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CONTENTS

INFRAORDER ANOMURA MACLEAY, 1838[1])

BY

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Contents. – **Introduction and definition** – Remarks – Diagnosis. **External morphology** – General habitus – Cephalothorax – Pleon – Appendages. **Internal morphology** – Muscles – Nervous system – Sense organs – Digestive system – Circulatory system – Excretory system – Genital apparatus and reproduction – Endocrine system. **Development and larvae** – Paguroidea and Lithodoidea – Galatheoidea and Chirostyloidea – Aegloidea – Hippoidea. **Ecology and ethology** – Ecological distribution – Shell and other object use – Symbiotic association – Parasites – Predators – Ethology. **Economic importance** – Paguroidea – Lithodoidea – Galatheoidea. **Phylogeny and biogeography** – Phylogeny – Biogeography. **Systematic** classification. **Appendix. Acknowledgements. Bibliography.**

INTRODUCTION AND DEFINITION

Remarks

Anomura, of all the decapod infraorders, has had a particularly unstable taxonomic history, with groups such as the dromiacean crabs and the thalassinidean shrimps being variously included and excluded over the years (see reviews by Martin & Davis, 2001 and McLaughlin et al., 2007a). The name for the group (Anomala versus Anomura) has also been vigorously debated (McLaughlin & Holthuis, 1985). Most classifications recognize three major groupings: Galatheoidea (squat lobsters and porcelain crabs), Paguroidea (symmetrical and asymmetrical hermit crabs and king crabs), and Hippoidea (mole crabs), but with other smaller independent groups (e.g., Lomisoidea, Aegloidea, Kiwaoidea) adding to the incredible morphological diversity. More recently the classification of the squat lobsters was revised to recognize Galatheoidea (restricted to Galatheidae, Munididae, and Munidopsidae), and Chirostyloidea (for Chirostylidae, Eumunididae, and

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[1]) Manuscript concluded 19 June 2010; revised December 2010.

Kiwaidae) (Ahyong et al., 2010; Schnabel & Ahyong, 2010). The monophyly of Anomura is now well established, as is its sister group relationship to the infraorder **Brachyura** (the true crabs); together forming the **Meiura** of Scholtz & Richter (1995). Anomura, as currently conceived, comprises 7 superfamilies, 20 families, over 200 genera, and 2200 species.

Unlike the more speciose Brachyura, the **fossil record** for Anomura has been limited (Burkenroad, 1963; Glaessner, 1969), and it has only been in the last decade that their known fossil occurrence has really been expanded both in time and in diversity. The oldest known anomuran, *Platykotta akaina* Chablais, Feldmann & Schweitzer, 2010 (Platykottidae), is of Upper Triassic age, but uncertain superfamilial affinities. Other known fossil anomurans span the following ranges: Aegloidea from Early to Late Cretaceous (marine) (Feldmann, 1984; Feldmann et al., 1998); Galatheoidea from the Lower Jurassic to Pleistocene (Glaessner, 1969; Schweitzer & Feldmann, 2000, 2005; De Angeli & Garassino, 2002); Hippoidea from Middle and Late Eocene (Boyko, 2002); Paguroidea from Jurassic to Oligocene (Glaessner, 1969; Feldmann & Keyes, 1992; Karasawa, 2002; Fraaije, 2003; Schweitzer et al., 2005; Jagt et al., 2006; Van Bakel et al., 2008); and Lithodoidea from the Miocene (Feldmann, 1998). No fossils of Lomisoidea are known at present, and the oldest chirostyloid is of Cretaceous age (Schweitzer & Feldmann, 2000). All of these fossil occurrences are younger than the recently proposed divergence times for Anomura (Carboniferous 350-300 mya) and some subclades (Permian-Triassic 250 mya) inferred from molecular data (Porter et al., 2005).

