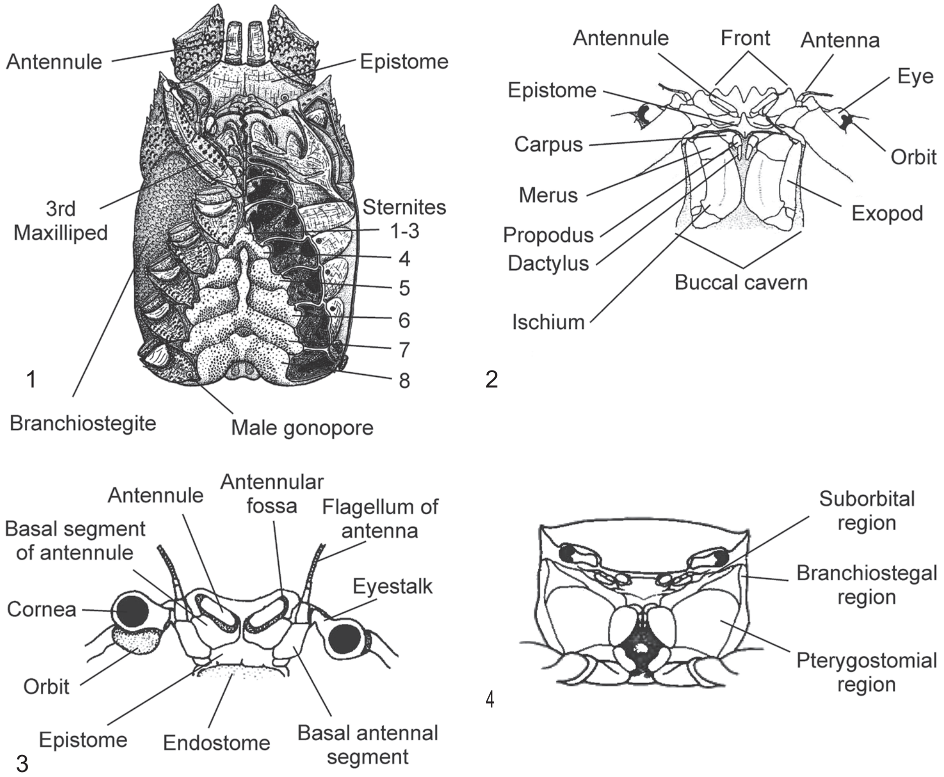


Fig. 6. Ventral carapace features: *1,* ventral morphology of palinurid lobster (adapted from Lavalli & Spanier, 2010, fig. 68.2); *2,* anterior oblique view of brachyuran; *3,* ventral view of brachyuran buccal area; *4,* anterior view of brachyuran with lateral margins (*2–4* adapted from Davie, Guinot, & Ng, 2015, fig. 71–2,13D–F).

nology is not typically used; instead, the carapace is referred to as cephalic (anterior to cervical groove) and thoracic (posterior to cervical groove). Very different terminology from that applied to the brachyurans has been developed for Anomura and Glypheidea. Regional development of the carapace is thus discussed under each decapod group.

CARAPACE ORNAMENTATION

Macroscopic carapace ornamentation is typically comprised of spines, carinae, tubercles, granules, pits, or other structures. (For microscopic elements of the carapace, please see an upcoming *Treatise Online* article on cuticle.) Holthuis (1974) provided an extremely detailed set of terms for spines and carinae of nephropid lobsters, based on their position on the carapace (Fig. 5). These terms are typically used for lobsters and can be applied to shrimps in which the main ornamentation is comprised of spines and carinae, although the terms used for shrimp may differ (Pérez Farfante & Kensley, 1997). A variety of terms have been used for other ornamentation types, which can seem arbitrary; therefore, ornamentation terms used in all Part R articles are defined below. Note that these ornamentation types can occur anywhere on the cuticle, including on appendages.

Spines.—Sharp macroscopic protuberances extending distally from the surface of the exoskeleton (Fig. 7.1, 7.6). Blunt spines have been called teeth in some literature, which is avoided here (with the exception of on fingers of the chelae) because teeth are defined as occluding or intermeshing surfaces (see the Oxford English Dictionary definition, for example).

Tubercles.—Large, prominent, blunt, of varying shapes—but typically spherical structures—that stand above the surface. Tubercles are frequently broadly spaced on the surface (Fig. 7.1).

Granules.—Small, but still macroscopic, blunt, spherical, and ordinarily densely spaced, standing minimally above the surface. These structures are more likely to be densely spaced than are tubercles (Fig. 7.1). (There is certainly a size continuum between granules and tubercles, but the aim here is to reflect the general usage of the terms.)

Carinae, keels, or ridges.—Narrow, elongate, upraised structures on the surface that that may be ornamented with spines or tubercles (Fig. 7.1).

Pits.—Concave, sunken structures, also called punctae (Fig. 7.2). If they are perforated, they are probably setal pits, but some pits can be remnants of hollow spines (Charbonnier & others, 2014).

Terraced ridges.—These are transverse ridges that may be continuous (Fig. 7.3, 7.5) or discontinuous (Fig. 7.4), and they have the upraised, steep slope directed anteriorly grading posteriorly into the carapace surface. The anterior edges can be spinose or setose (Fig. 7.5). Short and discontinuous ridges are termed scabrous or squamate. In Raninoida (frog crabs), they facilitate burying behavior (Savazzi, 1981).

Carapace lineae.—Some decapod groups exhibit *lineae,* which are longitudinal, narrow grooves or linear weakly calcified areas that constitute an interruption in the cuticle. They facilitate molting, as the carapace separates along these *lineae* during ecdysis. Decapod groups have specific types of *lineae* which help to diagnose them, discussed under each group in which they occur. Homologies between and among *lineae* have yet to be determined (Glaessner, 1969).

THORACIC STERNUM

All decapods possess a thoracic sternum comprised of individual sternites, which form the ventral surface of the thoracic somites (Fig. 8.1–2). The sternites are fused to one degree or another, but in all cases, sutures can be seen as remnants of segmentation unlike on the carapace, which does not display remnants of segments. The sternites articulate laterally with the thoracic appendages. The shape and size of sternites, their degree of fusion, and the means of articulation with the appendages is diagnostic at the family—and, in some cases—at the infraordinal level. The sternum has received varying amounts of attention and description. In some groups it is not typically illustrated, such as in caridean shrimp, whereas in Brachyura and Anomura, sternal features are diagnostic at the family or higher levels (Davie, Guinot, & Ng, 2015). Sternites 1–3 are smallest and reduced in size; sternites 1 and 2 are seldom seen in fossils.

PLEON

The pleon of Decapoda (called the abdomen in older literature) is comprised of six somites plus a telson (Fig. 8.3). Pleon has become the preferred term because the

Fig. 7. Carapace and pereiopod ornamentation in decapods (see facing page). *1, Mursia marcusana* Rathbun, 1926 (Calappidae), UWBM 103145, Oligocene-Miocene, with granule (Gr), keel (K), spine (Spi), and tubercle (Tu) labeled (Schweitzer & Feldmann, 2019a, fig. 2,*3a*); *2, Mesostylus mortoni* (Pilsbry, 1901), MMNS IP-2368, (Callianassidae), chela of shrimp with pit labeled; *3,* galatheoid carapace, *Mesogalathea striata* (Remeš, 1895) (Paragalatheidae), NHMW 2007z0149/0260, Tithonian, with terraced transverse ridges; *4,* galatheoid carapace, *Ankylokypha parabola* Robins, Feldmann, & Schweitzer, 2012 (Munidopsidae), NHMW 2007z0149/0119, Tithonian, with transverse scabrous ridges; *5, Vegaranina precocia* Feldmann & others, 1996 (Raninidae), KSU D 642 brachyuran carapace with terraced ridges with tiny spines on anterior edge; *6, Ranina ranina* Lamarck, 1801 (Raninidae), USNM 268506, Holocene, brachyuran carapace with forward-directed spines (*2,* Schweitzer & others, 2019, fig. 9, *3–4,* photo by C. Robins, University of Alabama; *5,* new, photo by R. Feldmann; *6,* Feldmann & Schweitzer, 2007, fig. 1C).

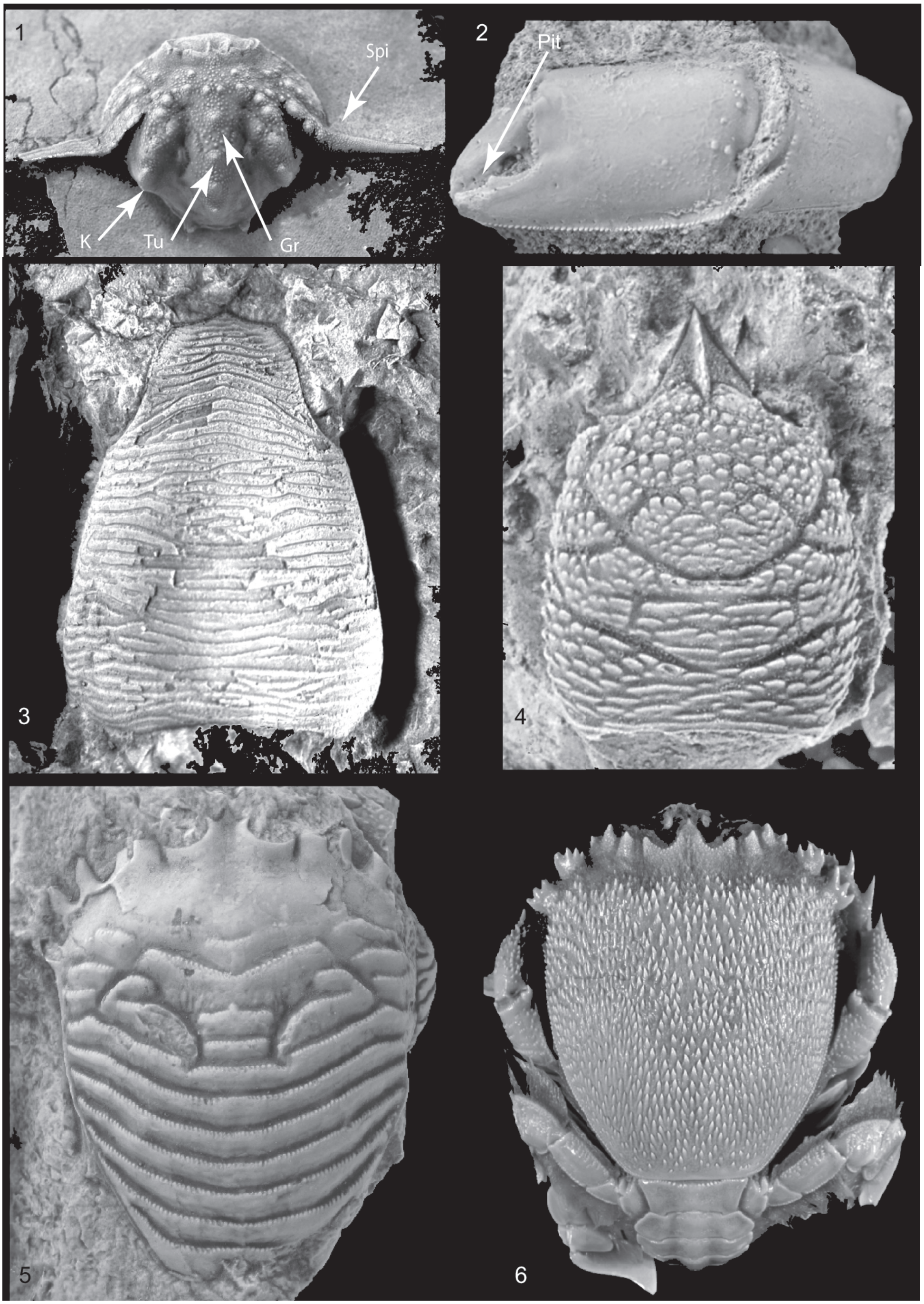


Fig. 7. Carapace and pereiopod ornamentation in decapods. See explanation on facing page.

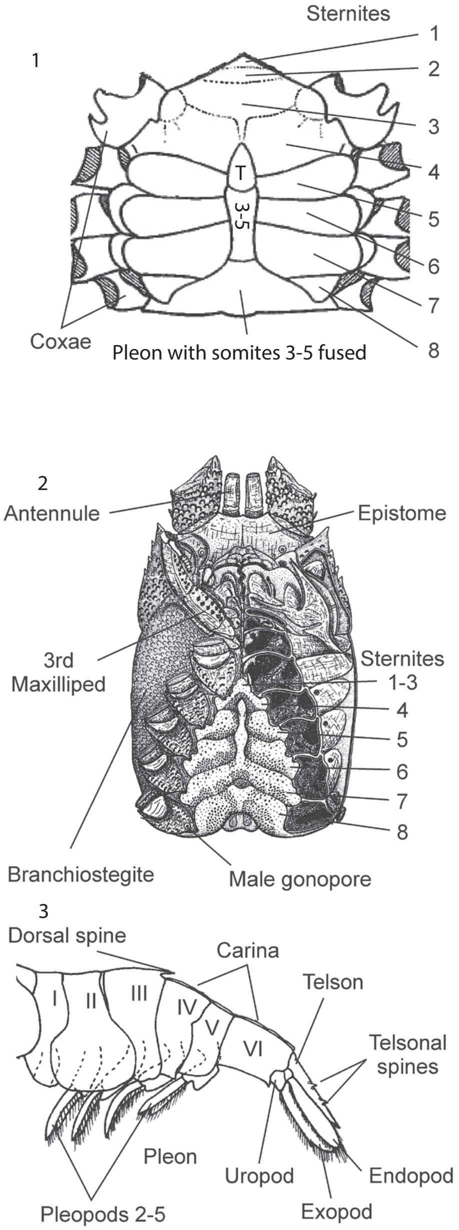


FIG. 8. Sternal and pleonal morphology. *1,* Brachyuran sternum (adapted from Rathbun, 1930, fig. 2A), (T=telson, 3–5=pleonites with 3–5 fused, sternites 1–8 numbered); *2,* palinurid lobster sternum (adapted from Lavalli & Spanier, 2010, fig. 68.2), sternites 1–8 numbered; *3,* caridean shrimp pleon (Roman numerals indicate pleonites I–VI), note that pleonite II overlaps pleonites I and III (adapted from McLaughlin, 1980, fig. 45A).

individual somites bear appendages and display a well-developed nervous system, whereas in an abdomen, the somites lack appendages and a well-developed nervous system (Schram & Koenemann, 2004, 2021; Schram, 2013). These differences are fundamental in the development of the animal as they are based upon HOX gene expression (Schram, 2013). Research on developmental patterns in crustaceans is proceeding apace, not to mention the recovery of older and older fossil crustaceans and crustaceomorphs, which will continue to affect our interpretations of decapod morphology, development, and phylogeny (Schram & Koenemann, 2021) Herein, the term thorax, as it has traditionally been used in the literature, is retained. Pleonal appendages are called pleopods, also called swimmerets in shrimp or crayfish, and may be modified for reproduction, notably in males, in which the first one or two pairs of pleopods may handle spermatophores during copulation. The pleon is elongate and can be held posteriorly from the posterior margin of the carapace or folded under the sternum to varying degrees. Each pleonal somite (pleonite) is comprised of the dorsally situated tergum and the laterally placed pleura, which generally extend at least a bit ventral to the sternite (Fig. 9). In Decapoda, the telson is not a true somite; rather, it is an extension of the sixth pleonite, and the uropods are the appendages of that somite (Bowman, 1971). The position of the anus on the telson is variable but it is never at the posterior terminal of the telson (Bowman, 1971). In some astacideans, the telson has a diaresis.

DECAPOD EYES

Eyes are not true appendages because they are not associated with their own body segment. As for most malacostracans, decapod eyes can be chiefly divided into two main types, depending on their internal optical characteristics and image-forming mechanisms: apposition and superposition eyes. Apposition optics occur in all larvae, adult axiideans, and several species of anomurans and brachyurans. In this type of eye, each ommatidium collects light independently from its neighbor. For each ommatidium, light enters a corneal lens, travels down the crystalline cone, and reaches the rhabdome, the light-sensing area of the ommatidium. In this eye type, the ommatidial facet is usually hexagonal, but local variations may occur. The second main type of eye exhibits superposition optics and occurs in adults of most decapods. In this eye type, the dioptric apparatus, comprised of the corneal lens and the underlying crystalline cone, of each ommatidium is separated from the light sensitive elements of the eye by a clear-zone. This organization allows the ommatidial lenses to unite to form an erect image on the light sensitive layer of the eye, increasing considerably the amount of light collected and hence the sensitivity of the eye. Ommatidial facets of superposition eyes are usually square (reflective superposition) or hexagonal (refractive and parabolic superposition). On the surface of the eye, a few ommatidia may have a different shape as a result of packing. Fossil decapods regularly preserve traces of the ommatidial facets or even the ommatidial facets themselves (Tanaka & others 2009, Charbonnier & others, 2013, Audo & Charbonnier 2013, Audo & others 2016, Audo, Winkler, & Charbonnier, 2021; Luque & others, 2019a, 2019b).

DECAPOD APPENDAGES: GENERALIZED

Limbs of Decapoda are considered to be biramous, although in many cases one of the rami is lost, usually the exopod. The generalized decapod appendage is comprised of a basipodite carrying an endopod and an exopod (Fig. 10).

Basipod.—The basipod is comprised of the most proximal podomeres of the appendage, called the pre-coxa, coxa, and basis. The coxa may carry an epipod. All elements of the

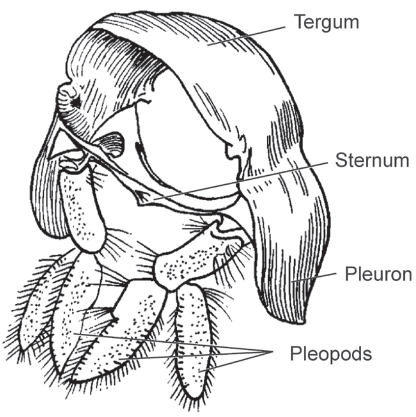


Fig. 9. Pleonal segment. Tergum is dorsal portion, pleuron is lateral portion, and sternum is ventral portion (adapted from Glaessner, 1969, fig. 230).

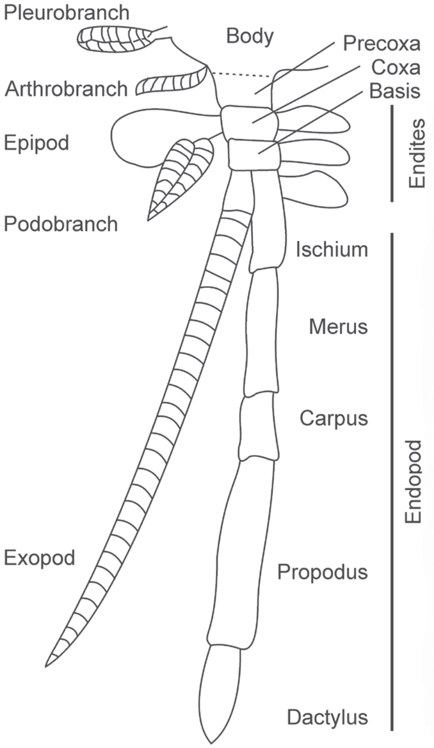


Fig. 10. Generalized decapod limb (adapted from Holthuis, 1993, fig. 2)

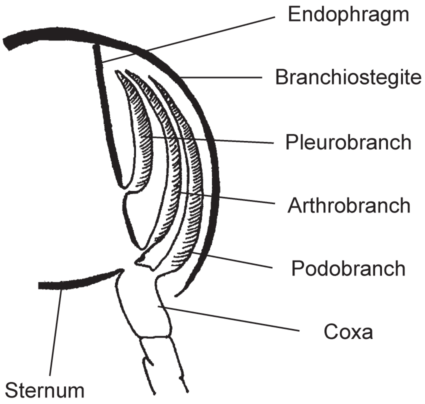


Fig. 11. Position of gill origins in generalized decapod. Space between branchiostegite and endophragm is branchial chamber (adapted from Boxshall & Jaume, 2009, fig. 11, and Fox, 2001, fig. 5).

basipod may carry endites, which are lobate projections toward the axis of the body and used in manipulating food for buccal appendages.

Exopod.—The exopod is the outer branch of the biramous appendage arising from the basis. In adult decapods it is reduced or absent in thoracic appendages. When present, for instance in larvae, it comprises numerous short articles (multiarticulate) and is used for swimming. Exopods develop on the anteriormost appendages such as the mandible, maxillae and maxillule, and maxillipeds.

Endopod.—The endopod is the inner branch of the biramous appendage, arising from the basis, and is variously specialized and modified and forms what is considered the leg of decapods. In fossil decapods, the endopod is most important in taxonomy and in interpretation of the paleoecology of the animal. The endopod is comprised of podomeres called the ischium, merus, carpus, propodus, and dactylus, from proximal to distal. These elements can be variously modified across taxa, and various combinations of elements can exhibit fusion. The endopod can be modified in some mouthparts into a palp, which is a reduced structure that can be foliaceous, tubular, or flattened.

Epipod.—The epipod is a small extension from the coxa. They are used in gill cleaning.

Endites.—These are lobes extending medially from the basal elements of the endopod. They usually occur on the mouthparts (maxillules, maxillae, and maxillipeds).

Gills.—Gills in decapods are complex. Podobranchs are attached to the coxa of the endopod or to the epipod. Arthrobranchs are attached to the arthrodial membrane between an appendage and the body wall. Pleurobranchs are attached to the endophragm (internal body wall) (Wirkner & Richter, 2013). The number, type, and arrangement of gills varies among decapod groups. In fossils, these details unfortunately are almost entirely unavailable, but they are of chief importance in biological classification of many decapod groups. In most decapods each somite and/or appendage bears four gills, a pleurobranch, two arthrobranchs, and a podobranch, depending on their position (Fig. 11). Gills are rarely preserved in fossils (Robin & others, 2018; Luque & others, 2021). Gills have varying structures, depending on the shape and organization of the gill filaments and on the decapod group (Fig. 12). Dendrobranchiate gills, with branching filaments, are present in Dendrobranchiata. Trichobranchiate gills are comprised of a series of hairlike, radiating filaments around the axis and are present in Astacida, Achelata, some Anomura (hermit crabs), and some Dromiacea in Brachyura (Wirkner & Richter, 2013). Phyllobranchiate gills are comprised of flat filaments attached to the axis and are present in most Brachyura, some Anomura, and Caridea (Wirkner & Richter, 2013) (Fig. 12).

DECAPOD APPENDAGES: SPECIFIC

Decapods are part of the larger group Eumalacostraca, itself nested within Multicrustacea. Among these, decapods are recognized by their appendage formula of 5-8-6, meaning five cephalic, eight thoracic, and six pleonal somites and corresponding pairs of appendages (Schram, 2013). The eyes are not considered homologous with other appendages. Among Decapoda, specific appendage types are present in most members (Fig. 13).

Antennules (*a1*).—Antennules, alternatively referred to as first antennae or antennae 1, are associated with the first cephalic somite (Fig. 13.1). There are basal articles and one or two flagella, occasionally three in some carideans. The first article may have a spine, called a stylocerite, which protects the statocyst in the first article (McLaughlin, 1980). Flagella are preserved in exceptional fossils. This pair of appendages functions primarily for sensing with olfactory setae or sensilla (Bauer, 2013).

Antennae (*a2*).—Antennae, also called second antennae or antennae 2, are associated with the second cephalic somite and comprise basal articles, which are endopodal, followed by a single flagellum (Fig. 13.1). The antennal exopod is modified and called the scaphocerite (sc), also referred to as the antennal scale. In swimming decapods, the scaphocerite serves to stabilize the animal during swimming/locomotion (Glaessner, 1969; Boxshall & Jaume, 2013). The scaphocerite is reduced or absent in some Decapoda. As in the case of the antennules, antennae are present in exceptionally preserved fossil specimens. The functions of the antennae are primarily sensorial, but they also house the excretory pore of the excretory glands (Felgenhauer, 1992) and may assist in filter feeding and directing water flow (Luque & others, 2019a). The antennae are used defensively, as in the spinous antenna of palinurid lobsters, which may also stridulate to produce a deterrent noise (Boxshall & Jaume, 2013). Antennae may even be modified to form a tube to facilitate breathing in burrowing crabs (Boxshall & Jaume, 2013).

Mandibles.—The mandibles are associated with cephalic somite 3. In Decapoda, the mandibles typically are comprised of a molar and an incisor process, and some with

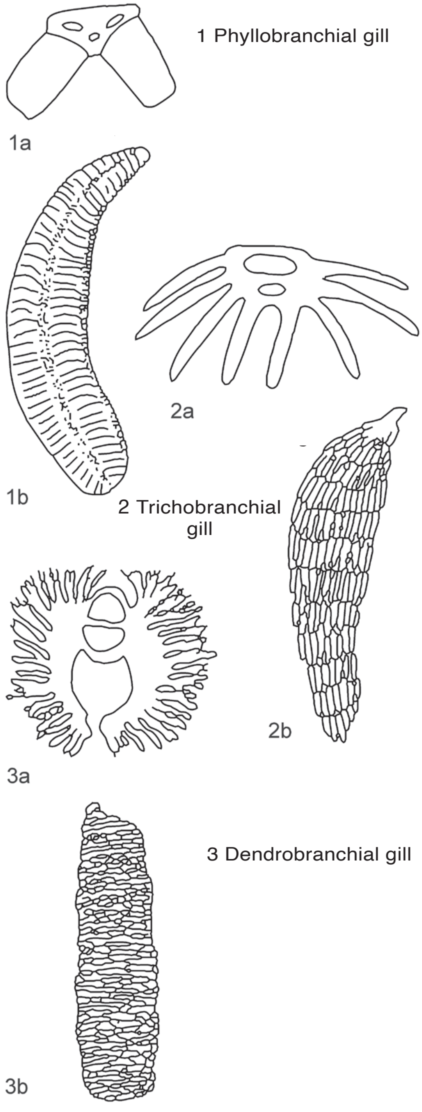


Fig. 12. Gill types present in decapod crustaceans: *1a*, cross section of phyllobranchial gill; *1b*, transverse section of phyllobranchial gill; *2a,* cross section of trichobranchial gill; *2b,* transverse section of trichobranchial gill; *3a,* cross section of dendrobranchial gill; *3b,* transverse section of dendrobranchial gill (adapted from McLaughlin, 1980, fig. 42).

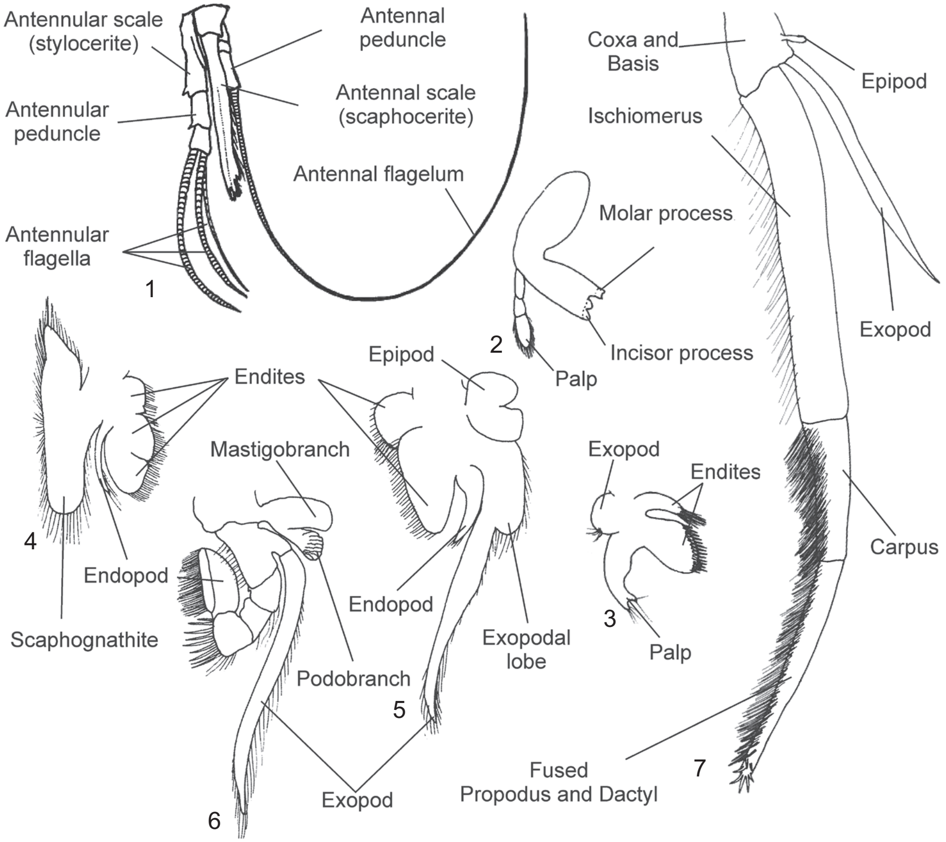


FIG. 13. Decapod appendages including antennules, antennae, and mouthparts: *1,* antennules and antennae; *2,* mandible; *3,* maxillule; *4,* maxilla; *5,* first maxilliped; *6,* second maxilliped; *7,* third maxilliped (adapted from McLaughlin, 1980, fig. 45).

a palp (Fig. 13.2). They are the primary food processing appendages, and their size and shape determine the food particles that a decapod can ingest (WATLING, 2013). They consist of either a rolling crushing structure or a rolling cutting structure with an incisor process (WATLING, 2013).

Maxillules (*first maxillae*) (*mx1*).—These are associated with cephalic somite 4. They are foliaceous and are typically comprised of a palp (endopod), endites, and the exopod (Fig. 13.3). They are used for food handling.

Maxillae (*second maxillae*) (*mx2*).—These are associated with cephalic somite 5. They are foliaceous and are comprised of endites, a palp (endopod), both for food handling, and a scaphognathite, which is a large foliaceous structure, also called the gill bailer, that functions to circulate water over the gills (Fig. 13.4).

Maxilliped 1 (*mxp1*).—This appendage is associated with thoracic somite 1 and therefore sternite 1, which along with thoracic somites 2 and 3, are fused to the cephalon in Decapoda. This structure consists of an endopod, an exopod, and various endites (Fig. 13.5). An epipod may be present, and it is used to clean the gills (WARNER, 1977).

Maxilliped 2 (*mxp2*).—This appendage is associated with thoracic somite 2. It is similar to the first maxilliped, but typically more distinct segmentation is seen in the endopod, and the exopod is usually flagellate and long (Fig. 13.6). An epipod may be present, and it is used to clean the gills (Warner, 1977).

Maxilliped 3 (*mxp3*).—This appendage is associated with thoracic somite 3 and sternite 3. Of the five pairs of mouthparts, it is most likely to be preserved in fossils because it is the largest and best developed of them. Among the mouthparts, this appendage displays the most distinct segmentation, comprising the basis through dactyl but frequently with fusion of articles (Fig. 13.7). The exopod can be flagellate. The third maxilliped can be pediform, as in dendrobranchiates, carideans, stenopodeans, and several groups of Eureptantia, in which case in fossils it may appear very similar to a pereiopod, or it can be rectangular or operculiform, forming a cover for the buccal frame, as in most brachyurans. Because it is more robust and better biomineralized than the other mouthparts, it is occasionally included in diagnoses for fossil groups.

The third maxilliped has multiple functions. It is used to clean the antennules of fouling and other material (Bauer, 1981, 2013; Boxshall & Jaume, 2013). An epipod may be present, and it is used to clean the gills (Warner, 1977). In some decapods, the third maxilliped is setose and is used for filter feeding (Watling, 2013). Because the mouthparts are superposed over one another (Fig. 14), they are difficult to see in fossils and only the third maxilliped is visible, because it is largest and on the outside.

Pereiopods (*P*).—Decapoda possess five pairs of pereiopods, with few exceptions, associated with thoracic somites 4–8, and therefore sternites 4–8. Pereiopods 2–5 may be referred to as walking legs. They are described as chelate, achelate, or pseudochelate and function for food procurement, locomotion, digging, grooming, carrying objects or other organisms, and in courtship (Bauer, 2013; Belanger, 2013; Faulkes, 2013). Epipods are absent from most decapod pereiopods as are the exopods, which are present only in some shrimp (Glaessner, 1969). In pereiopods of all groups except shrimp, the basis and ischium are fused. The carpus or other podomeres may be subdivided into multiple units, most commonly exhibited in the second pereiopod of dendrobranchiate and caridean

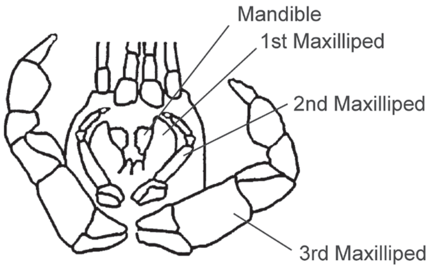


Fig. 14. Mouthparts of generalized decapod, showing their superimposition. Maxillae and maxillules hidden by first maxilliped in this view (adapted from Stamhuis, Dauwe, & Videler, 1998, fig. 1A).

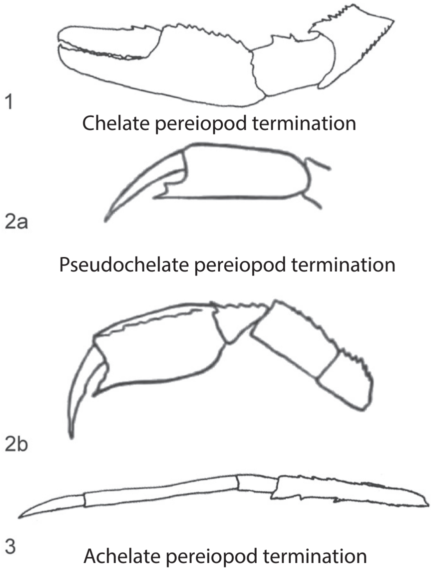


Fig. 15. Various types of pereiopod terminations: *1,* fully chelate pereiopod (adapted from McLaughlin, 1980, fig. 46A); *2a–2b,* pseudochelate (subchelate) terminations in which the movable finger largely occludes with the distal end of the propodus (adapted from Glaessner, 1969, fig. 235); *3,* achelate termination (adapted from McLaughlin, 1980, fig. 48C).

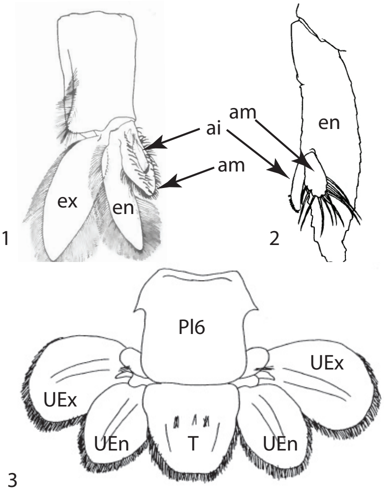


FIG. 16. Generalized pleopod morphology: *1,* second male pleopod (adapted from Hobbs & Hart, 1982, fig. 5b; *2,* second male pleopod (adapted from Chace, 1997, fig. 16h); *3,* uropods and telson of an axiidean ghost shrimp (adapted from Schweitzer Hopkins & Feldmann, 1997, fig. 2P). ai=appendix interna; am=appendix masculina, en=endopod; ex=exopod; Pl=pleonite; T=telson; UEn=uropodal endopod; UEx=uropodal exopod.

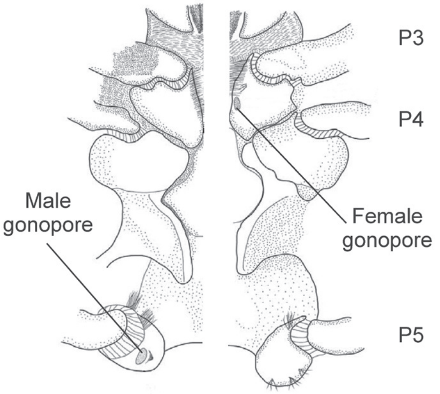


FIG. 17. Position of gonopores in all decapods except some brachyurans (adapted from Hernáez, 2018, fig. 3A). P=pereiopod.

shrimps. Specific arrangements of pereiopods are illustrated for each group.

Pereiopods are variously modified for lifestyle. They tend to be long and slender but can be flattened and paddle-like, and they are ornamented with spines, keels, tubercles, or setae, or are unornamented. Spoon-shaped tips of fingers of chelae facilitate feeding on algae (WATLING, 2013).

Most importantly for classification, various combinations of pairs of pereiopods are chelate, pseudochelate (subchelate), or achelate (Fig. 15). In an achelate appendage, the dactylus extends distally from the propodus and cannot occlude with it (Fig. 15.3). A fully chelate appendage is one in which the propodus has a distoventral extension more-or-less parallel to the propodal axis, called the fixed finger or pollex, which occludes with or crosses the dactylus, or movable finger; this condition is seen in the first pereiopods of most decapod groups (Fig. 15.1). In pseudochelate or subchelate appendages, the propodus lacks a long extension forming the fixed finger. They can lack an extension at all or display a spine or short projection, and the dactylus then partially occludes with a spine or, by pivoting approximately 90°, with the distal margin of the propodus (Fig. 15.2). This type of pereiopod termination is typical of members of Glypheoidea and is seen in some Achelata, Gebiidea, and Axiidea and rarely in Anomura and Brachyura. Pseudochelae apparently have arisen more than once.

Pereiopods can be setose for cleaning the antennules, and pereiopods 4 and 5 may bear setae for cleaning the carapace in shrimp (BAUER, 1981, 2013). Smaller chelae of pereiopods 2 and/or 3 are commonly used for cleaning the gills (BAUER, 1981). Flattened dactyls of pereiopods are modifications for burrowing, digging, or swimming (FAULKES, 2013; LUQUE & others, 2019a). Pereiopod 5 may be used for gill cleaning (BAUER, 2013).

Pleopods (*pl*).—The pleonal appendages are called pleopods. They are typically comprised of basal articles (protopod) and the endopod and exopod (Fig. 16.1–2). In shrimp, they may be multiarticulate or foliaceous and used for swimming. In most decapod females, the pleopods hold the eggs. In males, pleopods function in sperm transfer; typically the first one or two pairs are modified to transport spermatophores to the female (BAUER, 2013).

The sixth pair of pleopods is modified into uropods, which with the telson form the tail fan in most decapods (Fig. 16.3). The uropods are comprised of foliaceous endopods and exopods, which may bear a transverse suture called a diaresis. Uropods are reduced or even absent in Brachyura and some Anomura.

GENITAL OPENINGS

In most Decapoda, the female genital openings reside on the coxae of the third pereiopod and the male genital openings reside on the coxae of the fifth pereiopod (Fig. 17). The only exceptions to this are within Brachyura (illustrated on p. 99). In several brachyuran taxonomic sections, the ancestral state is retained, with both male and female genital openings on the coxae of the appendages. These taxonomic sections have been referred to as podotrematous because the pores occur on the pereiopods and include Dromiacea, Homoloida, Callichimaeroida, Torynommoida, Etyoida, Raninoida, Dakoticancroida, and Cyclodorippoida (Karasawa, Schweitzer, & Feldmann, 2011; Luque & others, 2019a, 2019b). In some brachyurans, the female genital pore is located on the sixth thoracic sternite (associated with pereiopod 3) and the male gonopore remains on the coxa of the fifth pereiopod; these are termed heterotrematous. Those with the female genital pore located on the sixth thoracic sternite (associated with pereiopod 3) and the male genital pore located on sternite 8 (associated with pereiopod 5) are termed thoracotrematous.

NATANT MORPHOLOGY: Infraorders Dendrobranchiata, Procaridea, Caridea, and Stenopodea

The shrimps, a paraphyletic group, include those decapods with relatively soft cuticle and a pleon extending posteriorly from the thorax. They are arrayed in four infraorders, Dendrobranchiata, Caridea, Procaridea, and Stenopodea. Schram and Koenemann (2021) are followed here in using the simpler forms for the latter two groups. Older literature classifies shrimp as Natantia, or swimmers, but in fact many shrimps live on the substrate. Although the four infraorders listed here differ in substantial ways, there is enough similarity across them to discuss them as a group. In fossils, it can be difficult to discern the critical characters to differentiate them.

CARAPACE

In all shrimp, the carapace is elongate and is cylindrical or laterally compressed (Fig. 18, Fig. 19, Fig. 20), with some notable exceptions such as Crangonidae (Caridea). Calcification of the cuticle is weak or absent (Amato & others, 2008). There is almost always a rostrum extending between the eyes, and the presence or absence of suprarostral and subrostral spines, and their number, can be diagnostic for families and genera. Spines, carinae, and grooves of the carapace are identified here using the schematic of Holthuis (1974) (see Fig. 5) and Pérez Farfante and Kensley (1997) (Fig. 18.2–3). These spines, grooves, and carinae are named based on their position on the carapace. These features are difficult to discern on fossilized specimens, which are almost always laterally compressed. It is notable that most shrimp families, regardless of infraorder, are diagnosed by biologists using morphological characters not typically preserved as fossils, such as features of the gills and mouthparts. Of the carapace features, the rostrum and carapace spines and grooves are most useful in classifying fossils. In fossils, supra- and subrostral spines and the length and shape of the rostrum may be observable.

THORACIC STERNUM

The sternum of shrimp receives little descriptive attention (Bauer, 2004; Tavares & Martin, 2010; Wicksten, 2010). It is narrow and elongate in all forms. In stenopodeans, the sternites become wider posteriorly but are overall proportionally narrower in males and are ornamented with spines in males and rounded protuberances in females (Goy, 2010). Dendrobranchiate females are characterized by a thelycum, which is

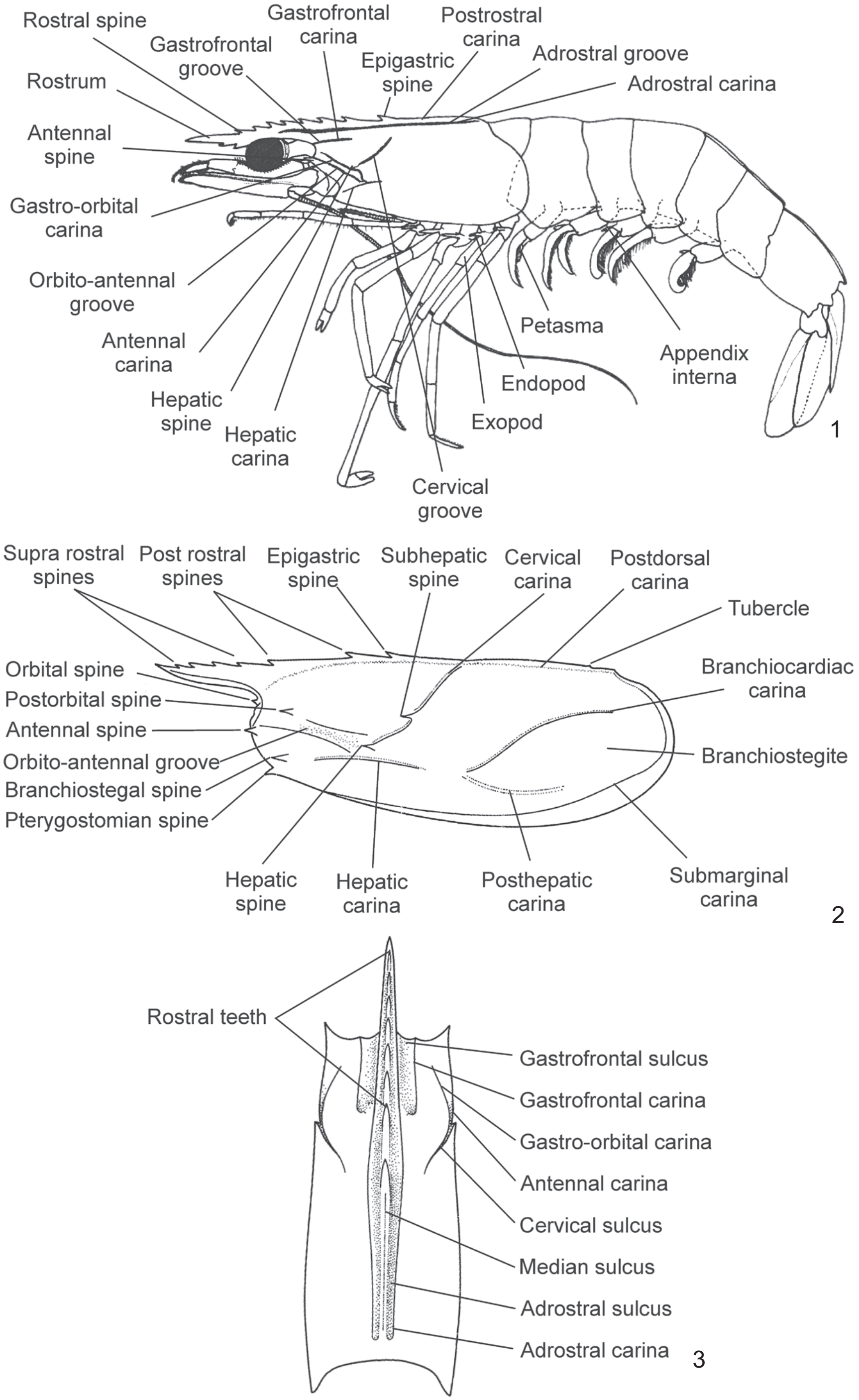


FIG. 18. Generalized dendrobranch shrimp morphology:*1,* lateral view of dendrobranch (adapted from McLaughlin, 1980, fig. 43A); *2,* lateral view of carapace; *3,* dorsal view of carapace (*2* and *3* adapted from Pérez Farfante & Kensley, 1997, fig. 2).

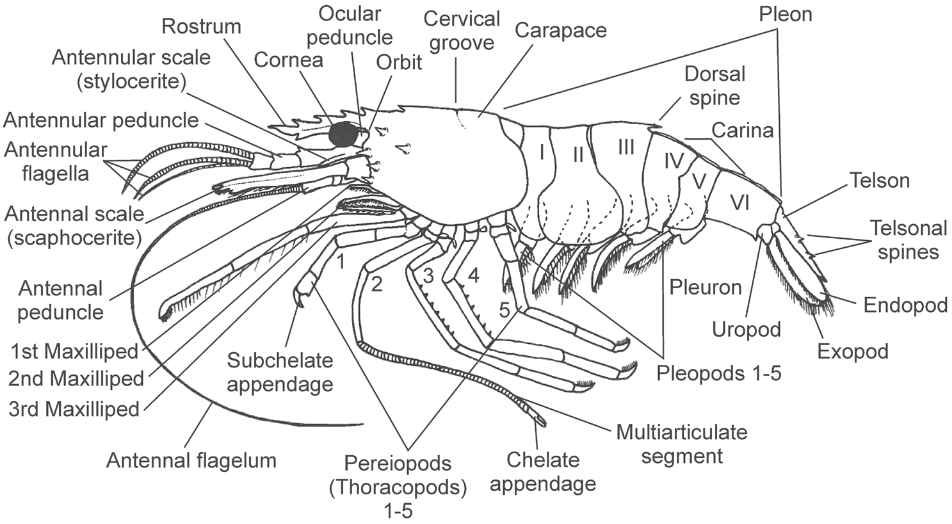


Fig. 19. Generalized caridean morphology. Note pleonite II overlaps pleonites I and III. Adapted from McLaughlin (1980, fig. 45A).

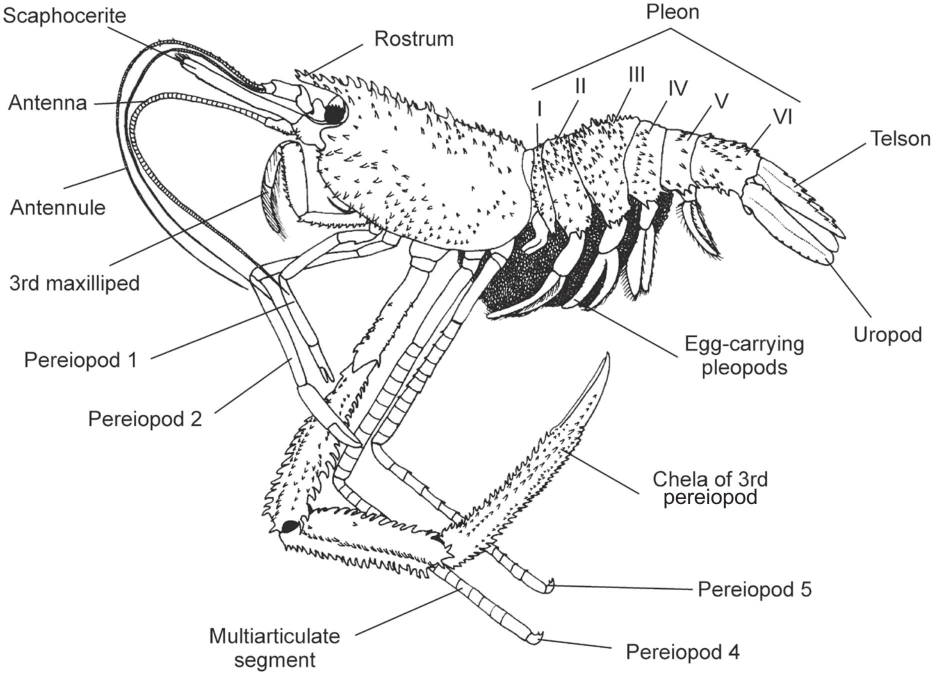


Fig. 20. Generalized stenopodidean shrimp morphology (adapted from McLaughlin, 1980, fig. 43E).

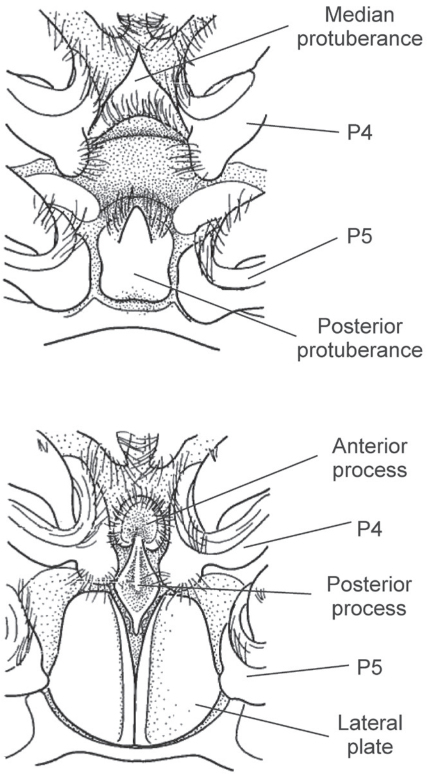


Fig. 21. Thelycum of two different dendrobranch shrimp (adapted from Pérez Farfante & Kensley, 1997, fig. 4A). P4=pereiopod 4, P5=pereiopod 5.

a modification of the posteriormost two or three sternites for sperm storage (Pérez-Farfante & Kensley, 1997) (Fig. 21).

PLEON

The pleon is the most easily identified feature useful in differentiating among shrimp infraorders. In dendrobranchiate shrimp, the pleura of the second pleonite overlap somite 3 but not somite 1 (Fig. 18). In procaridean and caridean shrimps, the pleuron of somite 2 is convex anteriorly and posteriorly, overlapping somites 1 and 3 (Fig. 19). In stenopodean shrimp, pleonites 1 and 2 are narrow and their pleura at most barely overlap the succeeding somite (Fig. 20). As obvious as this feature should be, it can be very difficult to discern the outline of the pleonites in fossil shrimp due to the introduction of cracks and breakage during burial and diagenesis and taphonomic factors, as well as the lateral compression of the body. Another useful character to consider is the mid-lateral hinge typical of Dendrobranchiata, but also occurring in a few carideans. The mid-lateral hinge is a notch and socket system at mid-height of each pleonite interlocking each with the next. This character was notably used in the systematic determination of Late Cretaceous shrimps from Lebanon by Charbonnier and others (2017).

In general, the shrimp pleon is elongate and extends posteroventrally from the thorax. The pleuron of each somite overlaps the succeeding somite. Some genera and families among all types of shrimp may possess carinae and/or spines on pleonites as diagnostic characters. Male stenopodid shrimp have a ventral median spine on pleonites 1–5, a useful diagnostic feature if it were to be found in fossils (Goy, 2010) (Fig. 20).

The telson in shrimps can be ornamented with movable or immovable spines or setae on the dorsal surface, lateral margins, and posterior margin. Caridean shrimps almost always bear dorsolateral telsonal spines (Wicksten, 2010) (see Fig. 8.3). In caridean shrimp, pleonal somites may be ornamented with spines or keels, and the third somite may be humped or spinose (Wicksten, 2010) (Fig. 8.3).

EYES

Fossilized ommatidial networks have been documented in a few species of dendrobranchiates from the Callovian of La Voulte-sur-Rhône (France) and Santonian of Sahel-Alma (Lebanon). In all cases, when preserved, the ommatidial facets have a square outline (Fig. 22). In the case of the Santonian shrimps from Sahel-Alma, the eyes are bilobed, a peculiar morphology interpreted as an adaptation to a low-light, deep-water, paleoenvironment (Fig. 22).

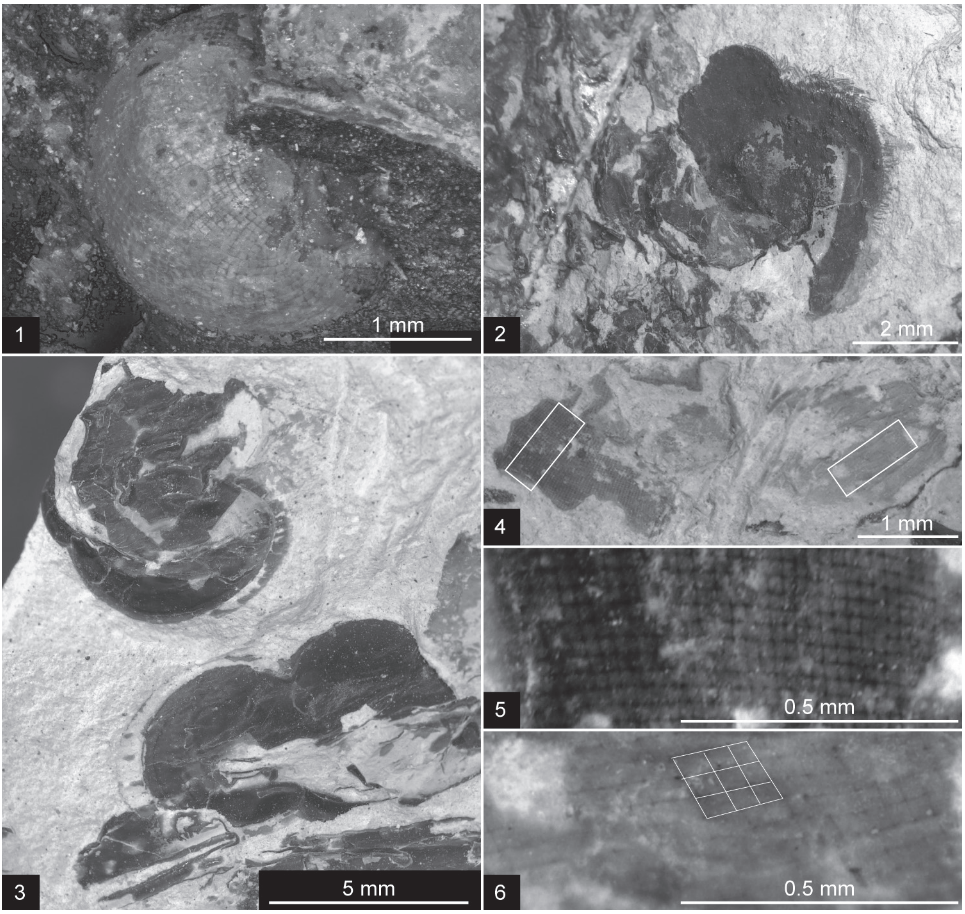


Fig. 22. Dendrobranch shrimp eye morphology. *1, Archeosolenocera straeleni* Carriol & Riou, 1991, note the square ommatidia, specimen UCBL-FSL 710076; *2. Pseudodrobna natator* (Glaessner, 1945), note the setae fringing the bilobed eyes; *3–6, Palaeobenthesicymus libanensis* (Brocchi, 1875), specimen MNHN.F.A30607 (3) and MNHN.F.A30587 (4–6), note the bilobed eyes, square ommatidia of different sizes on each lobe. Photos by S. Charbonnier (*1*) and M.-B. Forel (*2–6*).

APPENDAGES

The morphology of the antennae, antennules, and mouthparts is very important for biological classification of shrimp. Generalized mouthparts are illustrated in Figure 13. For more detailed perspective on shrimp mouthparts, consult Goy (2010), Tavares and Martin (2010), and Wicksten (2010). Of the anterior appendages in shrimp, only the antennae, antennules, and third maxillipeds are well known in fossils and therefore useful for their identification. Antennules are biflagellate in shrimp but are uniflagellate in some dendrobranchiates (Tavares & Martin, 2010) and can have an additional third branch in some carideans (Wicksten, 2010). Maxillae and maxillules have little chance of preservation in any decapod crustacean. Audo and Charbonnier (2013) illustrated the exopod of the second maxilliped in a dendrobranchiate shrimp. The third maxilliped, pediform in shrimp, is very commonly fossilized. Its ornamentation and shape are diagnostic for some extinct families,

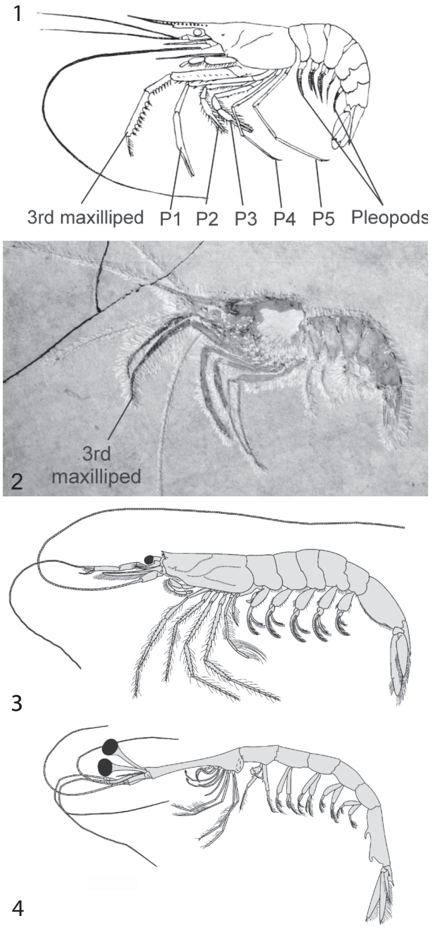


FIG. 23. Dendrobranch shrimp morphology: *1–2,* appendages of Aegeridae, extinct family of dendrobranch shrimp; *1, Aeger* MÜNSTER, 1839 (adapted from Glaessner, 1969, fig. 252.3), P=pereiopod; *2, Aeger spinipes* (DESMAREST,1822), CM 33222, note spines on third maxilliped (photo by R. Feldmann); *3,* Sergestidae (adapted from Pérez Farfante & Kensley, 1997, fig. 137); *4,* Luciferidae, note reduced pereiopods (adapted from Pérez Farfante & Kensley, 1997, fig. 126).

such as Aegeridae of the Dendrobranchiata, in which it is spinose and as long as or longer than the pereiopods (Fig. 23.1–2). Observers must be cautious in recognizing it as a maxilliped and not a pereiopod, because they can look quite similar.

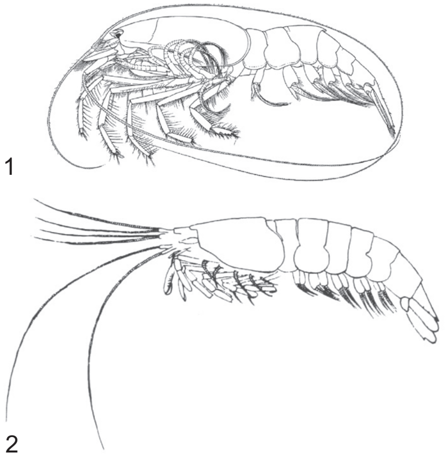


FIG. 24. Shrimp of Procaridea. *1, Procaris ascensionis* CHACE & MANNING, 1972 (adapted from Chace & Manning, 1972 fig. 4); *2, Udorella agassizi* OPPEL, 1862 (adapted from Glaessner, 1969, fig.257.5). Note achelate pereiopods.

For fossil shrimp, as for extant shrimp, the nature of the pereiopods is very important and they may be preserved in fossils. The chelae in shrimp can be very small, so that much care must be taken in preparation and observation of pereiopod terminations so as not to destroy or overlook morphological features. In dendrobranchiate shrimp, the first three pairs of pereiopods are minutely chelate in most cases (see Fig. 18.1), and yet rarely, the pereiopods are achelate (Luciferidae) (Fig. 23.4) or pereiopod 1 is achelate (in some Sergestidae) (Fig. 23.3). Among dendrobranchiates, some groups have pereiopods 4 and/or 5 reduced or absent (Sergestoidea).

In Procaridea, all of the pereiopods are achelate (Fig. 24), a condition seen in some fossil shrimp. Most Caridea exhibit chelate pereiopods 1 and 2, usually with the second pair being more robust. There is extreme variability in the development, size, and length of pereiopods 1 and 2 in caridean shrimp (Fig. 25). Another unusual feature seen in caridean shrimp is the subdivision of the carpus, but in some cases other articles, into multisegmented articles (Fig. 25.7). The number of segments varies from 2 to as many as 29 (WICKSTEN, 2010) and can be observed in fossils (Fig. 25.7). Stenopodean shrimp have chelate pereiopods 1–3, with

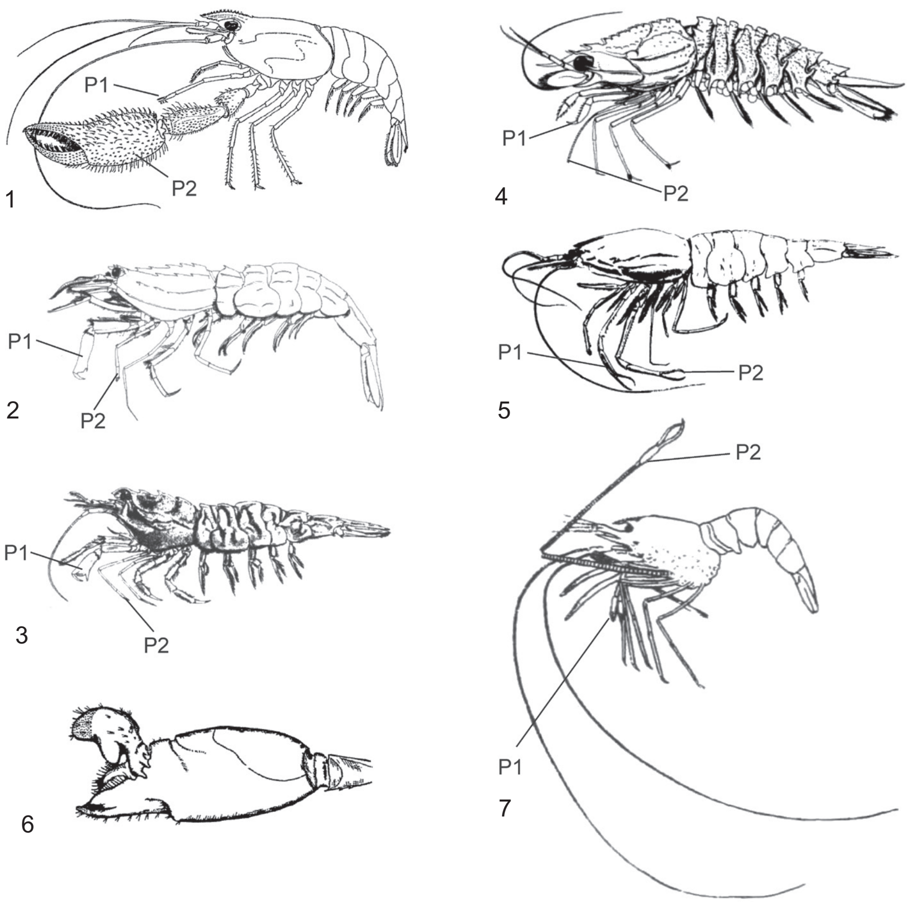


Fig. 25. Various caridean shrimp with pereiopods. Pereiopod 1 (P1) and pereiopod 2 (P2) indicated. *1, Macrobrachium olfersii* (Wiegmann, 1836), note very heterochelous P1 and P2; *2, Pontocaris vicina* (Dardeau & Heard, 1983), note pseudochelate P1; *3, Sclerocrangon boreas* (Phipps, 1774), note pseudochelate P1; *4, Glyphocrangon aculeata* A. Milne-Edwards, 1881, note dactyl; *5, Pasiphaea tarda* Krøyer, 1845, note forceps-like chelae on P1 and P2; *6, Alpheus californiensis* Holmes, 1900, note highly modified dactyl of P1; *7, Blaculla nikoides* Münster, 1839, note long multiarticulate carpus of P2; (*1–6* adapted from Bauer, 2004, fig. 2.7A, 3.7A, 3.7B, 3.10, 2.8B, 3.19; *7,* adapted from Glaessner, 1969, fig. 257.4).

pereiopod 3 very robust and pereiopod 2 longer than pereiopod 1 (Fig. 20).

Pleopods of shrimp are well developed and usually biramous. In dendrobranchiate shrimp, the pleopods are primarily used for swimming. In dendrobranchiate males, the first pleopods are modified to form the petasma (Fig. 18.1, Fig. 26), which is used during reproduction and rarely described in fossils (but see Polz, 2007; Audo & Charbonnier, 2013, fig. 6A2; Charbonnier & others, 2017; Audo, Winkler, & Charbonnier, 2021, appendix 1). Pleopods of many fossil dendrobranchiate taxa preserve two multisegmented flagella (Schweitzer & others, 2014) (Fig. 27.1).

In caridean shrimp, the male second pleopod exhibits an appendix interna and an appendix masculina (see Fig. 16). Some extinct groups have highly unusual pleopods, for example, *Pleopteryx* Schweigert & Garassino, 2004, in which the pleopods terminate in long, branching structures (Fig. 27.2). The pleopods 2–5 of stenopodids

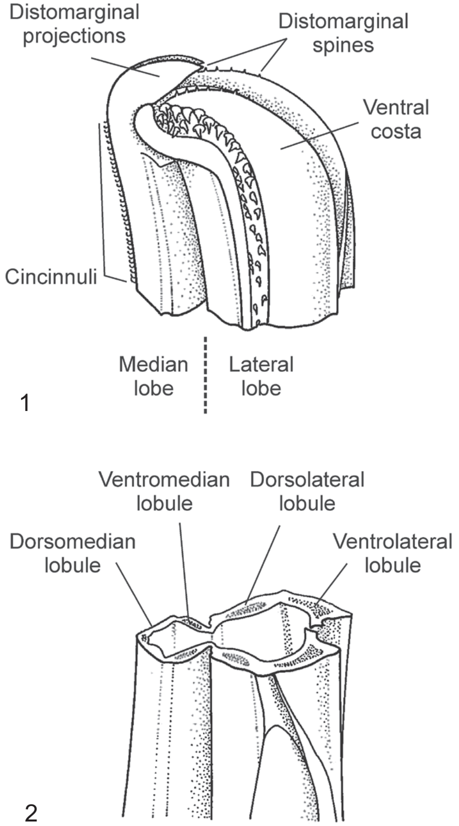


Fig. 26. Petasma of dendrobranch shrimp: *1,* overall view; *2,* cross-sectional view (adapted from Pérez Farfante & Kensley, 1997, fig. 4B).

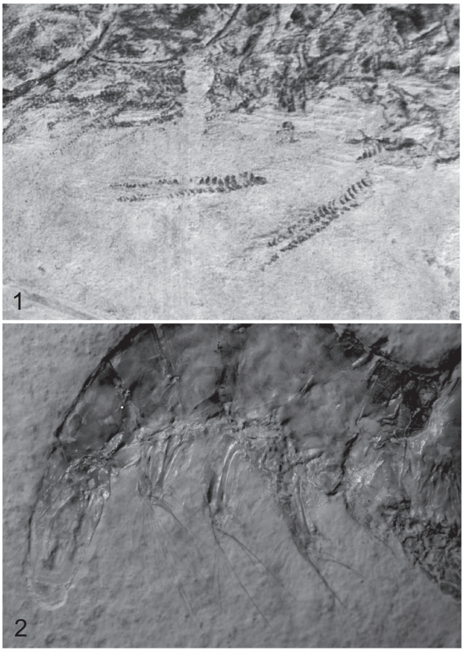


Fig. 27. Pleopods in extinct shrimp. *1,* Penaeoidea, *Anisaeger brevirostrus* Schweitzer & others, 2014, LPI-40792 (Schweitzer & others, 2014, fig. 5.4), multiarticulate flagellae on pleopods; *2,* Caridea, *Pleopteryx kuempeli* Schweigert & Garassino, 2004, SMNS 64942, dendritic pleopods (Schweigert & Garassino, 2004, fig. 16).

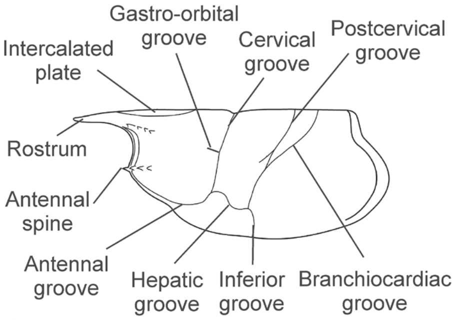


Fig. **28**. Erymoidea lobster morphology (adapted from Devillez, Charbonnier, & Barriel, 2019, fig. 2B).

are foliaceous and lack appendices internae (Goy, 2010).

The presence of a diaresis on the exopod of the uropods in dendrobranchiates has been noted in fossil forms (Schweitzer & others, 2014), illustrated but not mentioned for extant forms (Pérez Farfante & Kensley, 1997), and noted as absent in extant forms (Tavares & Martin, 2010). This structure is absent in stenopod and caridean shrimps.

INFRAORDER GLYPHEIDEA

Morphology in lobsters referred to Glypheidea is quite variable. The infraorder is divided into two superfamilies, Erymoidea and Glypheoidea (*sensu* Karasawa, Schweitzer, & Feldmann, 2013), which are substantially different from one another, especially in terms of pereiopods and chelae. A different classification scheme has been proposed by Devillez, Charbonnier, and Barriel (2019), in which Erymoidea was placed within Astacidea, and by Charbonnier and others (2014) who considered Erymoidea as not included within Glyphe-

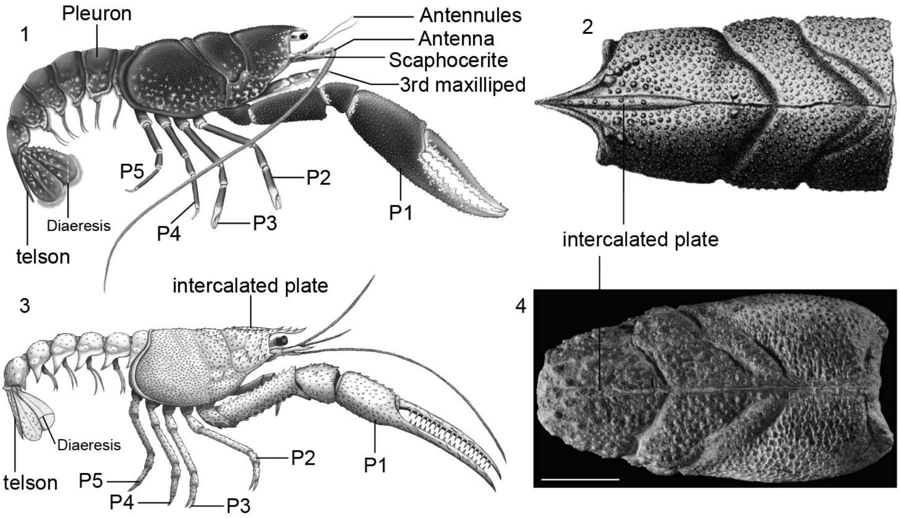


Fig. 29. Generalized erymoidean body form. *1–2, Eryma ventrosum* (Von Meyer, 1835), reconstruction by C. Letenneur (adapted from Charbonnier, Pérès, & Letenneur, 2012, fig. 17 and Oppel, 1862, pl. 4,*9b*; *3,* reconstruction of *Enoploclytia leachii* (Mantell, 1822), drawing by J. Devillez; *4, Enoploclytia collignoni* Secrétan, 1964, carapace in dorsal view, MNHN.F.F03925 (adapted from Charbonnier, Garassino, & Pasini, 2012, fig. 7a). P1–P5=pereiopods 1 to 5.

idea. These issues are more fully considered in the Glypheidea classification article (Feldmann, Schweitzer, & Karasawa, 2015, *Treatise Online* 68). Each superfamily is discussed separately herein, as there seems little disagreement over their recognition as well as their family and generic composition, with the exception of Pemphicidae, which is discussed in the following Erymoidea section.

CARAPACE

Erymoidea.—Members of Erymoidea are characterized by strong cervical, postcervical, and branchiocardiac grooves and lack some of the complex groove patterns seen in glypheoid lobsters (Fig. 28). Erymidae are unique among Decapoda in possessing an intercalated plate, an elongate-ovate structure bounded by sutures positioned on the dorsal axis and just posterior to the rostrum (Fig. 28, Fig. 29). The function of this intercalated plate is unknown, but it has been suggested that it aids in molting (Glaessner, 1969). Pemphicidae has deep, wide grooves and carapace swellings that differentiate it from other erymoid lobsters (Fig. 30). The carapace of erymoids is sexually dimorphic in some taxa. Those specimens with a larger carapace and a better-developed branchial region are interpreted as females and specimens with a longer carapace as males (Charbonnier, Pérès, & Letenneur, 2012).

Glypheoidea.—The glypheoid lobsters typically bear cephalic carinae anterior to the cervical groove. They have a complex set of grooves arrayed between the cervical and branchiocardiac grooves that are not seen in other decapods (Fig. 31, Fig. 32). The varying degree of development of these grooves is diagnostic for genera and families within Glypheoidea (Karasawa, Schweitzer, & Feldmann, 2013; Feldmann, Schweitzer, & Karasawa, 2015). Glypheoids have a long branchial area posterior to the branchiocardiac groove that is granular or scabrous.

The epistome of extinct glypheideans is long, occupying a long space between the anterior margin and the buccal cavity, with an axial tubercle (Feldmann & de Saint Laurent, 2002; Charbonnier, Pérès,

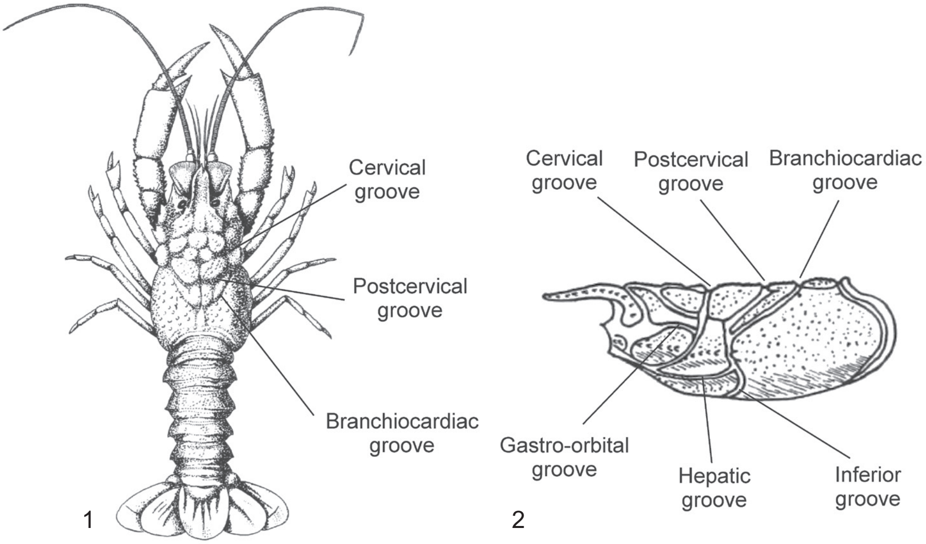


FIG. 30. Pemphicid lobster morphology: *1,* dorsal view; *2,* left lateral view (adapted from Glaessner, 1969, fig. 2a, b).

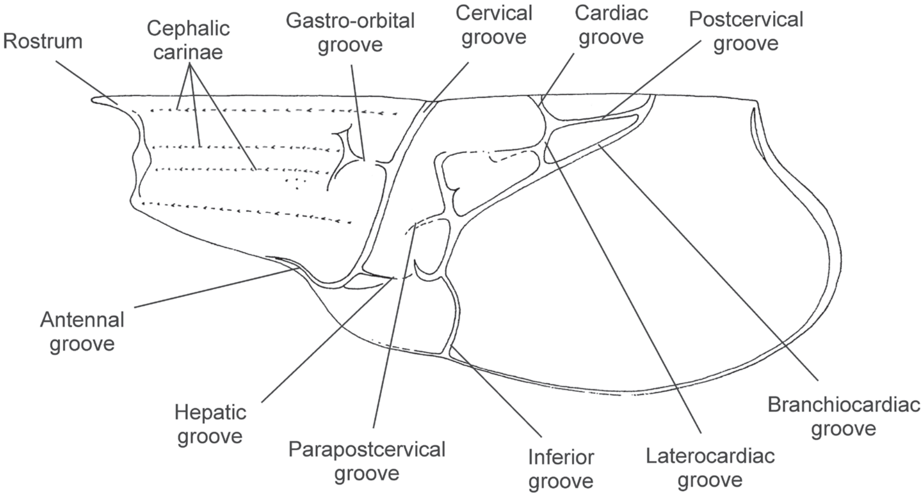


FIG. 31. Glypheoid lobster morphology (adapted from Förster & Matyja, 1986, fig. 4).

& LETENNEUR, 2012) (Fig. 33.1–3). The epistome of the extant Neoglypheidae is wide and spinose, and—similar to the fossil glypheoid—occupies a long space between the anterior margin of the carapace and the buccal cavity (Fig. 34).

THORACIC STERNUM

The ventral surface of extinct erymoids is known from *Eryma ventrosa* (VON MEYER, 1835), and the epistome is short and slightly wider than long (CHARBONNIER, PÉRÈS, & LETENNEUR, 2012) (Fig. 35). Sternites of the same specimen are poorly known but very narrow.

In glypheoids, the sternum is quite narrow in both extinct and extant forms (Fig. 36, Fig. 33.4) (CHARBONNIER & others, 2013), and the last somite is not fused to the remainder of the sternum, called the frac-

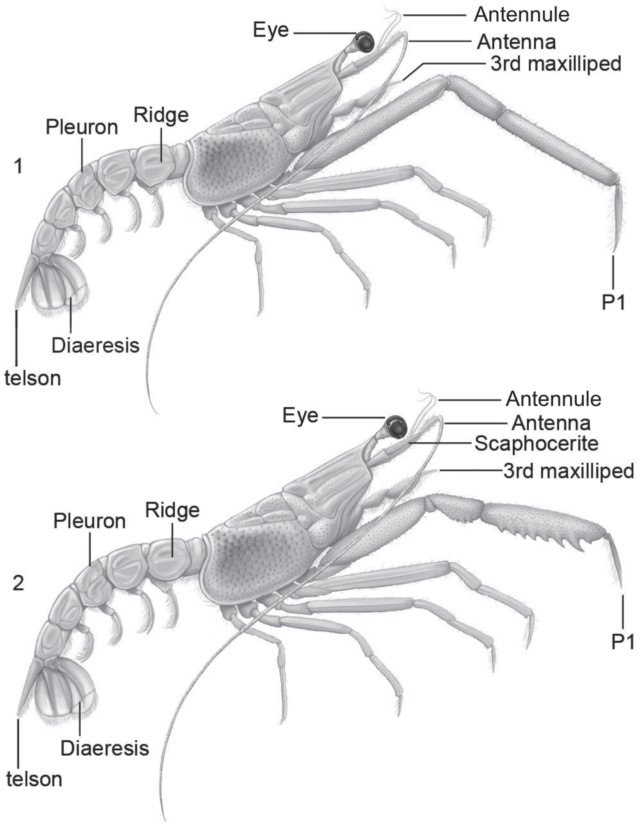


Fig. 32. Generalized glypheoidean body form; *1,* male, notice sharp pleurae and elongated, cylindrical first pereiopod (P1); *2,* female, notice rounded pleura and short, laterally flattened P1 (adapted from Charbonnier, Pérès, & Letenneur. 2012; reconstructions by C. Letenneur).

tosternal condition (Scholtz & Richter, 1995), seen in *Rectaglyphea howardae* (Charbonnier & others, 2013) (Fig. 33.4).

PLEON

Erymoidea.—The pleon of erymoids is comprised of robust, well-calcified somites. The pleura are sharply directed posteriorly (Fig. 29).

Glypheoidea.—Glypheoid pleonites may have pointed or rounded ventral edges, and this can be sexually dimorphic (Fig. 32). The terga and the pleura are generally strongly separated by a ridge or groove.

EYES

Fossilized eyes of glypheoid lobsters are known only in specimens from Konservat-Lagerstätten. They are situated at the end of long eyestalks. In the Middle Jurassic *Glypheopsis voultensis* Charbonnier & others, 2013, the eyes are large and show a framework of square ommatidia (Fig. 37). Eyes of erymoid lobsters are rarely preserved in the fossil record. In the Jurassic *Eryma ventrosa* from the bathyal paleoenvironment of La Voulte Lagerstätte, the eyes are very large, whereas in the Cretaceous *Eryma sulcata* Harbort, 1905, the eyes are small and probably reflect shallower and more illuminated conditions (Fig. 38).

CEPHALIC APPENDAGES AND MAXILLIPEDS

Erymoidea and Glypheoidea.—Antennae and antennules are preserved in some of these lobster fossils. The antennules are biflagellate, with a three-segmented peduncle (Charbonnier & others, 2013) (Fig. 29, Fig.

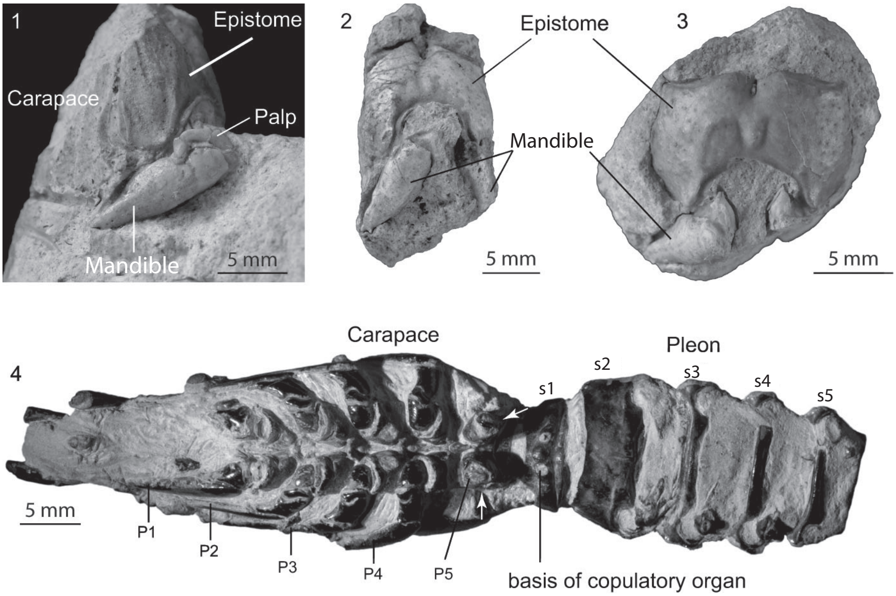


FIG. 33. Epistome and mandibles of Jurassic *Glyphea regleyana* (DESMAREST, 1822) (*1–2*) and *Squamosoglyphea dressieri* VON MEYER, 1840 (*3*). (*1,* adapted from Charbonnier, Pérès, & Letenneur. 2012, 2013, fig. 4a; *2,* adapted from Charbonnier & others, 2013, fig. 21; *3,* adapted from Charbonnier & others, 2013, fig. 78); *4,* ventral morphology of Cretaceous *Rectaglyphea howardae* CHARBONNIER & others, 2013, fig. 453, white arrows indicate movable last thoracic sternite (fractosternal condition). P1–P5=pereiopods 1–5, s1-s5=pleonal somites 1–5.

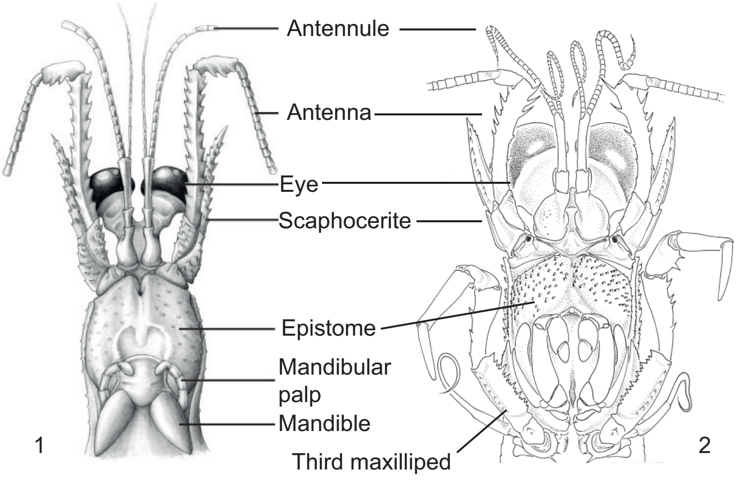


FIG. 34. Ventral morphology. *1,* Jurassic *Glyphea regleyana* (DESMAREST, 1822) (adapted from Charbonnier, Pérès, & Letenneur, 2012, reconstruction by C. Letenneur); *2,* Holocene *Neoglyphea inopinata* FOREST & DE SAINT LAURENT, 1975 (adapted from Richer de Forges, 2006, fig. 5).

32). As is typical, antennae are much longer than the antennules and can be longer than the carapace, plus the pleon. Antennae have a three-segmented peduncle and a scaphocerite (Charbonnier & others, 2013). Of the mouthparts, only the third maxilliped is commonly preserved in erymoids, and it is pediform (Fig. 29, Fig. 32). Mandibles are known from *Glyphea regleyana* (Desmarest, 1822) and appear to be rather long and large (Charbonnier, Pérès, & Letenneur, 2012) (Fig. 33.1–3). Mandibles in the erymoid *Eryma ventrosa* are short, approximately as wide as long and are bulbous (Charbonnier, Pérès, & Letenneur, 2012) (Fig. 35). Only the maxillipeds of the extant Neoglypheidae have been described, because the material is very rare and examination of the mandibles and inner mouthparts might result in damage (Forest & de Saint Laurent, 1989; Richer de Forges, 2006). Maxillipeds 2 and 3 are pediform and ornamented with spines (Fig. 34).

THORACIC APPENDAGES

Erymoidea.—In erymoid lobsters, pereiopod 1 is strongly chelate but not strongly heterochelous. Erymoid lobsters have chelate terminations of the first pereiopod and chelate or pseudochelate terminations of pereiopods 2 and 3 (Fig. 30, Fig. 29). The form of the chelae, which are known to be quite variable among erymoids, may change with growth (Charbonnier, Pérès, & Letenneur, 2012).

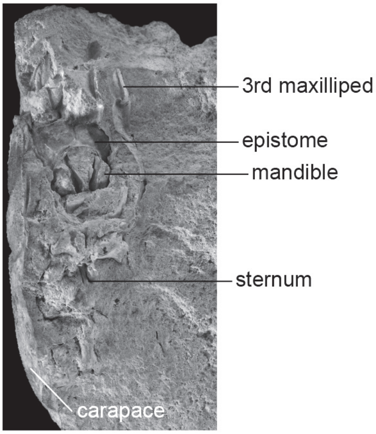


Fig. 35. Ventral morphology of *Eryma ventrosum* (von Meyer, 1835) (adapted from Charbonnier, Pérès, & Letenneur, 2012, fig. 14F).

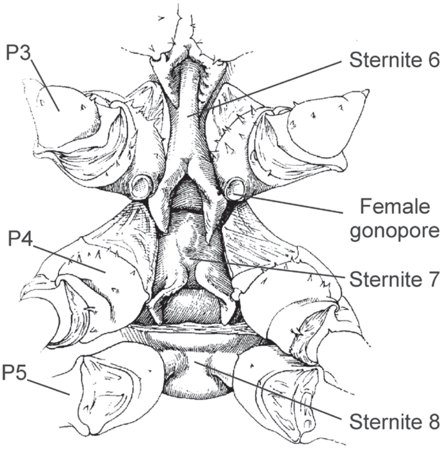


Fig. 36. Sternum of extant glypheidean, *Neoglyphea inopinata* Forest & de Saint Laurent, 1975 (adapted from Forest & de Saint Laurent, 1989, fig. 2). P=pereiopod.

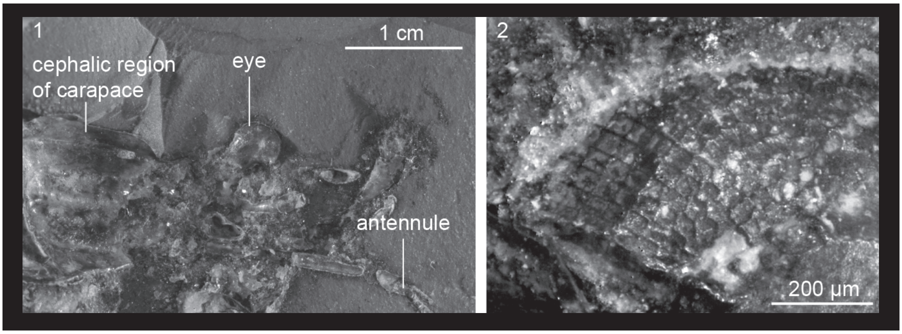


Fig. 37. Glypheoid eye morphology: *1,* eye of *Glypheopsis voultensis* Charbonnier & others, 2013; *2,* detail of the ocular surface with square ommatidia (adapted from Charbonnier & others, 2013, fig. 336, 337).

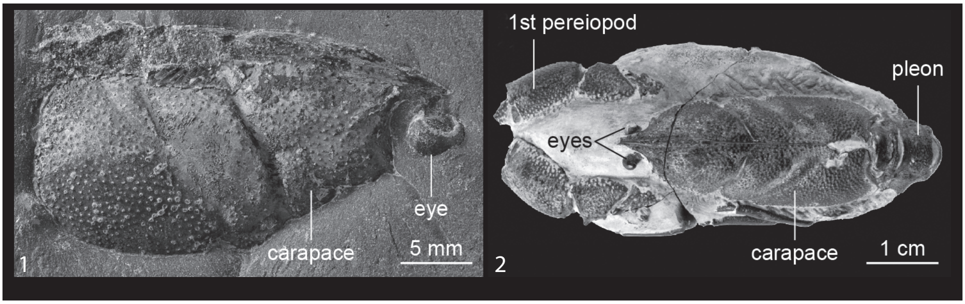


FIG. 38. Erymoid eyes: *1,* large eye of *Eryma ventrosa* (VON MEYER, 1835), MNHN.F.A59527 (photo by L. Cazes); *2,* small eyes of *Eryma sulcata* HARBORT, 1905, SM B11437 (adapted from Devillez & others, 2016).

Glypheoidea.—Glypheoid lobsters have pseudochelate first pereiopods which are commonly spinose, and the distal margin of the manus bears up to three spines, the largest of which occupies the position of the fixed finger in a chelate appendage (Fig. 32). Pereiopods 2 and 3 are chelate or pseudochelate. Pereiopod 4 is chelate, pseudochelate, or achelate, and pereiopod 5 is achelate. Some glypheoids are sexually dimorphic in the nature of the first pereiopods. For *Glyphea regleyana*, the longer, more slender first pereiopod is interpreted as the male form, and the shorter, more robust pereiopods are thought to belong to females (CHARBONNIER, PÉRÈS, & LETENNEUR, 2012).

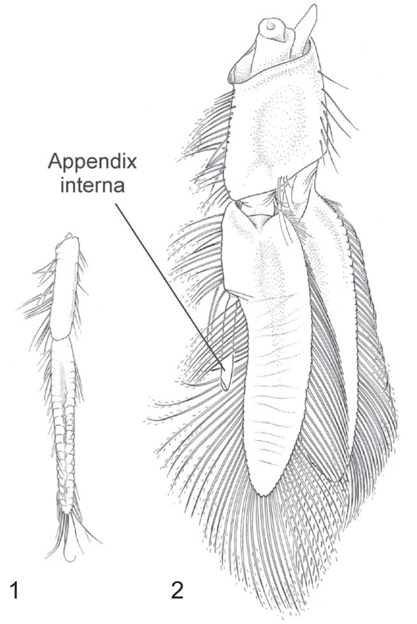


FIG. 39. Glypheidean female pleopods, *Laurentaeglyphea neocaledonica* RICHER DE FORGES, 2006: *1,* pleopod 1; *2,* pleopod 2 (adapted from Richer de Forges, 2006, fig. 8).

PLEOPODS

Erymoidea.—Pleopods are not known except for the uropods, which have rounded exopods and endopods and a diaresis on the uropodal exopod (CHARBONNIER, PÉRÈS, & LETENNEUR, 2012) (Fig. 29).

Glypheoidea.—Pleopods are not known for extinct glypheoids, except the uropods. Pleopods 1 and 2 are illustrated for extant females of Glypheoidea, and pleopod 2 has an appendix interna (Fig. 39); males bear an appendix masculina on pleopod 2 (FOREST

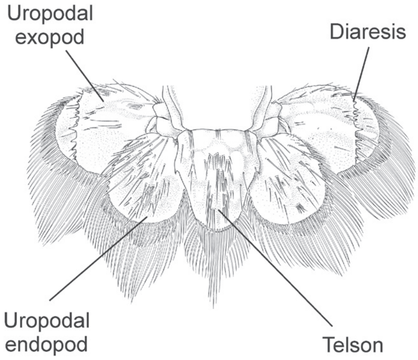


FIG. 40. Glypheidean tail fan, *Laurentaeglyphea neocaledonica* RICHER DE FORGES, 2006 (adapted from Richer de Forges, 2006, fig. 7).

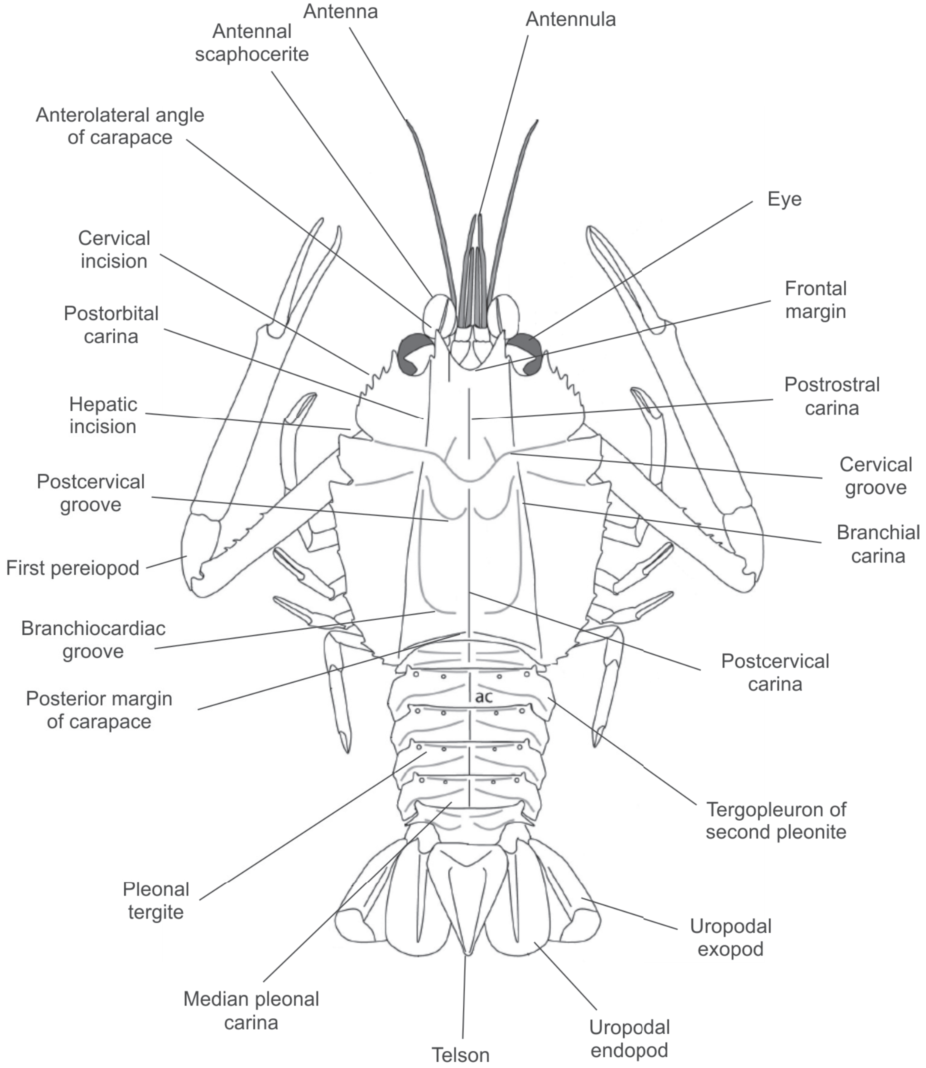


Fig. 41. Generalized polychelidan overall morphology, *Coleia antiqua* Broderip, 1835 (adapted from Audo, Barriel, & Charbonnier, 2021). ac=axial carina.

& de Saint Laurent, 1975). Glypheoid lobsters have a diaresis in the uropodal exopod in both extinct and extant forms (Fig. 32, Fig. 40).

INFRAORDER POLYCHELIDA

Infraorder Polychelida includes extinct and extant lobster-like decapods. All adults have a dorsoventrally flattened carapace, at most a short rostrum, and strongly chelate first pereiopods, with pereiopods 2–4 (and in some cases, 5), also chelate.

CARAPACE

The carapace of polychelidan lobsters is dorsoventrally flattened—and may be very strongly so, widened, and longer than wide (Fig. 41). The carapace features a frontal margin with, at most, a small rostral spine. This margin is concave, but, differing from

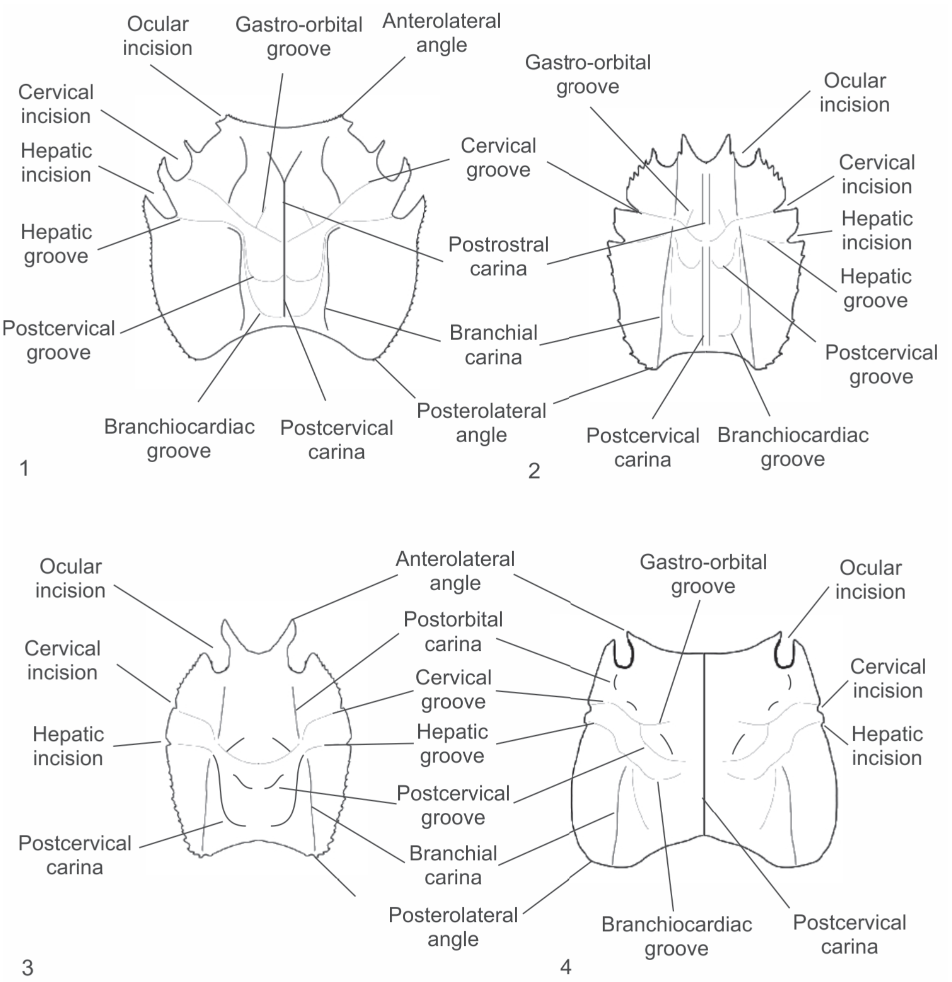


Fig. 42. Carapace morphology of extinct polychelidans, generalized at the generic level. *1, Eryon* Desmarest, 1822; *2, Coleia* Broderip, 1835; *3, Palaeopentacheles* Von Knebel, 1907; *4, Tetrachela* Reuss, 1858 (adapted from Audo & others, 2014a, fig. 2B(1) and Audo & others, 2017, fig. 2C, I, Q).

Achelata, the antennular somite is covered by the carapace and not visible dorsally. The lateral margins are strongly or weakly convex and spinose, ornamented with long spines or tiny serrations. Ocular incisions vary in size depending on the development of the eyes. They are just distal to the anterolateral angle of the carapace, except when the lateral margin projects laterally along the eye (e.g. Polychelidae) or when the ocular incision is set in a stalklike extension of the lateral margin (*Eryon* Desmarest, 1822) (Fig. 41, Fig. 42). Grooves are less pronounced in this group than on some other lobster groups, and the cervical and/or hepatic grooves intersect the lateral margins, each in a notch (Fig. 41, Fig. 42). Lateral longitudinal carinae, the branchial and postorbital, typically characterize the cephalic and branchial regions, and median carinae, the postrostral and postcervical, are almost always present and can be intersected or not by the cervical groove (Fig. 41, Fig. 42). *Knebelia* Van Straelen, 1922, within Eryonidae has been interpreted as having a pair of frontal lobes, located between the ocular incision and the

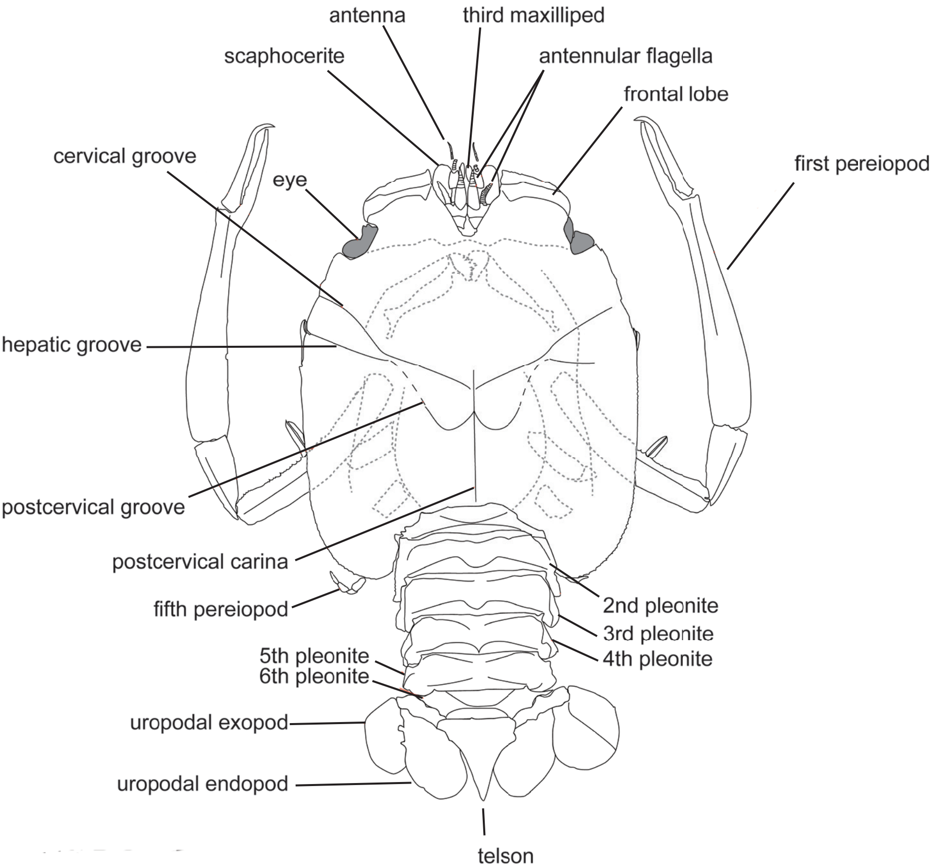


Fig. 43. Morphology of extinct Polychelida, generalized *Knebelia* Van Straelen, 1922 (adapted from Audo & others, 2014b, fig. 2B).

frontal margin, and articulating with the rest of the carapace (Fig. 43).