Diagnosis

Carapace variable in shape, not fused to epistome; epistome protected by sides of carapace; eyes well-developed, stalked, compound; antennulae with peduncle 3-segmented, flagella usually paired; antennal peduncle with 5 (sometimes 6) or fewer segments, exopod reduced to acicle, flagellum variable in length; maxillipeds usually pediform, exopod usually with flagellum, crista dentata usually well developed; first pereiopod usually chelate; second and third, and often fourth pereiopods ambulatory; fourth pereiopod sometimes chelate or subchelate; fifth pereiopod usually chelate or subchelate; male fifth pereiopod sometimes with sexual tubes; eighth thoracomere loosely connected to seventh thoracomere; pleopods rarely well-developed, often reduced or present only on one side; first and second pleopods often modified as gonopods in both sexes; uropods often reduced or modified, occasionally absent; uropodal exopod without suture; telson occasionally reduced or absent; first pleomere innervation from ganglion attached to thoracic ganglionic mass [after Davie, 2002; Poore, 2004].

EXTERNAL MORPHOLOGY

General habitus

Anomura exhibit a great diversity in body form. In the asymmetrical hermit crabs (**Paguroidea**: Paguridae, Diogenidae, Coenobitidae, Parapaguridae, and Pylojacquesidae),

the pleon is generally soft, membranous, and dextrally twisted (but see "Pleon" below for exceptions) (fig. 70.1C-I). In the hermit crab family, Pylochelidae, however, the pleon is well developed and symmetrical, and the segmentation is clearly defined, so that the general appearance is more crayfish-like (fig. 70.1A, B).

Lithodoidea generally present a crab-like (**carcinized**) body form, in which the pleon is mostly folded beneath the cephalothorax (fig. 70.2A-C). The pleon is symmetrical in male lithodoids, asymmetrical in females.

Members of **Galatheoidea** and **Chirostyloidea** are the anomurans known as squat lobsters, porcelain crabs, and the yeti lobster. Most have crayfish-like body forms in which the pleon is well developed, straight, and symmetrical, and the tergites and most sternites are strongly calcified (figs. 70.3C-E, 70.17A, 70.18A). The porcelain crabs (Porcellanidae), however, usually exhibit a crab-like body form, in which the cephalothorax is strongly flattened and the pleon is almost fully folded beneath the cephalothorax and not visible from the dorsal aspect (figs. 70.3F, 70.19A).

The endemic South American freshwater group **Aegloidea** generally resemble galatheoids in body form (where they were originally placed), but have shorter chelae and a rounder posterior end (fig. 70.3A). The pleon is well developed, elongated, and symmetrical, and is carried partially under the cephalothorax, with 3 or 4 pleonites visible dorsally; the tergites and most sternites are strongly calcified (see Martin & Abele, 1988 for review of aeglid external morphology).

Lomisoidea is represented by only one species, *Lomis hirta* (Lamarck, 1818), and the general appearance is superficially very similar to porcelain crabs or some lithodoids in which the pleon is almost completely folded beneath the cephalothorax (fig. 70.3B) (see McLaughlin, 1983a).

The almost universal burrowing habit of **Hippoidea** has presumably placed some restriction on the somatic morphology in this group, but albuneids and blepharipodids show a generally crab-like body form (similar to brachyuran raninids) with their walking legs visible dorsally, while the hippids are more elongate, oval in outline, and all of their limbs can be tucked under the body to be invisible in dorsal view (fig. 70.4A-D).

Cephalothorax

The **cephalothorax** consists of a head with five **cephalic somites** bearing antennulae, antennae, mandibles, maxillules, and maxillae, plus three **thoracomeres** bearing first through third maxillipeds, and a **thorax** with five somites bearing first through fifth pereiopods. All of these somites are completely fused so that the **segmentation** is not immediately recognized externally. The cephalothorax is entirely covered by the **carapace** in all anomuran taxa, but the degree of **calcification** varies in hermit crabs.