THORACIC STERNUM

The sternum is not well known in fossil forms but has been documented for one species (Jauvion & others, 2020). It is apparently quite narrow, as in extant forms, because the bases of the pereiopods are situated close together (Fig. 44) and in extant forms, the sternum widens at the position of sternites 7 and 8 (Fig. 45).

PLEON

Like the carapace, the pleon is dorsoventrally flattened. The tergites have a median carina, and the ventral margins of the pleonites are round or pointed. The telson is usually triangular and may be distinctively laterally concave (Fig. 41, Fig. 43). The telson is rounded in a few extinct genera (*Rogeryon* Audo & others, 2017; *Tetrachela* Reuss, 1858; *Rosenfeldia* Garassino, Teruzzi, & Vecchia, 1996; *Tethyseryon* Bravi & others, 2014). The exopods of the uropods are without a diaresis. In extant males, the first pleopods are spatulate and the remaining pleopods are biramous with an appendix interna (Lavalli & Spanier, 2010).

EYES AND APPENDAGES

Eyes are reduced in extant species but can be well developed in extinct taxa (Ahyong, 2009; Audo & others, 2016, 2019; Audo,

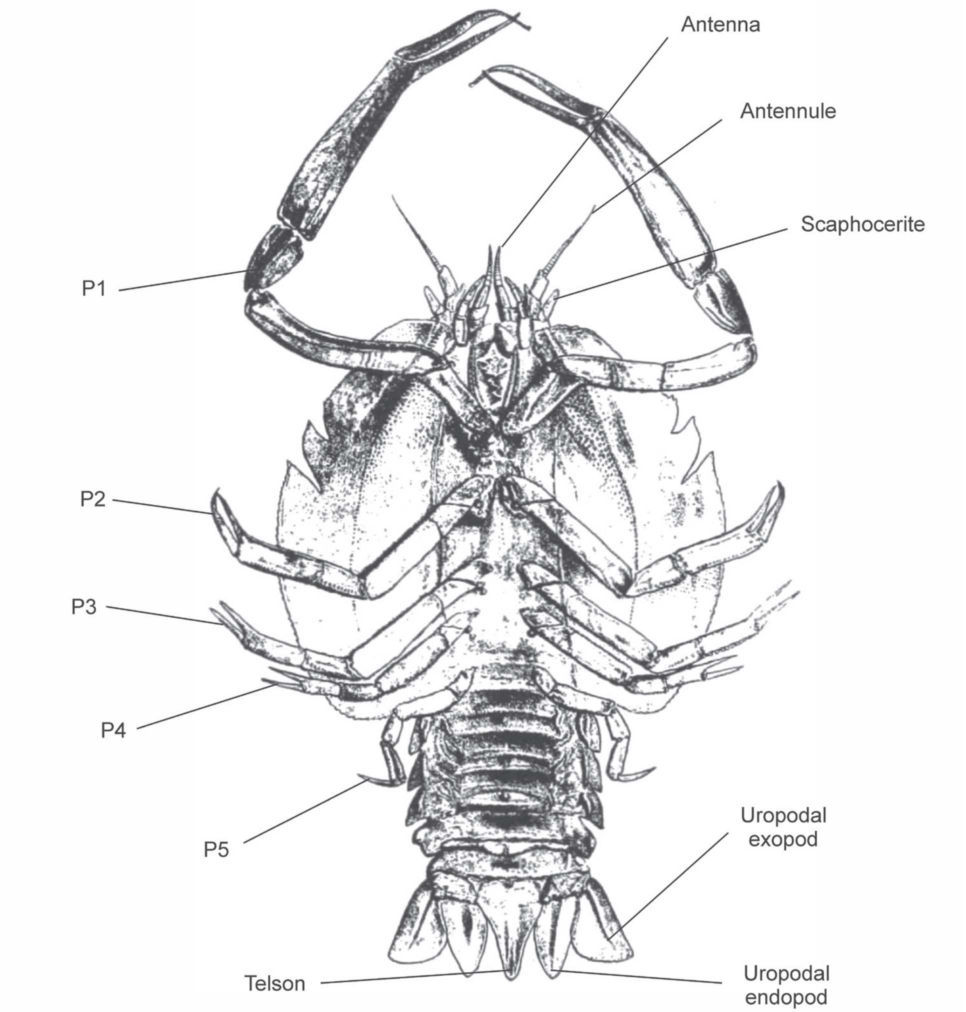


Fig. 44. Extinct polychelid ventral surface, generalized *Cycleryon* Glaessner, 1965 (adapted from Glaessner, 1969, fig. 274.4b). P=pereiopod.

Winkler, & Charbonnier, 2021). The eyes generally have squared ommatidial facets, or in some cases, hexagonal facets (Fig. 46). Hexagonal facets have been interpreted as representing apposition eyes. Squared facets are most likely reflective superposition eyes. The antennules and antennae bear long flagella in extant forms (Fig. 41) but they are short in many fossil forms (Fig.44, Fig. 47). They have a stylocerite and scaphocerite respectively (Fig. 41, Fig. 43, Fig. 44) (Ahyong, 2009); scaphocerites are known from fossil forms (Fig. 47). Generalized mouthparts of extant polychelidans are herein illustrated for reference (Fig. 48). In extinct forms, the third maxillipeds are pediform and have ischia of various widths, narrow in Polychelidae (tied to a loss of the *crista dentata*, a dentate ridge of the inner margin of the ischium) and wider in other families, notably the Eryonidae and Coleiidae. The mandibles only feature the incisor process, comprising a large median triangular tooth flanked anteriorly and posteriorly by smaller triangular teeth (Fig. 48). As the infraorder name implies, pereiopods 1–4 are chelate, with the first pair longest (Fig. 41, Fig. 44). Pereiopod 5 is the shortest and may be chelate, especially in females (Ahyong, 2009) (Fig. 41). Notably, the basis, ischium, and merus of pereiopods 3 to 5 (and usually pereiopod 2) are fused (Ahyong, 2009).

LARVAE

Larvae are known from the fossil record of Polychelidae, and their morphology deserves brief mention here. They can resemble tiny adults in some fossil species (direct development) (Audo & others 2014a; Bravi & others 2014), or they can be giant larvae with an inflated carapace (metamorphic development). In the latter case, the cephalothorax is inflated and rounded, covered in spines, and the pleon is comparatively smaller, shorter than, or approximately as high as wide, and

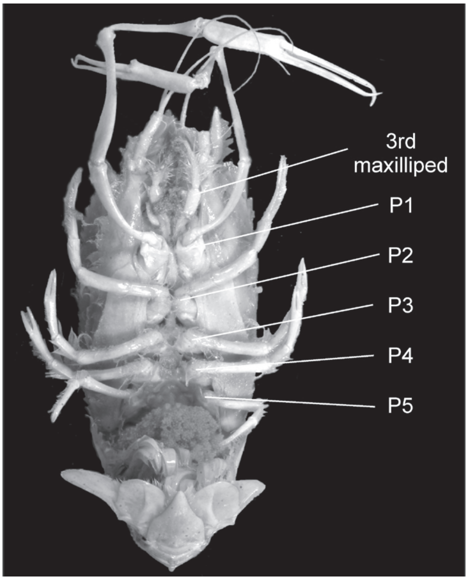


Fig. 45. *Stereomastis sculpta* (Smith, 1880), USNM CRT 292599, ventral surface (photo by K. Ahlfeld). P=pereiopod.

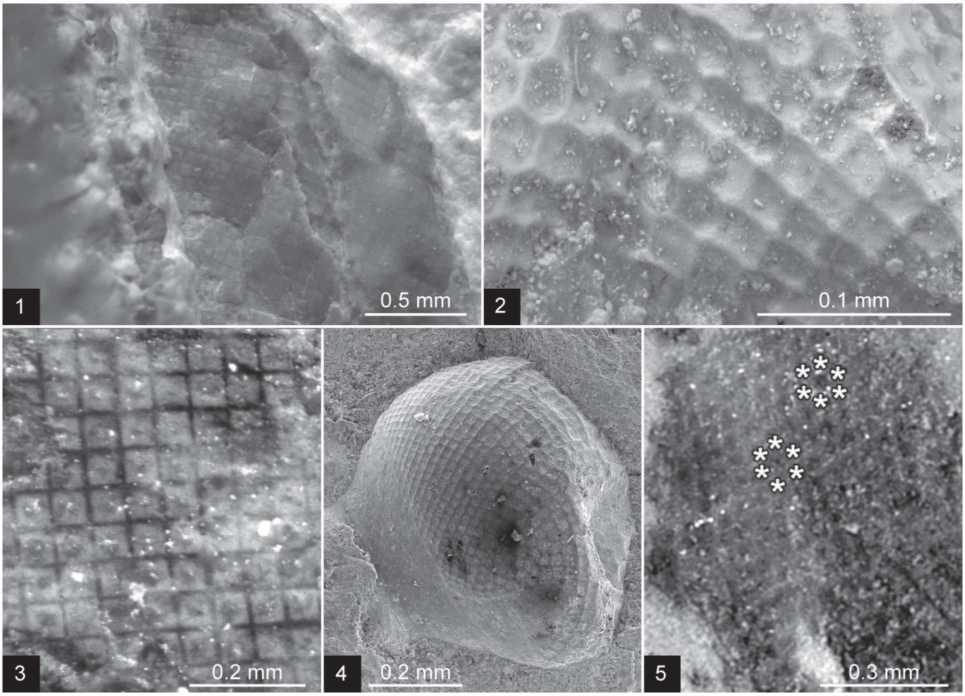


Fig. 46. Polychelidan eye specimens. *1, Knebelia totoroi* Audo & others, 2014b with square ommatidial facets, SMNS 67916. *2. Voulteryon parvulus* Audo & others, 2014a, with association of squared and hexagonal ommatidial facets, MNHN.F.50708. *3. Willemoesiocaris ovalis* (Van Straelen, 1923), notice the square ommatidial facets, MNHN.F.29521. *4. Hellerocaris falloti* (Van Straelen, 1923), with squared ommatidial facets, MNHN.F.50709. *5. Rogeryon oppeli* (Woodward, 1866), with hexagonal ommatidial facets, SMNS 66004. Photos: G. Schweigert (*1*); D. Audo (*2, 3*); P. Loubry (*4*), and J. T. & C. Haug (*5*).

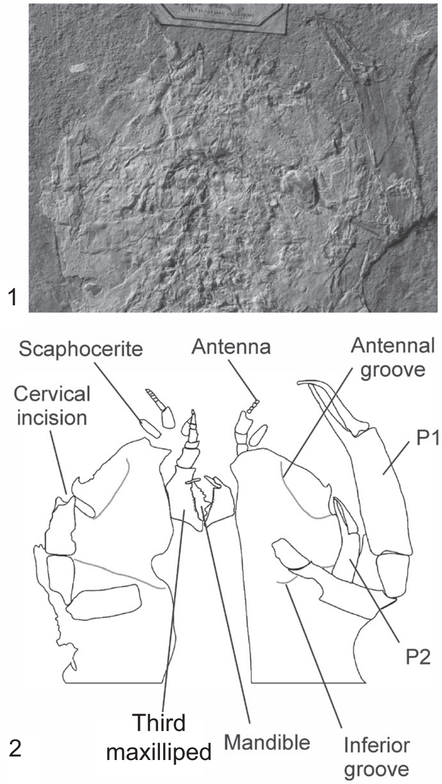


FIG. 47. Mouthparts of extinct polychelidan, generalized *Soleryon* AUDO & others, 2014c: *1,* fossil; *2,* interpretive drawing (adapted from Audo & others, 2014c, fig. 4A,B). P=pereiopod.

covered in spines (see MARTIN, 2014; HAUG & others, 2015; EILER, C. HAUG, & J. HAUG, 2016; EILER & HAUG, 2016).

INFRAORDER ACHELATA: SPINY AND SLIPPER LOBSTERS

Achelata includes three groups of achelate lobsters, the extinct Cancrinidae (Fig. 49.7), Palinuridae, or spiny lobsters (Fig. 49.1–3), and Scyllaridae, or slipper lobsters (Fig. 49.4–6).

CARAPACE

The carapace of achelatans varies by family but in all cases is heavily ornamented and possesses a reduced rostrum. Only the cervical groove is well developed in achelatans. In palinurid lobsters, the carapace is subcylindrical or rectangular in cross section. Palinurids are spinose and have large frontal horns situated above the eyes. The carapace is ornamented with several carinae which themselves may be spinose (Fig. 50). Scyllarid lobsters are dorsoventrally flattened, with well-defined orbits on the anterior margin or at the anterolateral angle (Fig. 51,

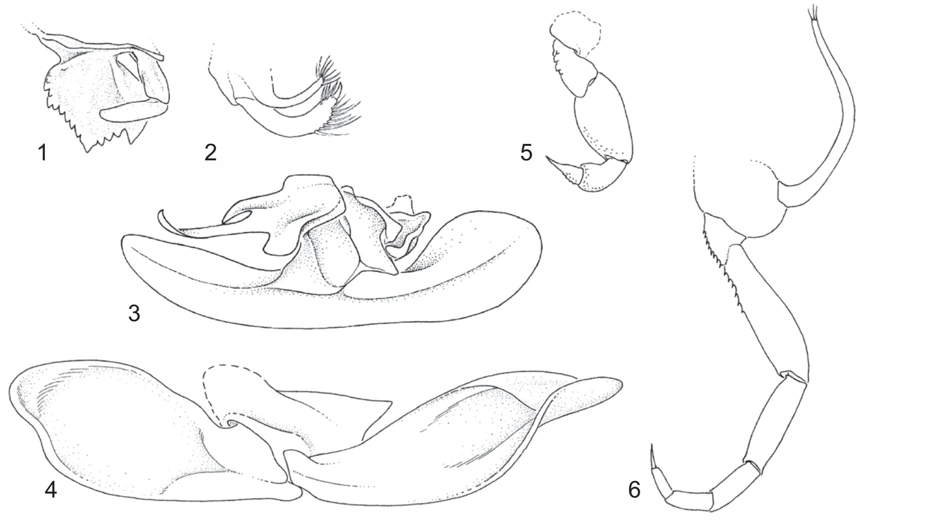


FIG. 48. Polychelidan mouthparts: *1,* mandible; *2,* first maxilla; *3,* second maxilla; *4,* first maxilliped; *5,* second maxilliped; *6,* third maxilliped (adapted from Galil, 2000, fig. 3).

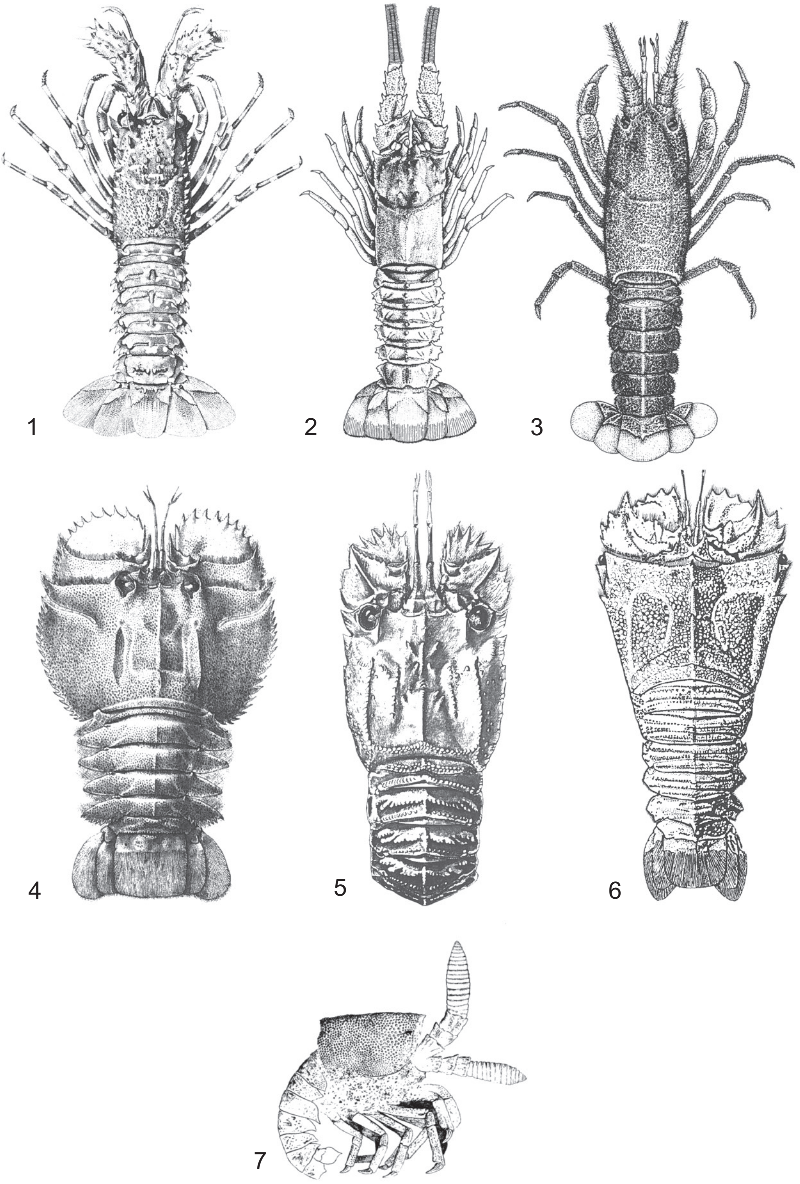
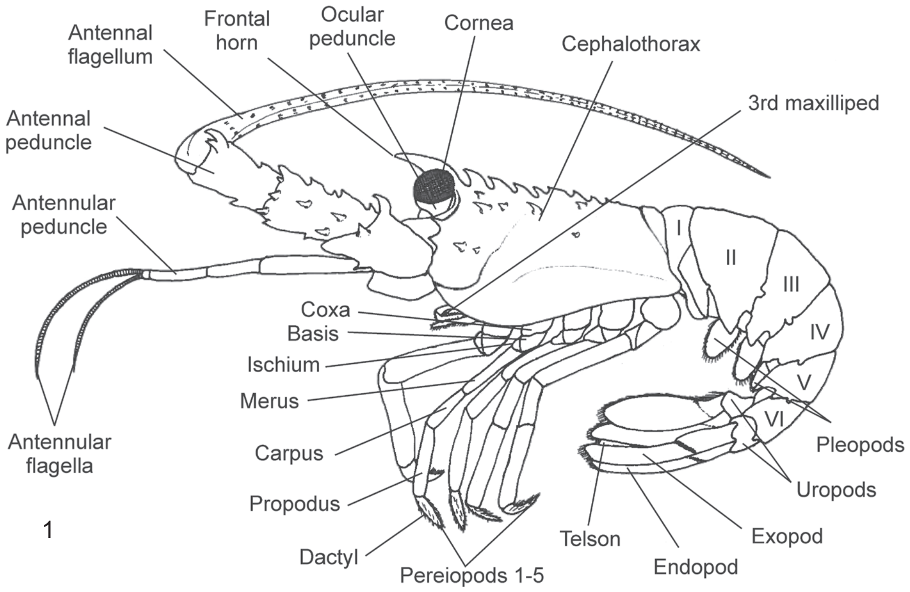


Fig. 49. Achelata body types. *1–3,* Palinuridae (adapted from Holthuis, 1991, fig. 220, 213, 313); *4–6,* Scyllaridae (adapted from Holthuis, 1991, fig. 384, 415, 427); *7,* Cancrinidae (adapted from Glaessner, 1969, fig. 280.2a).

Fig. 52). Dorsal carapace ornamentation in scyllarids frequently consists of weakly developed keels. Lateral margins can be spinose, and a marginal notch called the cervical incision, if present, is located at the intersection of the cervical groove (Lavalli & Spanier, 2010) (Fig. 51, Fig. 52). Cancrinids are characterized by a rectangular carapace with shallow, well-developed orbits (Haug & others, 2016) (Fig. 49.7).

THORACIC STERNUM

In palinurids and scyllarids, the sternum is distinctly triangular, widens posteriorly,



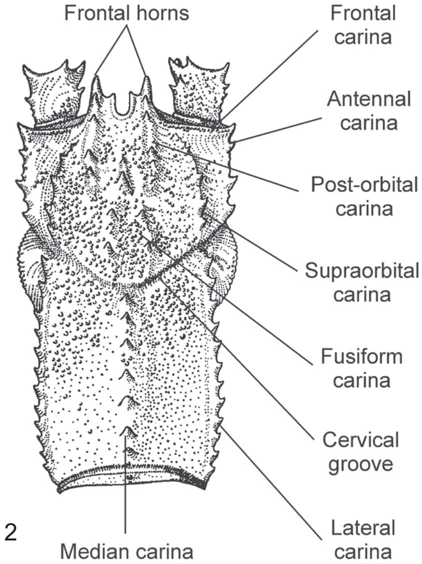


Fig. 50. Palinurid morphology: *1,* overall morphology (adapted from McLaughlin, 1980, fig. 46J); *2,* carapace morphology (adapted from Stenzel, 1945, fig. 4).

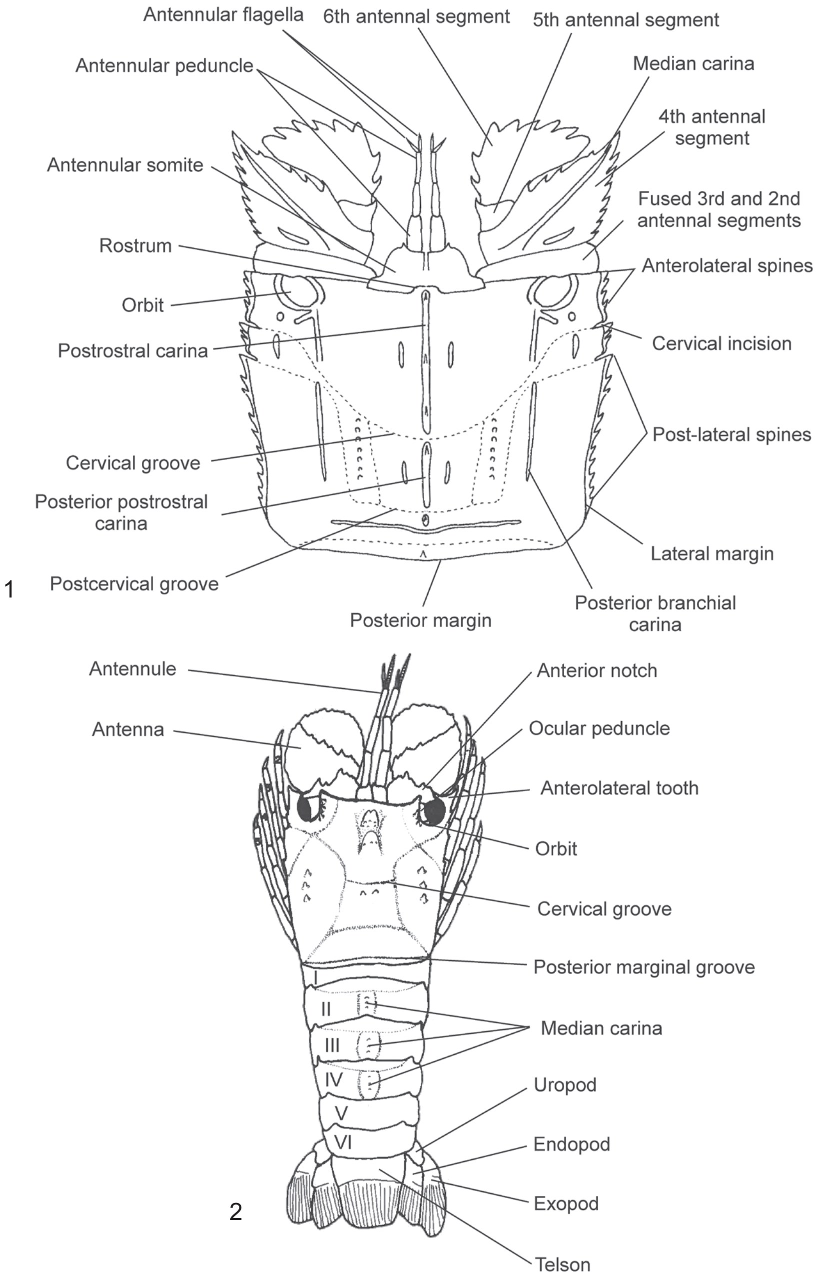


Fig. 51. Scyllarid morphology: *1,* carapace features (adapted from Holthuis, 1991, fig. 6); *2,* overall morphology (adapted from McLaughlin, 1980, fig. 46I).

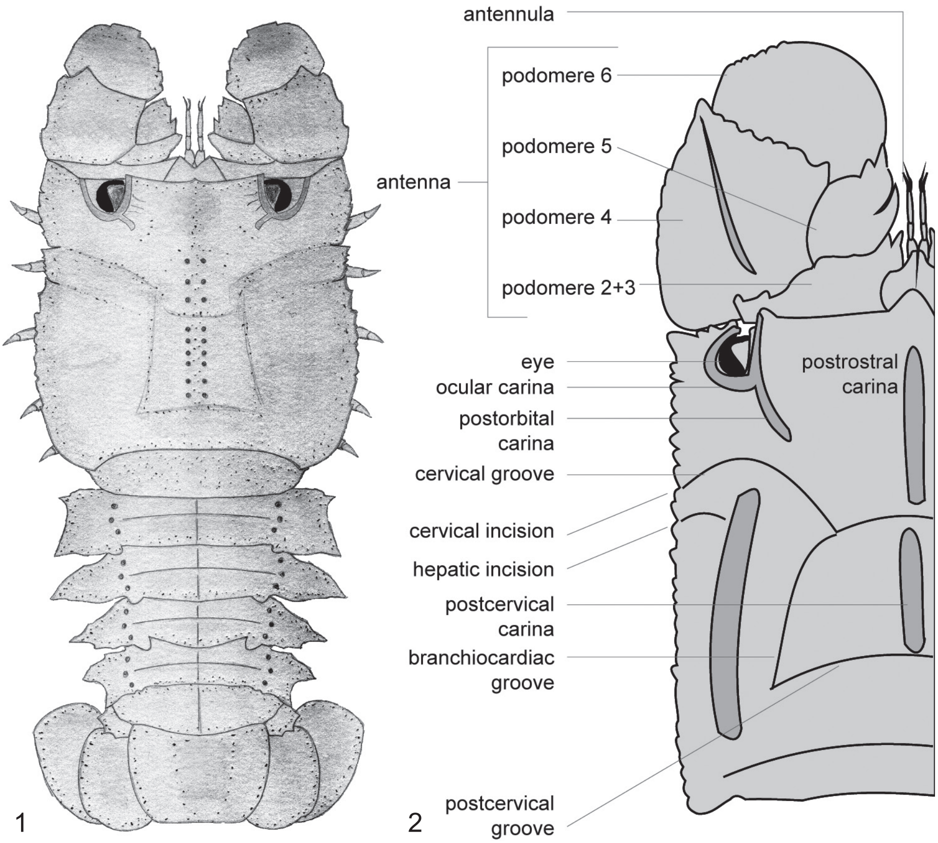


Fig. 52. Overall Scyllaridae morphology: *1,* extinct nisto (juvenile) slipper lobster (adapted from Audo & Charbonnier, 2012); *2,* adult scyllarid carapace morphology (adapted from Holthuis, 1985).

and is occasionally preserved in fossils (Schweitzer & others, 2015) (See Fig. 8.2*).*

PLEON

Like the carapace, the pleon is dorsoventrally compressed and strongly ornamented in achelatans (Fig. 49, Fig. 51, Fig. 52). Palinurids may have squamose tubercles or grooves on the pleonites (Lavalli & Spanier, 2010) and transverse ridges and lateral spines on the individual somites.

The pleon is dorsoventrally flattened in scyllarids and very wide, with longitudinal carinae (Lavalli & Spanier, 2010) (Fig. 49, Fig. 51, Fig. 52). The telson is typically calcified proximally and more weakly calcified or uncalcified distally, which can be evident in fossil preservation.

APPENDAGES

A diagnostic feature of Achelata is the lack of true chelae on pereiopods 1 through 4. They are also distinct from other decapods in the shape of their antennae (Fig. 53).

The antennules are reduced in length, usually with short flagella (Lavalli & Spanier, 2010) (Fig. 50, Fig. 51). The antennae are enlarged and well calcified in Achelata, forming a long, rigid structure (Fig. 50). In Palinuridae, the antennae are long and rigid, and in Cancrinidae, the antennae are tubular and very enlarged (Fig. 49.7, Fig. 53). In Scyllaridae, the fifth and sixth segments of the antennal peduncle are flattened into a flap-like shovel that can be ornamented with spines, keels, or tubercles

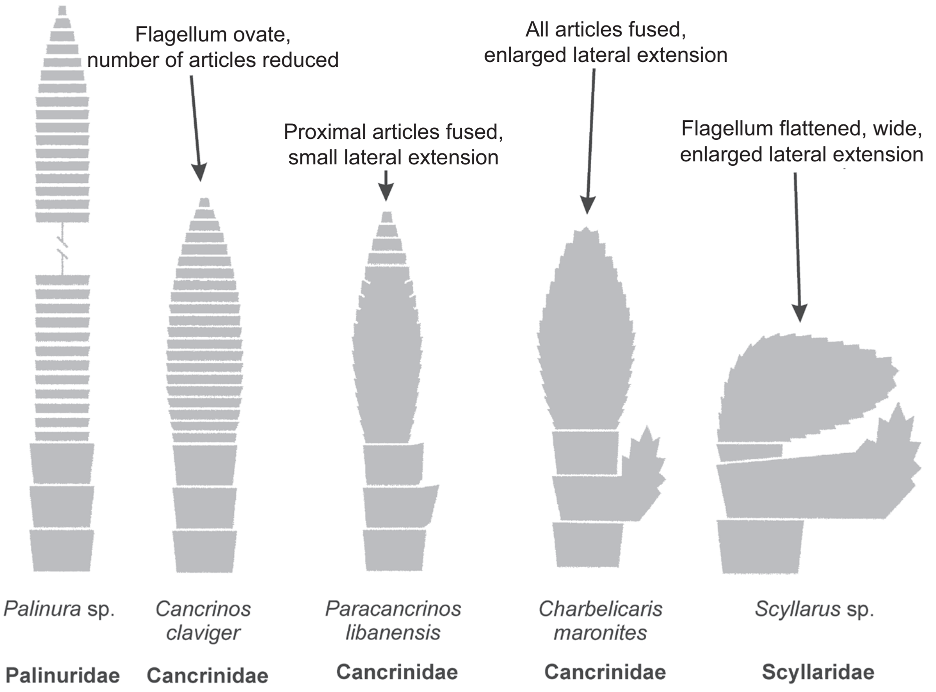


Fig. 53. Antennae of Achelata, interpreted as changing over time (adapted from Haug & others, 2016, fig. 7).

(Lavalli & Spanier, 2010; Schweitzer & others, 2015) (Fig. 52, Fig. 51).

In palinurids, the mandibles are well calcified and are occasionally preserved as fossils (Schweitzer & Feldmann, 2010). Other mouthparts are not known from the fossil record. The maxillae are foliaceous, and maxillipeds are characterized by large foliaceous epipods (Lavalli & Spanier, 2010). The third maxilliped is pediform (Fig. 54).

Pereiopods 1 through 4 lack chelae in Achelata (Fig. 55.2, 55.4), with a few exceptions in Palinuridae, in which pereiopod 1 is subchelate (Fig. 55.1, 55.3). In palinurids, the pereiopods are long and pediform, whereas they are shorter and heavier in scyllarids (Lavalli & Spanier, 2010) and cancrinids (Fig. 55.4–55.5).

Pereiopod 5 is chelate or subchelate in females and is used in egg care (Lavalli & Spanier, 2010) (Fig. 55.5). Scyllarid pereiopods decrease in robustness posteriorly (Lavalli & Spanier, 2010). Typically, in Achelata, pereiopods 2 and 3 are longer than pereiopod 1.

Pleopods are foliaceous and pleopod 1 is absent in both palinurids and scyllarids (Lavalli & Spanier, 2010) (Fig. 56). The telson is strongly calcified anteriorly and is soft posteriorly as are the uropods (Lavalli & Spanier, 2010) (Fig. 50, Fig. 51).

LARVAE

As with the Polychelida, achelatan larvae have a modest but notable fossil record (Fig. 52). Achelatans are metamorphic and possess giant larvae, the phyllosoma, with an extremely flattened body. Despite their weak mineralization, these larvae are present in the fossil record thanks to Konservat Lagerstätten (Haug & others, 2011; Audo & Charbonnier, 2012; Haug & Haug, 2012). The larvae are easily differentiated from the adult by the presence of long multiarticulated swimming exopods on pereiopods, the extremely dorsoventrally flattened carapace,

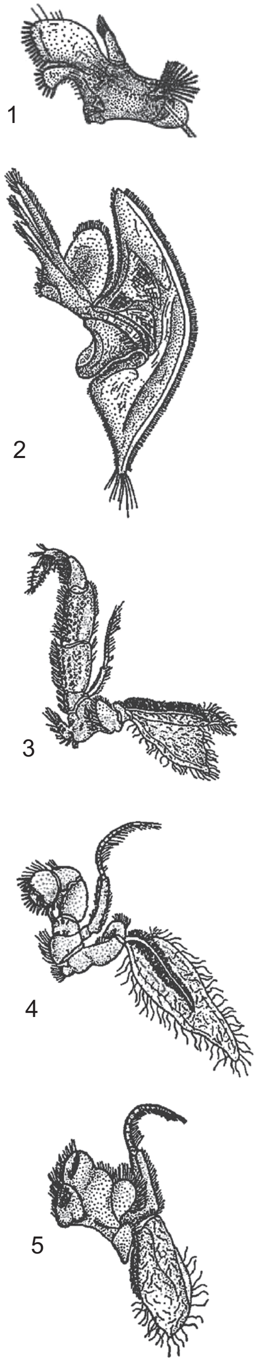


Fig. 54. Palinurid mouthparts: *1,* first maxilla; *2,* second maxilla; *3,* third maxilliped; *4,* second maxilliped; *5,* first maxilliped (adapted from Lavalli & Spanier, 2010, fig. 68.10D–H, 68.11D, I, and N, respectively).

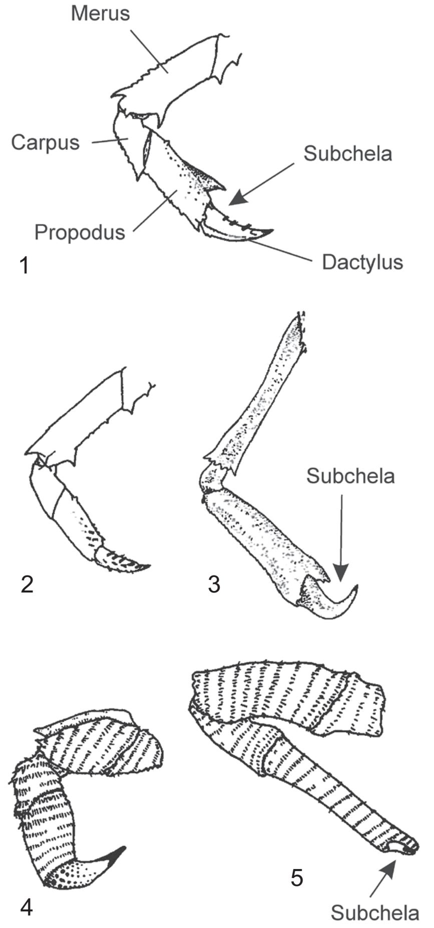


Fig. 55. Achelata pereiopods: *1,* first pereiopod of palinurid with subchelate termination; *2,* first pereiopod of palinurid with achelate termination; *3,* first pereiopod of palinurid with subchelate termination; *4,* first pereiopod of scyllarid with heavily mineralized tip of dactyl; *5,* fifth pereiopod of scyllarid lobster with subchelate termination (adapted from Lavalli & Spanier, 2010, fig. 68A–E).

with a cephalic region much larger than the thoracic region, and a comparatively small pleon (Palero, Clark, & Guerao, 2014).

INFRAORDER ASTACIDEA: LOBSTERS AND CRAYFISH

Astacidea comprises marine lobsters (Homarida Scholtz & Richter, 1995) and the freshwater crayfish (Astacida Scholtz & Richter, 1995) (Scholtz & Richter, 1995;

Feldmann, Schweitzer, & Karasawa, 2016; Schram & Koenemann, 2021). Their morphology is similar overall. They can be distinguished easily by the reduction of the cervical groove in marine lobsters, which is only visible in the ventral part of the cephalothorax, contrary to that of Astacida, in which the cervical groove intersects the median line. Additionally, the freshwater crayfish have mobility of the last thoracic segment (Rode & Babcock, 2003), and some (Astacoidea) have a diaresis on the telson.

CARAPACE

The carapace in astacideans is cylindrical, slightly laterally compressed, and marked at approximately the mid-length by a cervical or postcervical groove. The groove and ornamentation terminology for Nephropidae was developed by Holthuis (1974) and is still the standard for reference for Astacidea. The anterior margin of the carapace bears a rostrum, the lateral margins of which extend onto the carapace as postorbital ridges (Gherardi & others, 2010) (Fig. 57).

In homaridans, the anterior margin of the carapace is characterized by a rostrum extending anteriorly between the eyes, the lateral margins of which extend onto the carapace to border the orbits. The rostrum may bear supraorbital and/or suborbital spines (see Fig. 5). The anterior region can be ornamented with median, subdorsal, supraorbital, postorbital and/or metorbital spines (Fig. 5). Nephropoids may bear what Holthuis (1974, p. 737) termed the incisura clavicularis, a small notch in the anterolateral margin of the carapace that fits around a tubercle or ridge (the clavicular carina) on the epistome and evidently serves to lock the carapace to the epistome. In some nephropids (e.g., *Homarus* Weber, 1795), the epistome ridge fits the notch well. In others, the ridge or rounded ridge fits the notch poorly (e.g., *Metanephrops* Jenkins, 1972) or insignificantly (e.g., *Acanthacaris* Bate, 1888) (Tshudy, unpublished data).

Glaessner (1969) considered the longitudinal axis of homaridan lobsters to function similar to a *linea*, because it splits when the animal molts. The groove and ornamentation terminology of Holthuis (1974) was developed primarily for the Homarida (Fig. 5, Fig. 58). Of the grooves, the cervical and postcervical grooves are most prominent. The homology of the cervical groove among the Nephropoidea is suggested because its position is constant. The same is true for the postcervical groove where it crosses the dorsomedian and for the antennal groove. Also typically observed on nephropoids is the branchiocardiac groove.

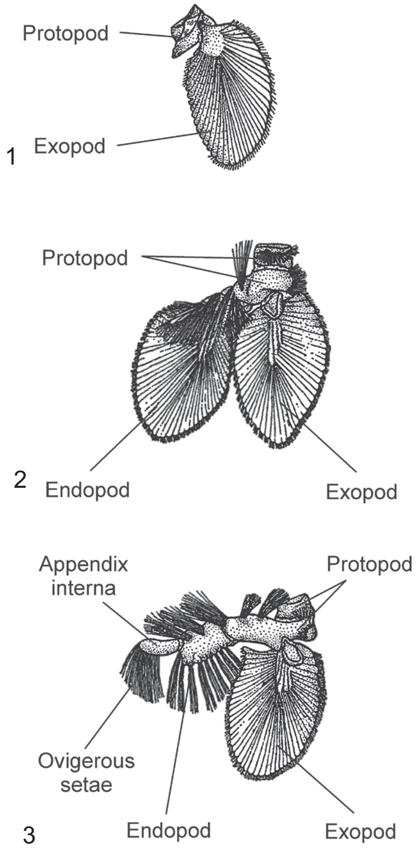


Fig. 56. Palinurid pleopods; *1,* male pleopod; *2,* female pleopod 2; *3,* female pleopods 3–5 (adapted from Lavalli & Spanier, 2010, fig. 68.13B–D, respectively).

In many of the nephropid lobsters, the branchiocardiac groove and postcervical groove merge at approximately the mid-

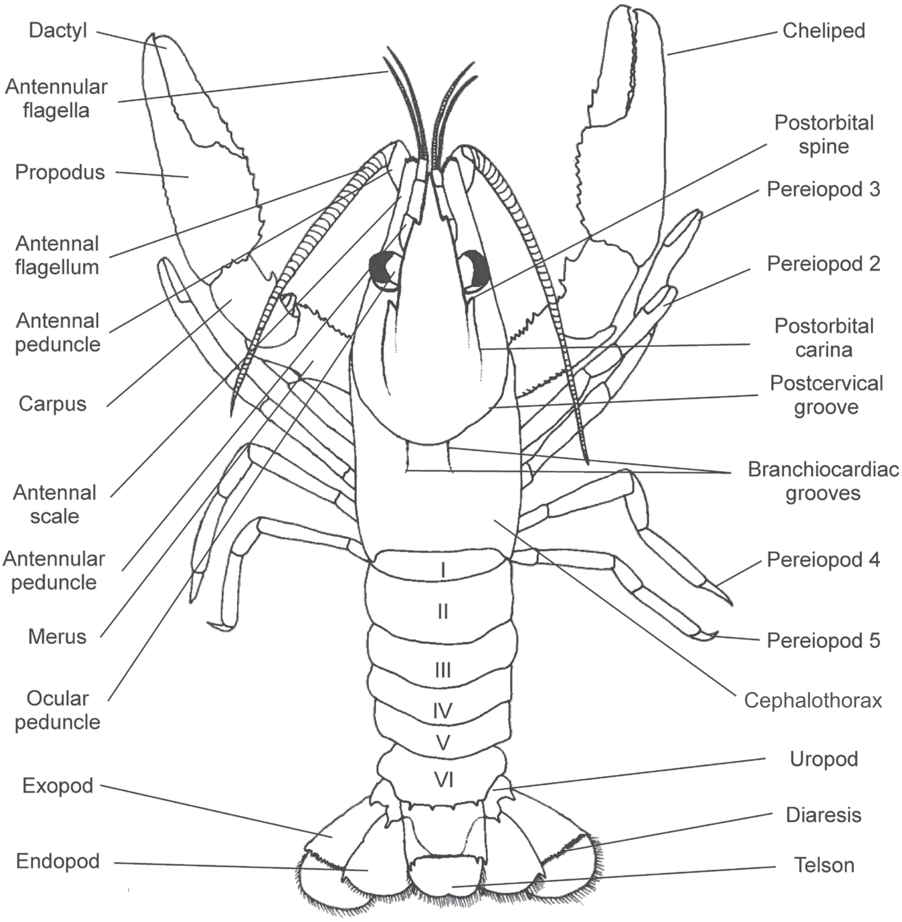


Fig. 57. Generalized freshwater astacidan morphology (adapted from McLaughlin, 1980, fig. 46A). Pleonal somites numbered with Roman numerals.

height of the carapace and extend anteroventrally, sometimes connecting to a small, U-shaped hepatic groove. The homologies of these grooves were revealed by examination of older, related lobsters, particularly the Stenochiridae, in which the branchiocardiac and postcervical grooves are separate. The postcervical groove in some forms extends anteriorly as the intercervical groove.

THORACIC STERNUM

The thoracic sternum of astacideans is narrow. The eighth sternite is not fused to the other seven in Astacida, termed the fractosternal condition (Scholtz & Richter, 1995) (Fig. 59). In homaridans, the eighth sternite is fused to the seventh sternite. The sternum in astacideans is thickest axially and thinnest laterally, and females have a thelycum (Wahle & others, 2012) (Fig. 59, Fig. 60).

PLEON

The pleon in both astacidans and homaridans is comprised of well-calcified pleonites. Each exhibits a tergum and pleuron, and articulating rings of the terga ensure that the pleon is fully movable. Depending on the taxon, the terga and pleura are smooth or ornamented with spines, ridges, or tubercles

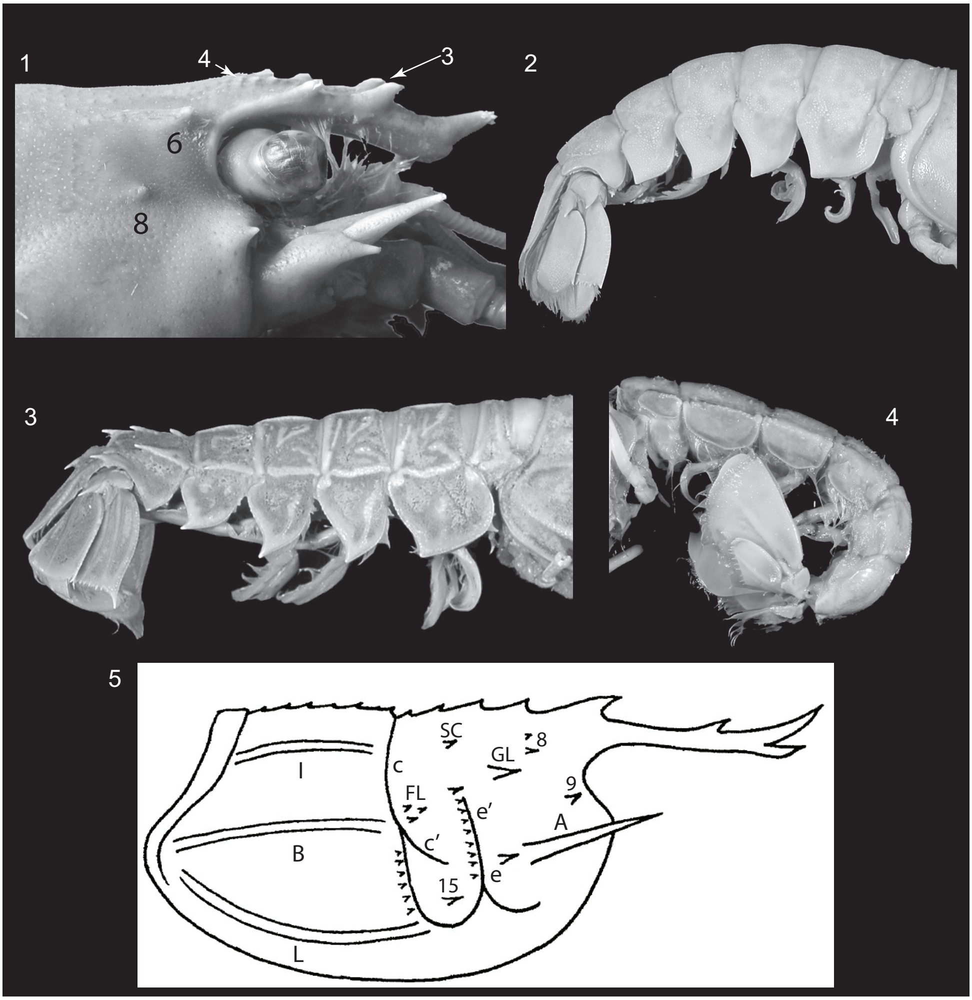


Fig. 58. Features of nephropid lobster carapaces and pleons. *1, Homarus americanus* (Linnaeus, 1758), spines numbered following Holthuis (1974); *2, Homarus gammarus* H. Milne-Edwards, 1837, with simple ornamamentation on pleura of pleonites, USNM 2085; *3,* sculptured ornamentation on pleura of *Metanephrops japonicus* (Tapparone Canefri, 1873), USNM 104182; *4,* short, rounded pleura of *Thaumastocheles massonktenos* Chang, Chan & Ahyong, 2014, holotype MNHN-IU-2008-10556N (photo by L. Flamme, RECOLNAT (ANR-11-INBS-0004); *5,* nephropid carapace (*1–3,* photos by D. Tshudy; *5,* adapted from Tshudy, Chan, & Sorhannus, 2007, fig. 2A). FL=flank spine, GL=gastro-lateral spine, SC=supra-cervical spine, other labels as in Fig. 5 on p. 6.

(Wahle & others, 2012) (Fig. 61). In the marine clawed lobsters, the smooth condition is shown well on *Homarus* (Fig. 58.2) whereas both the smooth and ornamented condition is shown well among different species of *Metanephrops* (Fig. 58.3), the most speciose nephropid genus.

Pleuron shape in the Nephropidae varies from the more common cordate (Fig. 58.2–3) to rather quadrate in the thaumastochelid clade (Fig. 58.4). The morphology of the telson is important for distinguishing among astacidans. In Astacoidea, the telson has a diaresis (Fig. 62.1).

In Parastacoidea, the telson lacks a diaresis but may have a membranous termination (Feldmann, Schweitzer, & Karasawa, 2016) (Fig. 62.2).

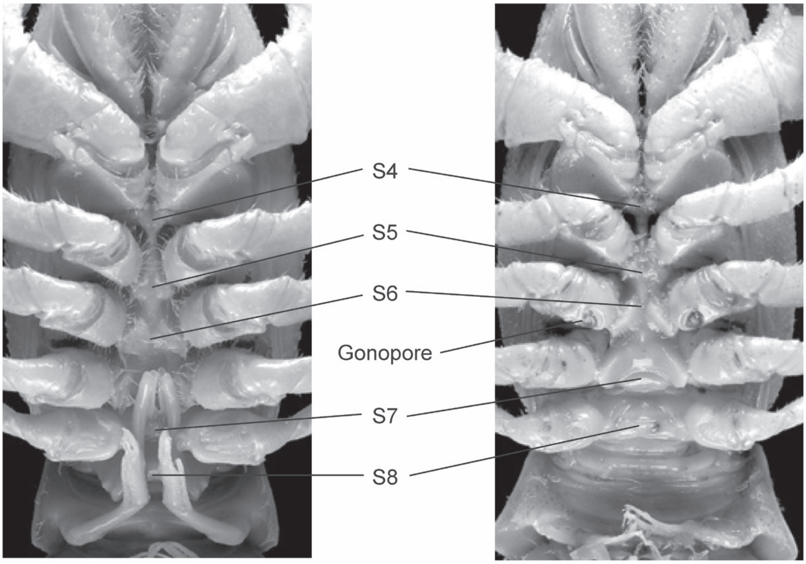


Fig. 59. Astacidan sterna, male at right, *Astacus astacus* (Linnaeus, 1758), and female at left, *Austropotamobius torrentium* (Schrank, 1803) (adapted from Feldmann, Schweitzer, & Karasawa. 2016, fig. 1b and 2b). S=sternite.

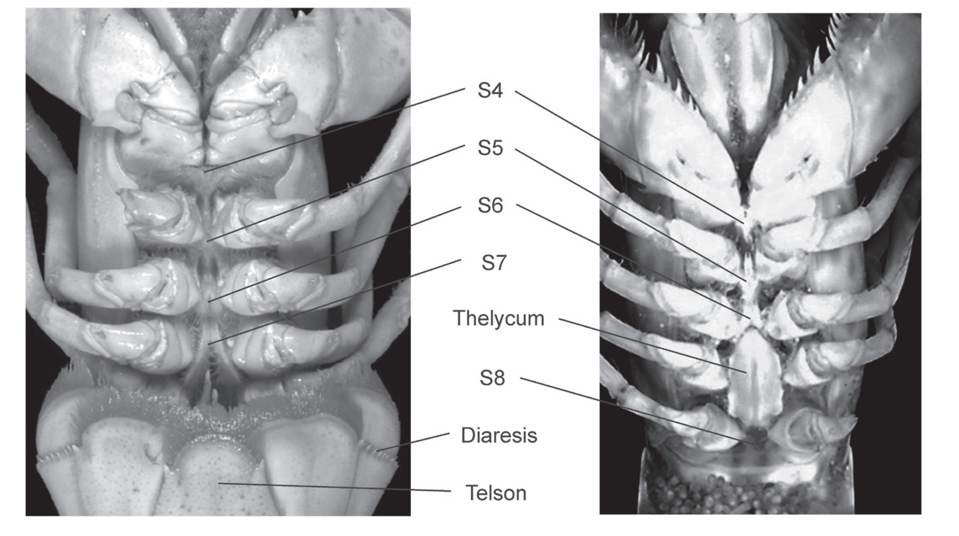


Fig. 60. Homarid sterna, left, male, *Homarus americanus* H. Milne-Edwards, 1837, and right, female, *Enoplometopus debelius* Holthuis, 1983 (adapted from Feldmann, Schweitzer, & Karasawa, 2016, figs. 16b and 10c). S=sternite.

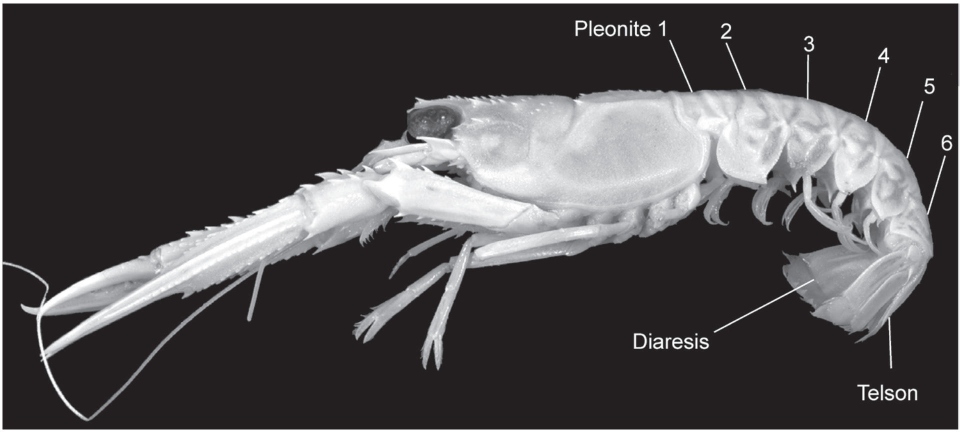


Fig. 61. Homarid pleon, *Nephrops norvegicus* Leach, 1814 in 1813–1814 (adapted from Feldmann, Schweitzer, & Karasawa, 2016, fig. 20,*1*).

APPENDAGES

Antennules are biflagellate in both astacidans and homaridans, with a tri-segmented peduncle, the basalmost of which contains a statocyst. This structure contains a statolith suspended in fluid to help keep the animal oriented (Gherardi & others, 2010; Wahle & others, 2012). Antennae are biramous with a scaphocerite in most cases and a long flagellum (Fig. 57). Maxillules, maxillae, and maxillipeds are similar to those of other decapods (Fig. 63). The third maxillipeds are long and pediform and thus are sometimes visible in fossils.

Both astacidans and homaridans are diagnosed by chelate pereiopods 1–3 (Fig. 57). The first pair is by far the strongest and is typically heterochelous. Heterochely may be expressed as a crusher claw, which is heavier, more robust, and stronger for crushing shells and other prey, and a more slender cutter claw for tearing apart food (Wahle & others, 2012) (Fig. 64). A bulbous manus and long, slender, spinose fingers on the first pereiopod characterize some groups (Fig. 65). Pereiopods 2 and 3 bear smaller chelae used for a variety of functions, including locomotion, feeding, and grooming (Fig. 64, Fig. 65). Pereiopod 4 is achelate except in Uncinidae, and pereiopod 5 is almost always achelate (Wahle & others, 2012; Feldmann, Schweitzer, & Karasawa, 2016). Enoplometopidae is characterized by weak pseudochelae on pereiopods 2–5 (Feldmann, Schweitzer, & Karasawa, 2016). The first male pleopods are modified for reproduction and sperm transfer in males (Fig. 66). In females, the pleopods are modified to carry the eggs. In both males and females, the pleopods move to circulate water over the gills and for locomotion (Gherardi & others, 2010; Wahle & others, 2012). The uropods always have a diaresis on the exopod (Feldmann Schweitzer, & Karasawa, 2016) (Fig. 62). In thaumastocheliforms, the exopod diaresis is smaller than in other nephropids. The endopod on most nephropids is as wide

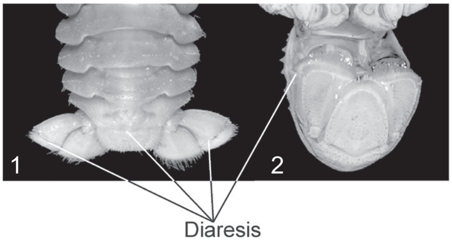


Fig. 62. Tail fan in Astacidae and Parastacidae. *1,* Astacidae, *Austropotamobius torrentium* Schrank, 1803, diareses on telson and uropods indicated (Feldmann, Schweitzer, & Karasawa, 2016, 1,*2a*; *2,* Parastacidae, *Astacopsis franklinii* Gray, 1845, diaresis on uropods only (Feldmann, Schweitzer, & Karasawa, 2016, fig. 6,*2a*).

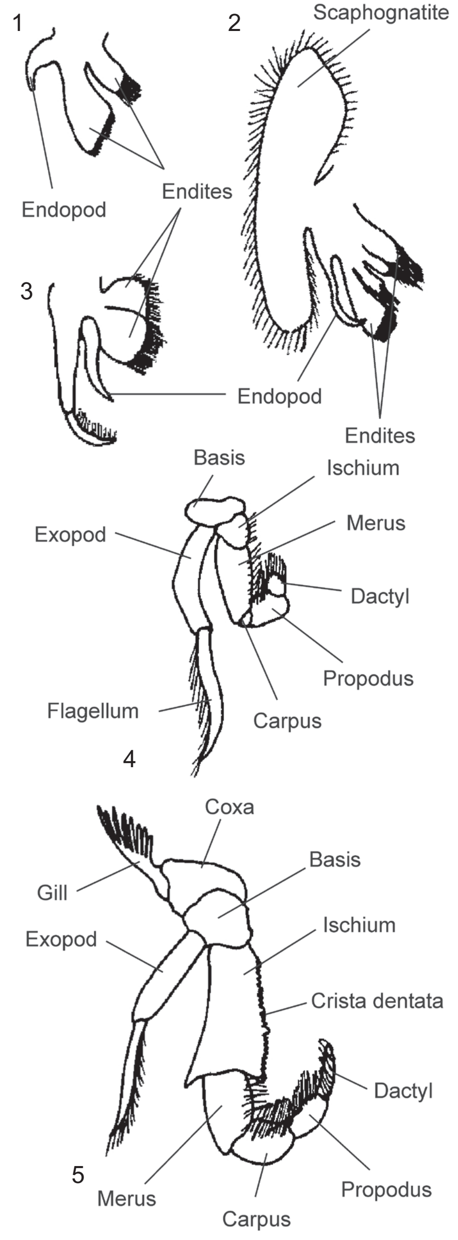


FIG. 63. Astacidan mouthparts: *1,* first maxilla, *2,* second maxilla; *3,* first maxilliped; *4,* second maxilliped; *5,* third maxilliped (adapted from MCLAUGHLIN, 1980, fig. 46 B–F).

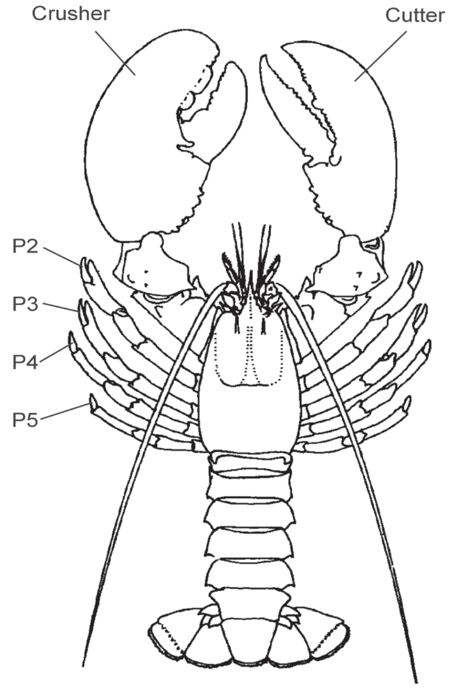


FIG. 64. Typical astacidan pereiopods (adapted from HOLTHUIS, 1991, fig. 26). P=pereiopod.

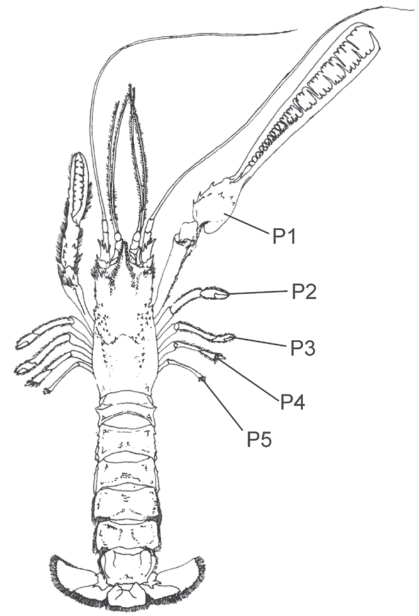


FIG. 65. Pectinate claws on first pereiopod, *Thaumastocheles japonicus* CALMAN, 1913 (adapted from HOLTHUIS, 1991, fig. 33). P=pereiopod.

as the exopod, but on thaumastocheliform homaridans, the endopod is much smaller than the exopod.

INFRAORDERS AXIIDEA AND GEBIIDEA: GHOST AND MUD SHRIMP AND MUD LOBSTERS

Axiidea and to a lesser extent Gebiidea have an extensive fossil record based mostly on chelae of the first pereiopods (Hyžný & Klompmaker, 2015). Common names for these animals include ghost or mud shrimp, mostly applied to axiideans, and mud lobsters, mostly used for *Thalassina* Latreille, 1806,

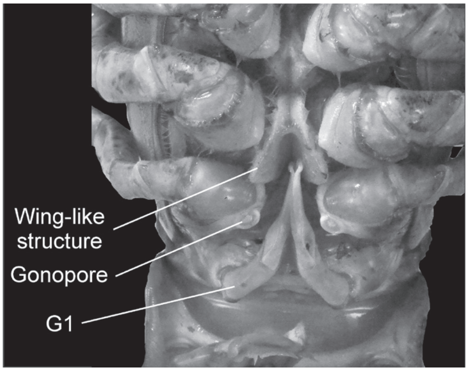


Fig. 66. Astacid male pleopod one and wing-like structure, *Homarus americanus* H. Milne-Edwards, 1837 (adapted from Feldmann, Schweitzer, & Haggart, 2020, fig. 3C).

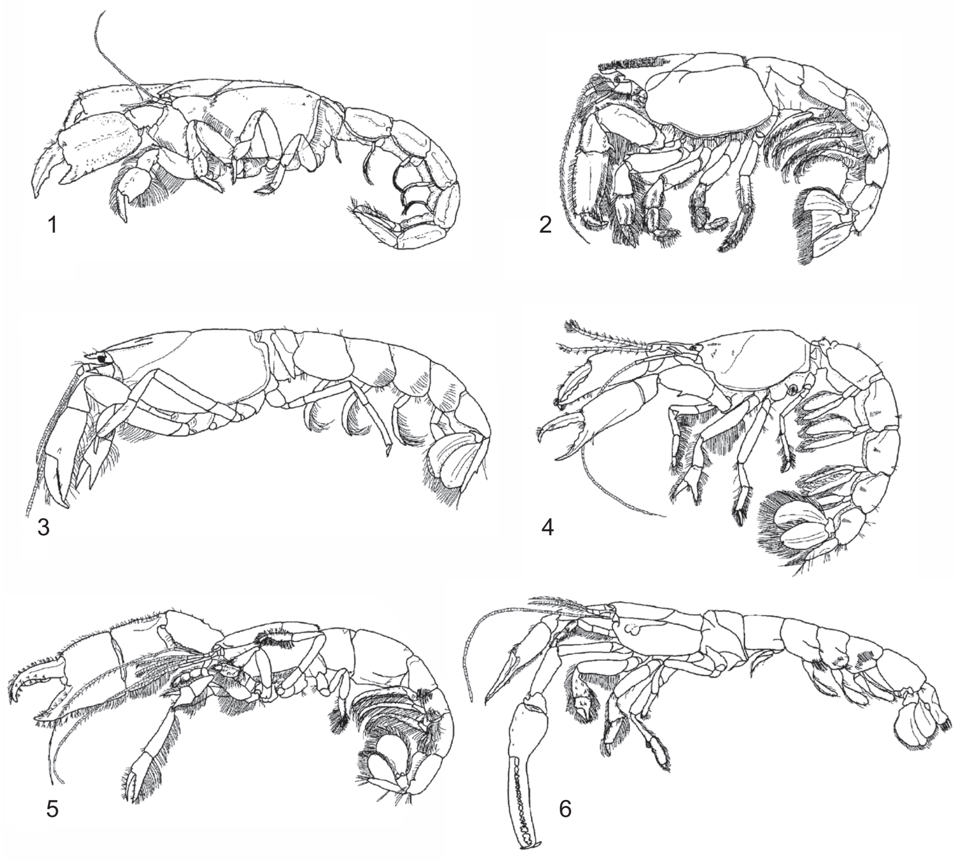


Fig. 67. Overall axiidean and gebiidean morphology. *1, Thalassina anomala* (Herbst, 1804 in 1782–1804) (Gebiidea, Thalassinidae); *2, Upogebia affinis* (Say, 1818 in 1817–1818) (Gebiidea, Upogebiidae); *3, Axius stirhynchus* Leach, 1815 (Axiidea, Axiidae); *4, Michelea pillsburyi* Kensley & Heard, 1991 (Axiidea, Micheleidae); *5, Callianassa subterranea* (Montagu, 1808) (Axiidea, Callianassidae); *6, Ctenocheles balssi* Kishinouye, 1926 (Axiidea, Ctenochelidae) (adapted from Dworschak, Felder, & Tudge, 2012, fig. 69.1A, B, E, I, K, L, respectively).

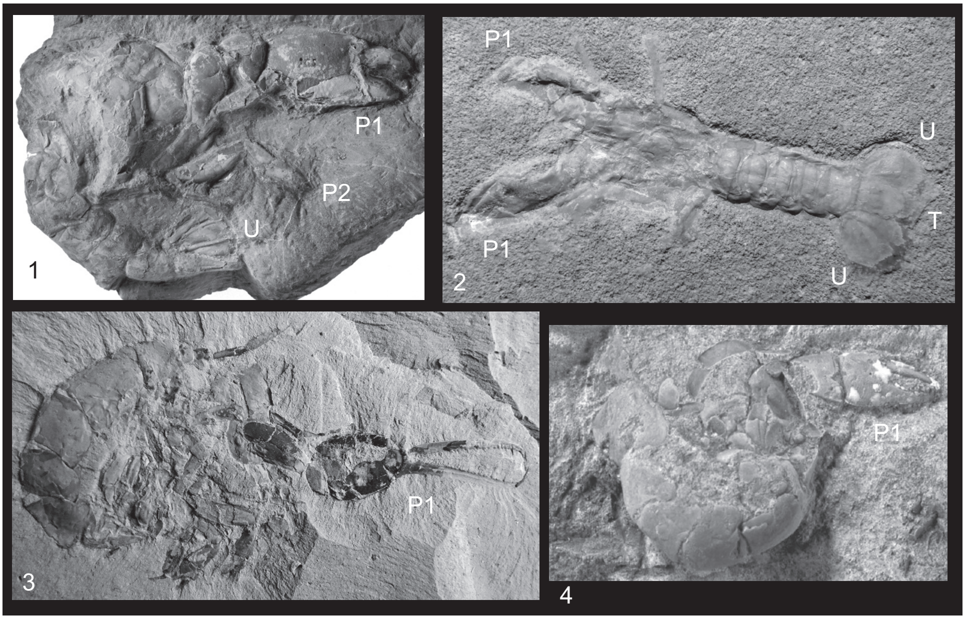


FIG. 68. Overall axiidean morphology in fossils. *1, Axius hofstedtae* HYŽNÝ, JAKOBSEN, & FRAAIJE, 2017 (Axiidae), MGUH31573; *2, Magila latimana* (MÜNSTER, 1839) (Axiidae), BMNH 44788; *3, Ctenocheles fritschi* HYŽNÝ, VESELSKÁ, & DVOŘÁK, 2014 (Ctenochelidae), 4, *Comoxianassa haggarti* SCHWEITZER & others, 2009 (Callianassoidea), GSC 27156. Photos by S. Jakobsen (*1*); by M. Hyžný (*2*); by P. Dvořák (*3*); and *4* adapted from Schweitzer & others, 2009, fig. 3H. P=pereiopod, T=telson, U=uropods.

and potentially for Gebiidea (SCHRAM & KOENEMANN, 2021). In the literature, they have been together formerly known as Thalassinidea or even just as callianassids, stemming from the common practice in the past of naming each claw fragment of the typical ghost shrimp morphology as *Callianassa.* Part of this proliferation of names for the group stems from a convoluted systematic history (SCHRAM & KOENEMANN, 2021), in addition to the immense variability in the group. Because of this, morphology for this group is described at the family level herein, as advocated by SCHRAM and KOENEMANN (2021), so that identification of these animals as well as study of their evolution can be best achieved.

More recently, in addition to the abundant cheliped elements, dorsal carapace elements and pleonites have been described from the fossil record (SCHWEITZER & others, 2009; HYŽNÝ, JAKOBSEN, & FRAAIJE, 2017; HYŽNÝ & SUMMESBERGER, 2019). The general body form of most axiideans and gebiideans is of a weakly calcified, shrimp or lobster-like animal, with large chelipeds as compared to body size, adapted for a burrowing habit (Fig. 67, Fig. 68).

CARAPACE

The carapace in axiidean and gebiidean shrimps is poorly to moderately calcified, elongate, and cylindrical or laterally compressed (Fig. 69, Fig. 70). It is sporadically preserved in the fossil record (Fig. 71). Anteriorly, most axiideans and gebiideans have a rostrum, which extends between the eyestalks (Fig. 69). It can be triangular or spinelike and can have serrations or lateral spines. In some representatives, the rostrum is tiny or absent (Fig. 69.5). Some taxa bear dorsal carapace keels anteriorly, which can be spinose, and diverge posteriorly from the base of the rostrum (Fig. 69.3). Axiideans and gebiideans may have a cervical groove, usually best expressed dorsally. All gebiideans and some axiideans are diagnosed by a *linea thalassinica*, a suture that extends anterior

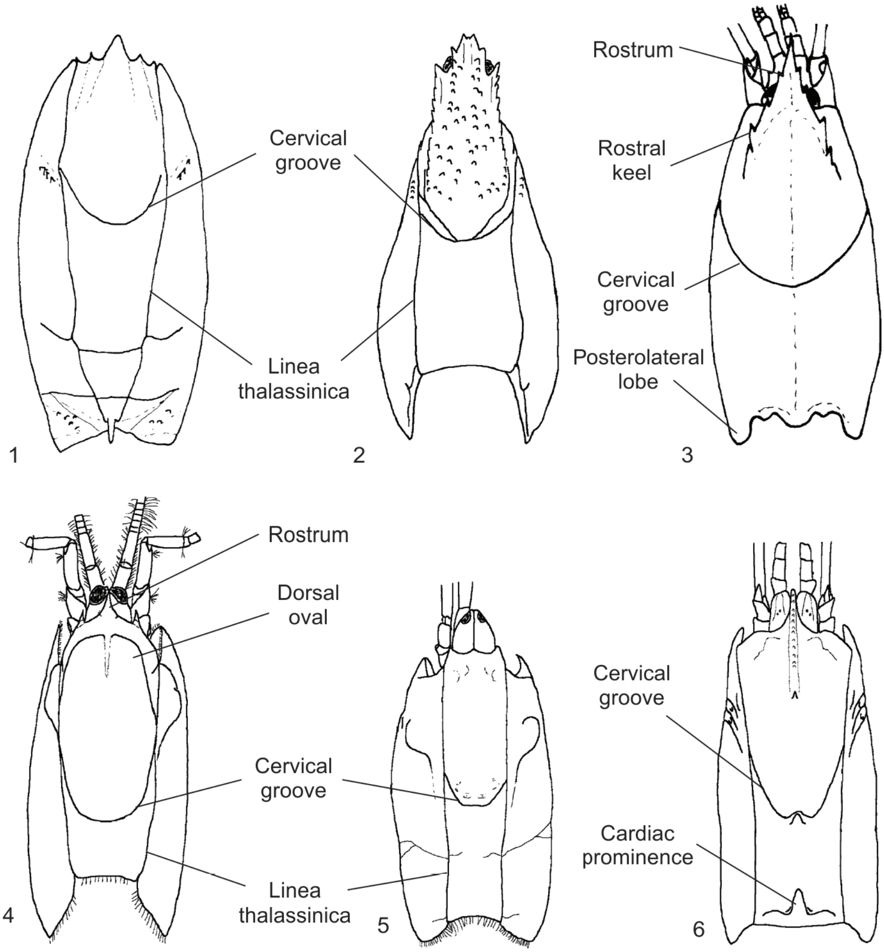


Fig. 69. Dorsal axiidean and gebiidean morphology. *1, Thalassina krempfi* Ngoc-Ho & de Saint Laurent, 2009 (Gebiidea, Thalassinidae); *2, Upogebia deltaura* (Leach, 1815) (Gebiidea, Upogebiidae); *3, Eiconaxius hakuhou* Sakai & Ohta, 2005 (Axiidea, Axiidae); *4, Corallianassa hartmeyeri* (Schmitt, 1935) (Axiidea, Callichiridae); *5, Eucalliaxopsis aequimana* (Baker, 1907) (Axiidea, Eucalliacidae); *6, Ctenocheles serrifrons* Le Leouff & Intès, 1974 (Axiidea, Ctenochelidae). Adapted from Dworschak, Felder, & Tudge, 2012, fig. 69.2A, 2B, 2G, 2M, 2N, 2O, respectively.

to posterior, separating the dorsal carapace from the lateral branchiostegite (Fig. 70). The branchiostegal area extends quite far ventrally from the *linea thalassinica* when present or from the bases of the antenna when it is not present (Fig. 70). The *linea thalassinica* may intersect the cervical groove. A few families are characterized by a dorsal oval which is comprised of an arcuate groove anteriorly, the *linea thalassinica*, and the cervical groove, forming a distinct, elevated oval shape (Fig. 69.4, Fig 70.4, Fig. 71.1, Fig. 72). The cardiac prominence, consisting of a strong swelling, is present in some axiideans near the posterior margin of the carapace (Fig. 69.6, Fig 70.6, Fig. 71.1, Fig. 72). Posterolateral lobes are convex projections on the posterior margin of the carapace of some axiideans that articulate with the first somite of the pleon (Dworschak, Felder, & Tudge, 2012) (Fig. 69, Fig 70).

PLEON

The pleon is weakly calcified and longer than the carapace (Fig. 67, Fig. 68). It is less common to find it preserved in fossils as

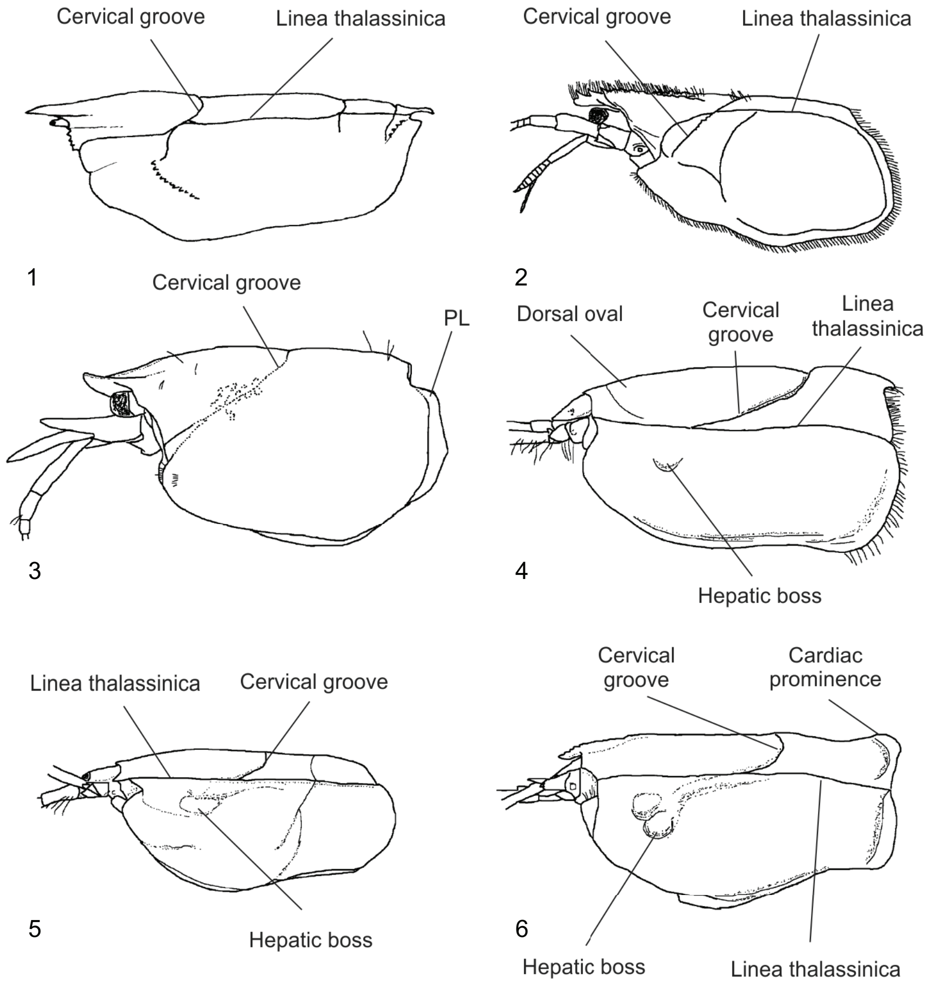


Fig. 70. Lateral axiidean and gebiidean carapace morphology. *1, Thalassina anomala* (Herbst, 1804 in 1782–1804) (Gebiidea, Thalassinidae); *2, Upogebia deltaura* (Leach, 1815) (Gebiidea, Upogebiidae); *3, Eiconaxius hakahou* Sakai & Ohta, 2005 (Axiidea, Axiidae); *4, Callianassa subterranea* (Montagu, 1808) (Axiidea, Callianassidae); *5, Eucalliaxopsis aequimana* (Baker, 1907) (Axiidea, Eucalliacidae); *6, Ctenocheles balssi* Kishinouye, 1926 (Axiidea, Ctenochelidae). Adapted from Dworschak, Felder, & Tudge, 2012, fig. 69.3A, B, E, J, L, M, respectively. PL=posterolateral lobe.

compared to the elements of the first pereiopods (Fig. 73). The pleonites are quite variable across these groups, but the first somite is typically shortest. The pleura are short in these groups, and are sharp or rounded. Notably, in some axiids the pleura of the second somite overlaps that of the first and third somites, similar to the condition seen in caridean shrimp, which is important for paleontologists examining fragmentary material (Fig. 67.3, Fig. 73.3). The telson is mostly oval to rectangular with rounded edges in most families (Fig. 68.2). In Thalassinidae, it is elongate, whereas in Strahlaxiidae it is characteristically rhomboid with several transverse carinae. In Upogebiidae, it can have various outlines, including oval, rectangular, or square. In *Pomatogebia* Williams & Ngoc-Ho, 1990, it forms an operculum together with the uropods (Dworschak, Felder, & Tudge, 2012). The telson of Axiidae and Calocarididae may have spines on its dorsal

Fig. 71. Fossil axiidean carapaces. *1, Callianopsis clallamensis* (Withers, 1924), note dorsal oval and cardiac prominence; *2, Axiopsis spinifera* Franţescu, 2014b, *3, Axiopsis pawpawensis* Franţescu, 2014b (lateral view); *4, Plioaxius texensis* Franţescu, 2014b, *5, Plioaxius texensis* (unusual mineralization); *6, Axiopsis eximia* Kensley & Williams, 1990, holotype, USNM PAL 219431 (*1,* adapted from Schweitzer Hopkins & Feldmann, 1997, fig. 7C; *2–5,* adapted from Franţescu, 2014b, fig. 2A, 2E, 4D, 4E, respectively. *6,* new; photo by R. Feldmann).

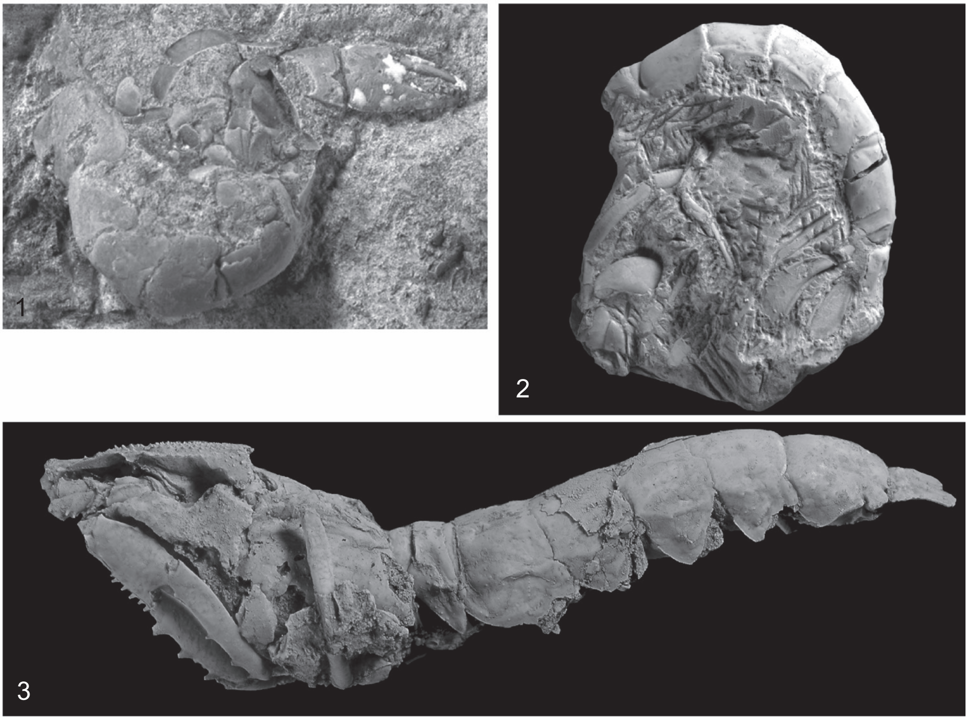
surface. In Callianassoidea *sensu* Poore and others (2019), the telson attains great morphological diversity, including broadly or elongately oval, trapezoid, or broadly rectangular. The posterior margin may exhibit a concavity (e.g., Anacalliacidae) or a terminal median spine (e.g. Paracalliacidae).

EYES AND APPENDAGES

Eyestalks, although not true appendages, are noted here as they are known from some fossil groups (Fig. 72), and in general, they are well developed, although the eyes themselves are apparently small and degenerate

Fig. 72. At left. Preserved eyes in Cretaceous axiidean, *Dawsonius tigris* Franţescu, 2014b (Ctenochelidae). Note also dorsal oval and cardiac prominence (adapted from Franţescu, 2014b, fig. 1A).

Fig. 73. Fossil axiidean pleons (below). *1, Comoxianassa haggarti* Schweitzer & others, 2009 (Callianassoidea) (adapted from Schweitzer & others, 2009, fig. 3E); *2, Metoconaxius rhachiochir* (Stenzel, 1945) (Micheleidae) (adapted from Franţescu, 2014b, fig. 3F); *3, Axiopsis eximia* Kensley & Williams, 1990, holotype, USNM PAL 219431 (Axiidae) (new, photo by R. Feldmann).



(Dworschak, Felder, & Tudge, 2012). Mouthparts are rarely known from the fossil record, nor are antennular or antennal flagella, although they are reasonably long in most taxa, with the antennal flagellum being longer than the carapace in most cases (Fig. 67). These appendages were well described and illustrated by Dworschak, Felder, and Tudge (2012) and representative appendages are illustrated here (Fig. 74).

The first pair of pereiopods is by far the most commonly preserved element of axiidean and gebiidean remains in the fossil record (Hyžný & Klompmaker, 2015). The vast majority of callianassoid taxa (*sensu* Poore & others, 2019; Robles & others, 2020) are known only from isolated cheliped elements, mostly propodi and fingers. For this reason, dozens of species based on claw fragments have been referred to *Callianassa sensu lato* (Schweitzer & others, 2010, for example). The morphology of the first pereiopod is therefore extremely important for the classification of fossils in these groups (Fig. 75). It is always chelate or subchelate and better biomineralized than any other part of the animal, resulting in its frequent fossilization. The merus is variously ornamented with spines, hooks, and keels, which can be diagnostic at the genus level. The carpus is highest distally and can display a bladelike ventral extension on the lower margin (Fig. 75). In many callianassoids *sensu* Poore and others (2019), the carpus of the first pereiopod has upper and lower margins subparallel with each other (Fig. 75.5–6, 75.8), whereas in axiids and some gebiideans, the carpus is very short and cup-shaped (Fig. 75.1–3).

The chelae of axiideans and gebiideans are remarkably variable. In some groups, the chelae are subchelate (Upogebiidae) (Fig. 75.1) and are subequal and similar whereas in others (Ctenochelidae, Callichiridae, Callianassidae, Axiidae), chelipeds are strongly heterochelous (Dworschak, Felder, & Tudge, 2012) (Fig. 76). In the latter family, however, they can also be elongate and very spiny (e.g., *Acanthaxius*

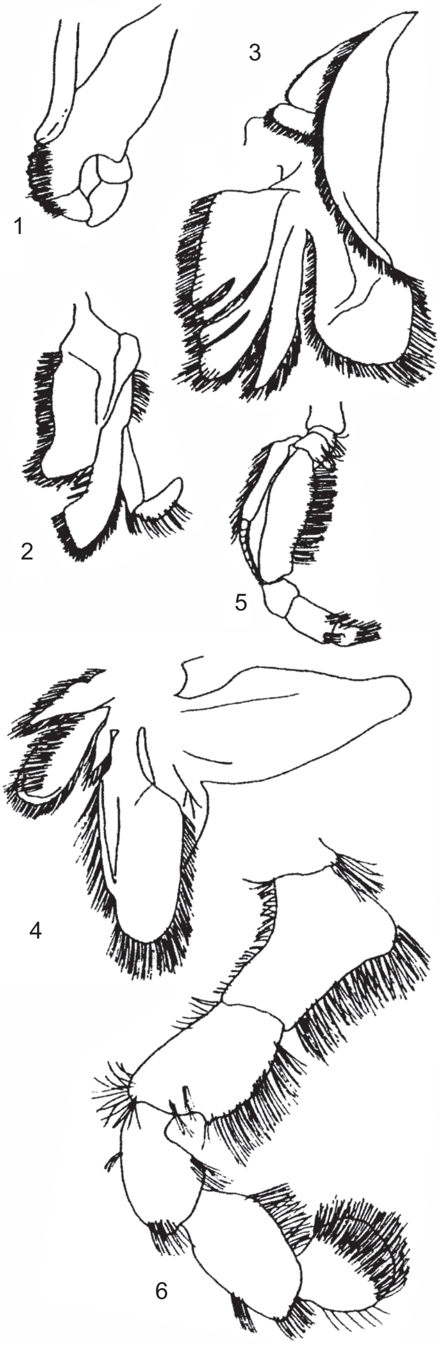


Fig. 74. Axiidean mouth parts: *1,* mandible; *2,* first maxilla; *3,* second maxilla; *4,* first maxilliped; *5,* second maxilliped; *6,* third maxilliped (adapted from Schweitzer Hopkins & Feldmann, 1997, fig. 1A, B, C, D, E, F).

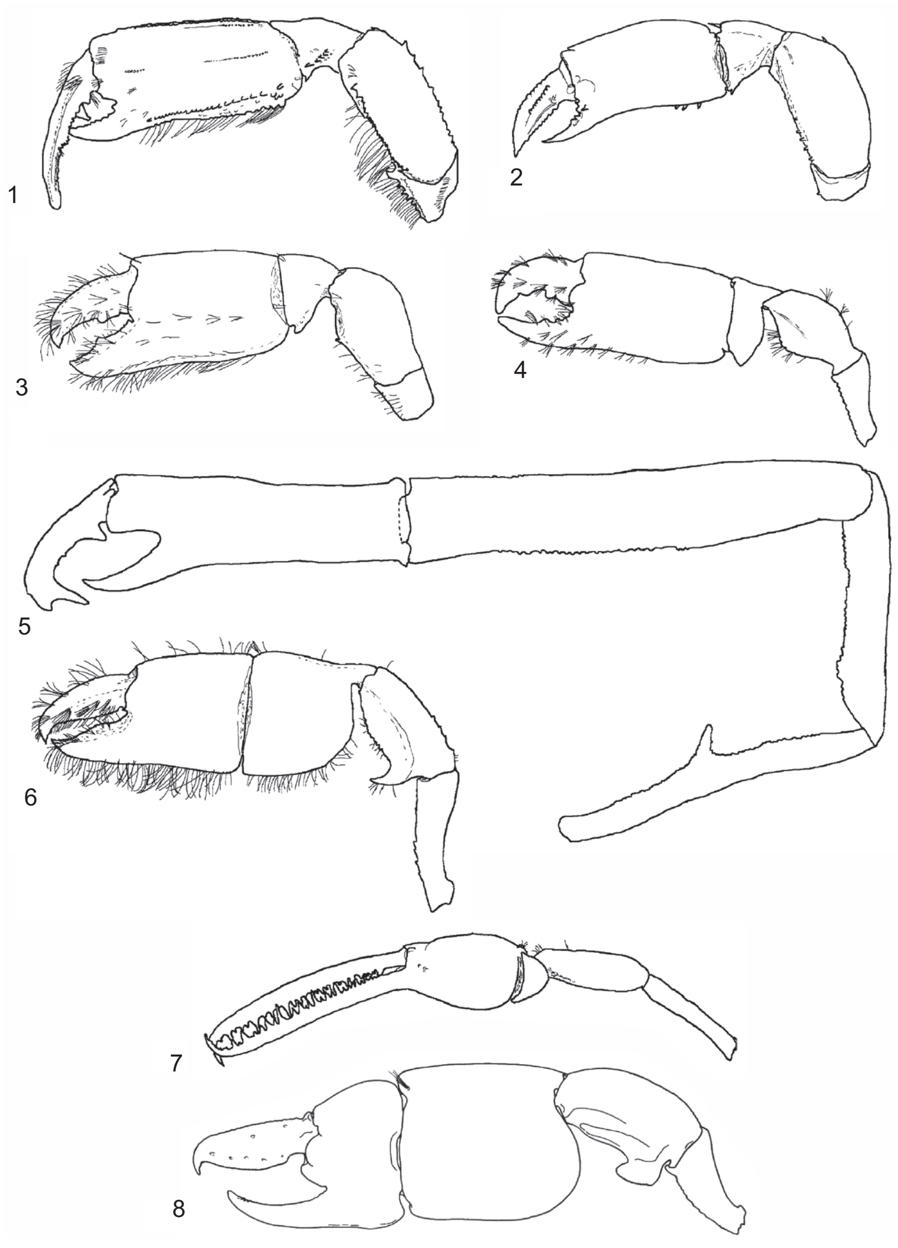


Fig. 75. Axiidean and gebiidean major chelipeds. *1, Thalassina emerii* Bell, 1844 (Gebiidea, Thalassinidae); *2, Upogebia deltaura* (Leach, 1815) (Gebiidea, Upogebiidae), *3, Axius stirhynchus* Leach, 1815 (Axiidea, Axiidae); *4, Callianidea laevicauda* (Gill, 1859) (Axiidea, Callianideidae); *5, Callichirus islagrande* (Schmitt, 1935) (Axiidea, Callichiridae); *6, Callianassa subterranea* Kishinouye, 1926 (Axiidea, Callianassidae); *7, Ctenocheles balssi* (Montagu, 1808) (Axiidea, Ctenochelidae); *8, Neotrypaea californiensis* (Dana, 1854) (Axiidea, Callianassidae) (*1–7,* adapted from Dworschak, Felder, & Tudge, 2012, fig. 69.13A, C, G, Q, 69.14A, C, E, respectively; *8,* adapted from Manning & Felder, 1991, fig. 10d).

Sakai & de Saint Laurent, 1989). In Anacalliacidae, Callianassidae, Callianopsidae, Callichiridae, Eucalliacidae, Paracalliacidae, and the majority of Ctenochelidae, the chelae are ventrally flattened, whereas in some Ctenochelidae (*Ctenocheles* Kishinouye, 1926; *Ctenocheloides* Anker, 2010; *Kiictenocheloides* Sakai, 2013) the pereiopod 1 propodus is bulbous and fingers are pectinate (Fig. 75.7, Fig. 68.3). The form of the distal margin of the manus is important, and can possess a deep reentrant or a spine positioned above the fixed finger (Fig. 75.8, Fig. 76.5).

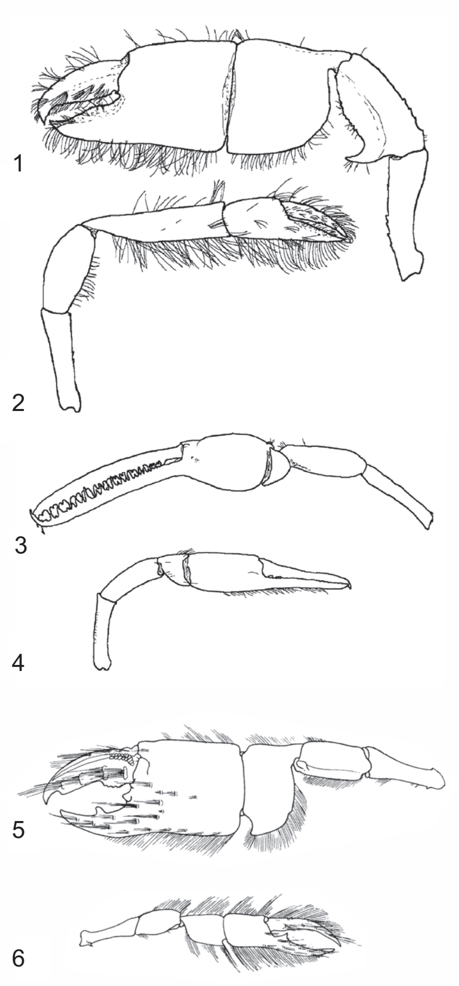


Fig. 76. Axiidean major and minor chelipeds. *1–2, Callianassa subterranea* (Montagu, 1808) (Axiidea, Callianassidae); *3–4, Ctenocheles balssi* Kishinouye, 1926 (Axiidea, Ctenochelidae); *5–6, Callianopsis goniophthalma* (Rathbun, 1902) (Axiidea, Callianopsidae). First member of each pair major cheliped, second member minor (*1–4* adapted from Dworschak, Felder, & Tudge, 2012, fig. 69.14A, B, E, F, respectively; *5–6* adapted from Manning & Felder, 1991, fig. 18).

The first pereiopod chelae are variously developed (Dworschak, Felder, & Tudge, 2012). Isochely or near-isochely can be observed in representatives of Upogebiidae, Laomediidae, Micheleidae, and Calocarididae (Fig. 77.1–2). Slightly unequal (subtle asymmetry *sensu* Babcock, 2005) first chelipeds are present in Thalassinidae, Axianassidae, Strahlaxiidae, many genera of Axiidae, some genera of Eucalliacidae (*Calliaxina* Ngoc-Ho, 2003; *Eucalliaxiopsis* Sakai, 2011), and the majority of Callianideidae. Strong heterochely (conspicuous asymmetry *sensu* Babcock, 2005) occurs in *Callianidea* H. Milne-Edwards, 1837 in 1834–1840 and *Paracallianidea* Sakai, 1992 (Callianideidae), some genera of Axiidae, and most representatives of Callianassoidea *sensu* Poore and others (2019), i.e., Anacalliacidae, Callianassidae, Callianopsidae, Callichiridae, Ctenochelidae, Eucalliacidae, and Paracalliacidae (Fig. 76, Fig. 77.3–4). In heterochelous species, the claws on the first pereiopods are termed major chela and minor chela. In some species, the chelae are similar in overall shape, differing mostly in size. However, in most heterochelous species, the chelae are dissimilar to such an extent that the isolated cheliped elements of major and minor chelae preserved in the fossil record have led to description of a single species as two separate species (e.g., Schweitzer Hopkins & Feldmann, 1997; Hyžný, 2012; Hyžný & Dulai, 2014). Where known, there is a lack of preference of handedness (random asymmetry *sensu* Babcock, 2005) in axiideans and gebiideans, which means that populations consist of a nearly equal number of left-handed and right-handed individuals (e.g., Felder & Lovett, 1989; Labadie & Palmer, 1996; Nates & Felder, 1999). This has also been demonstrated in the fossil record (e.g., Hyžný

FIG. 77. Gebiidean and axiidean major and minor chelae. *1, Jaxea kuemeli* BACHMAYER, 1954 (Gebiidea, Laomediidae), isochelous (Hyžný, 2011, fig. 7D); *2, Mesostylus faujasi* (DESMAREST, 1822) (Axiidea, Callianassoidea), weakly heterochelous, A5009-01, Ruhr Museum, photo by Hyžný); *3–4, Eucalliaxopsis pseudorakosensis* (LŐRENTHEY in LŐRENTHEY & BEURLEN, 1929 (Axiidea, Eucalliacidae), strongly heterochelous, minor chela (*3*) and major chela (*4*) (adapted from Hyžný & Klompmaker, 2015, fig. 9K, L).

& HUDÁČKOVÁ, 2012; HYŽNÝ & KLOMPMAKER, 2015). Handedness was suggested to be controlled by environmental factors (DWORSCHAK, 1998; SCHWEITZER & others, 2006). Minor chelipeds do not display the pronounced features as observed in major chelipeds, but there are exceptions; in some representatives of Axiidae, e.g., *Acanthaxius* spp., and Callichiridae, e.g., *Lepidophthalmus madagassus* (LENZ & RICHTERS, 1881), the minor chela has well-developed and unique ornamentation and/or armament.

Reproductive morphology of axiideans and gebiideans is very poorly known. Although hermaphroditism is present in axiideans and gebiideans (HERNÁEZ, 2018), many species are known from morphologically different males and females (DWORSCHAK, FELDER, & TUDGE, 2012). They differ primarily in the morphology of the first two pairs of pleopods, but may also show dimorphism in the first chelipeds, which commonly occur in the fossil record (BISHOP & WILLIAMS, 2005; HYŽNÝ & KLOMPMAKER, 2015). The male chela is stouter, more robust, and more strongly ornamented than that of females and even immature males (SCHWEITZER HOPKINS & FELDMANN, 1997) (Fig. 78) although some females exhibit stronger ornamentation. Sexually dimorphic chelipeds, accompanied by allometric growth enhancing the differences between male and female chelae, have been demonstrated for several representatives of Callichiridae (BOTELHO DE SOUZA, BORZONE, & BREY, 1998; FELDER & LOVETT, 1989; NATES & FELDER, 1999) and Callianassidae (HAILSTONE & STEPHENSON, 1961; LABADIE & PALMER, 1996; DWORSCHAK, 1998, 2012; SHIMODA & others, 2005).

Sexual dimorphs can express not only different growth rates of chelipeds but also different morphologies of the major chela, e.g., in Callianopsidae (SCHWEITZER HOPKINS & FELDMANN, 1997) and Callichiridae (MANNING & FELDER, 1986). In the fossil record, two morphologies of major claws, possibly sexual dimorphs, have also been identified for Eucalliacidae (HYŽNÝ & HUDÁČKOVÁ, 2012) and Callichiridae

(Hyžný & Hudáčková, 2012; Hyžný & Dulai, 2014). Interestingly, in sexually mature males of *Callichirus* Stimpson, 1866, all elements of the major cheliped are extremely elongate, which has been documented in the fossil record (Hyžný & Müller, 2010) (Fig. 75.5).

Ghost shrimps of Callianassoidea *sensu* Poore & others (2019) can express intraspecific variation in the major cheliped morphology, causing major difficulties for the taxonomic interpretation of isolated elements in the fossil record. The morphology of the pereiopod 1 merus and carpus are quite consistent within the genus, but the nature of the propodus and dactylus, especially the fixed fingers, can be variable. Unfortunately, isolated cheliped fingers are among the most common fossil remains of ghost shrimps (Schäfer, 1972; Bishop & Williams, 2005; Hyžný & Klompmaker, 2015). The variation in the morphology of cheliped fingers is observable mainly in the development of their occlusal margins (cutting edges).

Differences among individuals may include the morphology and/or number of teeth on these margins. For instance, in the major pereiopod 1 dactylus of Callichiridae and Callianassidae, blunt molariform teeth develop more proximally, whereas distal parts of the occlusal surfaces have sharper teeth alternating with gaps or more-or-less even dentition consisting of several smaller teeth, followed by a hooked fingertip. Yet, the other morphotype of the same species may have the major pereiopod 1 dactylus with a sinuous and edentulous cutting edge (Sakai, 1969; Hyžný & Hudáčková, 2012; Hyžný, 2020a). Also, the cutting edge of the pereiopod 1 fixed finger can be armed variously, corresponding to the armature of the dactylus. In some cases, the above-mentioned differences and distinguishing morphotypes are related to sex, with males having more heavily armed fingers with distinctly hooked fingertips (Sakai, 1969), but this is not always true. In some species of *Neocallichirus* Sakai, 1988, females are equally or even more heavily armed than males (Manning & Felder, 1995). In general, from the isolated cheliped fingers alone it is difficult to distinguish the mere intraspecific variation from sexual dimorphism and *vice versa*. There is a certain degree of overlap in the expressed morphologies of cheliped fingers.

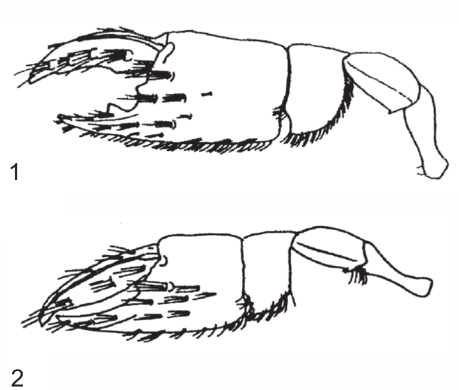


Fig. 78. Sexual dimorphism in Axiidea, Callianopsidae, *Callianopsis goniophthalma* (Rathbun, 1902); *1,* male; *2,* female (adapted from Schweitzer Hopkins & Feldmann, 1997, figs. 1G, 2G).