The cephalothorax is ventrally represented by a series of **sternal plates** (fig. 70.5G). The sternal plates in Galatheoidea and Chirostyloidea are broad and termed the **sternal plastron** (fused fourth to seventh sternites). In Galatheoidea, the eighth sternite is calcified and articulates with the sternal plastron. In Chirostyloidea, the eighth sternite is absent. The ventral parts of the antennular and antennal somites form the **epistome**, which may or
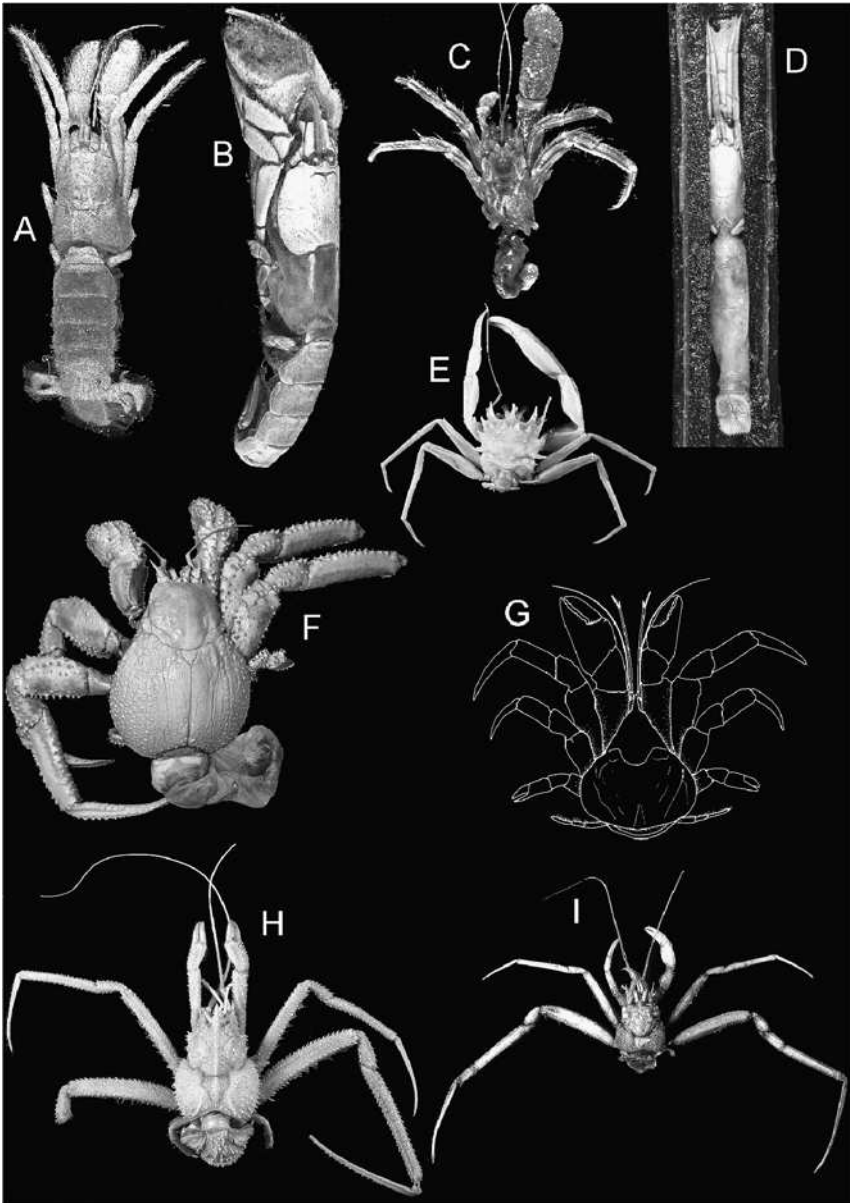
Fig. 70.1. ²) General habitus (dorsal) of Paguroidea. A, *Trizocheles caledonicus* Forest, 1987 (Pylochelidae); B, *Pomatocheles jeffreysii* Miers, 1879 (Pylochelidae); C, *Pagurus insulae* Asakura, 1991 (Paguridae); D, *Xylopagurus rectus* A. Milne-Edwards, 1880 (Paguridae); E, *Solitariopagurus triprobolus* Poupin & McLaughlin, 1996 (Paguridae); F, *Tisea grandis* Forest & Morgan, 1991 (Diogenidae); G, *Birgus latro* (Linnaeus, 1767) (Coenobitidae); H, *Probeebei mirabilis* Boone, 1926 (Parapaguridae); I, *Tylaspis anomala* Henderson, 1885 (Parapaguridae). [A, B, D, E, F, H, I, after Asakura, 2003; C, photo by Akira Asakura; G, after Alcock, 1905.]
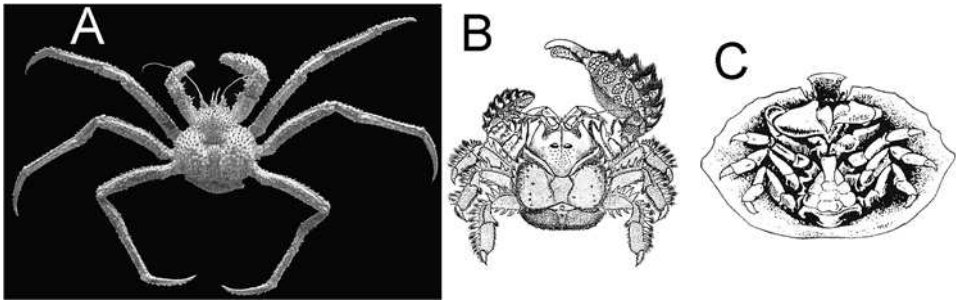
Fig. 70.2. General habitus of Lithodoidea. A, *Paralomis multispina*; B, *Hapalogaster dentata* (De Haan, 1849); C, *Cryptolithodes expansus* Miers, 1879. A, B, dorsal; C, ventral. [A, photo by Akira Asakura; B, after Kamita, 1956; C, after Makarov, 1938.]