Despite the variations mentioned above, many axiidean and gebiidean taxa can be differentiated from each other based on distal cheliped elements (propodus and dactylus) alone, at least to the family, but also to the genus or even the species level. This has major implications for taxonomic evaluation of (largely incomplete) fossil remains of these animals, as demonstrated in various families, including Axiidae (Hyžný Jakobsen, & Fraaije, 2017), Callianassidae (Hyžný, 2020b), Callianideidae (Ferratges, Hyžný, & Zamora, 2021), Callianopsidae (Schweitzer Hopkins & Feldmann, 1997; Hyžný & Schlögl, 2011; Ando, Kawano, & Ugai, 2019), Callichiridae (Schweitzer & Feldmann, 2002; Hyžný & Karasawa, 2012; Hyžný & Müller, 2012; Klompmaker, Hyžný, & Jacobsen, 2015; Hyžný, 2016, 2020a), Ctenochelidae (Schweitzer & Feldmann, 2002; Feldmann, Schweitzer, & Encinas, 2010; Hyžný & Dulai, 2014; Hyžný, Veselská, & Dvořák, 2014), Eucalliacidae (Hyžný,

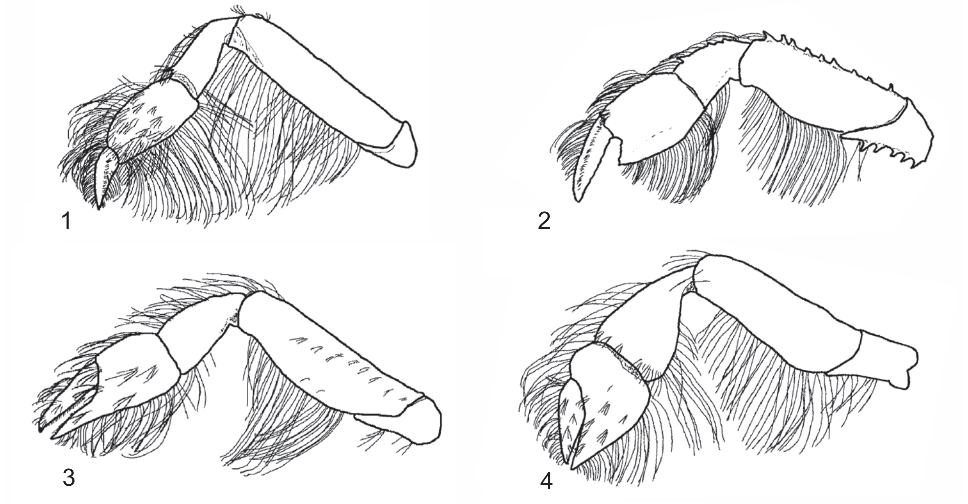


Fig. 79. Axiidean and gebiidean second pereiopod. *1, Upogebia deltaura* (Leach, 1815) (Gebiidea, Upogebiidae), achelate; *2, Thalassina spinosa* Ngoc-Ho & de Saint Laurent, 2009 (Gebiidea, Thalassinidae), subchelate; *3, Axius stirhynchus* (Leach, 1815) (Axiidea, Axiidae), chelate; *4, Callianassa subterranea* (Montagu, 1808) (Axiidea, Callianassidae), chelate (adapted from Dworschak, Felder, & Tudge, 2012, fig. 69.15B, A, E, L).

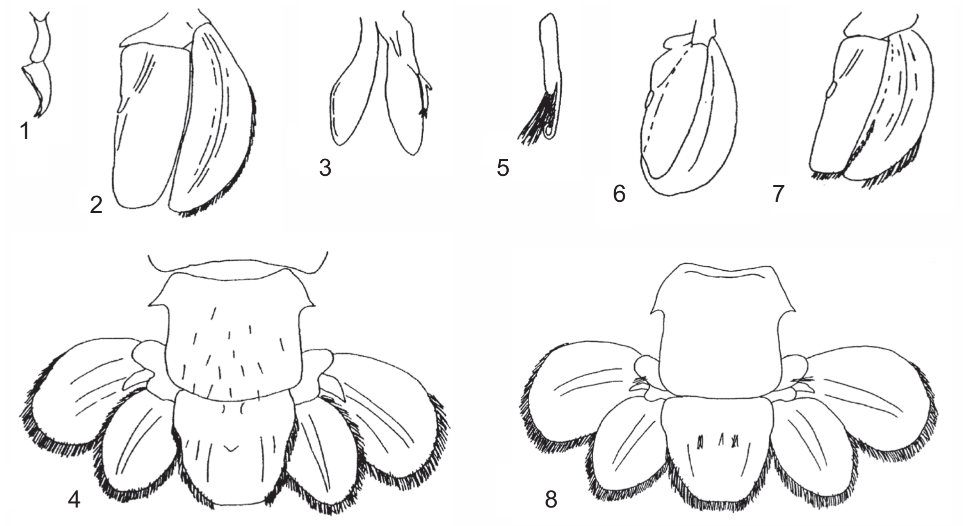


Fig. 80. Axiidean pleopods; *1,* male pleopod 1; *2,* male pleopod 3–5; *3,* male pleopod 2; *4,* male uropods and telson; *5,* female pleopod 1; *6,* female pleopod 2; *7,* female pleopod 3–5; *8,* female uropods and telson (adapted from Schweitzer Hopkins & Feldmann, 1997, fig. 1J, K, L, M; fig. 2M, N, O, P).

2012; Hyžný & Hudáčková, 2012; Hyžný & Gašparič, 2014), Micheleidae (Ferratges, Hyžný, & Zamora 2021), Axianassidae (Feldmann, Schweitzer, & Encinas, 2010), Laomediidae (Karasawa, 1989, 1993; Hyžný, 2011), Thalassinidae (Ando, Kishimoto, & Kawano, 2016), and Upogebiidae (Hyžný & others, 2021).

Pereiopod 2 is chelate in all Axiidea (Fig. 79.3–4), subchelate in the gebiidean Thalassinidae (Fig. 79.2), and achelate in the other gebiidean families (Fig. 79,1), and this is a

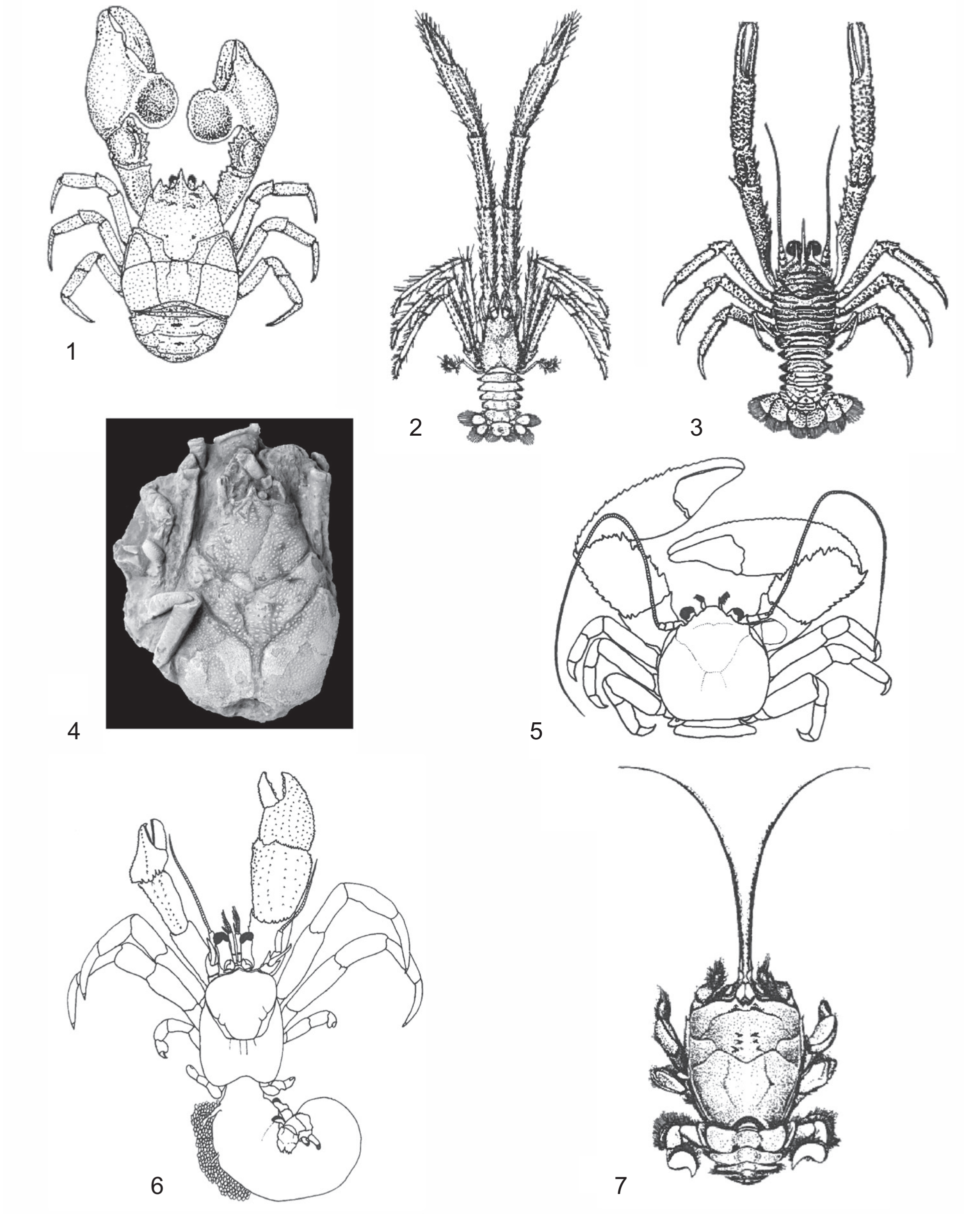


Fig. 81. Anomura body forms. *1,* Aeglidae; *2,* Chirostylidae; *3,* Munididae; *4,* Eocarcinidae; *5,* Porcellanidae; *6,* Paguridae; *7,* Hippoidea (*1–3,* adapted from Tudge, Asakura, & Ahyong, 2012, fig. 70.3A, 70.3C; *4,* Feldmann & Schweitzer, 2010, fig. 1,5–6; *5–6,* McLaughlin, 1980, fig. 48D and 48A, respectively; *7,* Tudge, Asakura, & Ahyong, 2012, fig. 70.4B.

diagnostic feature separating Axiidea and Gebiidea. Pereiopod 2 is seldom known in the fossil record (Fig. 68.1). The various modifications of pereiopod 2 render it useful in feeding or burrowing (Dworschak, Felder, & Tudge, 2012). Pereiopods 3–5 are achelate and are adapted for grooming, burrowing, or walking (Dworschak, Felder, & Tudge, 2012).Pleopods are variable (Fig. 80). Pleopod 1 is present in

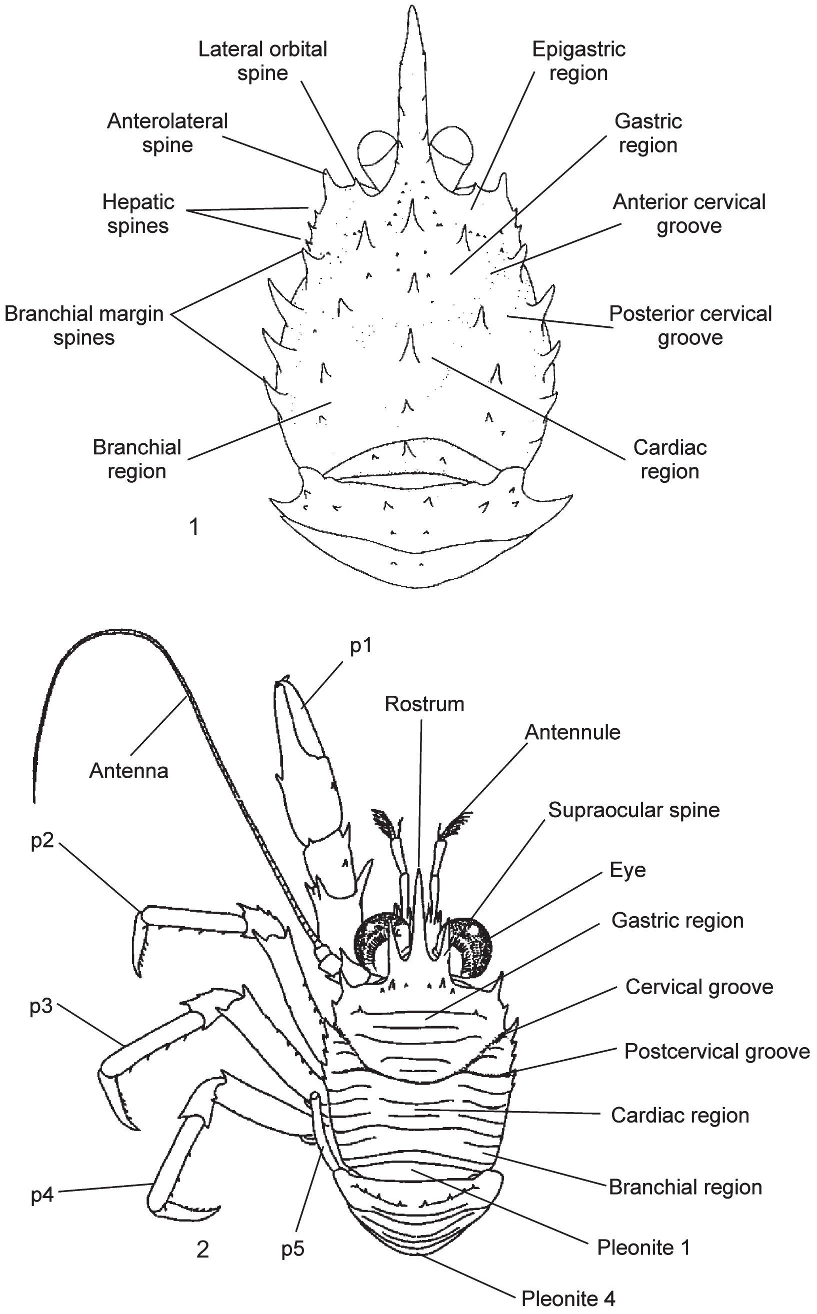


Fig. 82. Chirostyloid (*1*) and galatheoid (*2*) generalized morphology (adapted from Schnabel, 2020, fig. 4d and Tudge, Asakura, & Ahyong, 2012, fig. 70.17A). p=pereiopod.

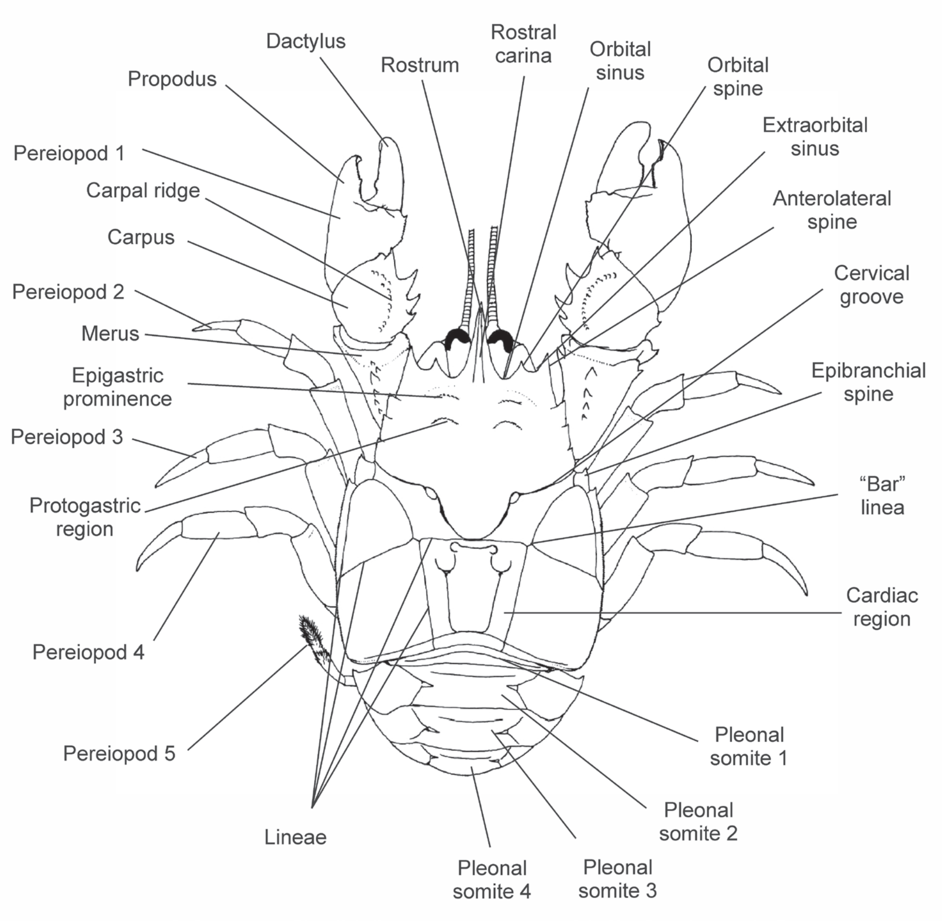


Fig. 83. Overall Aeglidae morphology (adapted from Martin & Abele, 1988, fig. 2).

all females but absent in males of several families (Dworschak, Felder, & Tudge, 2012). Males may possess an appendix interna on pleopod 1 (Fig. 80.1) and an appendix masculina on pleopod 2, but this is highly variable across families (Dworschak, Felder, & Tudge, 2012). Pleopod 2 is variable across the two infraorders, and an appendix masculina is usually present in males (Fig. 80.2). Pleopods 3–5 are similar to pleopod 2 (Fig. 80) with a few exceptions. The exopods and endopods of the uropods are ovate, rarely elongate and narrow (Dworschak, Felder, & Tudge, 2012) (Fig. 80.4, Fig. 68.2). Uropods are spinose in axiids with a diaresis on the uropodal exopod (Dworschak, Felder, & Tudge, 2012). Members of most callianassoids (*sensu* Poore & others, 2019), except Callianopsidae, Ctenochelidae and Paracalliacidae bear an anteriorly thickened region on the uropodal exopod, called the dorsal plate (Poore & others, 2019).

INFRAORDER ANOMURA

Anomurans are incredibly diverse, ranging from hermit crabs to galatheoid squat lobsters to carcinized forms (Fig. 81). Each group is characterized herein separately due to this extreme disparity in morphology across the infraorder. Nearly all Anomura are diagnosed by a *linea anomurica* paralleling the

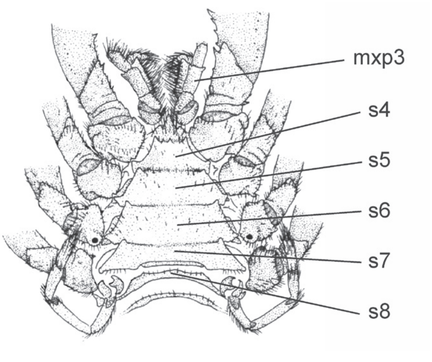


FIG. 84. Aeglidae sternum (adapted from Martin & Abele, 1988, fig. 10a). mxp=maxilliped, s=sternite.

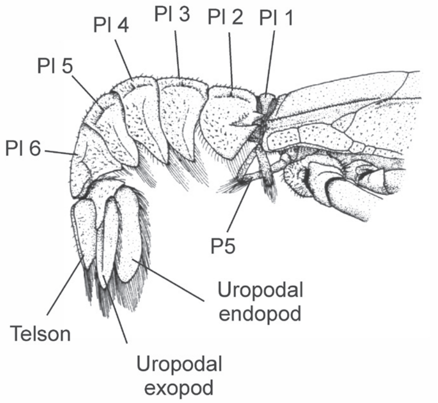


FIG. 85. Aeglid pleon (adapted from Martin & Abele, 1988, fig. 16a). P=pereiopod, Pl=pleonal somite.

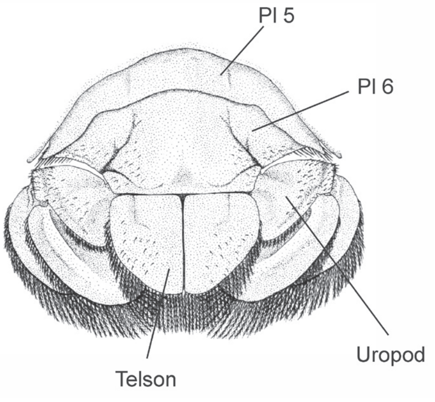


FIG. 86. Aeglidae tail fan (adapted from Martin & Abele, 1988, fig. 18c). Pl=pleonal somite.

lateral margins of the carapace and forming the boundary between the carapace and the branchiostegite (POORE, 2004).

AEGLIDAE

Aeglids are extant freshwater anomurans known only from the Southern Hemisphere; despite their restricted distribution, they do have a fossil record extending into the Late Cretaceous. Aeglids have a carcinized overall morphology (Fig. 81.1, Fig 83).

Carapace.—The carapace in aeglids is broadly triangular and flattened (Fig. 83). The anterior margin is characterized by a rostrum and shallowly excavated orbits. The groove pattern is simple, with only the cervical groove being well developed. The most distinctive feature of the aeglid carapace is the complicated series of *lineae,* separating the posterior half of the carapace into various polygonal regions (Fig. 83).

Thoracic sternum.—The sternum is broadly triangular, with sternite 8 reduced in size (Fig. 84).

Pleon.—In Aeglidae, only the posterior few pleonites are curled under the remainder of the pleon, and the pleonites are dorsally well calcified. Pleonite 1 is much reduced (Fig. 85).

Appendages.—Mouthparts in aeglids are similar to those of other anomurans and have been well illustrated (MARTIN & ABELE, 1988). The first pereiopods are strongly chelate and slightly heterochelous (Fig. 83). The upper margin of the carpus is typically enlarged into a prominent, ovate flap (Fig. 81.1). Pereiopods 2–4 are achelate and similar in length to one another, whereas pereiopod 5 is very reduced (Fig. 83). The telson is subdivided axially by a suture (TUDGE, ASAKURA, & AHYONG, 2012), and the uropods are strongly arcuate, concave axially (MARTIN & ABELE, 1988) (Fig. 86).

CHIROSTYLOIDEA AND GALATHEOIDEA

Chirostyloids and galatheoids have numerous morphological similarities and are grouped under the paraphyletic moniker

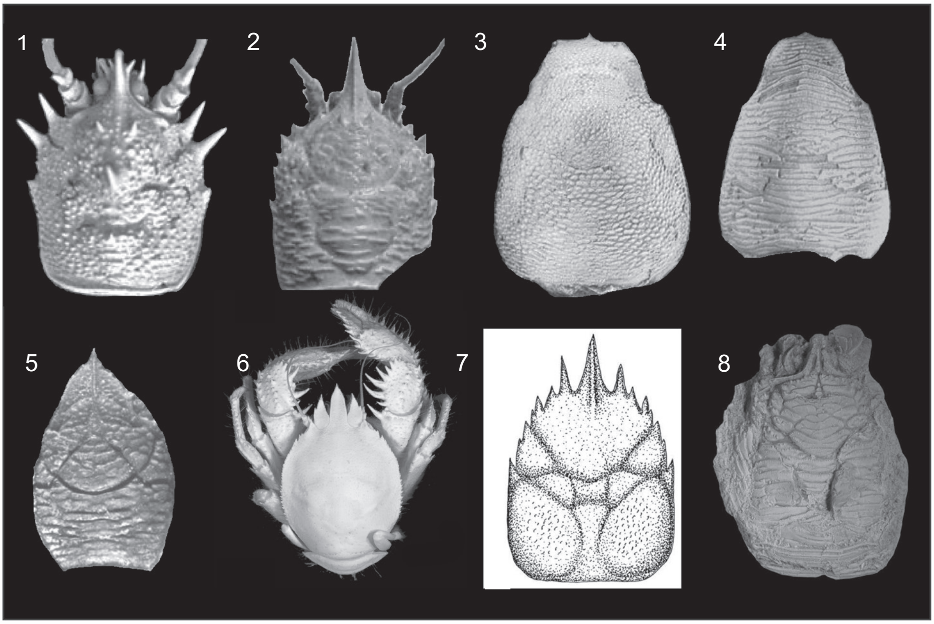


Fig. 87. Chirostyloidea and Galatheoidea body forms, *1, Galacantha rostrata* A. Milne-Edwards, 1880 (Munidopsidae), *2, Munidopsis starmer* Baba & de Saint Laurent, 1992 (Munidopsidae), *3, Paragalathea arcella* Robins & others, 2016 (Paragalatheidae), *4, Mesogalathea striata* Remeš, 1895 (Paragalatheidae), *5, Galatheites zitteli* Moericke, 1889 (Catillogalatheidae), *6, Shinkaia crosnieri* Baba & Williams, 1998 (Munidopsidae); *7, Pristinaspina gelasina* Schweitzer & Feldmann, 2000 (Pristinaspinidae), *8, Munida limonitica* (Stenzel, 1945) (Munididae) (*1–2,* adapted from Robins, Feldmann, & Schweitzer, 2013, fig. 6.10, 6.13; *3–5,* adapted from Robins & others, 2016, fig. 3.7, 5.2, 12.1; *6,* adapted from Schweitzer & Feldmann, 2008, fig. 1.1; *7,* adapted from Schweitzer & Feldmann, 2000, fig. 9; *8,* adapted from Franţescu, 2014a, fig. 4A).

squat lobster because they have a somewhat lobster-like body form and pleon extending posteriorly from the carapace. Galatheoids have a notable fossil record (e.g., De Angeli & Garassino, 2002; Klompmaker, Feldmann, & Schweitzer, 2012; Robins, Feldmann, & Schweitzer, 2013, Robins & others, 2016; Beschin & others, 2016; Robins & Klompmaker, 2019); however, there are few fossils attributed to the Chirostyloidea. Both groups are very diverse in modern oceans (Fig. 87) (Baba, 2005; Macpherson & Robainas-Barcia, 2015).

Carapace.—The carapace in these groups is well calcified, longer than wide, dorsoventrally flattened, and almost always strongly ornamented. A rostrum is present and can be spinose, spatulate, or dentate; the nature of the rostrum is diagnostic at the family level (Ahyong & others, 2010). The orbits are not well excavated and are located at the base of the rostrum on the anterior margin of the carapace. The lateral margins of the carapace are commonly spinose, especially anteriorly, and are parallel or subparallel, and the posterior margin is weakly concave (Fig. 82).

Dorsally, ornamentation among these groups is varied. Many families are characterized by transverse ridges that are variously short, scabrous, or more-or-less continuous (Fig. 87). Epigastric spines may be present posterior to the frontal margin (Fig. 87, Fig. 82).

Groove patterns are varied and complex and tend to be more complicated and better expressed in extinct forms. Key grooves in extinct galatheoids and chirostyloids are the cervical groove, circumgastric groove, and branchiocardiac groove (Robins, Feldmann, & Schweitzer, 2013; Robins & others, 2016). Various shorter grooves and

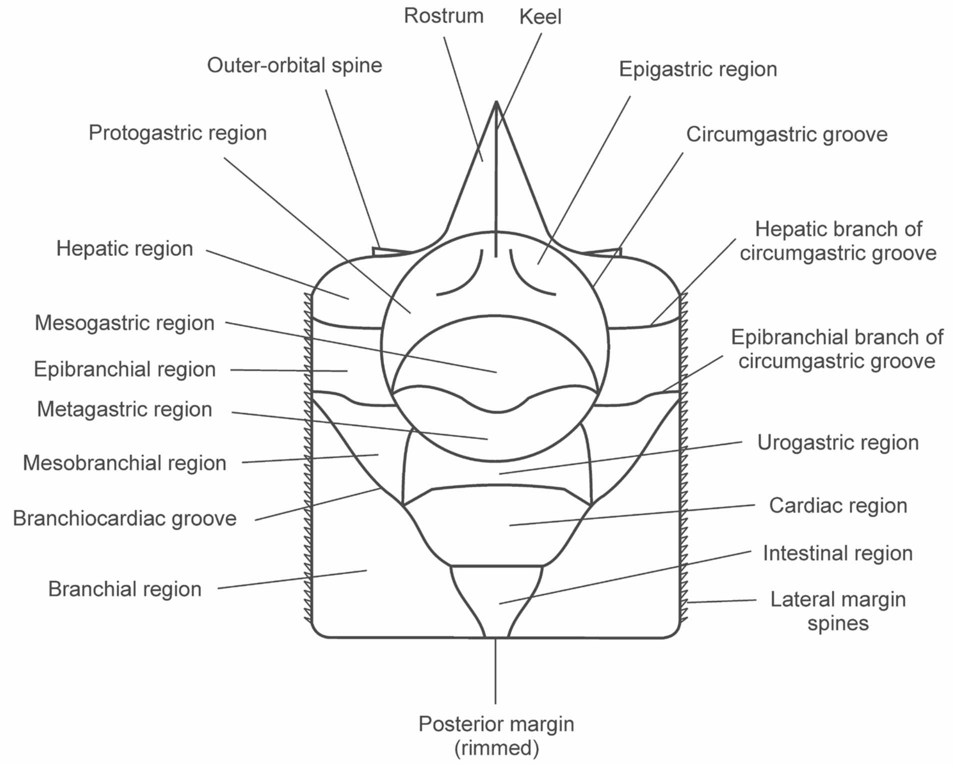


Fig. 88. Groove patterns for galatheoids (adapted from Robins, Schweitzer, & Feldmann, 2013, fig. 2.4).

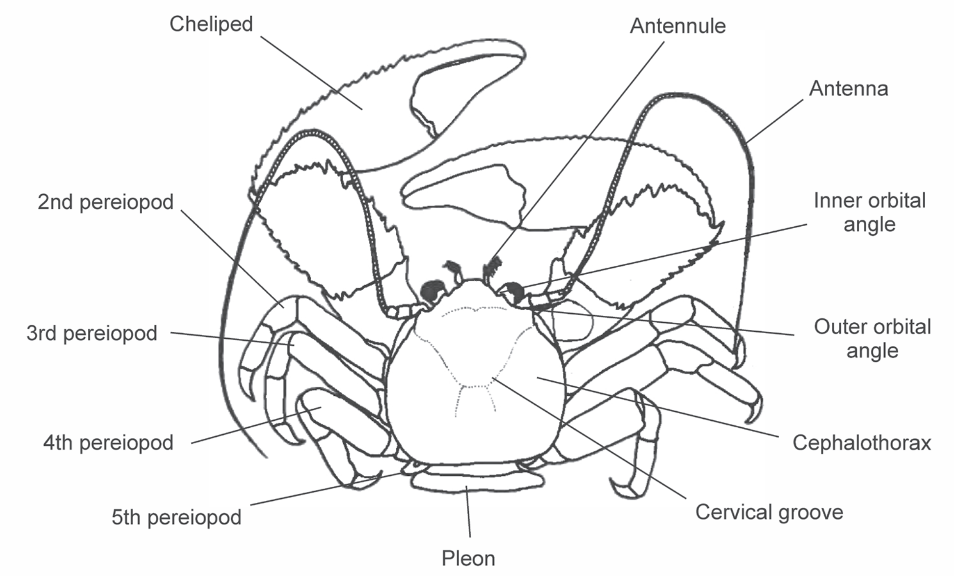


Fig. 89. Porcellanid morphology (adapted from McLaughlin, 1980, fig. 48D).

subdivisions of these three grooves can be present (Fig. 82, Fig. 88). Of note, especially in extinct forms, is the circumgastric groove, an ovate or circular groove surrounding the mesogastric, epigastric, and protogastric regions of galatheoids (Robins, Feldmann, & Schweitzer, 2013) (Fig. 88) that is generally recognized by biologists as several separate grooves. Robins, Feldmann, and Schweitzer (2013) noted two branches of this groove, a hepatic branch bounding the lateral margin of the protogastric region (cervical of Tudge, Asakura, & Ahyong, [2012]; anterior cervical of Schnabel [2020]) and an epibranchial branch, extending laterally to the lateral margin. The posterior axial portion of the circumgastric groove plus the epibranchial branch are equivalent, at least spatially if not homologously, to the cervical groove (postcervical groove of Tudge, Asakura, & Ahyong, [2012]; posterior cervical groove of Schnabel [2020]). Along with the groove patterns, carapace regions are well expressed in these groups, especially in the extinct forms. Regions are named based upon terminology applied to brachyurans (Fig. 82, Fig. 88).

In porcellanids, grooves and regional development are subdued compared to other galatheoids and chirostyloids. Only the cervical groove typically is obvious, and ornamentation is comprised of weak ridges or tubercles. The rostrum varies from weak to strongly developed, and the orbits are shallow. The lateral margins are typically convex and bear spines (Fig. 89).

Thoracic sternum.—The sternum of galatheoids and chirostyloids is wide and broadly triangular and may display spines or scabrous ridges as seen on the dorsal carapace (Fig. 90). Porcellanid sterna are more rectangular (Fig. 91.4, Fig. 90.4). In all cases, the sutures between the somites are shallow and sternite 8 is much reduced.

Pleon.—The general appearance of the pleon of chirostyloids and non-porcellanid galatheoids is lobster-like, earning these animals the common name squat lobster (Fig. 91). The pleon in these groups is symmetrical.

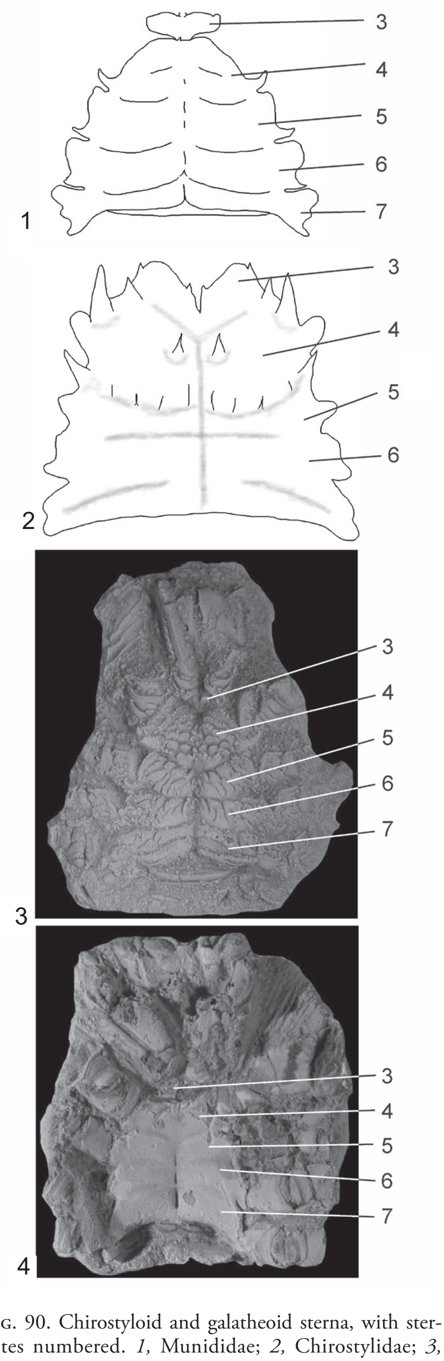


Fig. 90. Chirostyloid and galatheoid sterna, with sternites numbered. *1,* Munididae; *2,* Chirostylidae; *3,* fossil Munididae, *Munida limonitica* (Stenzel, 1945); *4,* fossil Porcellanidae, *Petrolisthes albianicus* Franţescu, 2014a (*1–2,* adapted from Tudge, Asakura, & Ahyong, 2012, fig. 70.17F, 70.18E; *3–4,* adapted from Franţescu, 2014a, fig. 4B, 5B).

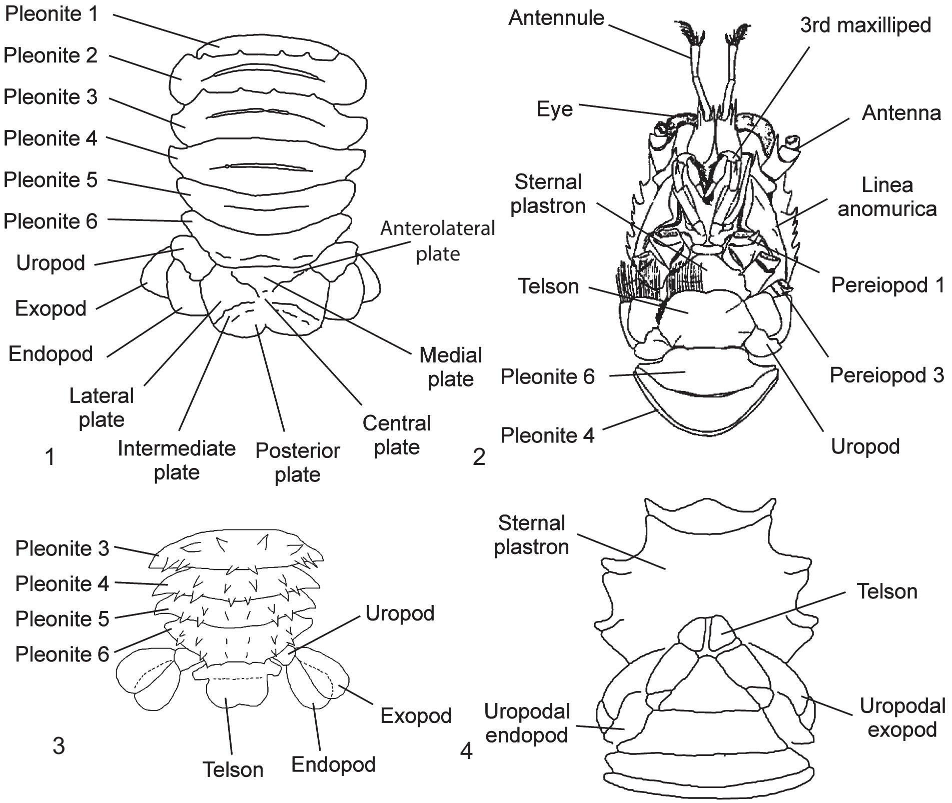


Fig. 91. Pleons and ventral views: *1,* galatheoid; *2,* munidid; *3,* chirostyloid; *4,* porcellanid (*1,* adapted from McLaughlin, 1980, fig. 48C; *2–4,* Tudge, Asakura, & Ahyong, 2012, fig. 70.17B; 70.18F; 70.19E).

In life, the pleon is carried loosely curled under the cephalothorax. In most galatheoids, the first pleonite is shortest and narrowest with a reduced pleuron (Fig. 91.1), whereas the remaining somites are larger and longer with distinct pleura (Tudge, Asakura, & Ahyong, 2012). The telson in galatheoids (including the porcellanids) is comprised of multiple plates separated by suture lines (Fig. 91.1, 91.4). In Chirostyloidea, the pleon is similar to that of galatheoids but the telson is only subdivided into two portions (Tudge, Asakura, & Ahyong, 2012) (Fig. 91.3).

Appendages.—Antennules in this group are biflagellate with a three-articled peduncle. The basal segment can be spinose or smooth, an important character in classification (Tudge, Asakura, & Ahyong, 2012). The antennal peduncle in chirostyloids is comprised of five articles, whereas in galatheoids, articles 2 and 3 are fused resulting in a total of four segments. Mandibles are strong, and maxillae and maxillules are as in other decapods, the latter of which has a large scaphognathite (Tudge, Asakura, & Ahyong, 2012). Maxilliped 3 is pediform and its appearance is important for classification (Tudge, Asakura, & Ahyong, 2012). The first pereiopods are strong in galatheoids and chirostyloids and are symmetrical or weakly asymmetrical (Fig. 81.2–3, Fig. 82.2). In porcellanids, the chelipeds are shorter and the chelae are stouter as compared to other galatheoids (Fig. 89). Pereiopods 2–4 are achelate, usually with the second longest. Pereiopod 5 is much reduced in size and is typically chelate; it is used for grooming (Tudge, Asakura, & Ahyong, 2012) (Fig. 82.2, Fig. 89).

Most male chirostyloids and galatheoids have paired gonopods 1 and 2 although females lack pleopod 1 as do males in some groups. Pleopods 3–5 are usually present. Uropods are well developed in all groups (Fig. 91).

HIPPOIDEA

Hippoidea includes sand crabs and mole crabs. Two of the three families, Albuneidae and Blepharipodidae, have a modest but well-documented fossil record.

Carapace.—Hippoids are characterized by a carapace with either a complicated groove pattern or an ovate, simple carapace. Albuneidae and Blepharipodidae have an overall rectangular carapace with up to 11 carapace grooves, which are transverse and vary in length. Anterior to the grooves lies a field of setae, and anterior to that, the rostrum is either reduced or absent (Tudge, Asakura, & Ahyong, 2012) (Fig. 92.1). Deep ocular sinuses are bordered laterally by a spinose field (Fig. 92.4). Hippidae have an ovate carapace narrowing anteriorly and posteriorly may have weak, irregular transverse grooves, especially anteriorly (Tudge, Asakura, & Ahyong, 2012 (Fig. 92.2).

Thoractic sternum.—The sternum within this group seems to have received little systematic descriptive attention and, thus, is not particularly useful in taxonomy. It appears to be very narrow, and in Hippidae is mostly obscured by the folded telson.

Pleon.—The pleon in this group is variable. In Albuneidae and Blepharipodidae, it is weakly held beneath the carapace. Pleonites 2–5 have pleura extending laterally (Fig. 92.2). In Hippidae, the pleon is held tightly beneath the carapace, the pleonites are small and rectangular, and the telson is notably very long and triangular (Tudge, Asakura, & Ahyong, 2012) (Fig. 92.3).

Eyes and appendages.—Although not a true appendage, the eyestalks deserve mention. They are wide and platelike and, thus, might be expected to fossilize (Fig. 92.4). The antennae and antennules in this group are well developed. In Albuneidae and Blepharipodidae, the antennules are long with stout basal articles and the antennae are shorter, whereas the antennules are short and the antennae are long in Hippidae (Fig. 92). The mandibles, maxillules, maxillae, and maxillipeds are similar to those of paguroids (Tudge, Asakura, & Ahyong, 2012). The pereiopods in this group are distinctive. In albuneids and blepharipodids, the first pereiopods are chelate with a hooklike dactylus (Fig. 92.4). In hippids, the first pereiopod is achelate (Fig. 92.2). In albuneids and blepharipodids, the dactyli of pereiopods 2–4 are distinctively hooked and flattened (Fig. 92.4). In hippids, the dactyli are flattened but not hooked (Fig. 92.2). Pereiopod 5 in all three families is much reduced, held under the carapace, and is chelate (Fig. 92.2).

PAGUROIDEA: HERMIT CRABS

Paguroidea has an extensive fossil record, based mostly upon chelae of the first pereiopods. More recently, dorsal carapace elements and sixth pleonites have been described from fossils (Fraaije & others, 2019, 2022). The general body form of most paguroids is a reduced carapace, membranous pleon, and well-developed chelae although many exceptions to this exist (Fig. 93).

Carapace.—Several schemes for naming the regions of paguroid carapaces have been proposed. Those used by biologists tend to be more simplistic, as identification and classification of modern forms is based upon the morphology of the entire animal. Many fossil paguroid taxa are only known from carapaces; thus, a more detailed terminology has been developed by paleontologists for carapace morphology. In general, the carapace of paguroids tends to be reduced in size compared to other decapods. It is better calcified anteriorly than posteriorly; the anterior portion of the carapace is called the shield (Fig. 94). A cervical groove positioned just anterior to the boundary between the shield and the less calcified part of the carapace, termed by biologists as the posterior carapace, are typical of most forms

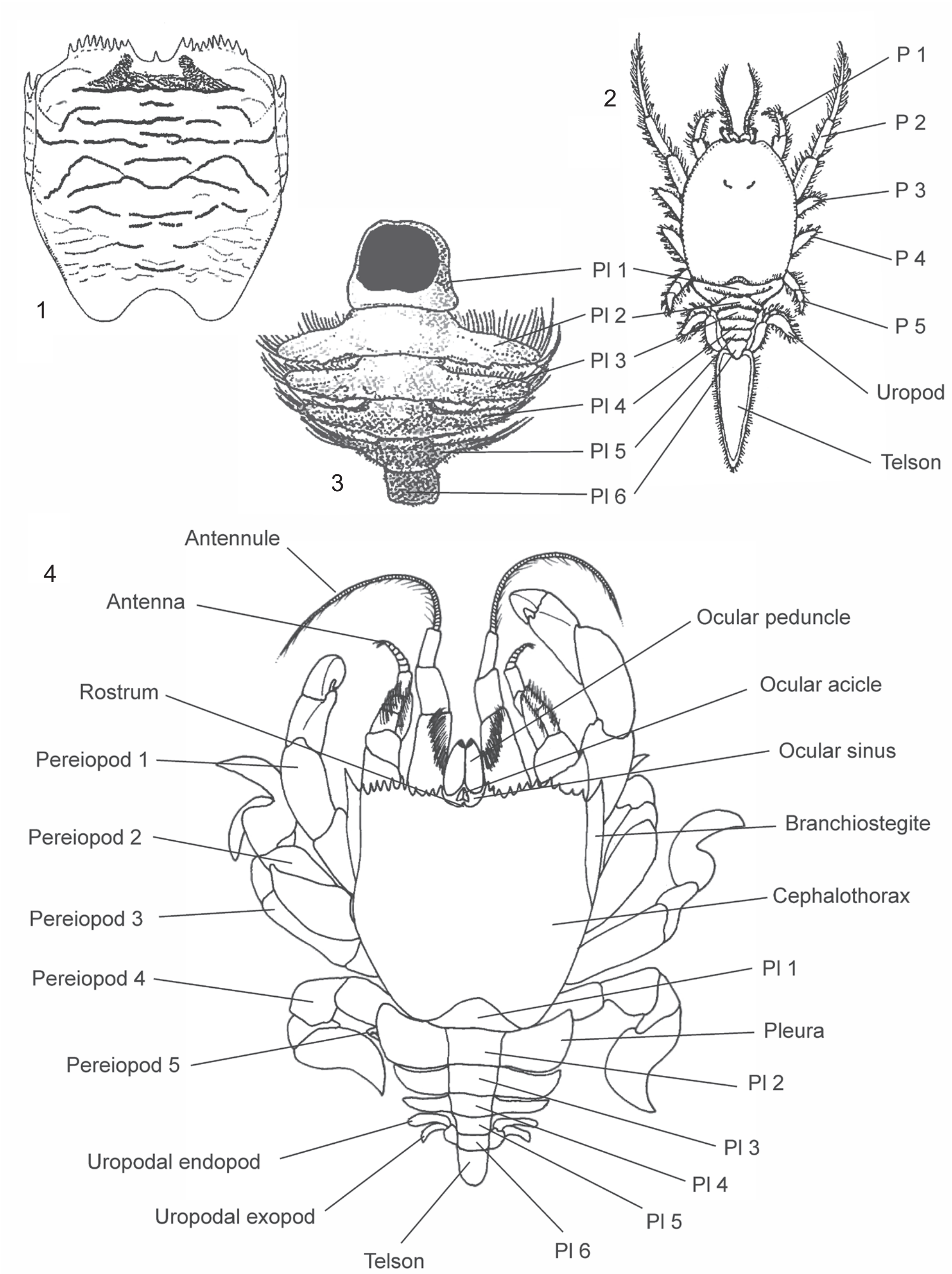


Fig. 92. Hippoidea morphology: *1,* carapace of Blepharipodidae; *2,* hippid carapace and pleon; *3,* pleon of Blepharipodidae; *4,* albuneid morphology (*1–3,* adapted from Tudge, Asakura, & Ahyong, 2012, 70.9A, D, H; *4,* McLaughlin, 1980, fig. 49F). P=pereiopod, Pl=pleonite.

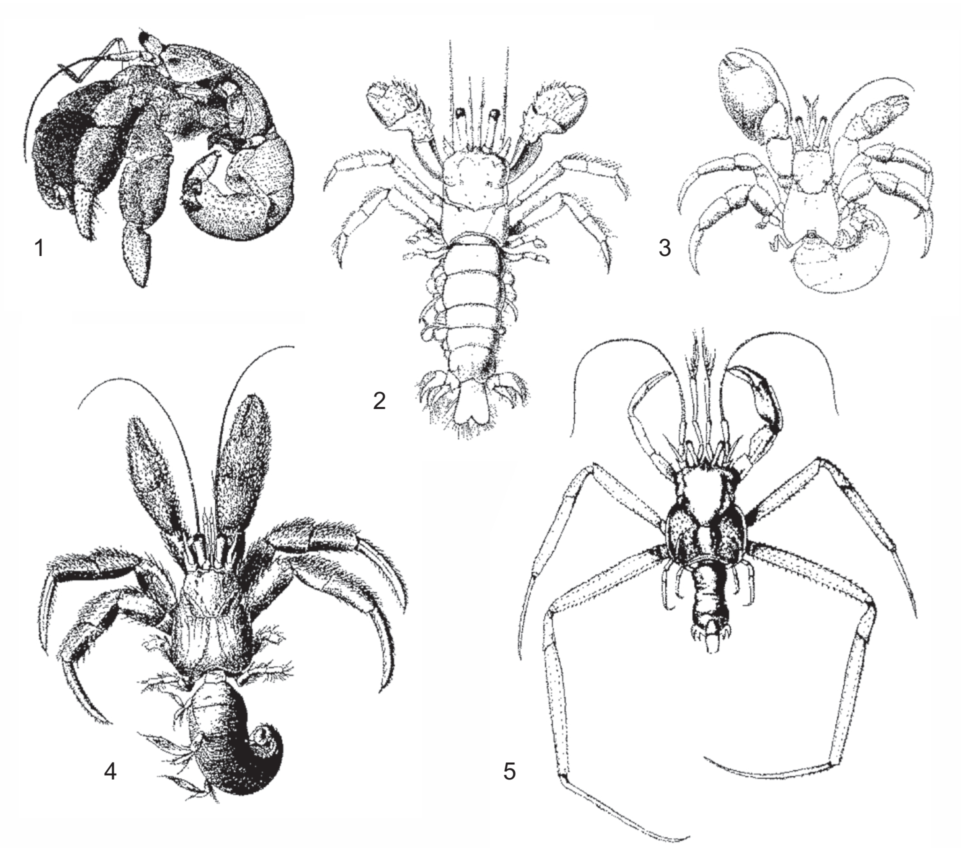


Fig. 93. Paguroid body forms. *1, Coenobita clypeatus* (Fabricius, 1787) (Coenobitidae); *2, Trizocheles spinosus* (Henderson, 1888) (Pylochelidae); *3, Allodardanus bredini* Haig & Provenzano, 1965 (Diogenidae); *4, Propagurus gaudichaudi* (H. Milne Edwards, 1836) (Paguridae); *5, Tylaspis anomala* Henderson, 1885 (Parapaguridae) (adapted from McLaughlin, 2003, fig. 1b, c, d, m, p, respectively).

(Fig. 94). The shield and posterior carapace are separated by the *linea transversalis*. The *linea-d,* present in some paguroids, extends from the posterolateral margin of the carapace toward the axis (Tudge, Asakura, & Ahyong, 2012) (Fig. 94.2). Some paleontologists have introduced terminology for the shield additional to and different from that used by biologists. The shield is characterized by a rostrum that is very reduced and may have lateral projections that are tiny spines on the anterior margins also referred to as postocular projections (Fraaije & others, 2019) (Fig. 95). Fraaije and others (2012) introduced the term massetic region for the part of the carapace termed the hepatic region in brachyurans. They correlated this region with areas of muscle attachments identified by Pilgrim (1973) and later subdivided it into an anterior and posterior part (Fraaije & others, 2014) (Fig. 95). The submassetic region is located posteriorly and axial to the massetic region. The term keraial region was applied (Fraaije & others, 2014) to the ovate area located anterior to the cervical groove and situated posterior to the submassetic region. It lies axial to the anterior branchial area. Also prominent in fossil paguroid carapaces is the post-frontal ridge, which may be bisected by the central gastric groove. The massetic and anterior branchial area could be homologous with the anterior carapace lobes 1–3 of Tudge, Asakura, and Ahyong (2012) (Fig. 94.3).

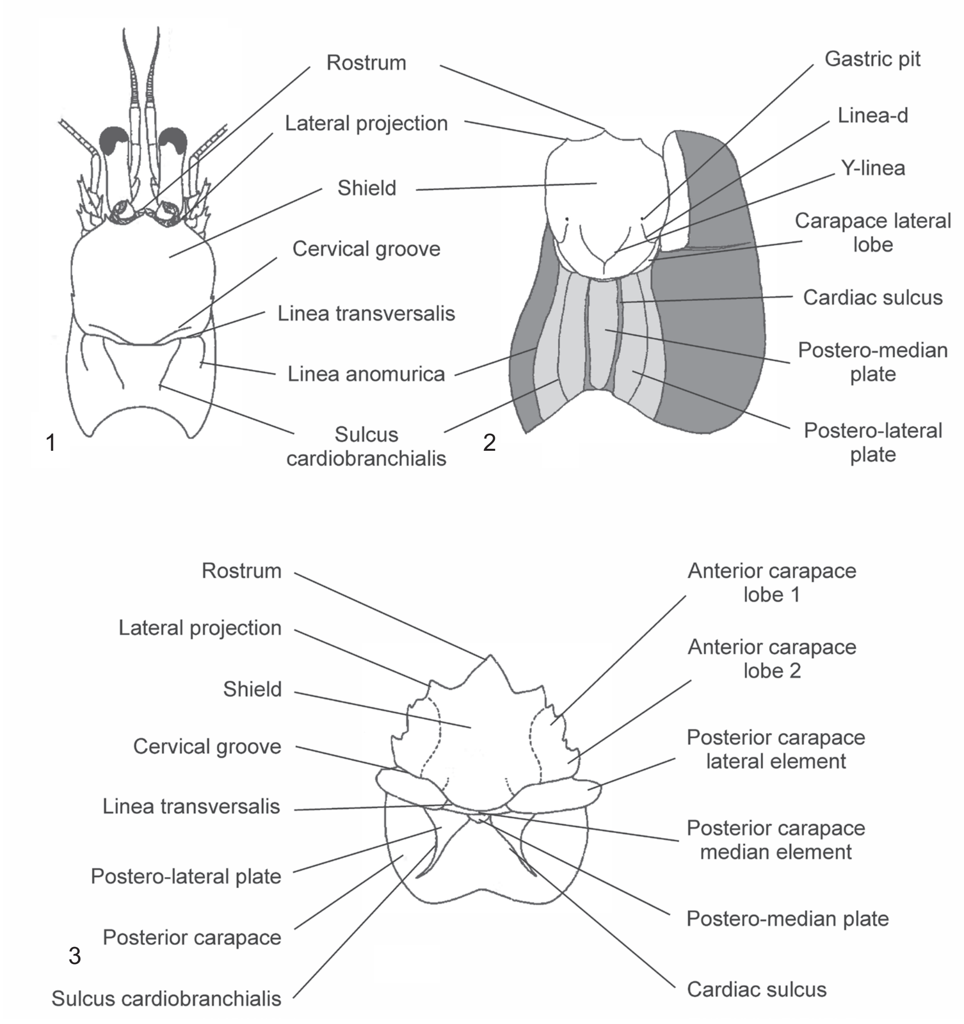


Fig. 94. Paguroid carapace terms as developed for extant specimens: *1,* pylochelid carapace; *2,* diogenid carapace; *3,* pagurid carapace (adapted from Tudge, Asakura, & Ahyong, 2012, fig. 70.6A, C, D).

Tudge, Asakura, and Ahyong, (2012) included a rather detailed morphology for the posterior carapace, seldom preserved in fossils, comprised of cardiac and intestinal regions as well as other regions (Fig. 94.3).

Thoracic sternum.—The sternum of paguroids in general is narrow and triangular and widens posteriorly (Fig. 96.1). Membranous areas separate the calcified sternites. The sternum is known from only one fossil specimen as far as we know (Franţescu, 2014a) (Fig. 96.2).

Pleon.—Paguroids have the most modified pleons among the anomurans. In most extant paguroid families, the pleon is overall soft, membranous, and dextrally twisted for carrying a shell or other structure (Fig. 93, Fig. 97.1). The tergites are small and thickened in most cases (Tudge, Asakura, & Ahyong, 2012). In a few extant families, the pleon is straight, and in Parapylochelidae and Pylochelidae, the pleon is straight and well calcified (Tudge, Asakura, & Ahyong, 2012) (Fig. 93.2, Fig. 97.1). The

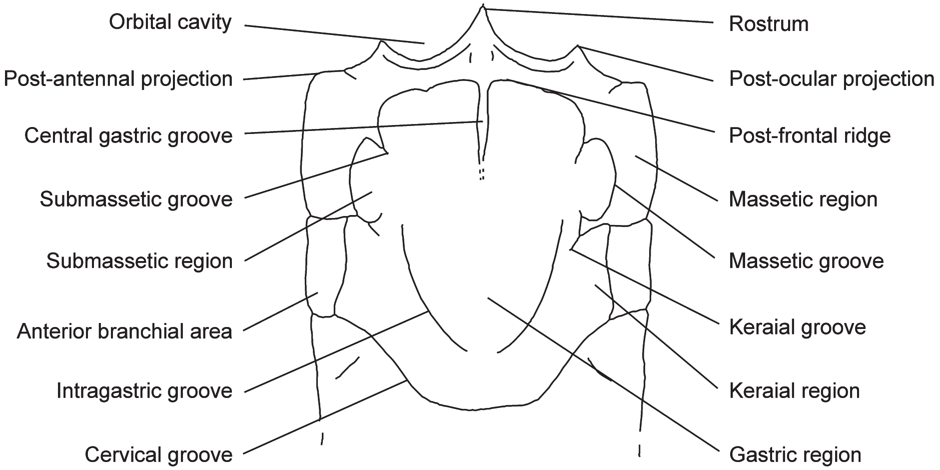


FIG. 95. Carapace terms developed for fossil paguroids, illustrated on a generalized member of Annuntidiogenidae (adapted from FRAAIJE & others, 2019, fig. 1).

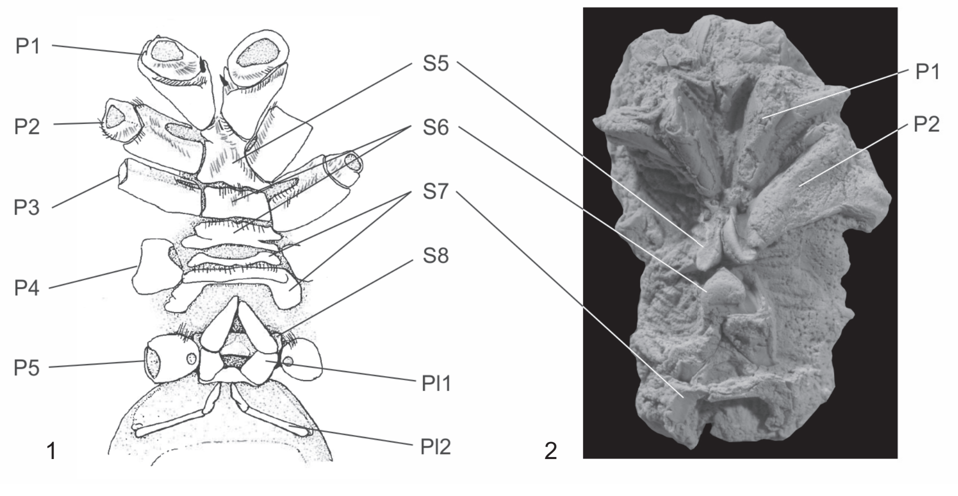


FIG. 96. Paguroid sterna. *1,* Diogenidae; *2,* fossil *Pagurus texensis* FRANŢESCU, 2014a (adapted from Tudge, Asakura, & Ahyong, 2012, fig. 70.5G and Franţescu, 2014a, fig. 6B). P=pereiopod, Pl=pleopod, S=sternite.

sixth pleonite can be well calcified and has been recognized in fossil forms (Fig. 98). It can function as an operculum, closing off the domicile of the animal (FRAAIJE & others, 2012). The shape is ovate or rounded-hexagonal. FRAAIJE and others (2012, 2013) recognized a longitudinal median groove as well as lateral grooves, transverse grooves, and a lateral bulge on fossilized forms (Fig. 98).

Appendages.—The antennules of paguroids are shorter than the antennae and are biflagellate, with the lower flagellum being shorter (Fig. 99). The antennular peduncle bears statocysts. The antennae have a five-segmented peduncle and long flagellum (Fig. 99). Mandibles in paguroids have both an incisor process and molar process. Maxillules and maxillae, and the first and second

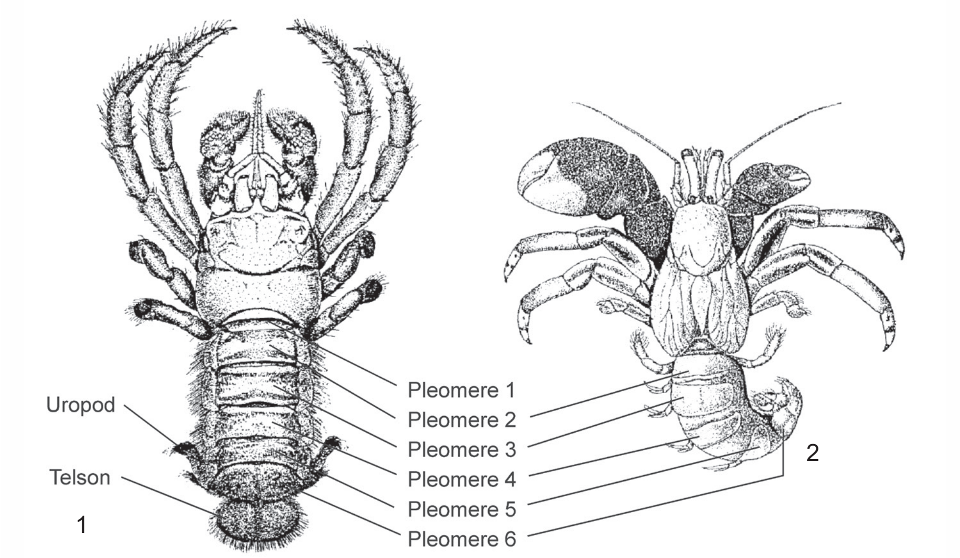


Fig. 97. Paguroid pleons. *1,* Pylochelidae; *2,* Diogenidae (adapted from Tudge, Asakura, & Ahyong, 2012, fig. 70.10A, B).

maxillipeds are similar to those of other decapods. The third maxilliped is notable in bearing a crista dentata in most cases and possibly other spines (Tudge, Asakura, & Ahyong, 2012).

The first pair of pereiopods is strongly developed into chelipeds. Comparative size is diagnostic for some families. In Parapylochelidae, Pylochelidae, and some Diogenidae, the chelipeds are equal or nearly so (Fig. 93.2). In Paguridae and Parapaguridae the right is always larger, and they are also dimorphic in form (Fig. 93.4). In coenobitines and most Diogenidae, the left is larger (Fig. 93.3). Thus, handedness is frequently used to place fossil paguroids within families. Chelipeds may be used as opercula to close off the snail shell or other objects that the animal uses for shelter. Chelae exhibit a wide range of shapes and ornamentations (Fig. 100). The second and third pereiopods are used for walking and can be asymmetrical with one side longer than the other. The fourth and fifth pereiopods are reduced in paguroids and are used to hold the animal within its shelter when present. The fifth pereiopods are chelate and the fourth varies, ranging from achelate to fully chelate (Tudge, Asakura, & Ahyong, 2012) (Fig. 99).

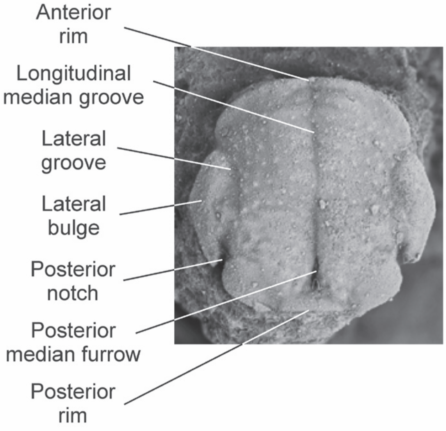


Fig. 98. Sixth pleonal somite of paguroid (adapted from Fraaije & others, 2013, fig. 2).

Pleopods are variable within Paguroidea. In some cases, the pleopods are absent, in some the first or second pair is missing, and in others, lefts are present and rights are absent (Tudge, Asakura, & Ahyong, 2012). Uropods and telson are present and well calcified, presumably to help hold

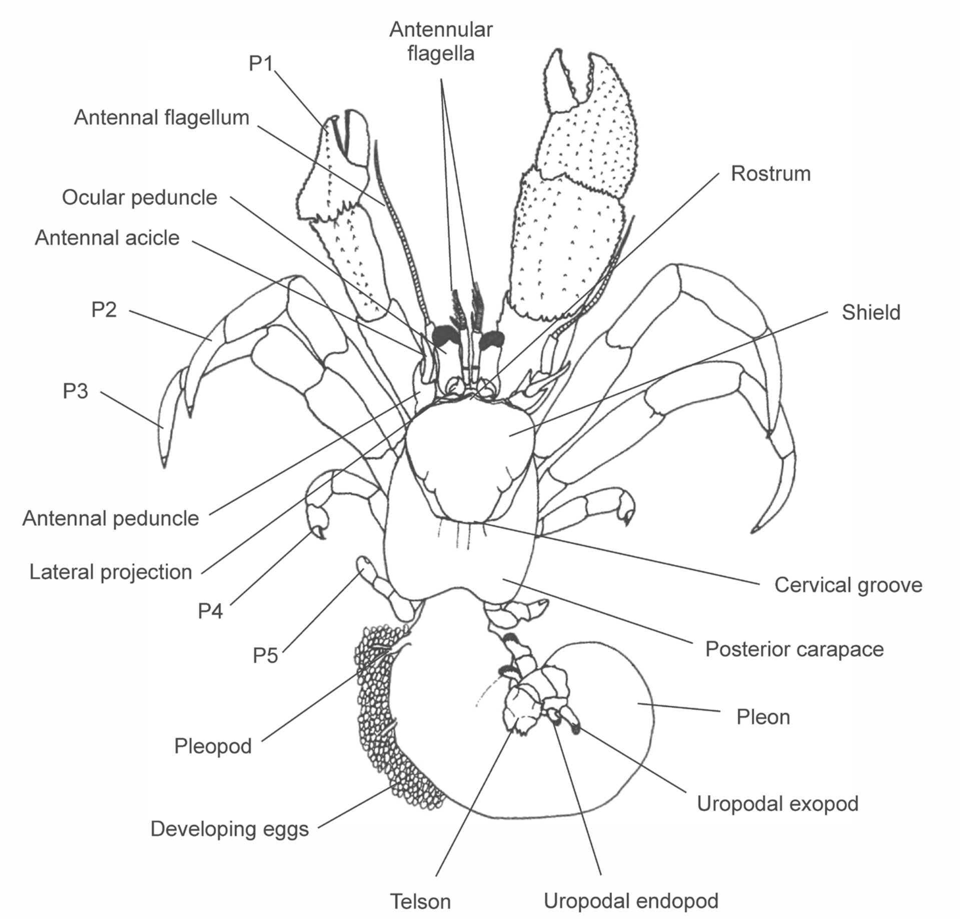


Fig. 99. Generalized paguroid with appendages labeled (adapted from McLaughlin, 1980, fig. 48A). P=pereiopod.

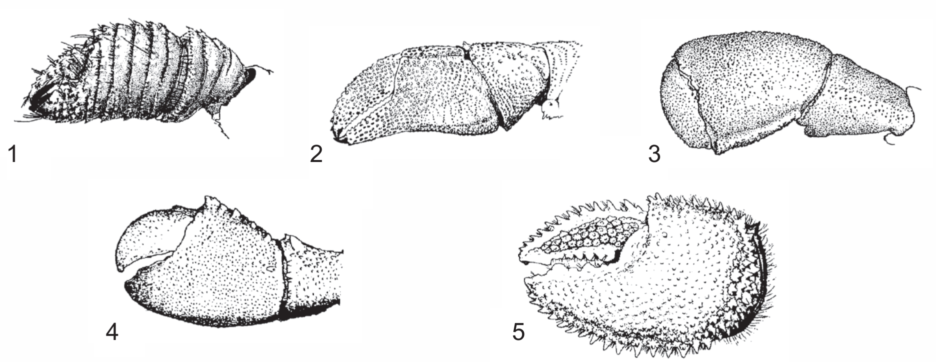


Fig 100. Paguroid chelae, generalized at generic level. *1, Ciliopagurus* Forest, 1995 (Diogenidae); *2, Loxopagurus* Forest, 1964 (Diogenidae); *3, Paragiopagurus* Lemaitre, 1996 (Parapaguridae); *4, Bathypaguropsis* McLaughlin, 1994 (Paguridae); *5, Rhodochirus* McLaughlin, 1981 (Paguridae); (adapted from McLaughlin, 2003, fig. 6c, g, h, k, and m, respectively).

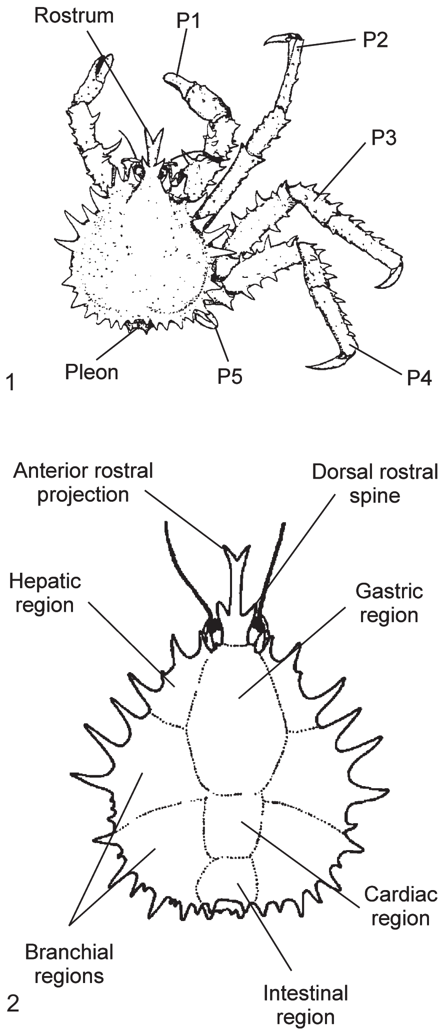


FIG. 101. Lithodoid carapace (*1, 2*) and appendages (*1*) (adapted from Pohle, 1990, p. 6; Tudge, Asakura, & Ahyong, 2012, fig. 70.6F). P=pereiopod.

the shelter in place (TUDGE, ASAKURA, & AHYONG, 2012) (Fig. 99).

Lithodidae have recently been found to be nested within Paguroidea, as highly derived forms (BRACKEN-GRISSOM & others, 2013). They have a meager fossil record with some Miocene occurrences (FELDMANN, 1998; KARASAWA & others, 2017). Lithodids have a different carapace form than other paguroids. Their carapace is similar to brachyurans in general form, and the carapace grooves and regions are described using brachyuran terminology (Fig. 101). The carapace of lithodids is densely covered with tubercles or spines, and the rostrum is almost always spinose and well developed (TUDGE, ASAKURA, & AHYONG, 2012). The sternum in lithodids is broadened. The pleon in lithodids is very large and wide, covering the entire sternum, even in males. In both males and females, somites 3–6 are reduced and separated axially by a central area. Marginal plates can be positioned lateral to somites 3–6. In females, the pleon is asymmetrical, with the right side of plates 3–5 larger than the left side (TUDGE, ASAKURA, & AHYONG, 2012) (Fig. 102). Antennules, antennae, and mouthparts in lithodoids are similar to those of other paguroids. The first pereiopod in lithodids is short, shorter than pereiopods 2–4, and chelate (Fig. 101.1). Pereiopods 2–4 in lithodids are longest and pereiopod 5 is reduced, with tiny chela (TUDGE, ASAKURA, & AHYONG, 2012) (Fig. 101).

LOMISOIDEA

No fossil Lomisoidea have been found to date. The lomisoid carapace is triangular, with a densely ornamented carapace that may exhibit transverse grooves (TUDGE, ASAKURA, & AHYONG, 2012) (Fig. 103). The rostrum and orbital spines in this group are reduced to blunt projections (TUDGE ASAKURA, & AHYONG, 2012). The sternum in lomisoids is broadened, with sternite 8 reduced (Fig. 104). They have an overall triangular shape, symmetrical pleon due to the narrowing of successive somites posteriorly, and an undivided telson (TUDGE, ASAKURA, & AHYONG, 2012).

In lomisoids, the antennules have short flagella, and the antenna lacks the scaphocerite. Mouthparts are similar to those of paguroids. Their chelae are dorsoventrally flattened and directed toward the body (Fig. 103.1). Pereiopods 2–4 are short and setose, (Fig. 103.1) and pereiopod 5 is reduced, with a tiny chela (TUDGE, ASAKURA, & AHYONG, 2012) (Fig. 103.1).

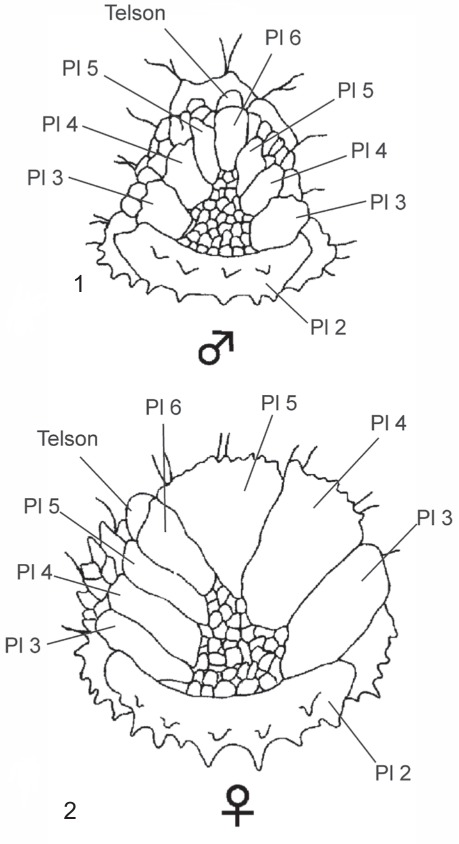


Fig. 102. Lithodid pleons showing tiny lateral and medial plates: *1,* male; *2,* female (adapted from Tudge, Asakura, & Ahyong, 2012, fig. 70.10E, F). Pl=pleonal somite.

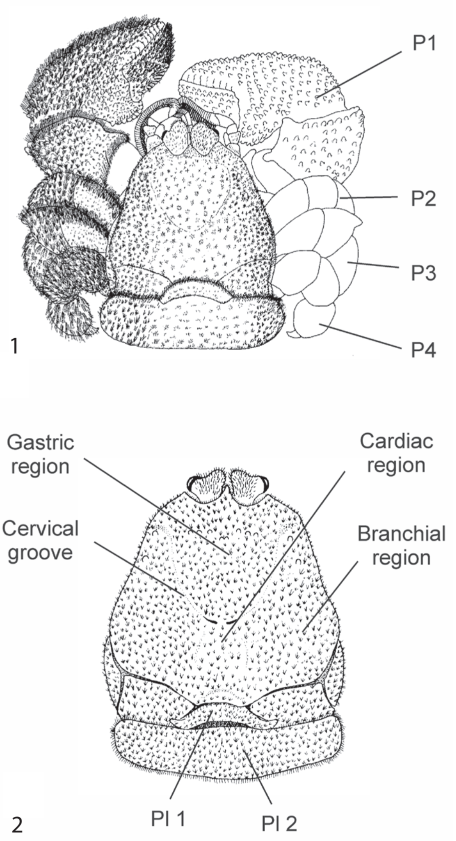


Fig. 103. Lomisidae morphology: *1,* carapace and appendages; *2,* carapace and pleon (adapted from Tudge, Asakura, & Ahyong, 2012, fig. 70.3B, 70.22A). P=pereiopod, Pl=pleonal somite.

INFRAORDER BRACHYURA: TRUE CRABS

Brachyura includes the so-called true crabs, those decapods with a carapace covering the entire cephalothorax, a reduced pleon carried at least partially against the thoracic sternum, and five pairs of appendages, the first of which is chelate. Other carcinized forms, those that have an overall body plan similar to true crabs, are present among Anomura, but in each case the pleon and pereiopods differ from those of true crabs (Keiler, Wirkner, & Richter, 2017).

True crabs are the most diverse group within Decapoda (De Grave & others,

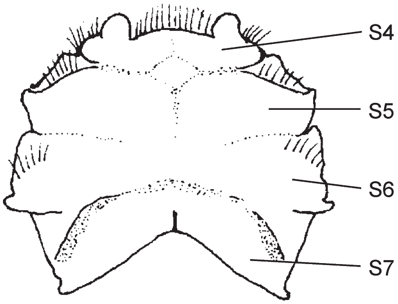


Fig. 104. Lomisidae sternum (adapted from Tudge, Asakura, & Ahyong, 2012, fig. 70.22D). S=sternite.

2009), and they are the only decapods with modifications of the position of the gonopores from the ancestral location on the coxae of the appendages. Brachyurans previously referred to Podotremata have subsequently been realigned into a series of taxonomic sections, which include Dromiacea, Homoloida, Callichimaeroida, Torynommoida, Etyoida, Dakoticancroida, Raninoida, and Cyclodorippoida (Ahyong & others, 2007; Karasawa, Schweitzer, & Feldmann, 2011; Luque & others, 2019a). The broad array of cephalothorax morphologies in these sections demonstrates convergence with Eubrachyura in having a more derived appearance of the carapace with reduced grooves and regional development but still retaining the ancestral condition of gonopores on the pereiopodal coxae. Eubrachyurans exhibit female or both male and female gonopores on the sternum. The range of variation among brachyuran body forms is vast (see Fig. 105–108).

CARAPACE

Morphology.—In Brachyura, the carapace is comprised of one cuticular plate covering the tagma of the head (five somites) and thoracic region (eight somites). It is variously shaped and subdivided into regions. The carapace of brachyurans is highly variable, even within families. Various terms are applied to carapace shapes, including those used for leaves (Fig. 109). Ng (1998) developed an illustrated terminology for carapace shapes as well (Fig. 110). Overall, carapace shape is similar among members of a family, with notable exceptions.

Carapace regions.—The scheme of naming regions of the carapace used today was originally devised by Dana (1852 in 1852–1853) and is based on a comparison of the dorsal position of the region with the internal anatomy situated below it. Thus, regions are referred to as gastric or branchial regions. Grooves are identified by the same terminology as that used for lobsters and other decapods, although homology among and between these grooves is not known. Carapace regional development is variable and somewhat different terminology is used for different taxa.

The gastric region corresponds to the position of the foregut of the animal and is subdivided—working anterior to posterior—into epigastric, protogastric, mesogastric, metagastric, and urogastric regions (see Fig. 111–115). The cardiac region corresponds to the position of the cardiac stomach (not the heart), and the intestinal region corresponds to the intestines. Anterolateral to the protogastric region lies the hepatic region, associated with the liver or hepatic gland. The branchial region, which houses the gills, is subdivided into epibranchial, mesobranchial, and metabranchial regions, anteriorly to posteriorly. In some podotrematous groups, the lateral portions of the carapace (extralineal in Homoloida) develop into a subhepatic region and a subbranchial region (Fig. 115.3), and the cervical and branchiocardiac grooves extend onto the flanks of the carapace.

Carapace grooves.—As in other decapods, the cervical groove separates the mesogastric, protogastric, and hepatic regions from the branchial regions. It is well developed in many groups but obscure in some eubrachyurans. Especially in those brachyurans that are podotrematous, a postcervical groove and branchiocardiac groove are well developed (Fig. 115.5). These are absent in eubrachyurans. Schweitzer and others (2012) defined branchial grooves 1 and 2 that are oblique from the posterolateral margin and bounding the mesobranchial region, present in Etyoida (Fig. 116).

Carapace *lineae*.—Nearly all crabs, with the exception of some podotrematous groups, have a *linea brachyura* (also called *linea dromica* and the pleural suture), which forms the boundary between the carapace and the branchiostegite (Davie, Guinot, & Ng, 2015) (see Fig. 6.4). Homoloida includes some families with a *lineae homolica*, which parallels the lateral margins of the carapace, intersecting the orbits or the carapace just lateral to the orbits and extending to the posterior margin (Fig. 115.1, 115.4). This suture facilitates molting (Davie,

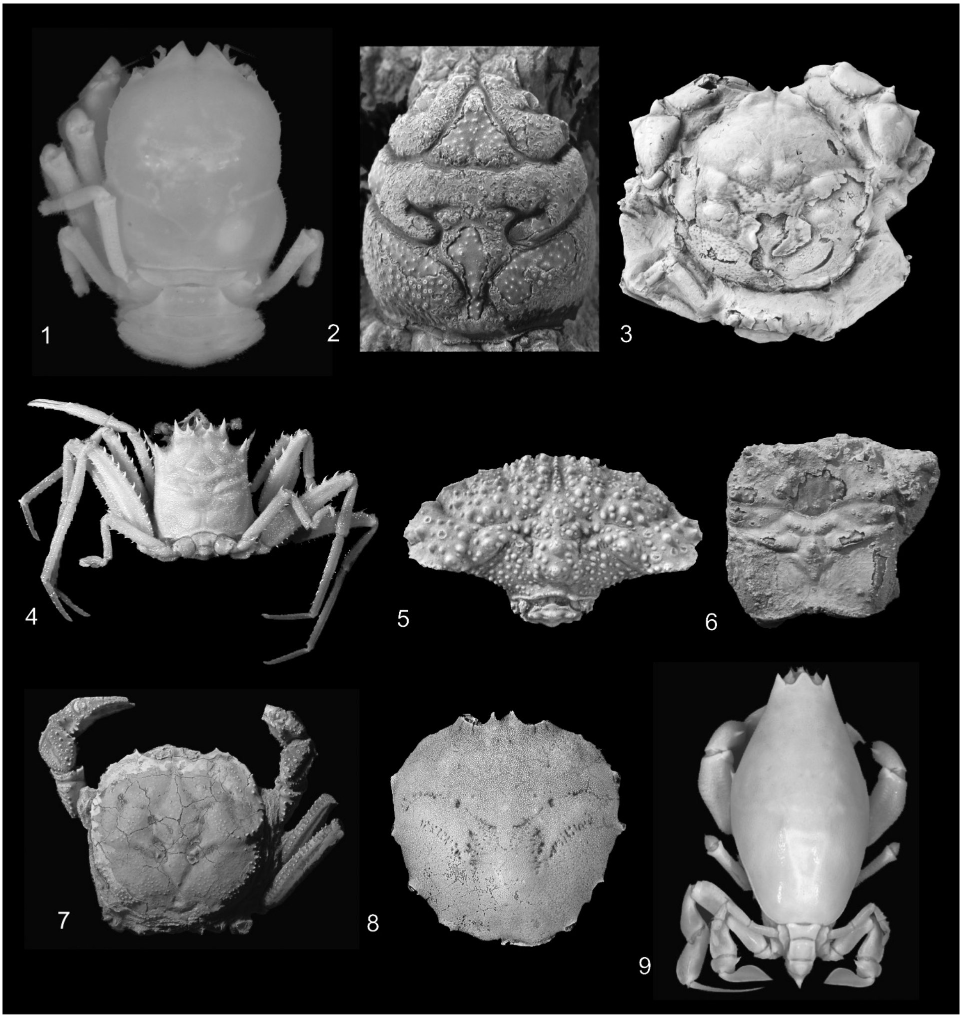


Fig. 105. Podotrematous crab morphology. *1,* Homolodromiidae, *Dicranodromia ovata* A. Milne-Edwards, 1880 (Dromiacea); *2,* Prosopidae, *Europrosopon aculeatum* (von Meyer, 1857) (Dromiacea); *3,* Sphaerodromiidae, *Dromilites bucklandi* H. Milne-Edwards, 1837 (Dromiacea); *4,* Homolidae, *Homola ranunculus* Guinot & Richer de Forges, 1995 (Homoloida); *5,* Etyidae, *Steorrosia aspera* (Rathbun, 1935) (Etyoida); *6,* Quadratoplanidae, *Quadratoplanus primitivus* Franţescu, 2014a (Cyclodorippoida); *7,* Dakoticancridae, *Avitelmessus grapsoideus* Rathbun, 1923 (Dakoticancroida); *8,* Camarocarcinidae, *Camarocarcinus arnesoni* Holland & Cvancara, 1958 (Raninoida); *9,* Lyreididae, *Lyreidus tridentatus* De Haan, 1841 in 1833–1850 (Raninoida). All images from previous Part R *Treatise Online* articles.

Guinot, & Ng, 2015). Many fossil homoloids are known chiefly from the interlineal portion of the carapace, as the extralineal portions are frequently missing (Fig. 115.4).

ORBITS AND FRONTAL STRUCTURES

Front.—The front lies between the orbits in brachyurans and ranges from spinose to lobate or straight (Fig. 117.2, Fig. 117.5). In many brachyurans, the front develops into a rostrum, which is the term used when the structure extends well beyond the orbits and is spinose (Fig. 112.1, Fig. 117.3–4). This is most commonly seen in podotrematous brachyurans and majoids.

In homoloidan brachyurans, spines located between the orbits are referred to

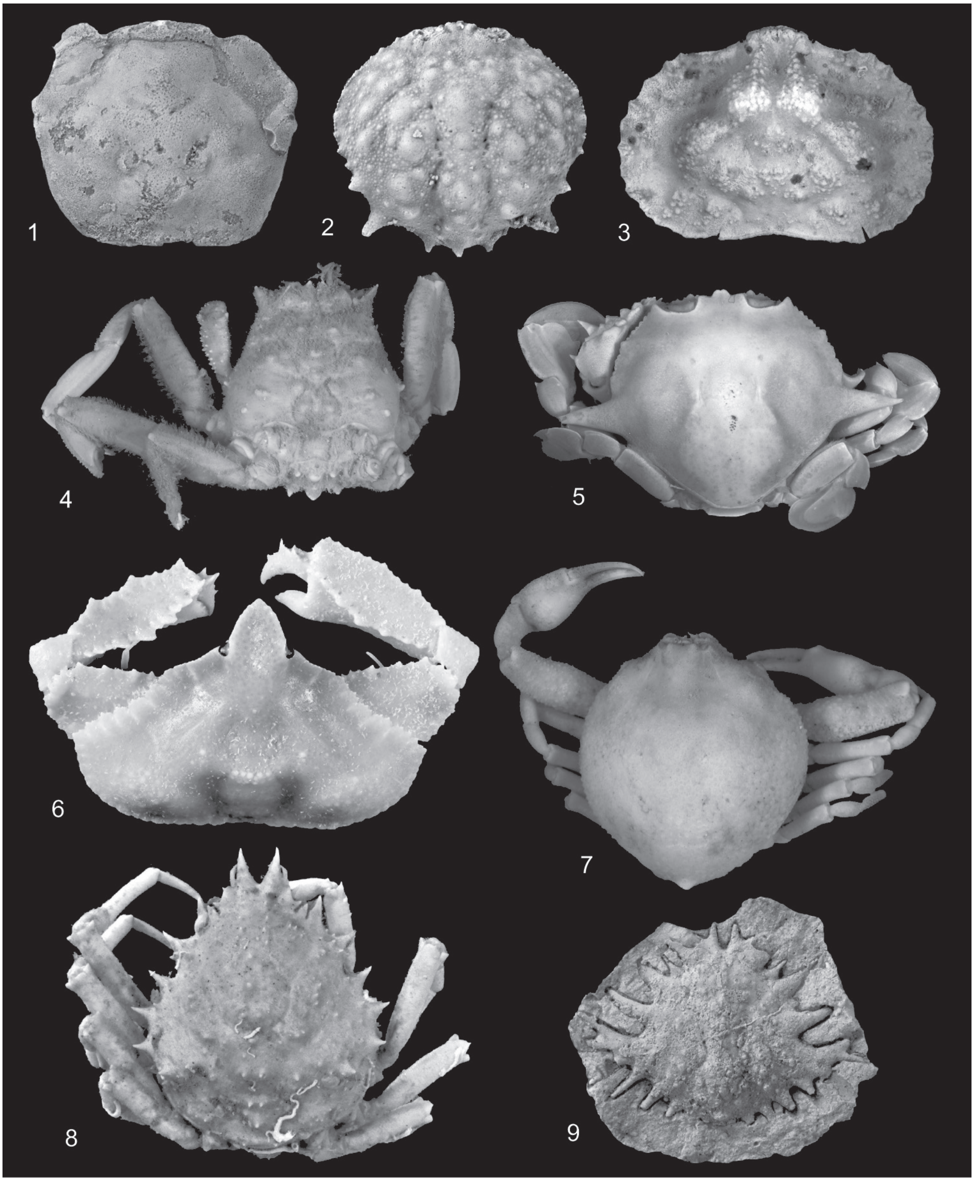


Fig. 106. Heterotreme crab morphology. *1,* Componocancridae, *Componocancer roberti* Feldmann, Schweitzer, & Green, 2008; *2,* Calappidae, *Calappa lanensis* Rathbun, 1926; *3,* Aethridae, *Aethra scruposa* (Linnaeus, 1764); *4,* Dorippidae, *Dorippe quadridens* (Fabricius, 1793); *5,* Matutidae, *Matuta victor* (Fabricius, 1781); *6,* Parthenopidae, *Cryptopodia fornicata* (Fabricius, 1781); *7,* Leucosiidae, *Leucosilia jurinei* (de Saussure, 1853); *8,* Majidae, *Leptomithrax garricki* Griffin, 1966; *9,* Epialtidae, *Periacanthus horridus* Bittner, 1875. All images from previous Part R *Treatise Online* articles.

Fig. 107. Heterotreme crab morphology (on facing page). *1,* Retroplumidae, *Loerenthopluma lata* Beschin & others, 1996; *2,* Cancridae, *Cancer pagurus* Linnaeus, 1758; *3,* Corystidae, *Corystes cassivelaunus* Pennant, 1777; *4,* Geryonidae, *Chaceon peruvianus* (d'Orbigny, 1842); *5,* Tumidocarcinidae, *Tumidocarcinus giganteus* Glaessner, 1960; *6,* Tumidocarcinidae, *Pulalius vulgaris* (Rathbun, 1926); *7,* Euryplacidae, *Orbitoplax weaver* (Rathbun, 1926); *8,* Hypothalassiidae, *Lathahypossia aculeata* (Busulini, Tessier, & Visentin, 1984); *9,* Hexapodidae, *Palaeopinnixa rathbunae* Schweitzer & others, 2000 (*4,* photo by P. Hurst, NHMUK; *7,* photo by G. Retallack, University of Oregon; *8,* photo by A. Busulini, Museo di Storia naturale, Venezia, Italy; all others from previous Part R *Treatise Online* articles).

Fig. 107. Heterotreme crab morphology. See explanation on facing page.

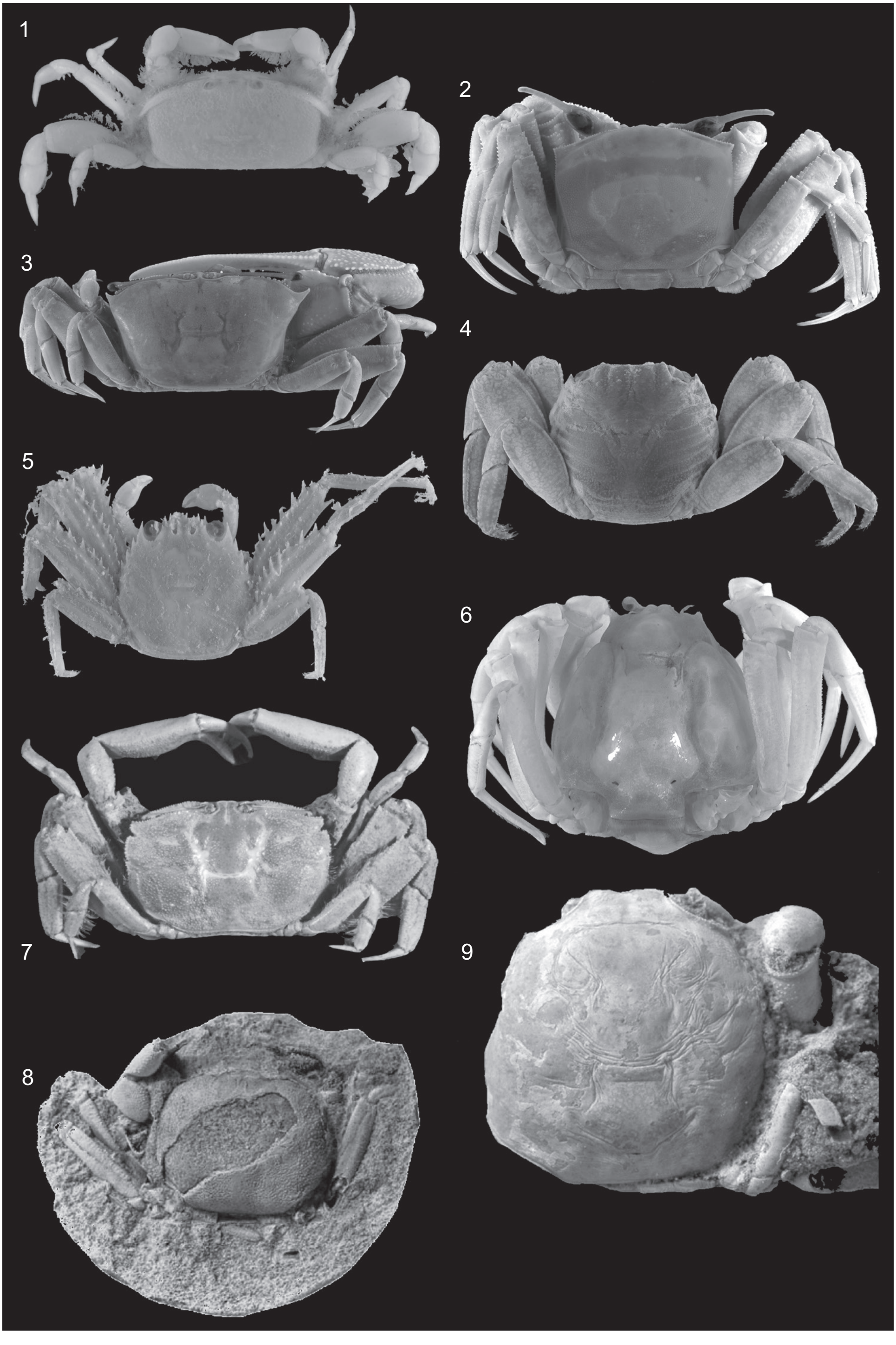


FIG. 108. Thoracotreme crab morphology. For explanation, see facing page.

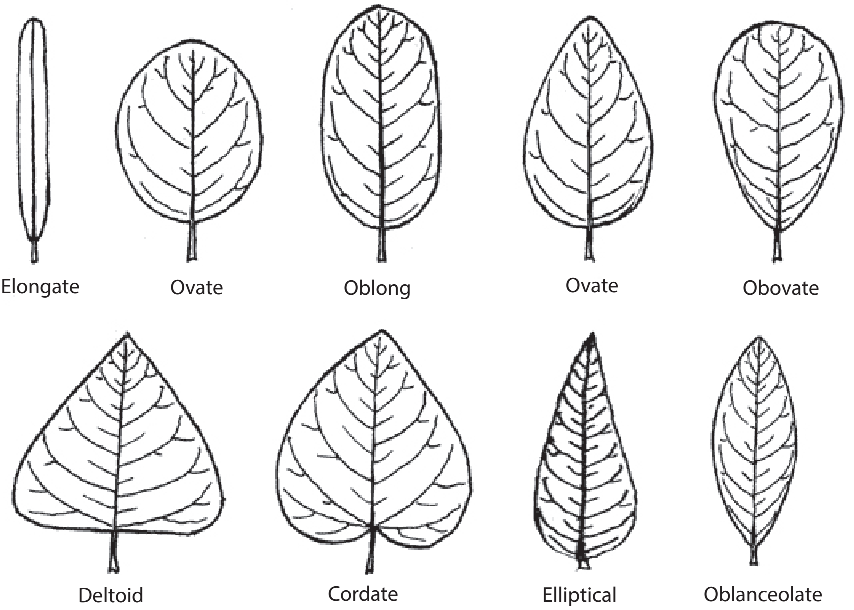


Fig. 109. Generalized leaf terminology used for brachyuran carapace shapes (adapted from Plant Inspection Guidebook, Philadelphia Water Department. p. 3).

as pseudorostral spines because the spines appear to originate on the dorsal carapace but extend into the region between the orbits (Fig. 115.1). In many groups, the number of frontal spines or lobes is diagnostic at the family or genus level.

Orbits.—The orbits are concave structures to house the eye and eyestalks, situated just ventral to the anterior or anterolateral margin of the carapace. The upper (or supra-) orbital margin is described separately from the suborbital margin, and each can be ornamented with rims, spines, notches, or fissures (Fig. 117). In many eubrachyurans, the orbit is elongate, housing long eyestalks and eyes. In fact, many types of structures have developed to protect the eye, and the specific orbital forms among brachyurans do not all appear to be homologous (Davie, Guinot, & Ng, 2015). In some podotrematous groups, the orbit is barely developed, such as in some dromiaceans and homoloidans, in the latter of which the orbital region is called a false orbit (Wright & Collins, 1972) or the plage orbitaire (Guinot & Richer de Forges, 1995) (Fig. 117). In majoids, a true orbit is typically absent, but a protective structure is formed by some combination of spines, eaves, and lobes (Fig. 117.3, 117.4).

An augenrest is present in many podotrematous groups, which is an extralimital orbit structure (Fig. 118). A low septum divides the orbital structure into two parts,

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Fig. 108. On facing page. Thoracotreme crab morphology. *1,* Pinnotheridae, *Pinnixa cylindrica* (Say, 1818 in 1917–1818); *2,* Ocypodidae, *Ocypode ceratiophthalma* Pallas, 1772; *3,* Ocypodidae, *Uca major* Herbst, 1782 in 1872–1804; *4,* Grapsidae, *Grapsus grapsus* (Linnaeus, 1758); *5,* Plagusiidae, *Percnon planissimum* (Herbst, 1804 in 1872–1804); *6,* Mictyridae, *Mictyris longicarpus* Latreille, 1806; *7,* Macrophthalmidae, *Macrophthalmus japonicus* (De Haan, 1835 in 1933–1850); *8,* Varunidae, *Asthenognathus urretae* Schweitzer & Feldmann, 2001; *9,* Pinnotheridae, *Pharkidodes agele* Feldmann & others, 2011b (*8,* Schweitzer & Feldmann, 2001, fig. 5.9; *9,* Feldmann & others, 2011b, fig. 12A). Photos for *1–7* are from Schweitzer, Feldmann, & Karasawa, 2023, *Treatise Online* 166, as follows: *1,* fig. 7,*2*; *2,* fig 6,*1*; *3,* fig. 63,*3*; *4,* fig. 1,*6*; *5,* fig. 2,*2*; *6,* fig. 5,*12*; *7,* fig.5,*9*.

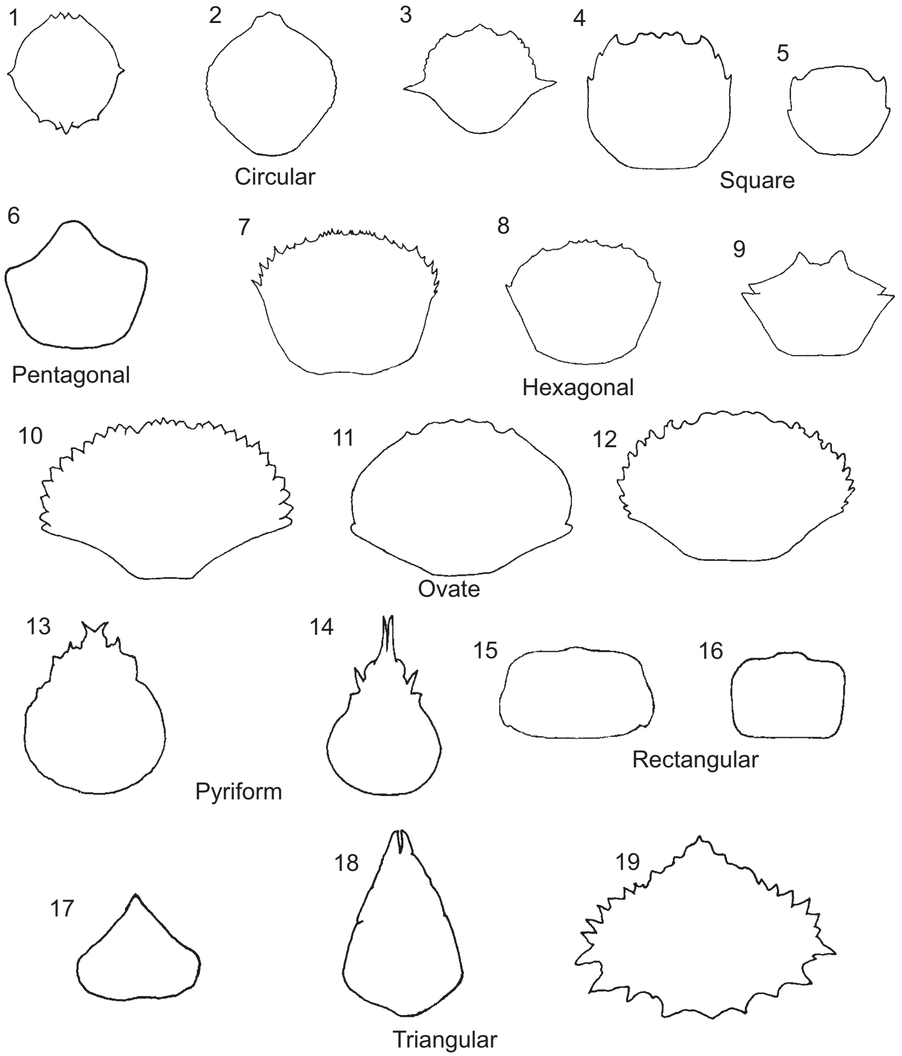

FIG. 110. Typical brachyuran carapace shapes: *1–3,* circular; *4–5,* square; *6,* pentagonal; *7–9,* hexagonal; *10–12,* ovate; *13–14,* pyriform; *15–16,* rectangular; *17–19,* triangular (adapted from Ng, 1998, fig. B, C, E, F, G, H, K, L, N).

seen in Goniodromitidae for example, the outermost part being termed the augenrest (SCHWEITZER & FELDMANN, 2009b). In other taxa, the augenrest is comprised of a circular or elongate cavity surrounded by a rim, spines, or both, separated from the orbit proper by a small ridge (Fig. 118.2) or a space (Fig. 118.1) (SCHWEITZER & FELDMANN, 2009b; STARZYK, 2016). In Bucculentidae, this structure is situated on the dorsal carapace (Fig. 118.3). The augenrest appears to be an independently derived, convergent structure that developed to provide protection for the eye and eyestalk in taxa in which the orbit is reduced.

Margins.—Lateral margins of the carapace are variously developed. The front (or rostrum) plus the orbits is referred to as the anterior margin or the fronto-orbital margin (Fig. 119). The margin extending from the outer orbital margin to the widest part of the carapace is called the anterolateral margin (Fig. 119). The margin extending from the

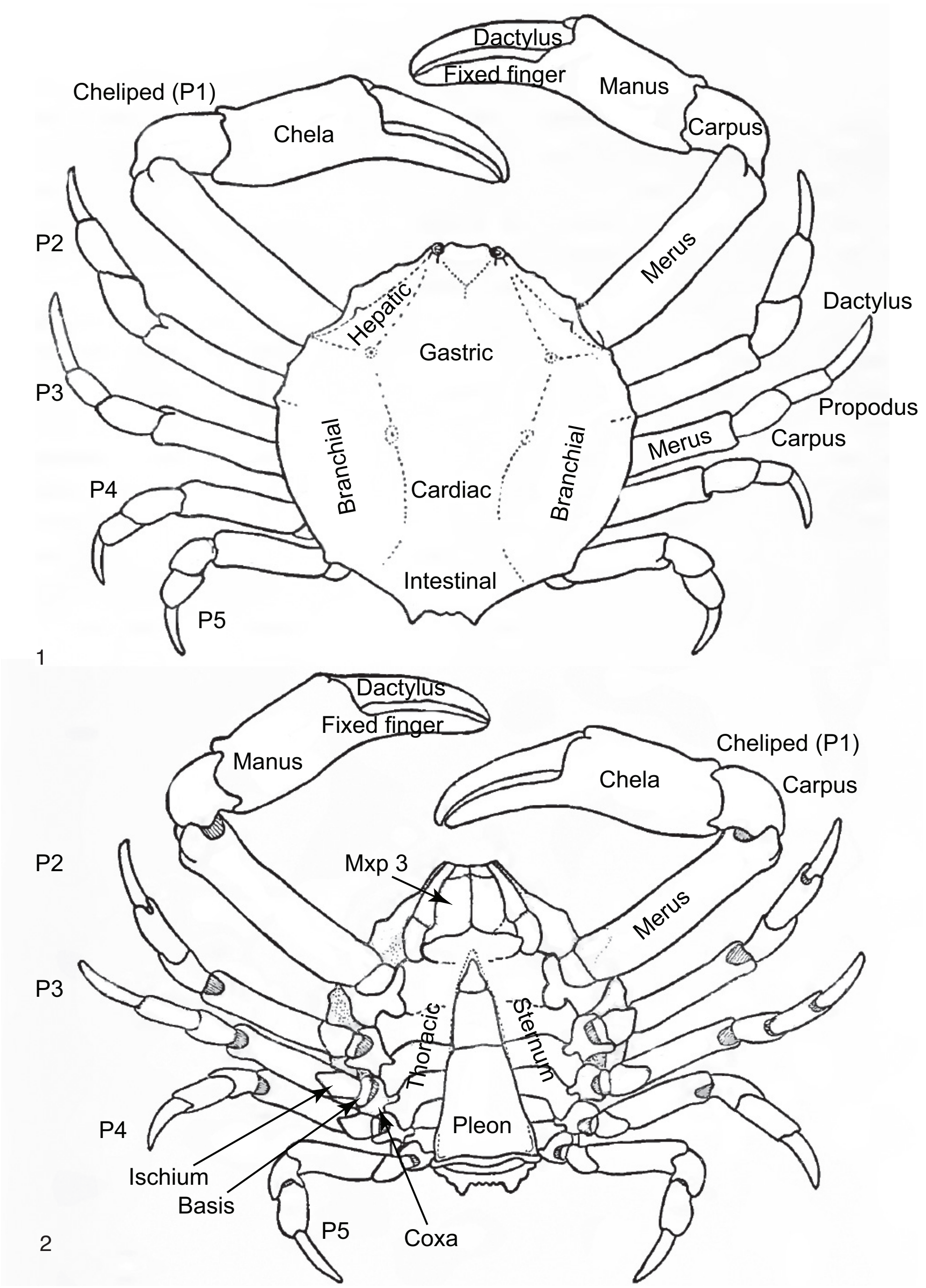

Fig. 111. Dorsal (*1*) and ventral (*2*) views of leucosioid crab (adapted from Rathbun, 1937, fig. 1–2). P=pereiopod, Mxp=maxilliped.