may not be fused into a single plate and is sometimes provided with a spine, the **epistome spine** (fig. 70.5D) (Sandberg & McLaughlin, 1998). In Parapaguridae, a single **"labral spine"** is provided on the anterior portion of the **labrum** that is generally fused to the epistome (fig. 70.5D) (Lemaitre, 1989). The **ophthalmic sternite** is generally membranous and unarmed, but in *Diogenes* (Diogenidae), a rostriform process, the **intercalary rostral process**, is developed (fig. 70.5A-C).

There is some debate concerning the validity of an **ocular sternite**, i.e., whether the **ocular peduncles** could or could not be interpreted as appendages of a true segment (cf. Mayrat & de Saint Laurent, 1996). The ocular peduncle was at one point thought to be 2 or 3 indistinguishable segments (Power, 1969). In this chapter, though, we regard the ocular peduncles as not being appendages, following McLaughlin (1980, 1983c). In Paguroidea, the ocular peduncle is provided basally with a small, calcified plate referred to as an **ocular acicle**, or in some genera of Pylochelidae, an **ocular plate** or **basal ocular piece** (Forest, 1987a; Forest et al., 2000). The ocular acicle is reduced or absent in Lithodoidea, and absent in Galatheoidea and Chirostyloidea.

In Albuneidae and Blepharipodidae, the ocular peduncles are composed of three segments but lack ocular acicles (Boyko, 2002). The proximal segments are fused to form the ocular plate. The median peduncle segments are either a pair of small, free, calcified elements, or are fused to the ocular plate. The distal peduncle segments contain the **corneas**. In *Blepharipoda*, the apparent division of the distal peduncle segment is recognized (fig. 70.9B). However, this is not a true segmentation, but is only a weak calcification separating the segment into two **pseudo-segments** (Boyko, 2002).

PAGUROIDEA

The dorsal surface of the carapace is generally very flat, but species in several genera including *Pylocheles* and *Cheiroplatea* in Pylochelidae, *Pylopagurus* and *Xylopagurus*