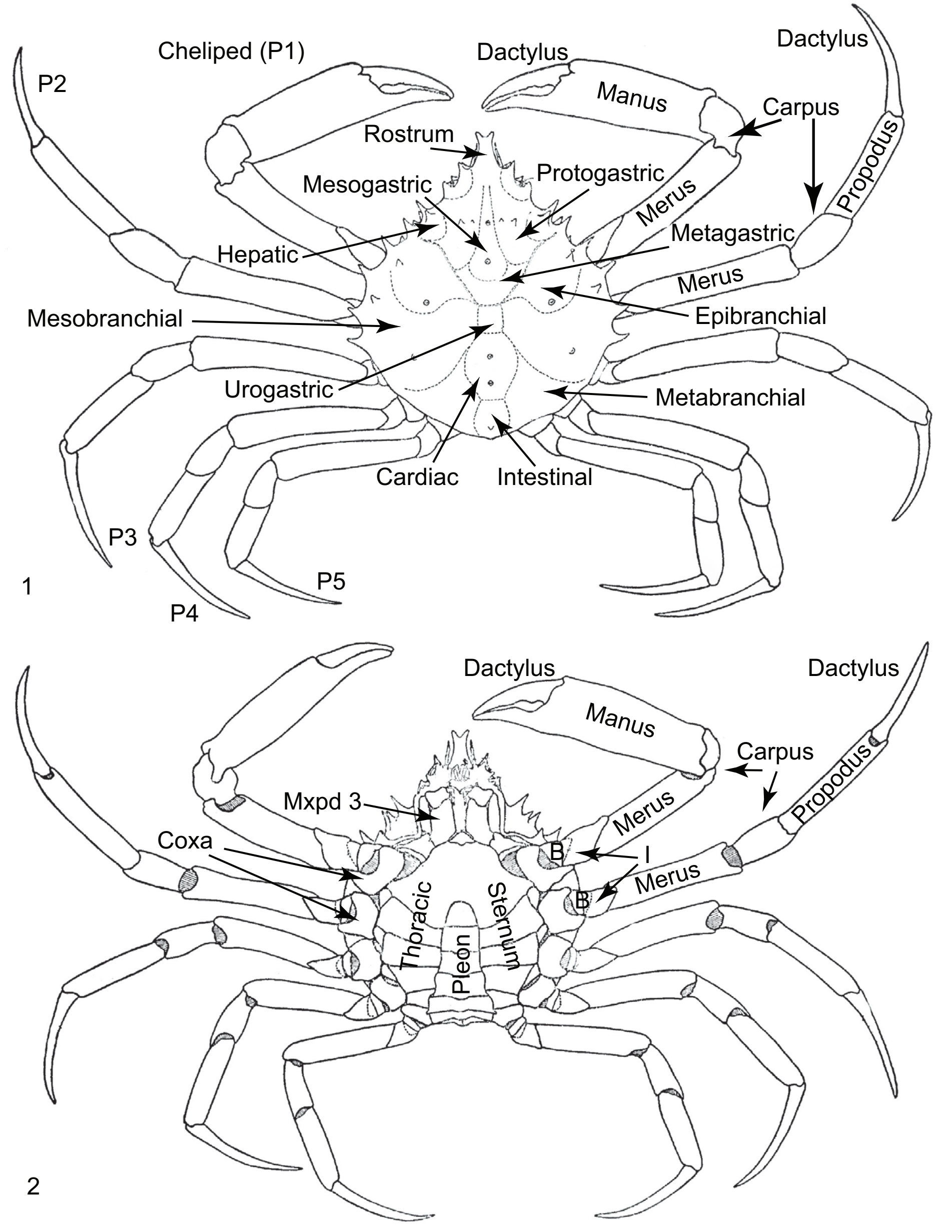

FIG. 112. Dorsal (*1*) and ventral (*2*) morphology of majoid crab (adapted from Rathbun, 1925, fig. 1–2). B=basis, I=ischium, Mxpd=maxilliped, P=pereiopod.

widest part of the carapace to the posterior corner is the posterolateral margin. The posterior margin extends from the posterior corners and parallels the pleonites. As in many podotrematous crabs, the anterolateral and posterolateral margins may not be well differentiated, and in this case, they are referred to as the lateral margins. These margins may or may not be rimmed.

The anterior margin is characterized in terms of the number and shape of frontal/rostral spines, the width and ornamentation

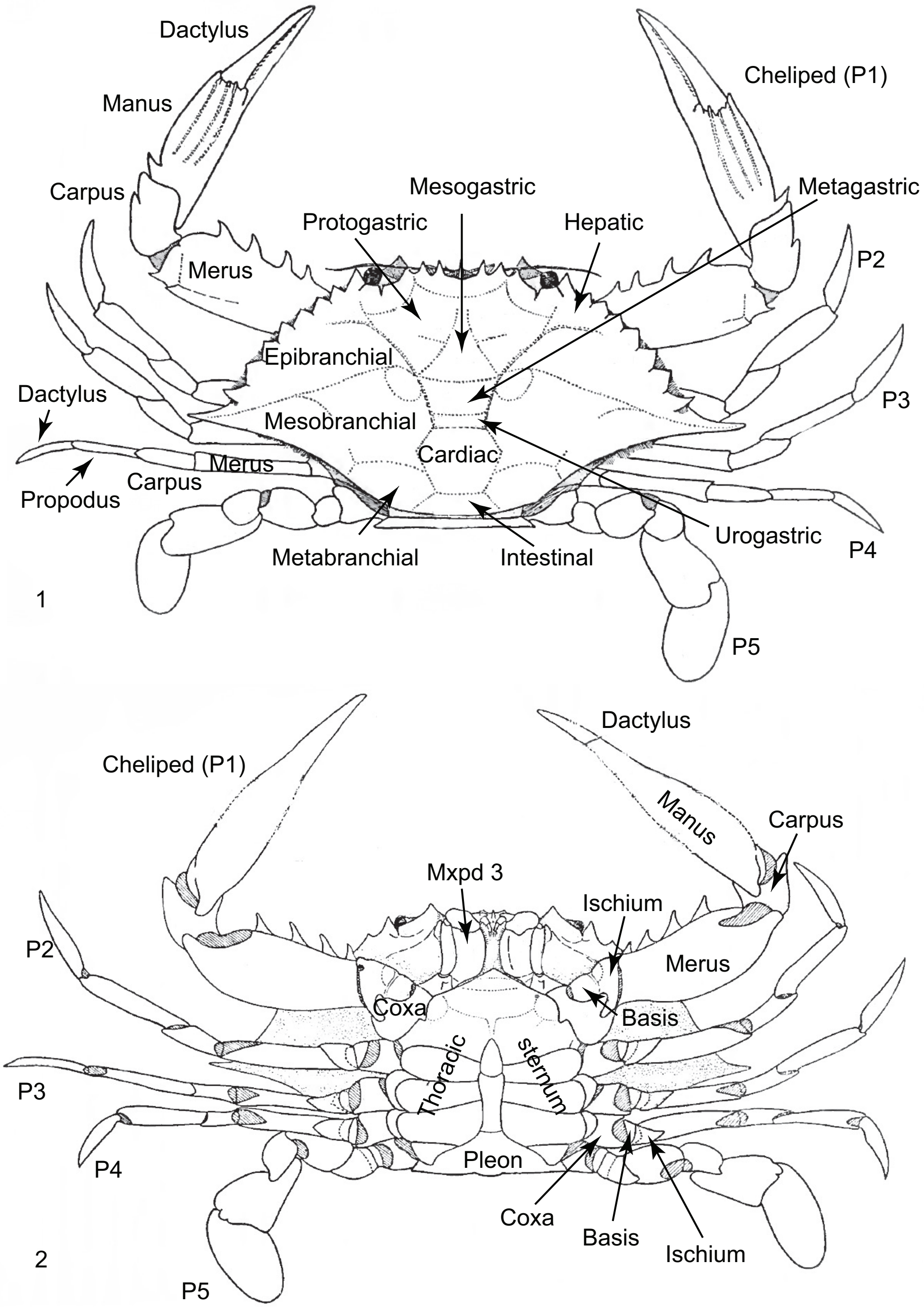

Fig. 113. Portunoid dorsal (*1*) and ventral (*2*) morphology (adapted from Rathbun, 1930, fig. 1–2). P=pereiopod, Mxpd=maxilliped.

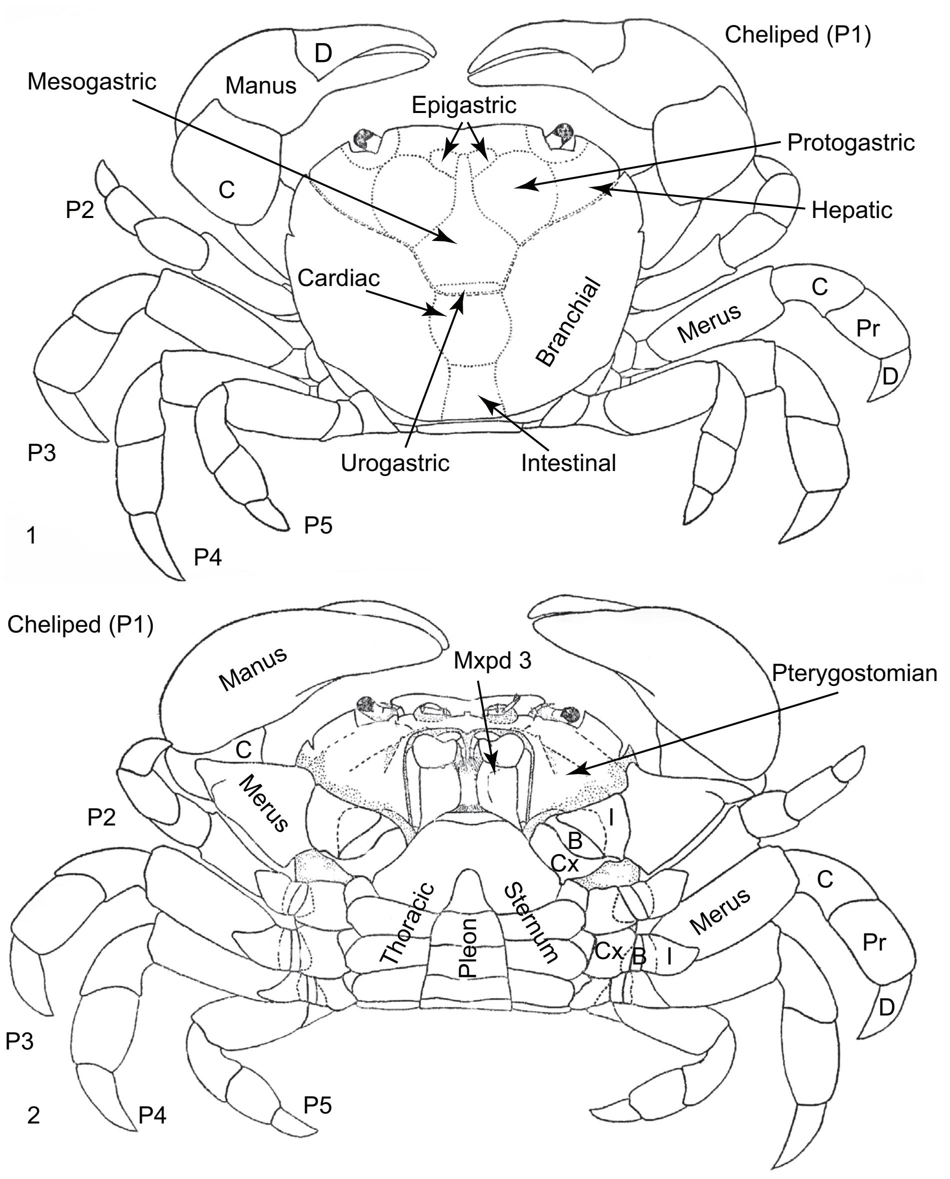

Fig. 114. Dorsal (*1*) and ventral (*2*) morphology of a grapsoid crab (adapted from Rathbun, 1918, fig. 1–2). B=basis, C=carpus, Cx=coxa, D=dactylus, I=ischium, Mxpd=maxilliped, P=pereiopod, Pr=propodus.

of the orbits, and whether it is perpendicular or oblique to the long axis of the carapace (Fig. 119). Anterolateral margins can be characterized as spinose (Fig. 106.8), crispate (Fig. 106.3), granular (Fig. 106.2), or entire (Fig. 108.6), and usually the degree of convexity is noted qualitatively. When counting the number of anterolateral spines, it is important to note whether the outer-orbital spine is included. Anterolateral spines can themselves be serrate (Fig. 106.6), spinose (Fig. 107.8) or bifid (Fig. 106.9). The posterolateral margin may have spines as seen on the anterolateral margins (Fig.

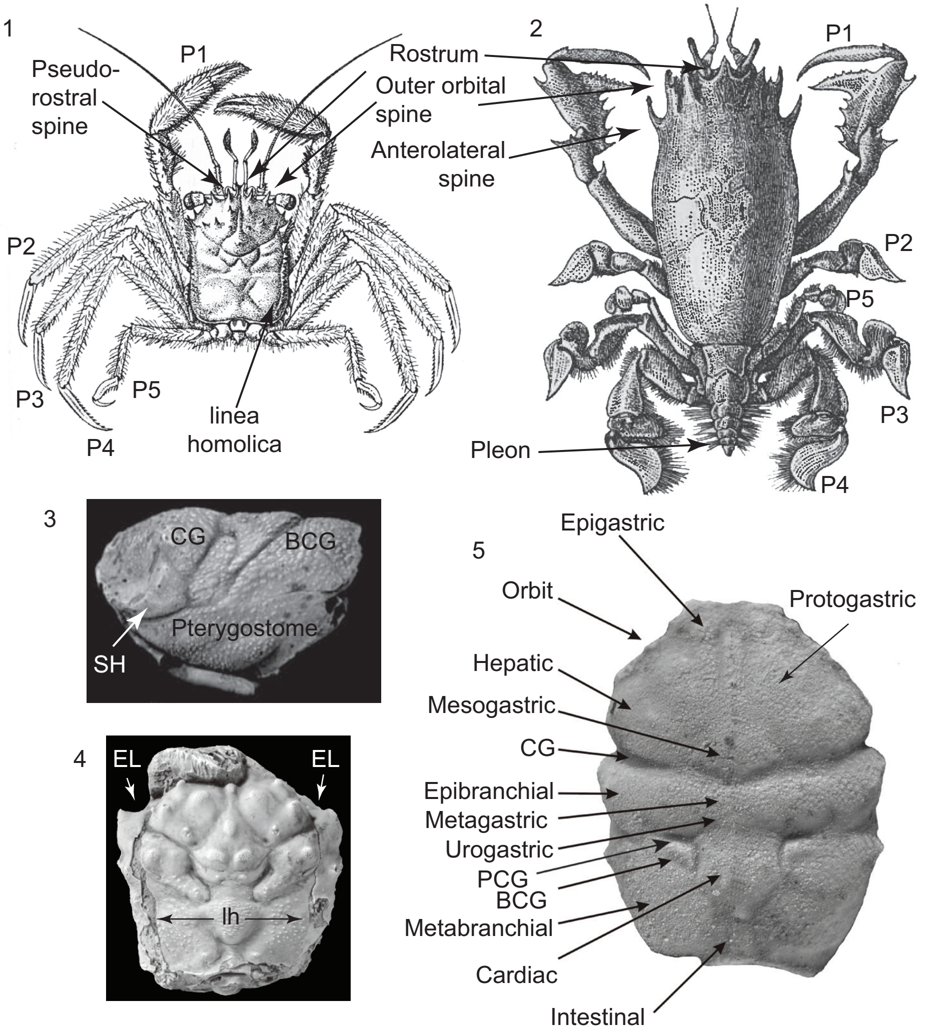

FIG. 115. General morphology of podotrematous crabs: *1,* homoloid general morphology; *2,* raninoid general morphology; *3,* dromioid general morphology, lateral view of longodromitid *Glaessnerella spinosa* (VAN STRAELEN, 1936); *4,* homolid morphology *Latheticocarcinus punctatus* (RATHBUN, 1917); *5,* generalized podotrematous crab morphology (*1–2,* adapted from Rathbun, 1937, fig. 4, 16; *3,* adapted from Schweitzer & Feldmann, 2011, fig. 3.4; *4,* adapted from Feldmann & Schweitzer, 2015, fig. 3.1). BCG=branchiocardiac groove, CG=cervical groove, EL=extra-lineal portion of carapace, lh=*linea homolica,* P=pereiopod, PCG=postcervical groove, SH=subhepatic region.

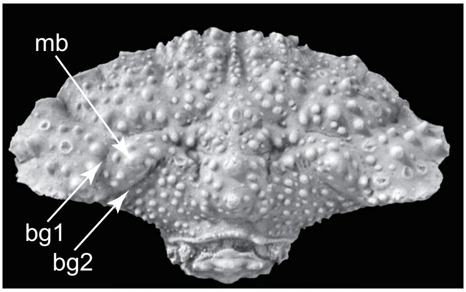

FIG. 116. Location of branchial groove 1 (bg1) and branchial groove 2 (bg2), bounding the mesobranchial region (mb) in etyoid crabs, *Steorrosia aspera* RATHBUN, 1935 (adapted from Schweitzer & others, 2012, fig. 1).

106.2). The posterior margin is rimmed (Fig. 107.3) and may be spinose (Fig. 106.9), and the presence and size of posterolateral reentrants, which accommodate the proximal articles of the posteriormost pereiopods or

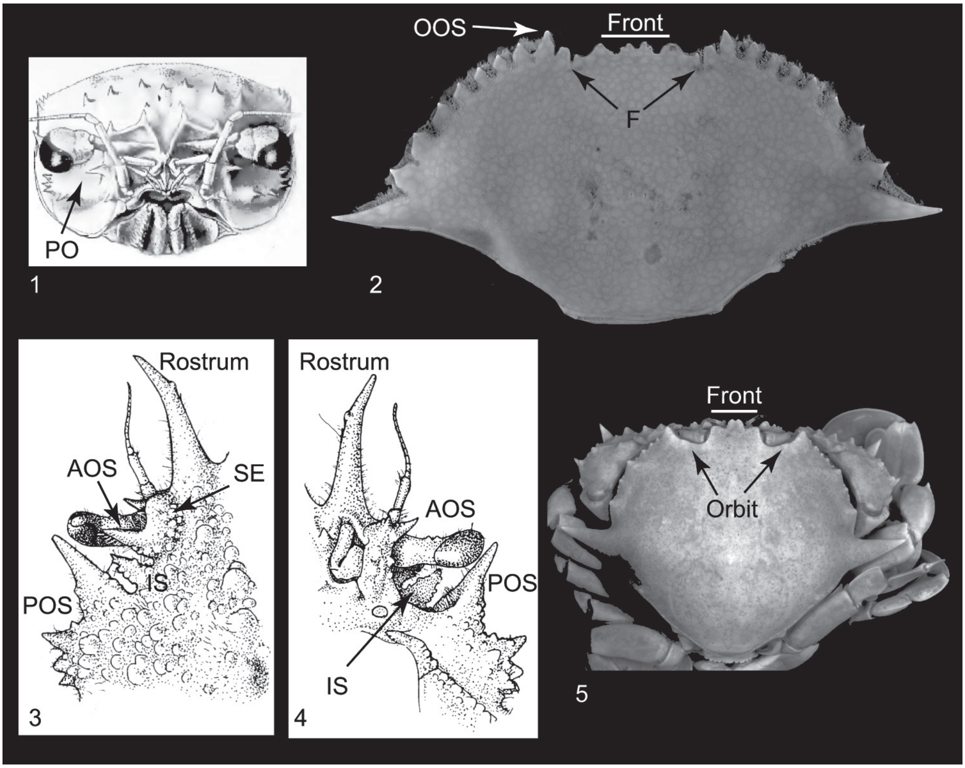

Fig. 117. Orbits and rostral and frontal structures in crabs. *1,* Plage orbitaire in homoloid crab; *2,* orbits and front in portunid crab; *3–4,* dorsal (*3*) and ventral (*4*) views of orbital structures in majoid crab; *5,* orbit and front in matutid crab (*1,* adapted from Alcock & Anderson, 1895, fig. 1; *2,* Karasawa, Schweitzer, & Feldmann. 2019, fig. 15,*3a*; *3–4,* adapted from Griffin & Tranter, 1986, fig. 72a and d; *5,* Schweitzer, Feldmann & Karasawa, 2021, fig. 13,*2a*). AOS=antorbital spine, F=fissure, IS=intercalated spine, OOS=outer orbital spine, PO=plage orbitaire, POS=postorbital spine, SE=supraorbital eave.

are concavities into which the posteriormost pereiopods can fold, can be diagnostic for families and genera (Fig. 107.9, Fig. 108).

Carapace ornamentation.—Regions of the carapace can be ornamented with keels, ridges, tubercles, granules, spines, and terraces or it can be punctate or smooth (see Fig. 7). Waugh, Feldmann, and Schweitzer, (2009) defined several cuticular structures ornamenting the carapace of raninoidan brachyurans.

Setae.—In fossils, the presence of setae is recognized by the pits that formed the setal insertions (Fig. 7), and only in exceptional cases are the setae themselves preserved (Luque & others, 2021).

Muscle scars and pits.—Prominent on many fossil crab carapaces are posterior gastric pits, a pair of pits located along the posterior margin of the mesogastric region and essentially in line with the cervical groove (Klompmaker & others, 2019). Several muscle scars are more prominent on internal molds than on the cuticle itself (Klompmaker & others, 2019).

Carapace measurement ratios.—Because the dorsal carapace is the only or the best-preserved part of the fossil crab in many cases, measurements and ratios between measurements are commonly used as diagnostic characters for families, genera, and species (Fig. 119).

Measurements are typically taken oriented parallel or perpendicular to the long axis. In fossils, maximum length is best measured excluding the rostrum, because it is usually broken. The length is measured from the furthest anterior point on the orbits to the posterior margin. The maximum width is measured between the bases of the most distal anterolateral spines, if present, or at the widest part of the carapace. The position of maximum width with respect to the carapace length is frequently included in fossil diagnoses; it is measured as the length from the furthest anterior point on the orbits toward the posterior margin to the point of maximum carapace width. Length-width ratios have been used for many diagnoses, but careful interpretation is needed because this ratio can change throughout ontogeny (e.g., Gómez-Cruz, Bermúdez, & Vega, 2015; Klompmaker & others, 2012, 2020; Klompmaker, Hyžný, & Jakobsen, 2015). The fronto-orbital width—the distance between the two outer-orbital spines—is an important measurement in fossil brachyurans. The frontal or rostral width is measured between the inner edge of the inner orbital spines, if present, or the widest part of the base of the rostrum. Posterior width can be measured including posterolateral reentrants, if present, or not; this should be indicated. The ratio of the fronto-orbital width to maximum width may be diagnostic, but it must be noted that carapace ratios may change with ontogeny, being greater in smaller (younger) specimens (e.g., Kornecki, Feldmann, & Schweitzer, 2017).

Molds of the interior versus external cuticular morphology.—It has been well documented that the external cuticle surface may differ substantially from the carapace surface known from a mold of the interior of the cuticle. Molds of the interior can have more subdued carapace regional definition and ornamentation, whereas carapace grooves can be more distinct on molds of the interior (Klompmaker, Jakobsen, & Lauridsen, 2016). Even different cuticular layers may bear different types of ornamentation (Waugh, Feldmann, & Schweitzer, 2009). Thus, it is crucial that paleontologists consider these potential differences, an issue neontologists do not have (Fig. 120).

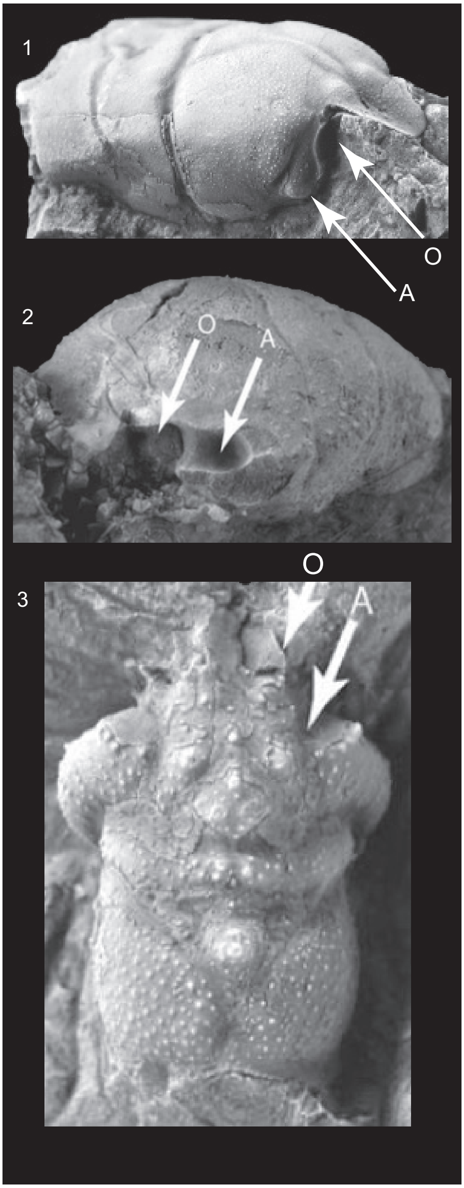

Fig. 118. Augenrest and orbits in podotrematous crabs: *1–2,* orbit and forward-directed augenrest lateral to it; *3,* laterally directed orbit and subdorsal augenrest (*1,* adapted from Schweitzer & Feldmann, 2009a, fig. 1.10; *2–3,* adapted from Schweitzer & Feldmann, 2009b, fig. 1.3, 1.4). A=augenrest, O=orbit.

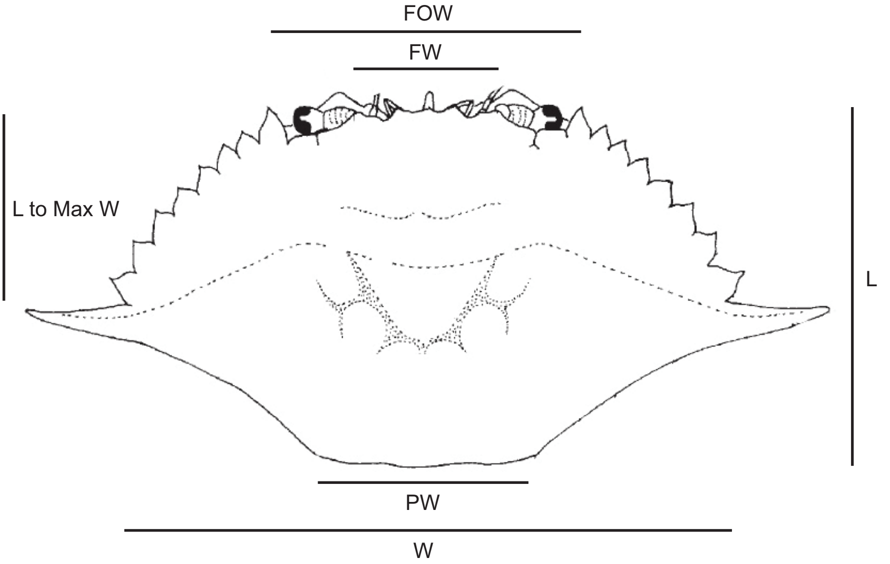

FIG. 119. Standard carapace measurements for brachyurans (adapted from Ng, 1998). FOW=fronto-orbital width, FW=frontal width, L=maximum carapace length, L to Max W=length from anterior to position of maximum width of carapace (excluding spines). PW=width of posterior margin, W=maximum width of carapace excluding spines.

Ventral carapace.—In crabs, the proepistome and epistome are located anteriorly and ventrally and are occasionally preserved as fossils (see Fig. 6.2). The buccal frame and cavern house the mouth parts and can be preserved as fossils; if so, the third maxillipeds cover the frame in many cases (Fig. 6.3). The branchiostegal region and pterygostome are positioned anteroventrally on the carapace (Fig. 6.4). The branchiostegal regions may be designated with subhepatic and suborbital regions. They are separated by what has been called the *linea brachyura* or pleural line from the pterygostomial region. This region forms the plate between the buccal area and the dorsal carapace. The pterygostome can be adapted for breathing, including structures to channel water over the gills (DAVIE, GUINOT, & NG, 2015).

THORACIC STERNUM: GENERAL MORPHOLOGY

The sternum is variably preserved in fossil specimens of Brachyura. The sternum is a ventral plate comprised of eight sternites, reflecting the eight somites of the thoracic region in decapods. It is highly variable in shape, ranging from very narrow and reduced in Raninoida to very wide in many eubrachyurans (Fig. 121). Sternites exhibit varying degrees of fusion, and the nature of the sutures between the sternites varies across taxa. The sutures may be continuous across the midline of the sternum or interrupted axially; this feature may be a family level diagnostic character (GUINOT, 1978). Sternites 1–3 are typically fused, although weak traces of the boundaries between sternites may be seen (Fig. 121, Fig. 122).

In general, the sternum serves as a point of articulation for the maxillipeds and pereiopods and as a plate to accommodate the pleonites, which in brachyurans are at least partially carried ventral to the carapace. Sternites 1–3 articulate with maxillipeds 1–3. Sternites 4–8 articulate with pereiopods 1–5, respectively (Fig. 122). The sternal portion lateral to the position of the articular condyle on sternites 4–8 is usually an episternite, also called the episternal projection (Fig. 121.2, 121.3). These are arcuate, hooklike structures in most cases that extend from

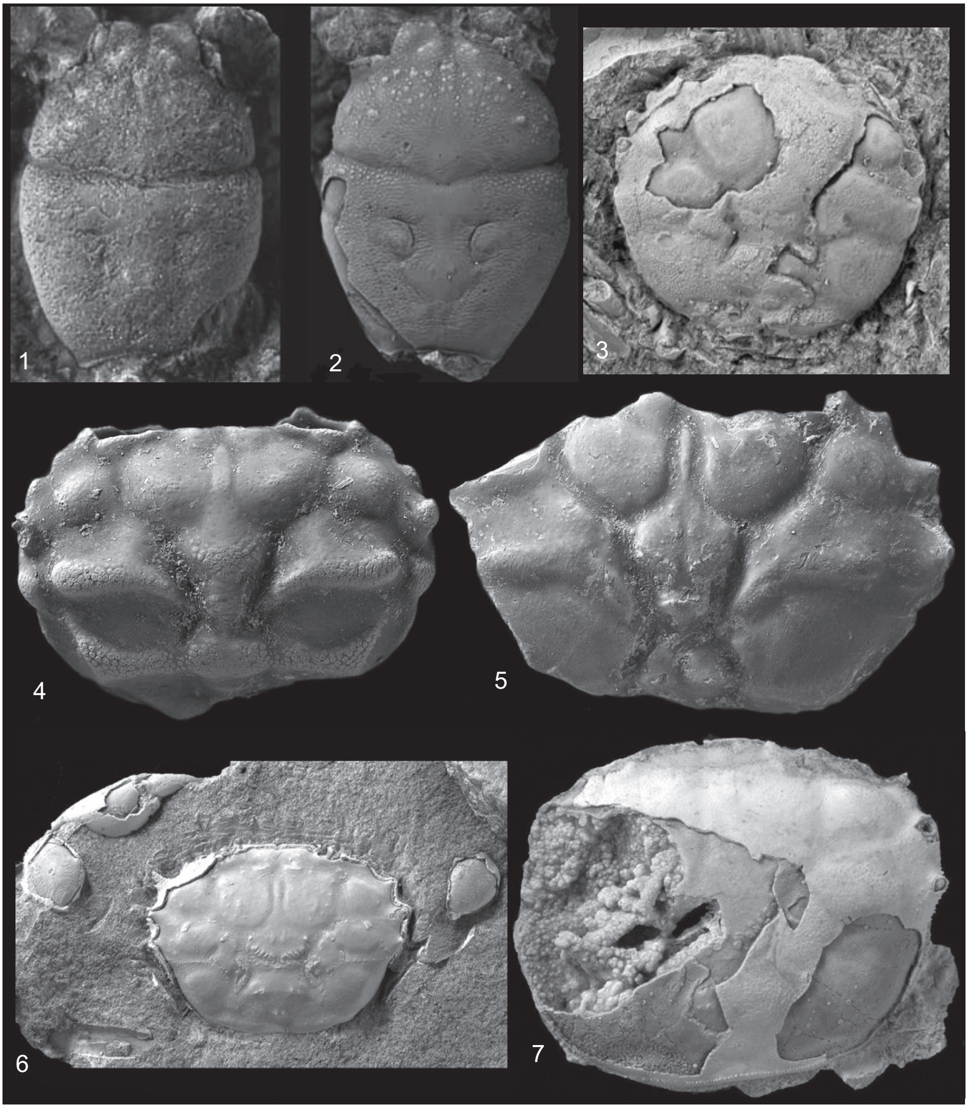

Fig. 120. Brachyuran carapaces with and without cuticle. *1–2, Longodromites excisus* (von Meyer, 1857), without (*1*) and with (*2*) cuticle; *3, Nitotacarcinus canadensis* Schweitzer & others, 2009, with mold of the interior as well as some cuticle; *4–5, Glyphithyreus bendensis* Schweitzer, Odumodu, & Feldmann, 2016, with (*4*) and without (*5*) cuticle; *6–7, Tierrapilumnus edseli* Feldmann & others, 2011, without (*6*) and with (*7*) cuticle (*1–2,* adapted from Schweitzer & Feldmann, 2009b, fig. 7.2 and 7.3); *3,* adapted from Schweitzer & others, 2009, fig. 9; *4–5,* adapted from Schweitzer, Odumodu, & Feldmann, 2016, fig. 5C, E); *6–7,* adapted from Feldmann & others, 2011, fig. 11A, E).

the disto-posterior corner of each sternite and wrap around the anterolateral edge of the succeeding sternite.

The cavity to accommodate the pleon is variously developed and differs by taxonomic section. Especially in podotrematous taxonomic sections, it is called a sterno-pleonal depression, as it is shallower than seen in other groups (Davie, Guinot, & Ng, 2015). In some podotrematous taxonomic sections, the male pleon covers the entire sternum, but this is not seen in the extinct Dakotican-

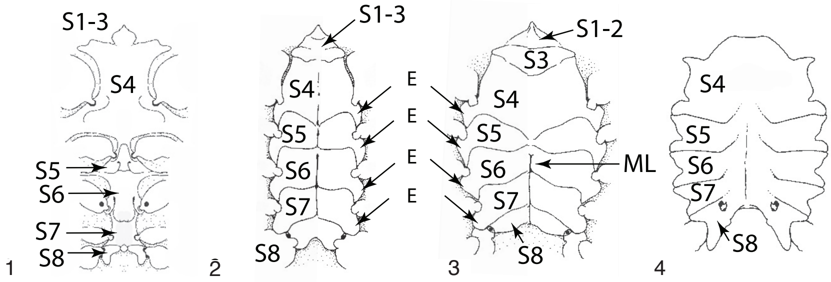

Fig. 121. General features of brachyuran sterna: *1,* raninoid form; *2–3,* heterotrematous forms; *4,* thoracotrematous form (adapted from Ng 1998, fig. 18.52). S=sternite, E=episternite, ML=median line.

croida and Etyoida. In Raninoida, a cavity or depression may not be developed at all. In eubrachyuran crabs, the cavity enclosed by the pleon is called the sterno-pleonal cavity. Compared to females, this cavity tends to be deeper and narrower in males to accommodate the gonopods.

STERNAL MORPHOLOGY in Sections Dromiacea, Homoloida, Callichimaeroida, Torynommoida, Etyoida, Raninoida, Dakoticancroida, and Cyclodorippoida

Sternal morphology in those brachyuran taxonomic sections previously referred to Podotremata, a non-monophyletic assemblage of brachyurans (Luque & others, 2019a), is very diverse, which may reflect several independent, convergent adaptations to a shortened pleon and wider carapace.

Dromiacea.—The morphology of the sternum is quite variable in Dromiacea. In general, sternites 1–3 are narrow, fused and situated slightly lower (more dorsal) than the other sternites. Sternite 4 is much wider, approximately as wide as sternites 5–7, and may have a long anterior process. Sternites 4, 5, and 6 terminate in triangular episternites, and sternites 7 and 8 are directed posteriorly. The sterno-pleonal depression holding the pleon is broad and shallow (Fig. 122.1).

Homoloida.—In Homoloida, sternal suture 6/7 is complete, separating the sternum into two parts. Sternites widen posteriorly, and sternites 7 and 8 are directed posteriorly (Fig. 122.2).

Callichimaeroida.—The sternum in this section is unusual, with sternites 5 and 6 much wider than sternites 1–4 (Fig. 122.3). Sternite 8 currently is not well known.

Etyoida.—Sternites 1–3 are fused into a triangular segment. Sternites 4, 5, and 6 are wide, and sternites 5 and 6 are situated at a high angle to sternite 4, nearly 90 degrees. Sternites 7 and 8 are narrow and directed posteriorly (Fig. 122.5).

Raninoida.—This section embraces a very diverse array of sternal morphologies. In nearly all, sternites 1–3 are fused into a crown-shaped structure. The sternum of Necrocarcinoidea is narrow, with a deep sterno-pleonal cavity; sternites 4, 5, and 6 are long and directed laterally, and sternites 7 and 8 are reduced and directed posteriorly. The walls of the sternites are nearly vertical in Camarocarcinidae and Necrocarcinidae. Members of Raninoidea display fusion and reduction in size of sternites and essentially lack the sterno-abdominal cavity (Fig. 122.4).

Torynommoida.—The sternum on this group is broad anteriorly with a transverse ridge on sternite 4. The sternopleonal depression houses well-developed sternal sutures.

Dakoticancroida.—In this section, the sternum is very wide and is strongly sexually dimorphic (Jones, Schweitzer, & Feldmann, 2022) (Fig. 122.6). Male sterna have a deeper pleonal cavity than females. Sternites 1–3 are fused, and sternites 4–7 are directed laterally or posterolaterally, similar

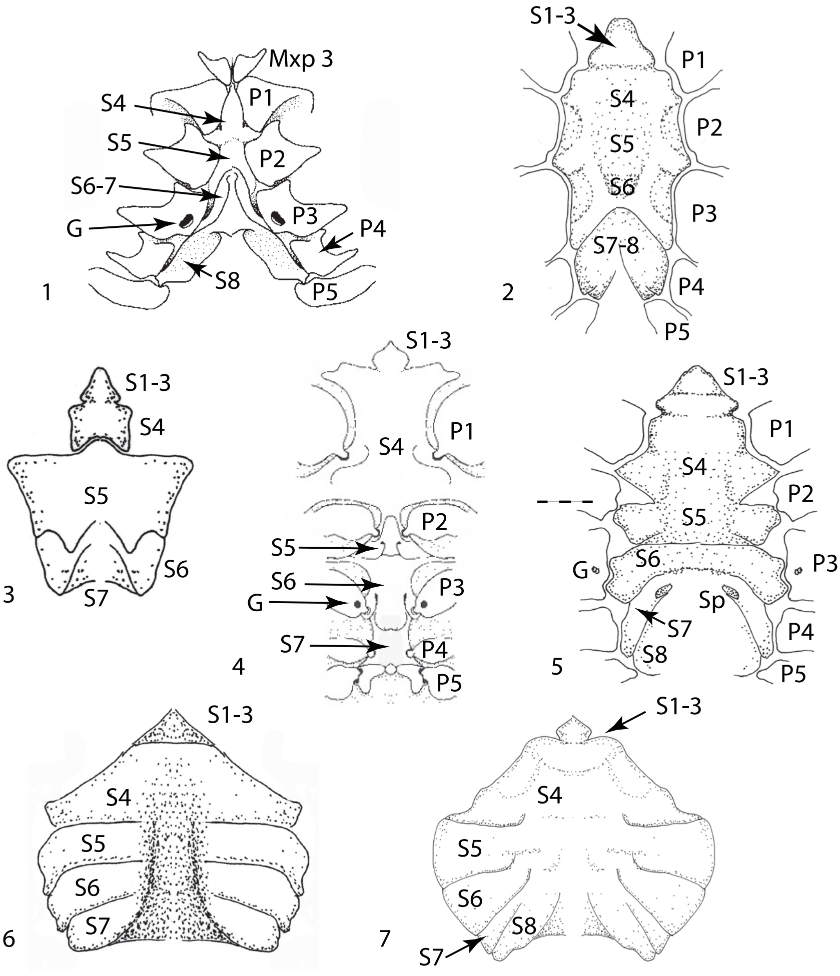

Fig. 122. Generalized sterna of the following: *1,* Dromiacea; *2,* Homoloida; *3,* Callichimaeroida; *4,* Raninoida; *5,* Etyoida; *6,* Dakoticancroida; *7,* Cyclodorippoida (*1* and *4,* adapted from Ng, 1998, fig. 11, 18; all others new, drawings by C. Schweitzer). G=gonopore, Mxp=maxilliped, P=pereiopod, S=sternite, Sp=spermatheca. Dashed line in *5* represents position at which the sternum is flexed at about 90 degrees.

to the condition seen in Eubrachyura. Sternal sutures are incomplete. The sternum in Dakoticancroida is wider than that seen in other podotrematous sections.

Cyclodorippoida.—Cyclodorippoids have wider sterna than other podotrematous crabs (Fig. 122.7).

STERNAL MORPHOLOGY OF EUBRACHYURAN CRABS

The sternum in Eubrachyura is wider than that seen in the podotrematous sections, with exceptions. Sternites 1–3 are fused, although sutures may be visible. In heterotrematous crabs, the sternum can be quite narrow (Fig. 111, 112) or very wide as in portunoids (Fig. 113). Thoracotreme crabs have wide sterna (Fig. 114). The nature of the sternal sutures is important among these groups, and it can be important to determine whether sutures 4/5, 5/6, 6/7, and 7/8 are complete or incomplete (Guinot, 1978). For some taxa, it is important to determine whether sternite 8 is visible in ventral

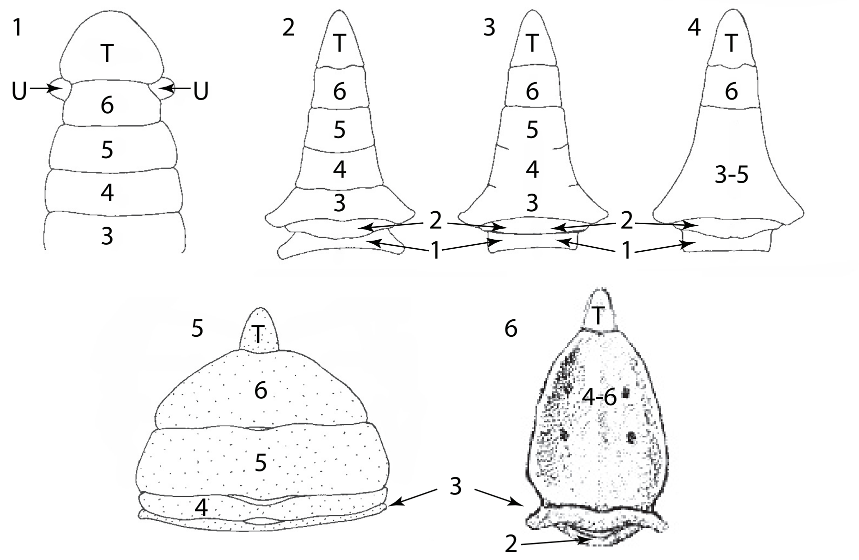

Fig. 123. Various brachyuran pleons, with pleonal somites numbered. *1,* Dromiidae; *2,* male with all somites free; *3,* male with somites 3–5 fused but with sutures visible; *4,* male with somites 3–5 completely fused; *5,* generalized female; *6,* female Leucosiidae, with somites 4–6 fused (*1–5* adapted from Ng, 1998, fig. 14, 20, 77; *6,* adapted from Rathbun, 1937, fig. 34). T=telson, U=uropod.

view or covered by the sternum (Karasawa, Schweitzer, & Feldmann, 2008).

PLEON

The pleon in brachyurans is comprised of six somites plus the telson, but varying degrees of fusion of somites may occur. In general, the pleonites are reduced in size compared to other decapods and are held against the sternum. In some groups, the first few pleonites may be visible in dorsal view, especially in some podotrematous taxonomic sections where the flexion of the pleon is less strong or in ovigerous females in which the egg mass may cause the pleon to bulge posteriorly and ventrally. The pleon retains pleopods to varying degrees. Retention of uropods is seen only in a few groups within Dromioidea and Hymenosomatoidea (Guinot, 2011) (Fig. 123.1). In some brachyurans, the pleon is held against the sternum by a locking mechanism. These mechanisms are diverse and appear to have evolved independently across lineages (Davie, Guinot, & Ng, 2015, p. 56). The telson is triangular but varies in length compared to width across taxa.

Somites of the pleon may be fused or free. Fusion with retention of visible sutures also occurs (Fig. 123). In general, somites are all free in female brachyurans (Fig. 123.5) with few exceptions in which fusion of somites creates a dome or pouch-like structure (Fig. 123.6). In males, somites 3–5 are the most typically fused. Vestigial sutures may be present, even when the somites are fused (Fig. 123.3). In fossils, the presence of sutures makes the pleonites appear to be free.

In addition to fusion of somites, the pleon of brachyurans is distinctly sexually dimorphic. In males, it is more narrow than in females, in the latter of which the expanded width accommodates the eggs (Fig. 123.5, 123.6). In males, the lateral margins of the entire pleon may be straight or concave, but are frequently concave, at times markedly so, as in some portunoids. In eubrachyurans, the male pleon is much narrower than the sternum (see Fig. 111–114). In mature females, the pleon is wide, covering most or all of the sternum, and has convex lateral margins (Fig. 123.5). In immature females, the pleon tends to have convex lateral margins but it is narrower than in mature individuals, even resembling males (Ng & Ahyong, 2022). In some raninoids, sexual dimorphism in the pleon is not well developed, with the females being slightly wider.

GONOPORES

Brachyurans can be divided into three major groups based on the position of the male and female gonopores. Sections Dromiacea, Homoloida, Callichimaeroida, Torynommoida, Etyoida, Raninoida, Dakoticancroida, and Cyclodorippoida, retain the decapod ancestral state of female gonopores on the coxae of the third pereiopod and male gonopores located on the coxae of the fifth pereiopods (Fig. 122, Fig. 124, Fig. 125). Within heterotrematous Eubrachyura, the female gonopore is located on the sixth sternite, whereas the male gonopore remains on the fifth coxae, as in podotrematous brachyurans and other non-brachyuran decapods (Fig. 126). In thoracotreme crabs, the female gonopore is located on the sixth sternite, and the male gonopore is located on the eighth sternite (Fig. 126.3).

Within these three categories, there is considerable variation in size and placement of the gonopores. Across the podotrematous crabs, the female gonopore is located in various orientations on coxae 3 (Fig. 124, 125). In palaeocorystoid crabs, the female gonopore on the coxa of pereiopod 3 is located ventrally (Fig. 124.3), whereas in Xandarocarcinidae, it is rotated so as to be positioned on the distal or posterior margin of the coxae (Fig. 125.1). In Etyidae, the female gonopores are situated on the ventral surface and close to the sternal edge of the coxae of pereiopod 3 (Fig. 124.1). Among heterotrematous crabs, the female gonopores in Componocancridae are very large, much larger than seen in other groups (Fig. 126.1). Guinot (1978) illustrated a broad variety of placements of male gonopores on the coxae

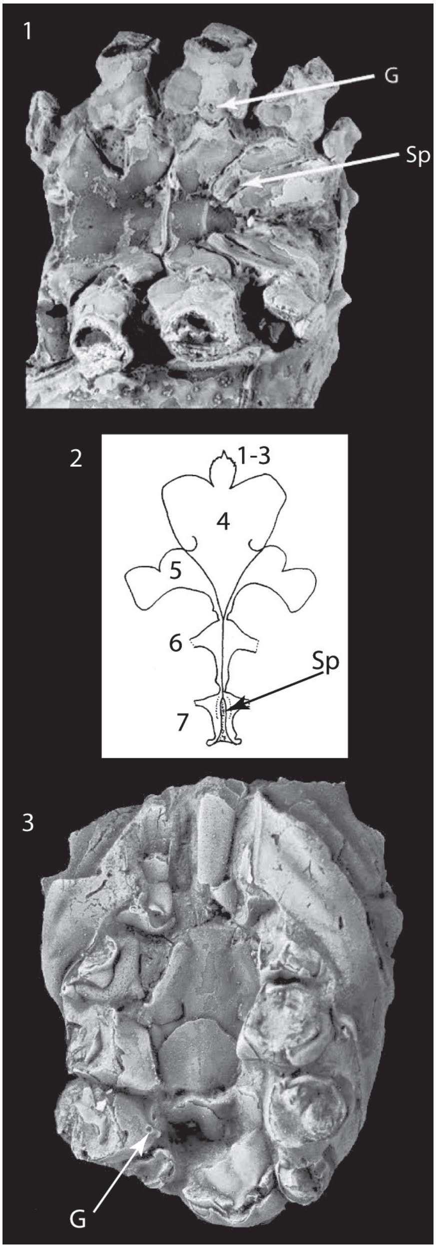

Fig. 124. Gonopores and spermatheca: *1,* gonopores and spermatheca on Etyoida, *Steorrosia pawpawensis* Schweitzer Hopkins, Salva, & Feldmann, 1999 (adapted from Schweitzer & others, 2012, fig. 2.3); *2,* axial spermatheca on Raninoida (adapted from Glaessner, 1969, fig. 229.1); *3,* female gonopore on Raninoida, *Eucorystes broderipi* Mantell, 1844 (adapted from Karasawa, Schweitzer, & Feldmann, 2011, fig. 11B; G=gonopore, Sp=spermatheca, sternites numbered.