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[2]) In this caption with habitus figures, all authorities and dates of species names are given, whereas in subsequent captions only names at first mention are provided with author and date; all authors and dates can be seen in the Appendix with the names of genera and species alphabetically arranged.
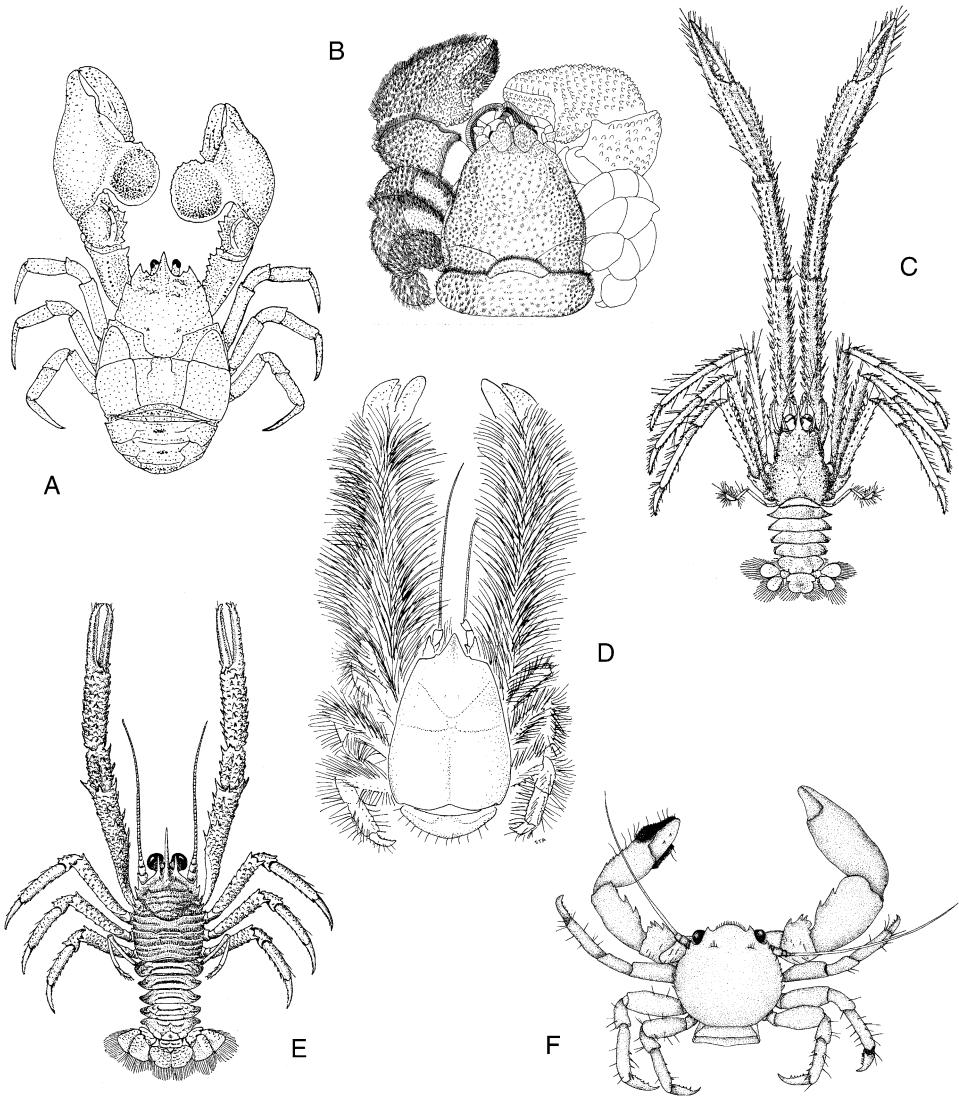
Fig. 70.3. General habitus (dorsal) of various Anomura. A, *Aegla schmitti* Hobbs, 1979 (Aegloidea, Aeglidae); B, *Lomis hirta* (Lomisoidea, Lomisidae); C, *Gastroptychus affinis* (Chace, 1942) (Chirostyloidea, Chirostylidae); D, *Kiwa hirsuta* Macpherson, Jones & Segonzac, 2005 (Chirostyloidea, Kiwaidae); E, *Munida quadrispina* (Galatheoidea, Munididae); F, *Pisidia inequalis* (Heller, 1861) (Galatheoidea, Porcellanidae). [A, after Martin & Abele, 1988; B, after McLaughlin, 1983; C, after Chace, 1942; D, based on Macpherson et al., 2005; E, after Benedict, 1902; F, after Werding & Hiller, 2007.]

in Paguridae, and *Cancellus* in Diogenidae have a more convex, subcylindrical carapace (fig. 70.6A-C). Usually, the carapace is calcified only in the anterior part, referred to as the **shield** (= **gastric region**, Pilgrim, 1973; **gastric carapace**, Sandberg & McLaughlin,
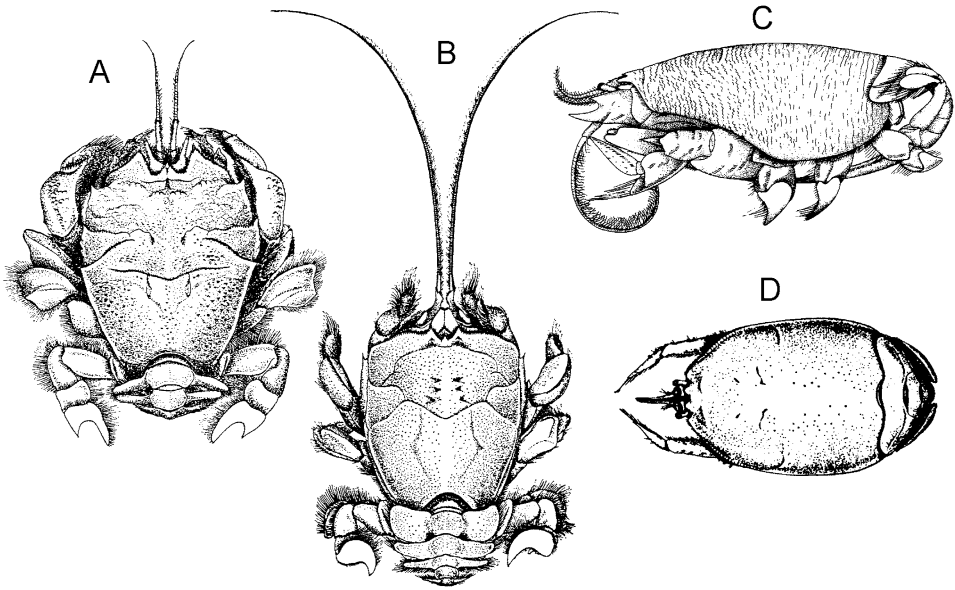
Fig. 70.4. General habitus of Hippoidea. A, *Lophomastix japonica* (Duruflé, 1889) (Blepharipodidae); B, *Albunea symmysta* (Linnaeus, 1758) (Albuneidae); C, *Emerita benedicti* Schmitt, 1935 (Hippidae); D, *Hippa pacifica* (Hippidae). A, B, D, dorsal; C, left lateral. [A, B, after Miyake, 1978; C, after Williams, 1984; D, after Miyake, 1982.]

1998). The posterior portion of the carapace is usually membranous and called the **posterior carapace** (= **posterior cardiac region**, Sandberg & McLaughlin, 1998) (fig. 70.6C).

The anterior dorsal surface of the shield is provided with a **rostrum** and a pair of **lateral projections**, or a **post antennal spine**, on the anterior margin. The rostrum is generally more or less reduced, but exceptions are species of *Labidochirus*, *Porcellanopagurus*, and *Solitariopagurus* in Paguridae, and *Probeebei* in Parapaguridae, that have a well-developed rostrum (fig. 70.6D-E). The rostrum is absent in species of *Pylocheles*, and, instead, a median concavity is provided on the anterior margin of the shield (fig. 70.6B). The lateral projections are usually small in species of Diogenidae and Parapaguridae and most species of Paguridae, but they are large in *Porcellanopagurus* and *Solitariopagurus*. A pair of grooves from each posterolateral margin to the anterior portion of the shield are sometimes recognized and referred to as **linea-d** (Pilgrim, 1973; Lemaitre, 1995). The linea-d is exceptionally long in *Xylopagurus* (Paguridae) and reaches the anterior margin of the shield (Lemaitre, 1995). A pair of **post-gastric pits** and sometimes a y-shaped groove called **Y-linea**, in particular in species of Diogenidae, can also be recognized posteriorly on the shield. The shield is delineated posteriorly and laterally by the **cervical groove** and separated posteriorly from the posterior carapace by a narrow, usually uncalcified hinge, the **linea transversalis**.