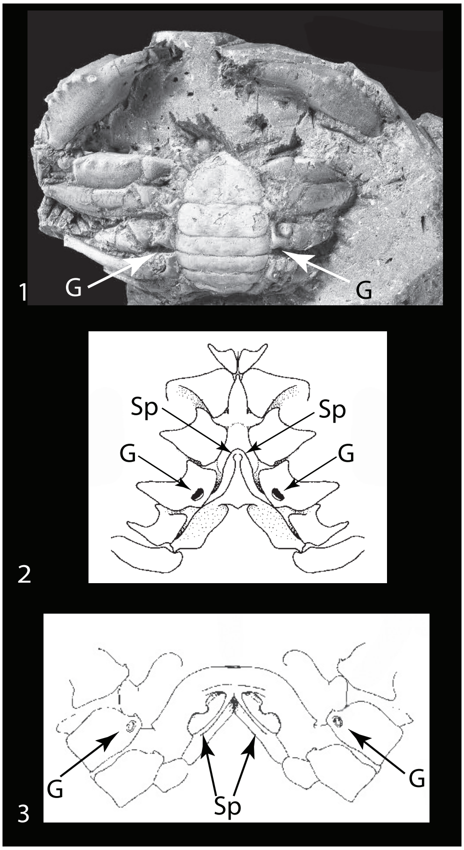

Fig. 125. Gonopores and spermatheca; *1,* posteriorly directed gonopores on Dromiacea, *Xandarocarcinus sternbergi* (Rathbun, 1926) (adapted from Karasawa, Schweitzer, & Feldmann, 2011, fig. 6E); *2,* anteriorly positioned spermatheca and ventral gonopores in Dromiacea; *3,* gonopores and spermatheca on Homoloida (*2–3* adapted from Ng, 1998, fig. 11, fig. 32). G=gonopore, Sp=spermatheca.

of pereiopods 5, on sternite 8, and intermediate between these two placements. Female gonopores and spermatheca are preserved occasionally in fossils, although it is not common (Fig. 124, 125, 126). Preservation of gonopores in male fossil crabs is rare (Bishop, 1983).

Spermatheca are present in podotrematous crabs. They are located along sternal sutures 7 and 8 and appear to be a sac or pouch formed between these two sternites (Fig. 124.1–2; Fig. 125.1–3). In raninoidans, the spermatheca form an opening along the axis of sternite 7, in what has been termed a paired spermatheca (Fig. 124.2). The size and position of the structure across the podotrematous crabs is variable; in some Dromioidea, it is located very far anteriorly because the sutures of sternite 7/8 arc anteriorly (125.2).

EYES

Eyes are rarely preserved in fossil brachyurans (Fig. 127) because they decay relatively fast compared to carapaces and chelipeds, as shown experimentally (Klompmaker, Portell, & Frick, 2017). Eyes are preserved occasionally though, and the outer corneal elements can preserve well across taxa under favorable taphonomic conditions (Luque & others, 2019b, 2021). The biology of eyes is well discussed by Davie, Guinot, and Ng (2015). The eyestalk is comprised of two articles, the basophthalmite and the podophthalmite, and the eyestalk terminates in the cornea (Davie, Guinot, & Ng, 2015) (Fig. 127). Across extant groups, eyes and eyestalks are variously adapted. For example, very long eyestalks are typical in crabs living in intertidal areas, and the eyes have a nearly 360-degree field of view (Davie, Guinot, & Ng, 2015) (Fig. 127.14).

In fossils, the eyestalk can be partially preserved, such as in species of *Orbitoplax* Tucker & Feldmann, 1990, suggesting that their eyestalks perhaps were more strongly calcified than is typical (Karasawa & Schweitzer, 2006) (Fig. 127.13). Corneae outlines are known in a Jurassic (Fig. 127.6) and a Cretaceous dromiacean (Fig. 127.7), while well-preserved corneae-bearing ommatidial facets are known in Cretaceous callichimaeroids (Luque & others, 2019a, 2022; Jenkins, Briggs, & Luque, 2022) (Fig. 127.8–10), etyoids (Vega & others, 2014; Luque & others, 2019b), cenomanocarcinids (Luque & others, 2019b, 2022), and several Cretaceous and Cenozoic eubrachyurans (Luque & others, 2019b, 2022 (Fig. 127.11–12). In fossils, length of eyestalks can be indicated by the length of the orbit, but there are several exceptions, either because the eyestalk exceeds the length of the orbit (Fig. 127.14) or because the eyes are much larger than the orbit itself (Fig. 127.7–9). Thus, using orbit length as a proxy for eye size may be problematic for those groups in which the eyestalks are routinely long.

Orbit height has in some cases been used as a proxy for eye size (Klompmaker, Jakobsen, & Lauridsen, 2016; Jenkins, Briggs, & Luque, 2022). Internal eye soft tissues such as retinotopic neuropils and even individual cells can also be preserved in great detail under exceptional conditions (Luque & others, 2019a; Jenkins, Briggs, & Luque, 2022).

GILLS

Gills in brachyurans are not as widely used in systematics and classification as they are in shrimp and other groups. Brachyuran gills are phyllobranchiate and have a flattened gill shaft, with one dorsally flowing afferent sinus and one ventrally flowing efferent sinus connected by gill lamellae (Luque & others, 2021). Davie, Guinot, and Ng (2015) summarized the state of knowledge on brachyuran gills. Brachyuran gills are rare in the fossil record but where known, they are similar to those in extant forms (Robin & others, 2018; Luque & others, 2021).

BRACHYURAN APPENDAGES

Antennae and antennules.—These are rarely preserved as fossils (Luque & others, 2019a, 2021) (Fig. 127.9, 127.12). The antennules are the first appendage and in brachyurans, are short and small. They fold into a cavity, which may be preserved, called the antennular fossa (Davie, Guinot, & Ng, 2015). The folding can be oriented parallel to or transverse to the long axis of the animal (Fig. 128). The antennules are biflagellate and not biramous (see discussion in Davie, Guinot, & Ng, 2015) and are used for sensing, both mechanically and chemically, as well as for maintaining equilibrium. The antennae are uniramous and comprise stout basal articles that contain the nephridiopore. They are quite variable in length, depending on the group (Fig. 128). The basal articles of the antennae are rarely preserved in fossil brachyurans.

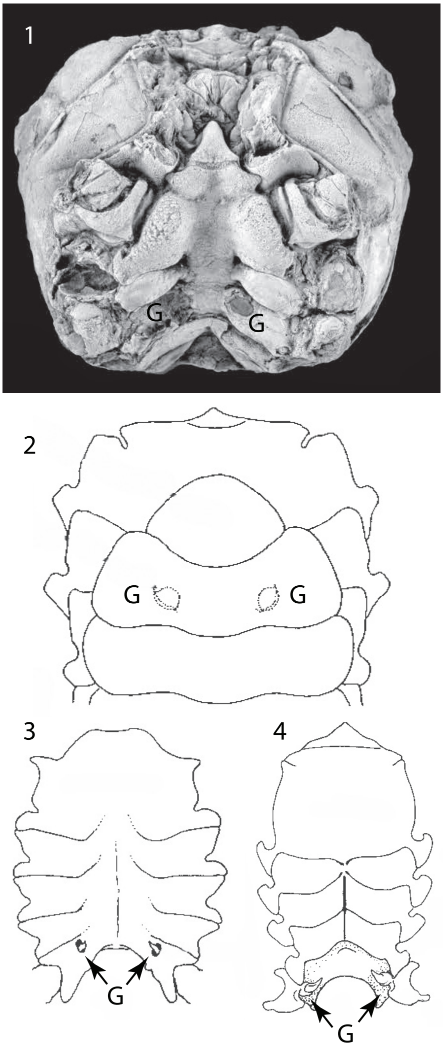

Fig. 126. Gonopore position in heterotreme and thoracotreme crabs; *1,* sternal female gonopores in Componocancroidea *Componocancer roberti* Feldmann, Schweitzer, & Green, 2008; *2,* heterotreme and thoracotreme female gonopores shown under the pleon; *3,* male gonopores in thoracotremes; *4,* male gonopores in podotrematous sections and heterotremes (*1* adapted from Feldmann & others, 2008, fig. 2D; *2–3* adapted from Ng, 1998, fig. 45, 52). G=gonopore.

Mandibles.—In brachyurans, the mandibles are well-calcified structures that are occasionally preserved. They are used for

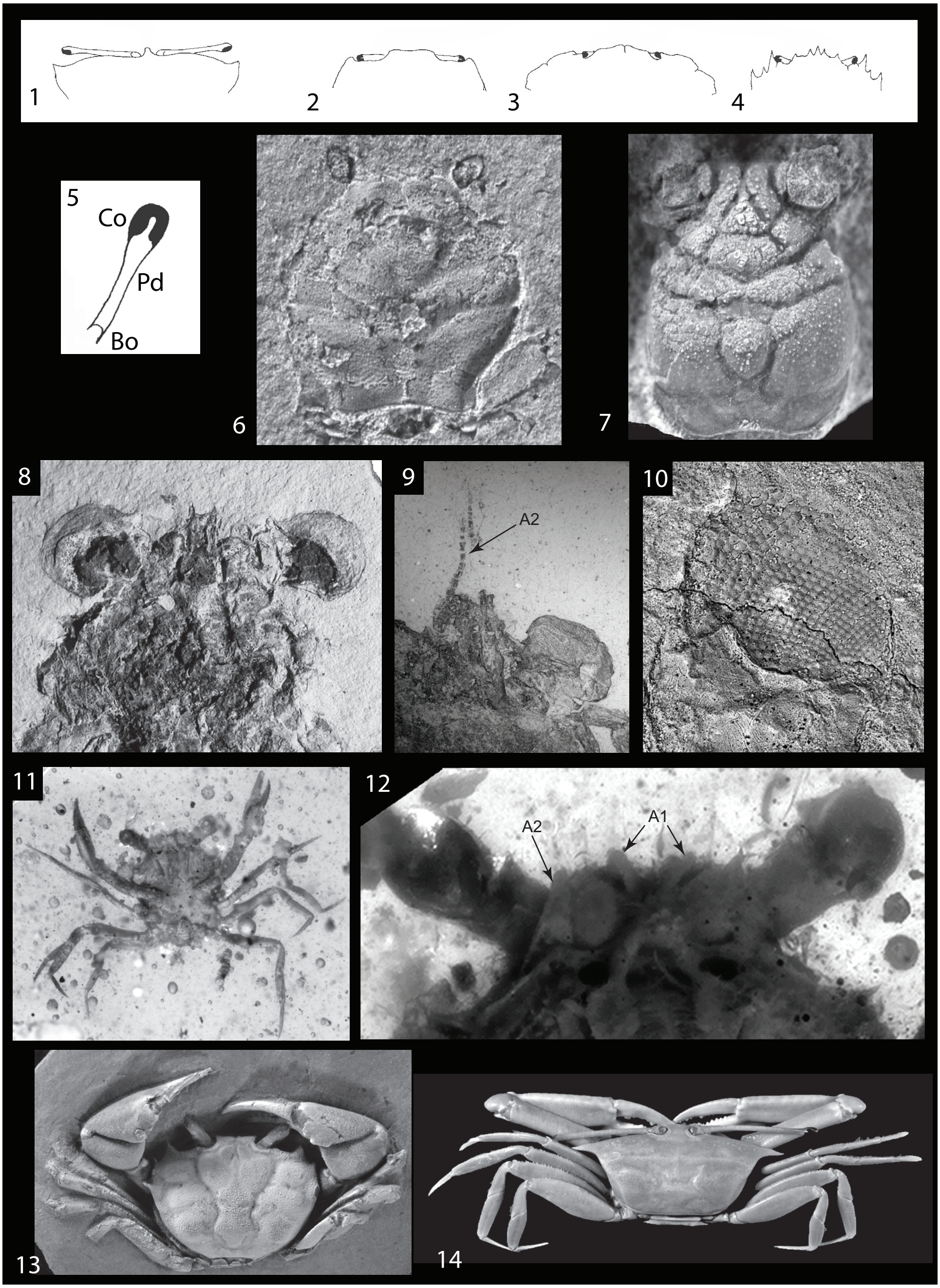

Fig. 127. Eyes and eyestalks in brachyuran crabs; *1,* long eyestalks; *2–4,* medium to short eyestalks (*1–4* adapted from Ng, 1998, fig. 2 and 60); *5,* generalized eye (Bo=basophthalmite, Co=cornea, Pd=podophthalmite); *6,* Jurassic dromiacean crab with preserved eyes, *Goniodromites serratus* Beurlen, 1929; *7,* Cretaceous dromiacean crab with very large eyes, *Ekalakia exophthalmops* Feldmann, Schweitzer, & Wahl, 2008; *8–10,* Cretaceous *Callichimaera perplexa* Luque & others, 2019a, very large eyes with reduced eyestalks and lacking orbits (*8*), a compound eye and slender antennae (A2) (*9*), and details of the corneal facets (*10*); *11–12,* Cretaceous heterotreme crab, *Cretapsara athanata* Luque in Luque & others, 2021, ventral view (*11*), and close-up of ventral anterior portion, (continued on facing page)

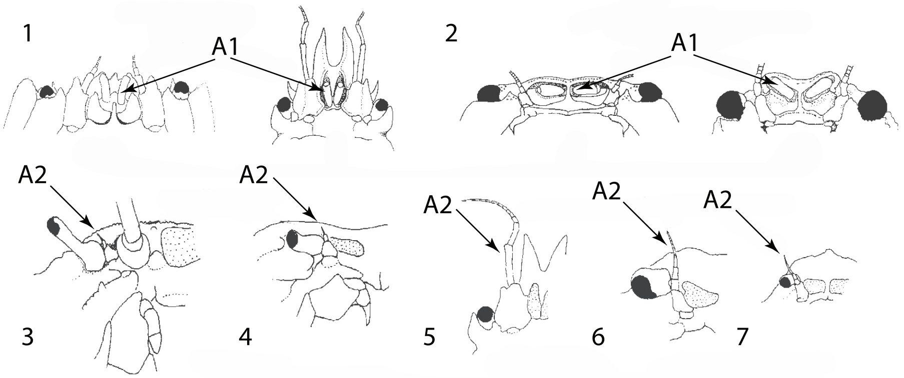

Fig. 128. Various sizes and positions of antennae and antennules in Brachyura: *1,* longitudinally folded antennules; *2,* horizontally folded antennules; *3–4,* very reduced antennae; *5–7,* examples of longer antennae (*1–2,* adapted from Ng, 1998, fig. 36; *3–7,* adapted from Ng, 1998, fig. 34). A1=antennules; A2=antennae.

processing food, and depending on diet, are crushing (molariform) or have sharper edges, called incisors. The mandible has lost the exopod, and the endopod exhibits fusion (Davie, Guinot, & Ng, 2015).

Maxillae.—These are not preserved in fossil brachyurans as far as is known. They are foliaceous structures used for manipulation of food and circulation of water. Both maxillae have a variety of endites used to manipulate food (Fig. 129.1–2). The second maxillae have a scaphognathite, or gill bailer, that is flap-like and pumps water over the gills (Fig. 129.2). They are rarely used for taxonomic purposes (Davie, Guinot, & Ng, 2015).

Maxillipeds.—The maxillipeds are biramous, represented by distinctly developed endopods and exopods. They are modified primarily for use in food handling. They all possess epipods, which are used as gill cleaners. The first maxilliped is the smallest and used in taxonomy in some heterotrematous crabs (Davie, Guinot, & Ng, 2015). It is comprised of an endopod, exopod, and endites. The third maxilliped is frequently found fossilized (Fig. 129.10–13) and can be useful in taxonomy. It can be either pediform or operculiform, in which case it covers or nearly covers the entire buccal frame (Fig. 129.3–13). The relative widths and lengths of the exopod versus the endopod are important taxonomically. In the podotrematous sections, the entire structure is elongate, as in Raninoida (Fig. 129.11–12) and rectangular in other crabs. A structure called the *crista dentata* is present on the ischium in some Dromiacea, Homoloida, and Callichimaeroida and is comprised of serrated ridges on the inner surface of the ischium (Davie, Guinot, & Ng, 2015; Luque & others, 2019a).

Pereiopods: general features.—Pereiopods in brachyurans function for locomotion, food procurement, defense, and reproduction. Morphology among groups varies widely (see Fig. 111–114). Chelae and/or isolated fingers are frequently the only evidence of brachyurans in the fossil record of an area and can be recovered by washing or screening samples (Feldmann & Schweitzer, 2017).

Fig. 127. (continued from facing page) showing large compound eyes with short eyestalks (*12*), antennulae (A1), and antenna (A2); *13,* Eocene heterotreme crab, *Orbitoplax weaveri* (Rathbun, 1926); *14,* extant heterotreme crab with eyestalks longer than orbits, *Ommatocarcinus macgillivrayi* White, 1851; (*1–4,* adapted from Ng, 1998, fig. 60; *5,* adapted from Ng, 1998, fig. 2b; *6,* adapted from Feldmann & others, 2016, fig. 6.2; *7,* adapted from Feldmann, Schweitzer, & Green, 2008, fig. 2.1); *8,* adapted from Luque & others, 2019a, fig. 2H; *9,* adapted from Luque & others, 2019b, fig. 11B–C; *10,* adapted from Luque & others, 2019a, fig. 2G; *11–12,* adapted from Luque & others, 2021, fig. 1B and 2A, respectively); *13,* new, by Bruce Theil; *14,* new, by H. Kato).

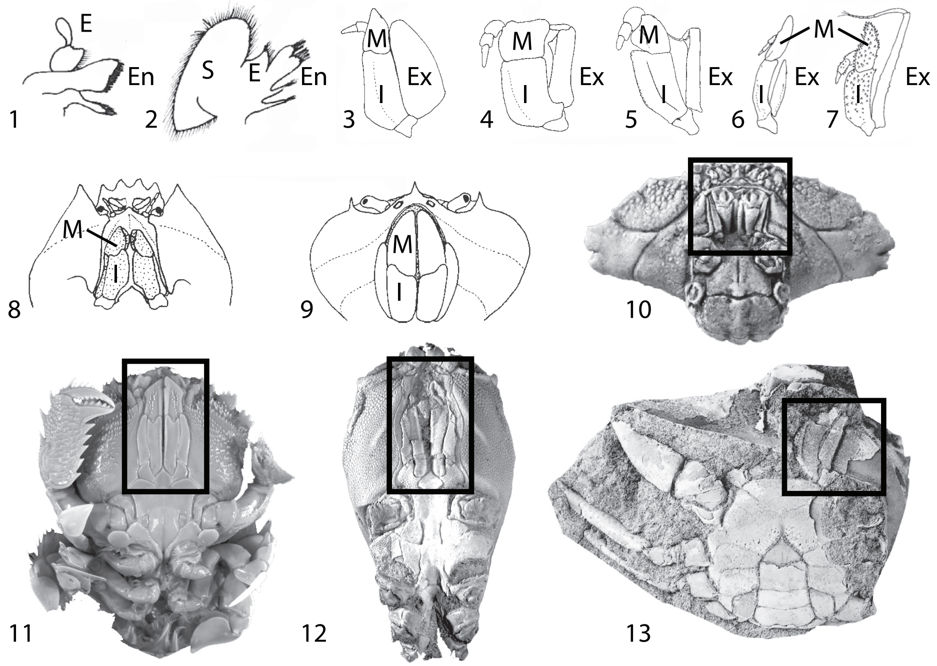

FIG. 129. Brachyuran mouthparts: *1,* first maxilla; *2,* second maxilla; *3–7,* various third maxillipeds; *8–9,* third maxillipeds in place in buccal frame; *10,* third maxillipeds in Cretaceous Etyoida, *Steorrosia aspera* (RATHBUN, 1935); *11,* elongate third maxillipeds in *Ranina ranina* (LINNAEUS, 1758); *12,* elongate third maxillipeds in Cretaceous Raninoida, *Marylyreidus punctatus* (RATHBUN, 1935); *13,* right third maxilliped in Eocene Goneplacoidea, *Pulalius vulgaris* (RATHBUN, 1926) (*1–2,* adapted from McLaughlin, 1980, fig. 51G, H; *3–9,* adapted from Ng, 1998, fig. 5, 6, 8; *10,* adapted from Schweitzer & others, 2012, fig. 6.2; *11,* adapted from Feldmann & Schweitzer, 2007, fig. 1D; *12,* adapted from Karasawa & others, 2014, fig. 14B; *13,* adapted from Schweitzer, 2000, fig. 3C). E=endopod, En=endite, Ex=exopod, I=ischium, M=merus, S=scaphognathite.

Pereiopod 1 (*Cheliped*).—The first pereiopod is most significant in identifying fossil brachyurans because it is typically the most robust and biomineralized pereiopod and thus most likely to be preserved (COLLINS, 1999). It is referred to as the cheliped, because it is the only appendage pair with fully developed chelae. Chelipeds are multi-use appendages, well documented for predation, defense (LAVALLI & SPANIER, 2015), attracting mates, eating vegetation (JORMALAINEN, 2015), and reproduction (DAVIE, GUINOT, & NG, 2015). Length, relative size, and ornamentation of the various articles of the cheliped are widely variable among crabs (Fig. 111–114, Fig. 130, Fig. 131).

The chelipeds are isochelous or heterochelous. Isochely, in which the right and left chelipeds do not differ substantially in size and shape, occurs frequently in the podotrematous sections and in females of many eubrachyuran groups (Fig. 130). Isochely is characteristic of, but not restricted to, nonpredatory crabs, those that are scavengers or detritus feeders (DAVIE, GUINOT, & NG, 2015).

Heterochely is widely recognized in heterotrematous and thoracotrematous brachyurans (SCHÄFER, 1954) (Fig. 131, Fig. 132). The earliest indications of heterochely in Brachyura appeared in the Early Cretaceous, with the radiation of more derived lineages, and was widespread by the Eocene (SCHWEITZER & FELDMANN, 2010). Heterochelous pereiopods may differ in size, length, and/or shape of the claws. Many crabs (and

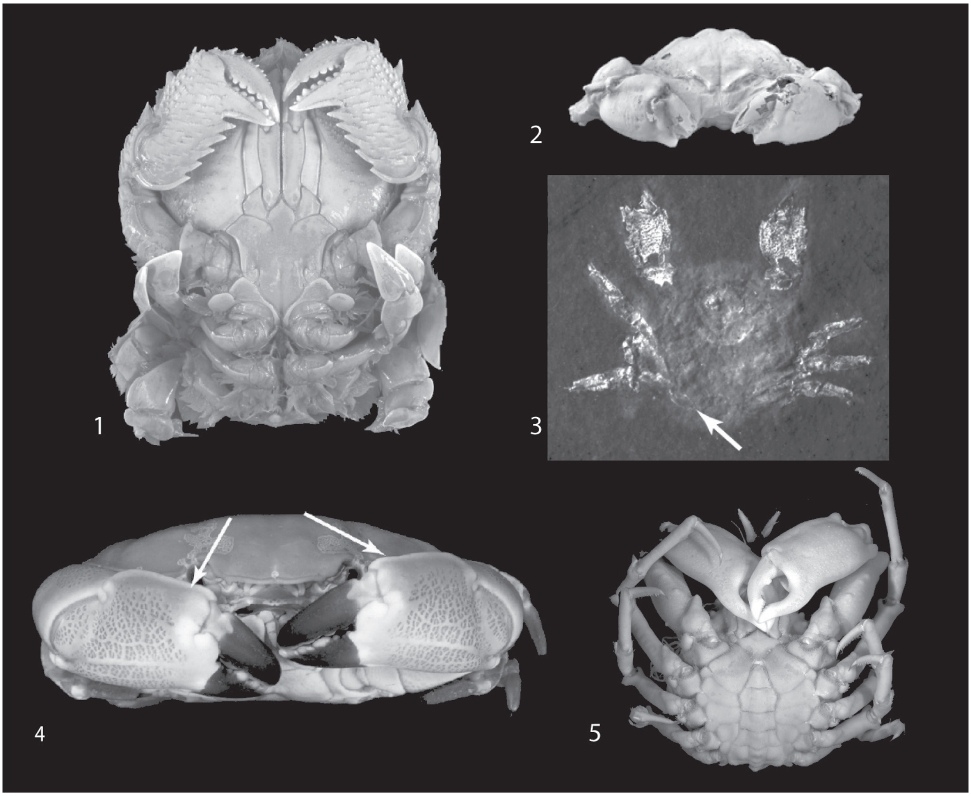

Fig. 130. Isochelous chelipeds. *1,* Raninidae, *Ranina ranina* (Linnaeus, 1758); *2,* Dromioidea, *Dromilites bucklandi* H. Milne-Edwards, 1837; *3,* Homolodromioidea, *Goniodromites serratus* Beurlen, 1929, under long wave UV illumination, *arrow* indicates subdorsal fifth pereiopod; *4,* Xanthoidea, *Atergatis floridus* (Linnaeus, 1767); *5,* Majoidea, *Pisa tetraodon* Pennant, 1777 (*1,* Feldmann & Schweitzer, 2007, fig. 1B; *2,* Schweitzer, Feldmann, & Karasawa, 2012, fig. 22,*1c*; *3,* adapted from Feldmann & others, 2016, fig. 7.6; *4,* adapted from Schweitzer & Feldmann, 2010, fig. 7B; *5,* adapted from Schweitzer, Feldmann, & Karasawa, 2020, fig. 3,*1b*).

lobsters) exhibit a heavier crushing claw and a more slender cutting claw, both for different aspects of feeding (Schweitzer & Feldmann, 2010) (Fig. 131.5). One claw may be larger or more robust than the other (Schweitzer & Feldmann, 2010). Heterochelous chelipeds are ordinarily seen in predatory crabs (Davie, Guinot, & Ng, 2015), but note that some predatory groups, such as cancroids, are only very weakly heterochelate (Schweitzer & Feldmann, 2010) (Fig. 131.7).

Chelipeds may display marked sexual dimorphism (Fig. 133). Heterochely is almost always better developed in males (Fig. 133.1, 133.4). In some cases, such as in fiddler crabs (Ocypodidae), marked heterochely in males is the result of sexual selection; the claws are not used in predation and are instead used in attracting mates and fighting for territory (Dennenmoser & Christy, 2013; Davie, Guinot, & Ng, 2015) (Fig. 133.1–2). Some studies have even found that such enormously heterochelous claws may be a hindrance for feeding in males of *Pseudocarcinus gigas* (Lamarck, 1818) (Pseudocarcinidae) (Heeren & Mitchell, 1997) (Fig. 133.5).

Brachyurans may exhibit handedness, with the right chela larger than the left as the most frequent pattern. There might be a genetic signal in handedness in some

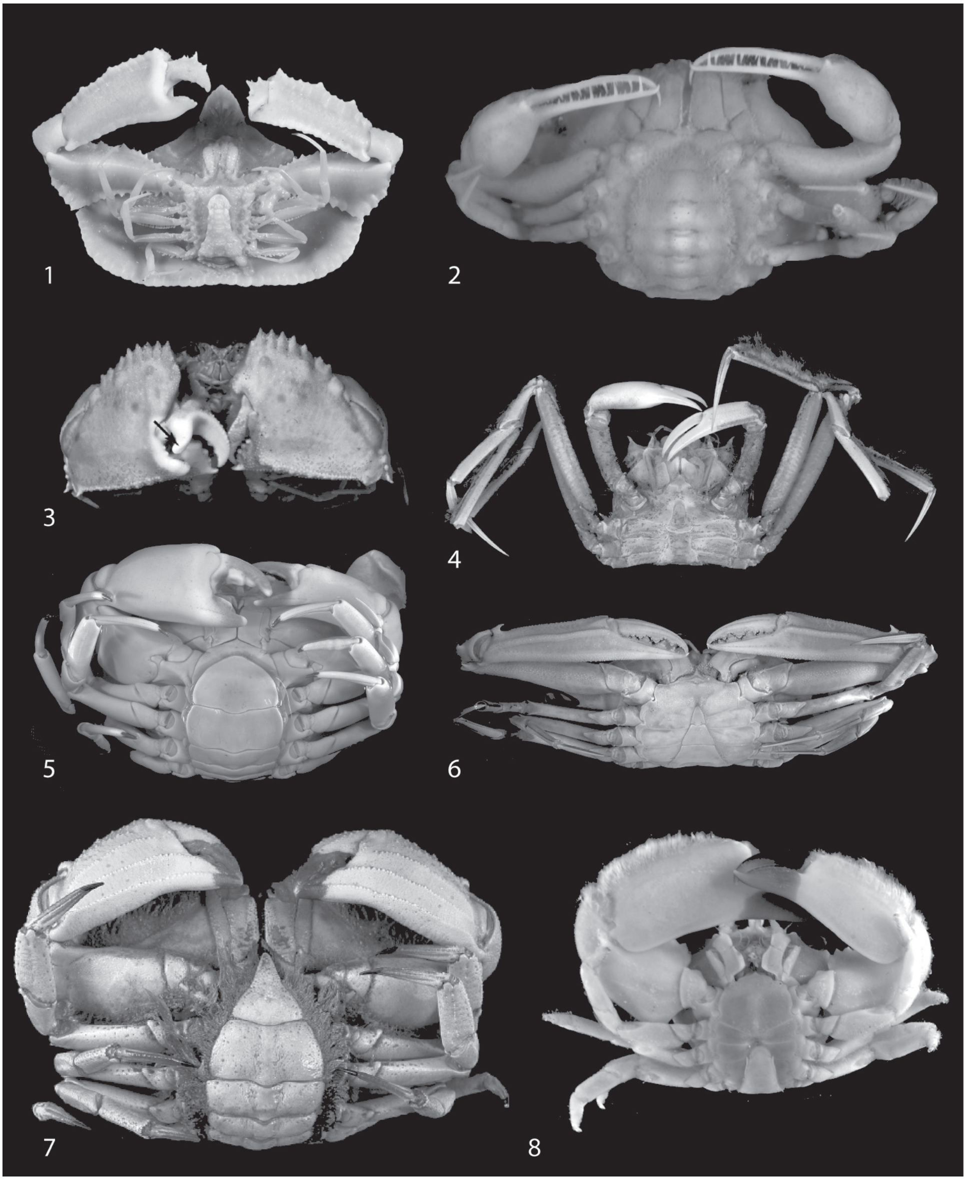

Fig. 131. Heterochelous chelipeds. *1,* Parthenopoidea, *Cryptopodia fornicata* (Fabricius, 1782); *2,* Leucosioidea, *Iphiculus spongiosus* Adams & White, 1849; *3,* Calappoidea, *Calappa lophos* (Herbst, 1785 in 1782–1804), *arrow* indicates hooklike tooth; *4,* Retroplumoidea, *Bathypluma forficula* de Saint Laurent, 1989; *5,* Carpilioidea, *Carpilius corallinus* (Herbst, 1783 in 1782–1804); *6,* Portunoidea, *Podophthalmus vigil* (Fabricius, 1798); *7,* Cancroidea, *Cancer* sp.; *8,* Trapezoidea, *Trapezia cymodoce* (Herbst, 1801 in 1782–1804) (*3,* adapted from Schweitzer & Feldmann, 2010, fig. 2B; *7,* photo by R. Feldmann (KSU specimen). All other images from the following numbered Part R *Treatise Online* articles: 131, fig. 5*b* (*1*); 115, fig 1*b* (*2*); 106, fig 1,*2b* (*4*); 112, fig. 2*b* (*5*); 151, fig. 13,*4b* (*6*); 153, fig. 2,1*b* (*8*).

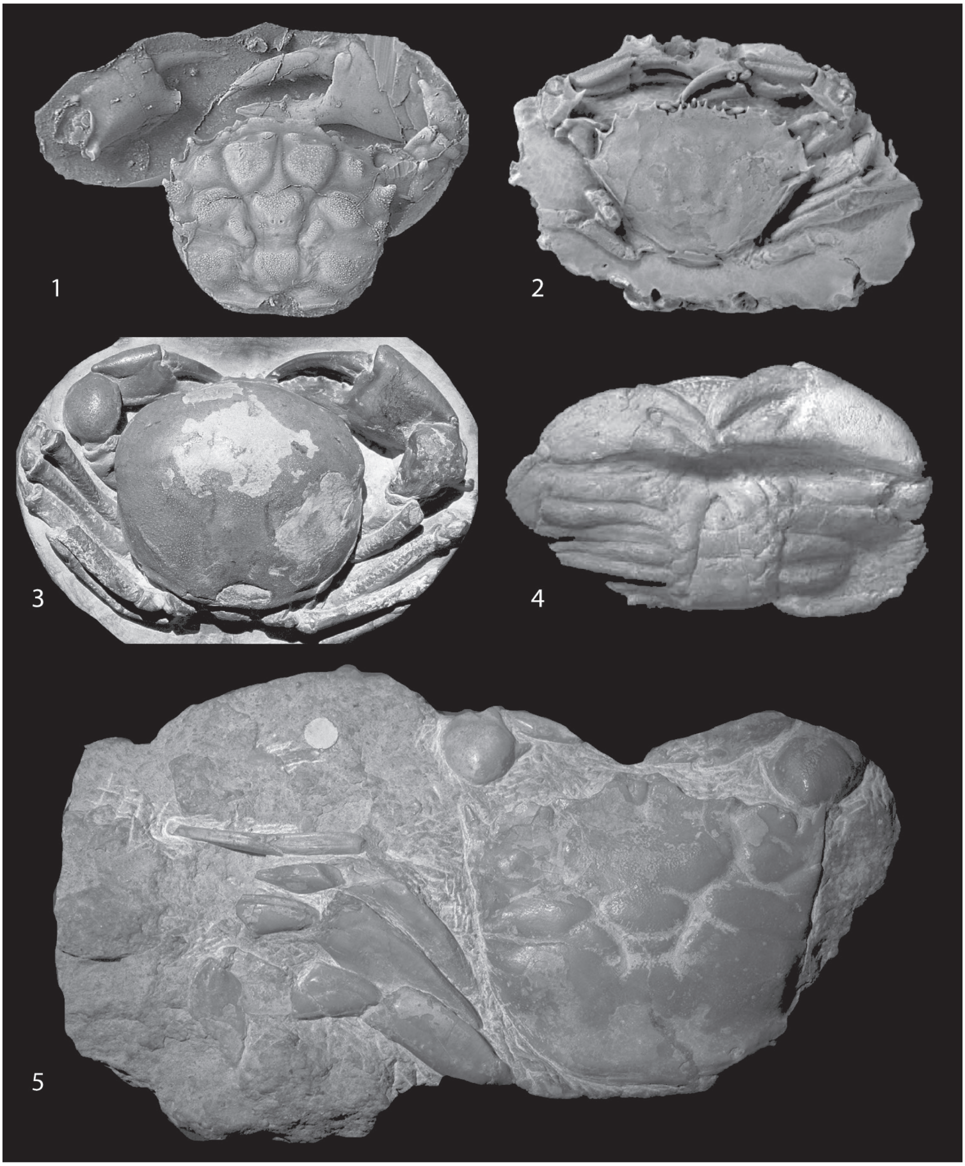

Fig. 132. Heterochelous chelipeds. *1,* Cretaceous Tumidocarcinidae, *Nitotacarcinus bituberculatus* (Collins & Jakobsen, 2003); *2,* Eocene Portunoidea, *Maeandricampus starri* Feldmann & others, 2018; *3,* Miocene Tumidocarcinidae, *Tumidocarcinus giganteus* Glaessner, 1960; *4,* Eocene Carpiliidae, *Laticarpilius aegypticus* Feldmann & others, 2011; *5,* Cretaceous Portunoidea*, Carcineretes woolacotti* Withers, 1922 (*2,* adapted from Feldmann, Schweitzer, & Goedert, 2018, fig. 1A; *3,* Schweitzer & Feldmann, 2015, fig. 10). All other images from the following numbered Part R *Treatise Online* articles: 112, fig. 9,*2a* (*1*); 112, fig. 4,*2b* (*4*); 121, fig. 1,*1* (*5*).

FIG. 133. Sexual dimorphism and heterochely. *1–2, Afruca tangeri* (EYDOUX, 1835); male with pronounced heterochely (*1*), female with similarly sized chelipeds (*2*) (photo by N. Mollaret, MNHN, RECOLNAT, MNHN-IU-2014-11951); *3, Podocatactes hamifer*, USNM 72485, ventral view (Schweitzer & Feldmann, 2019b, fig. 9,*4a*); *4, Trichopeltarion nobile* A. MILNE-EDWARDS, 1880, MNHN-IU-2013-18776, male, dorsal view (photo by L. Corbari); *5, Pseudocarcinus gigas* (LAMARCK, 1818), with very enlarged cheliped (www.fish.gov.au/2014-Reports/Giant_Crab).

groups (SCHWEITZER & FELDMANN, 2010). In addition, when chelipeds are lost due to autotomy, the opposite chela grows back as the major chela in most cases, with fiddler crabs as a notable exception (PALMER, 2016). Handedness is not as distinctive as that seen in anomuran and axiidean groups and is thus not used for systematics and classification.

The chela, as in all decapods, is comprised of an articulating propodus, with a long distal extension forming the fixed finger, and a movable dactylus, or movable finger, on the upper distal margin of the propodus. The chelae are adapted for feeding (SCHÄFER, 1954). The occlusal surfaces of the fingers may bear molariform teeth, and the entire distal ends of the fingers may be black, which indicates hardening for use in crushing (Schäfer, 1954; Schweitzer & Feldmann, 2010; Eastman & Thiel, 2015; Spiridonov, Neretina, & Schepetov, 2014) (Fig. 130.4, Fig. 131.7). Molariform teeth can be subdivided based on their shape (Spiridonov, Neretina, & Schepetov, 2014). In those crabs with crushing claws, as in homarid lobsters, the other claw is a cutting claw. Spinose occlusal surfaces are used for tearing (Davie, Guinot, & Ng, 2015) (Fig. 131.7). A strong, blunt, hook-shaped structure at the base of the movable finger is characteristic of calappoid crabs, used to crush and chip the aperture of snail shells (Schweitzer & Feldmann, 2010) (Fig. 131.3). The tips of fingers can terminate in spoon-shaped structures for scraping algae from surfaces (Davie, Guinot, & Ng, 2015). Delicate or slender fingers are frequently associated with a diet of algae (Davie, Guinot, & Ng, 2015; Jormalainen, 2015) (Fig. 131.2).

Because chelae and even isolated fingers are frequently the only preserved portion of fossil brachyurans, some literature has developed around identifying families, genera and species from just these fragments (Nations, 1975; Portell & Agnew, 2004). Chelae and fingers are most readily identifiable to the family level, but more specific identification typically is not possible. Identifications to the genus or species level are, not surprisingly, easiest on younger fossils, post-Miocene, which can be easily compared with extant congeners (i.e., Todd & Collins, 2005; Collins, Donovan, & Stemann, 2009; Garassino & others, 2012; Luque, 2017; Luque & others, 2018). Certain groups have very distinctive chelae, making them easier to recognize in fossils including Calappidae (Fig. 131.3), Cancroidea (Fig. 131.7), Portunoidea (Fig. 131.6), and Raninoida (Fig. 130.1).

Pereiopods 2–5.—Pereiopods 2–5 may be called walking legs and may be numbered separately from the cheliped in older literature. They are similar in shape to one another, with a common exception being pereiopod 5 (Fig. 134, Fig. 135). The

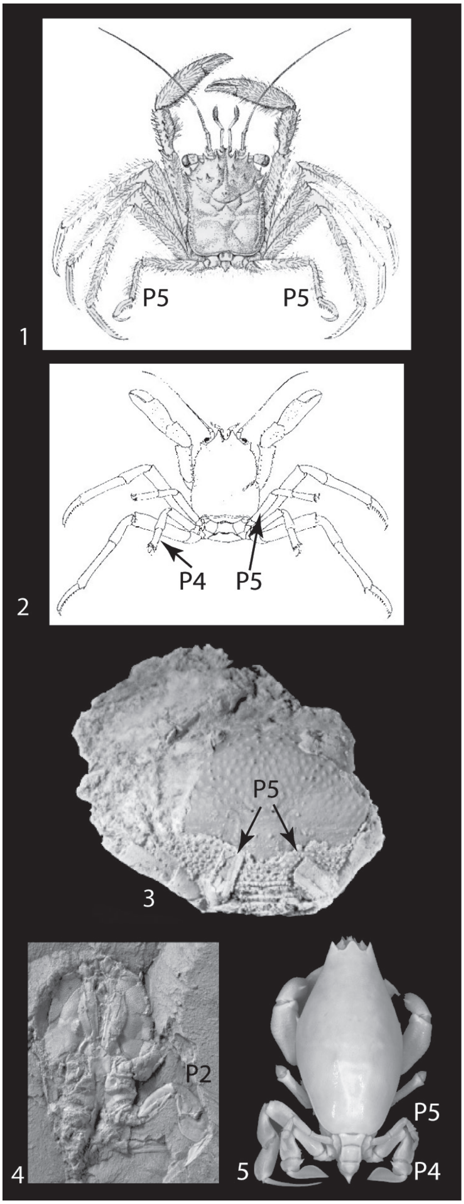

Fig. 134. Position of pereiopods 4 and 5 in several sections: *1,* hooklike dactyls of fifth pereiopods in Homolida; *2,* subdorsal fourth and fifth pereiopods in Dromiacea; *3,* subdorsal fifth pereiopod in Cretaceous Etyoida, *Caloxanthus americanus* Rathbun, 1935; *4,* paddle-like second pereiopod in Cretaceous Raninoida, *Marylyreidus punctatus* (Rathbun, 1935); *5,* flattened fourth pereiopod and reduced fifth pereiopod in extant Raninoda, *Lyreidus tridentatus* de Haan, 1841 in 1833–1850 (*1,* adapted from Rathbun, 1937, fig. 16; *2,* adapted from Ng, 1998, fig. 16; *3,* adapted from Schweitzer & others, 2012, fig. 11.1; *4,* Franțescu, Feldmann, & Schweitzer 2016, fig. 8.6; *5,* adapted from Feldmann & Schweitzer, 2007, fig. 4A). P=pereiopod.

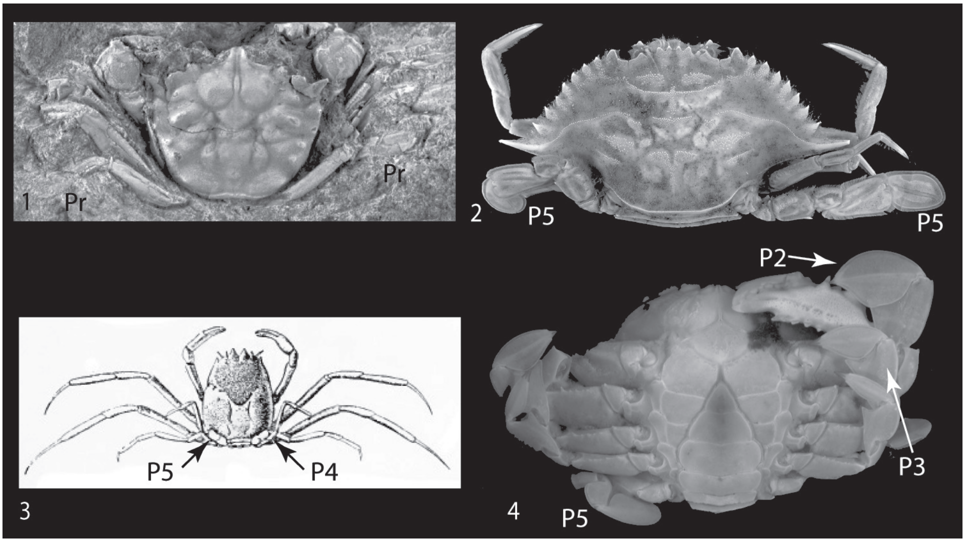

FIG. 135. Various pereiopods. *1,* Cretaceous Portunoidea with flattened propodi of fifth pereiopod, *Longusorbis cuniculosus* RICHARDS, 1975; *2, Thalamitoides quadridens* A. MILNE EDWARDS, 1869, USNM 1418391, flattened fifth pereiopod in extant Portunidae; *3,* subdorsal fourth and fifth pereiopods in Dorippoidea; *4,* flattened pereiopods 2, 3 and 5 in Matutidae, *Matuta victor* (FABRICIUS, 1781) (*1,* adapted from Schweitzer, Feldmann, & Karasawa, 2007, fig. 2A; *2,* new, photo by R. Feldmann; *3,* adapted from Rathbun, 1937, fig. 22; *4,* Schweitzer, Feldmann & Karasawa, 2021, fig. 13,*1b*). P=pereiopod, Pr=propodus.

main function of the pereiopods is motion, although pereiopod 5 is frequently modified for other activities. Pereiopods 2–5 are longer and more slender than the chelipeds, are used for locomotion, and terminate in sharp dactyls. In Matutidae, pereiopods 2–5 are flattened as an adaptation mainly for digging but also facultatively for swimming (DAVIE, GUINOT, & NG, 2015) (Fig. 135.4), whereas in Callichimaeridae pereiopods 2–3 are elongated, oar-like paddles for swimming. In some extinct raninoids, the propodi of pereiopods 2 and 3 are flattened, presumably for burrowing or digging (Fig. 134.4).

Pereiopod 5 may differ from pereiopods 2–4 and may terminate in a flattened dactyl and sometimes propodus used in either swimming (Portunoidea) or digging (Raninoida Matutidae, and Orithyiidae) (LUQUE & others, 2019a). The more proximal elements of the pereiopods also can be flattened (Fig. 132.5, Fig. 134.5, Fig. 135.1). Pereiopod 5 can be held subdorsally, with subchelate terminations adapted to holding sponges or other items as camouflage as in dromiaceans, some majoids, cyclodorippoids, and dorippoids (Fig. 134.1–134.3, Fig. 135.3). Hook-shaped dactyli can facilitate gripping corals, rocks, or other surfaces (DAVIE, GUINOT, & NG, 2015). In fossil specimens, it is common for the proximal elements of the pereiopods to be preserved and the distal elements to be missing or even vice versa (Fig. 134, Fig. 135.1). The coxae of pereiopods 3 and 5 bear gonopores in females and males respectively, as previously discussed.

Pleopods.—The pleopods in brachyurans are reduced compared to other decapod groups. In females, the pleopods, which are biramous (Fig. 136.8), hold the eggs under the pleon (Fig. 136.11). They also help to circulate water and thus oxygen around the eggs.Pleopods are more commonly specialized in males. Pleopods 1 and 2 are modified into gonopods, a condition not seen in other decapods. The first gonopod (pleopod 1) (Fig. 136.1–3) is modified to transfer sperm to the female gonopore, and the second gonopod (pleopod 2) (Fig.

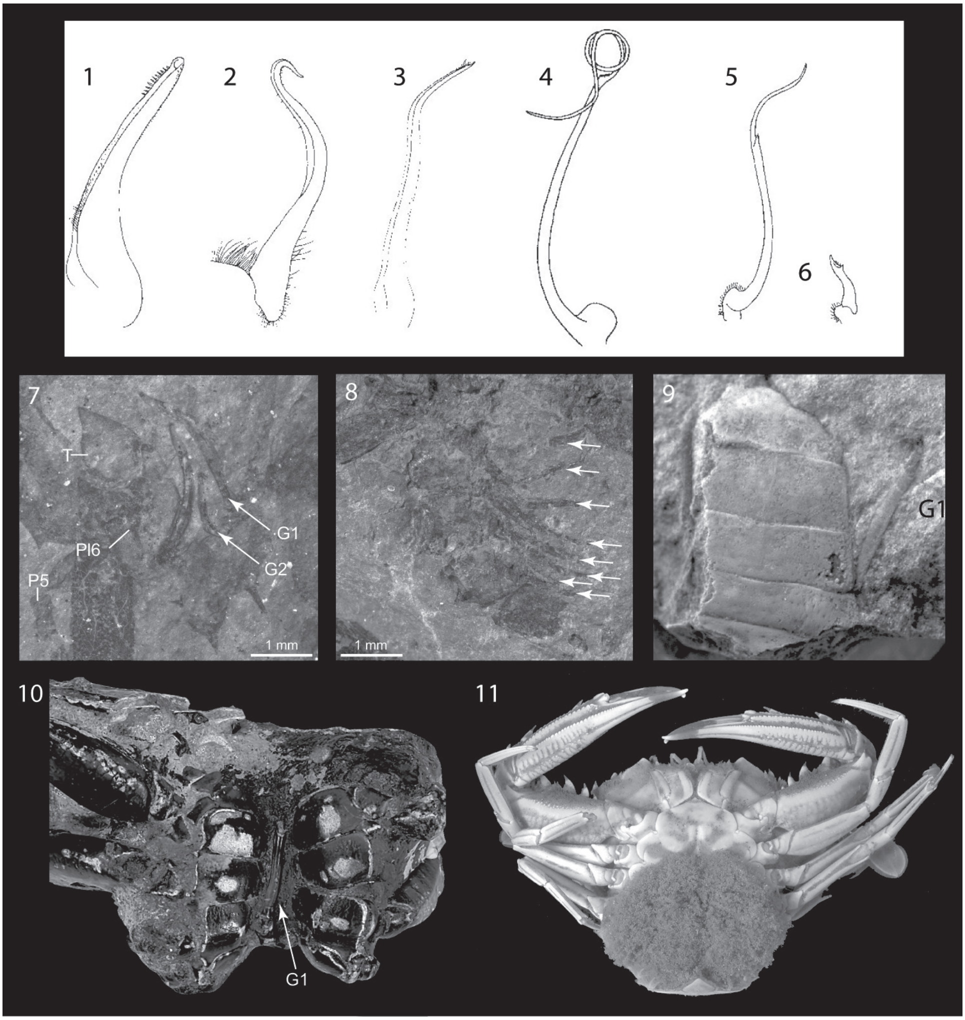

Fig. 136. Male and female brachyuran gonopods: *1–3,* examples of male gonopod 1; *4–6,* examples of male gonopod 2; *7–8,* Cretaceous podotreme, *Callichimaera perplexa* Luque & others, 2019a, male with gonopods 1 and 2 preserved (*7*) and female with pleopods preserved (*arrows*) (8); *9,* Miocene thoracotreme, *Asthenognathus australensis* Feldmann & others, 2011b, male with preserved gonopod 1; *10,* Quaternary thoracotreme, *Uca ornata* (Smith, 1870), male with gonopod 1 preserved; *11,* Portunidae, *Cronius ruber* (Lamarck, 1818), female with eggs carried on pleopods (*1–6,* adapted from Ng. 1998, fig. 82–83; *7–8,* adapted from Luque & others, 2019a, figs 3E and 3B, respectively); *9,* adapted from Feldmann & others (2011b, fig. 13D); *10,* adapted from Luque & others, 2018, fig. 2H; *11,* Schweitzer, Feldmann, & Karasawa, 2021, fig. 16,*3b.*). G1–G2=gonopods 1 and 2, P5=pereiopod, Pl6=pleonite 6, T=telson.

136.4–6) assists in the sperm transfer. Gonopod 1 is slender and elongate and is known occasionally from fossil forms (Smirnov, 1929; Secrétan, 1975; Karasawa & Kato, 2001; Feldmann & others, 2011b; Luque & others, 2018; Karasawa & Kato, 2019; Luque & others, 2019a) (Fig. 136.7, 136.9–10). Gonopod 2 is shorter but occasionally longer than gonopod 1 (Fig. 136.7). The form, length, and ornamentation of the gonopods is very important in brachyuran classification of living species but is not particularly useful for fossils because they are so infrequently preserved.

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This chapter is dedicated to Rodney M. Feldmann (deceased, May 2024, in the final proof stages of this article). He was president of the Paleontological Society and the Paleontological Research Institution, co-editor of the Journal of Paleontology, and he published over 450 scientific papers between 1962 and 2024 on fossils, primarily on decapod crustaceans (lobsters, crabs, and shrimps). He was a global expert on fossil lobsters and crabs, and his work placed him in the top 2 percent of scientists in the world. His work is pivotal to this *Treatise* article and many more in progress. Furthermore, his work inspired the co-authors of this article and more to come, for which we are all indebted.

ABBREVIATIONS FOR MUSEUM REPOSITORIES

BMNH/NHMUK: The Natural History Museum, London, UK

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

GSC: Geological Survey of Canada, Eastern Paleontology Division, Ottawa, Ontario, Canada

KSU D: Decapod Comparative Collection, Department of Geology, Kent State University, Kent, Ohio, USA

LPI: Invertebrate Paleontology Collection, Chengdu Institute of Geology & Mineral Resources, Chengdu, China

MGUH: Geologisk Museum, University of Copenhagen, Copenhagen, Denmark

MMNS: Mississippi Museum of Natural Science, Jackson, Mississippi, USA

MNHN.F: Muséum National d'histoire naturelle, Paris, Collection de Paléontologie, France

MNHN IU: Muséum National d'histoire naturelle, Paris, Crustacean Collection, France

NHMW: Naturhistorisches Museum Wien (Natural History Museum of Vienna), Austria

RECOLNAT: Réseau national des collections naturalists (National Network of Natural History Collections, France

SM B: Sedgwick Museum, Cambridge University, UK

SMF: Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt, Germany

SMNS: Staatliches Museum für Naturkunde, Stuttgart, Germany

UCBL-FSL: University of Lyon, France

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

UWBM: Burke Museum, University of Washington, Seattle, Washington, USA

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