A pair of **calcified regions** is most often recognized on either side of the posterior margin of the shield. Lemaitre (1995) designated this structure the "accessory portion" in his
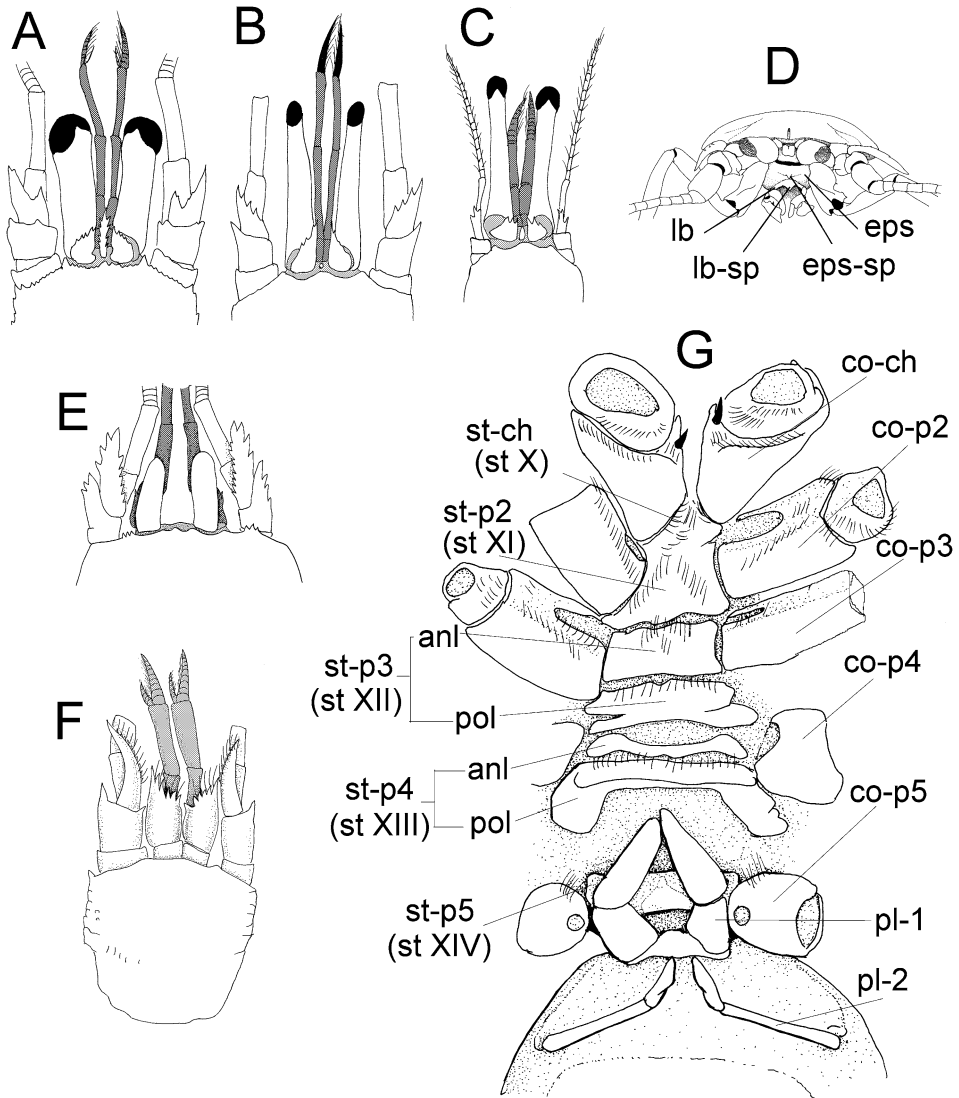
Fig. 70.5. Cephalothorax of Paguroidea. A-C, intercalary rostral process of *Diogenes* (Diogenidae): A, serrate; B, vestigial; C, simple; D, anterior portion of Parapaguridae: eps, epistome; eps-sp, epistomial spine; lb, labrum; lb-sp, labral spine; E, corneas without pigmentation, *Cheiroplatea laticaudata*; F, ocular peduncles without visible corneas, *Typhlopagurus foresti*; G, ventral view of cephalothorax, *Pseudopaguristes bollandi* Asakura & McLaughlin, 2003: anl, anteror lobe; co-ch, coxa of cheliped; co-p2 to co-p5, coxae of second to fifth pereiopod; pl-1, first pleopod; pl-2, second pleopod; pol, posterior lobe; st, sternite; st-ch, sternite of chelipeds; st-p2 to st-p5, sternites of second to fifth pereiopod. [A-C, illust. by Akira Asakura; D, after Lemaitre, 1989; E, F, after Asakura, 2003; G, after Asakura & McLaughlin, 2003.]
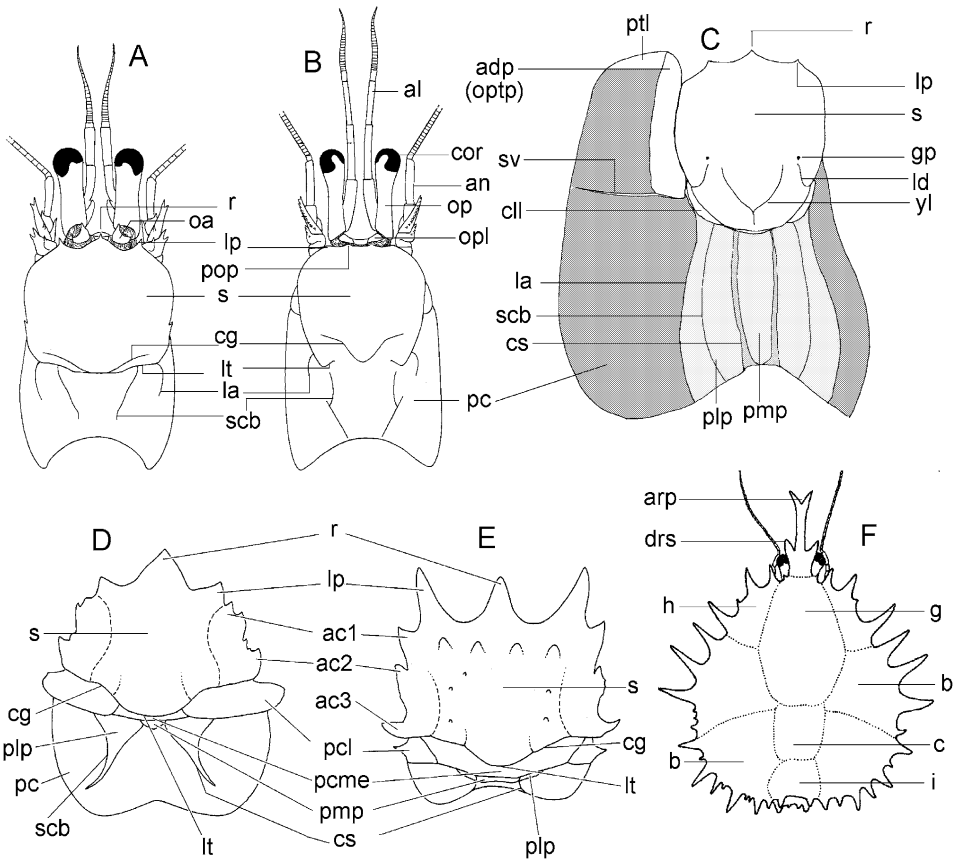
Fig. 70.6. Carapace (dorsal) of Paguroidea and Lithodoidea. A, *Trizocheles* (Pylochelidae); B, *Pylocheles* (Pylochelidae); C, *Calcinus* (Diogenidae); D, *Porcellanopagurus* (Paguridae); E, *Solitariopagurus* (Paguridae); F, diagrammatic lithodid. Abbreviations A-E: ac1, anterior carapace lobe 1; ac2, anterior carapace lobe 2; ac3, anterior carapace lobe 3; adp, anterodorsal plate; al, antennule; an, antenna; cg, cervical groove; cll, carapace lateral lobe; cor, cornea; cs, cardiac sulcus; gs, postgastric pit; la, linea anomurica; ld, linea-d; lp, lateral projection; lt, linea transversalis; op, ocular peduncle; opl, ocular plate (= basal ocular piece); optp, outer pterygostomial plate; pc, posterior carapace; pcl, posterior carapace lateral lobe (element); pcme, posterior carapace median element; plp, postero-lateral plate; pmp, postero-median plate; pop, post-ocular projection; ptl, pterygostomial lobes; r, rostrum; s, shield; scb, sulcus cardiobranchialis; sv, sulcus verticalis; yl, Y-linea. Abbreviations F: arp, anterior rostral projection; b, branchial region; c, cardiac regions; drs, dorsal rostral spine; g, gastric region; h, hepatic region; i, intestinal region. [A, B, after Forest, 1987a; C, illust. by Akira Asakura; D, E, after McLaughlin, 2000; F, after Sandberg & McLaughlin, 1998.]

review of *Xylopagurus*, presumably delineated anteriorly by the anterior prolongation of the cervical groove and posteriorly by the linea transversalis. This structure is incorporated into species descriptions as **"accessory portion of the shield"** (McLaughlin & Lemaitre, 2001). Although there is ongoing debate concerning interpretation of this structure, a similar structure found in *Porcellanopagurus* and *Solitariopagurus* is referred to as the **pos-**
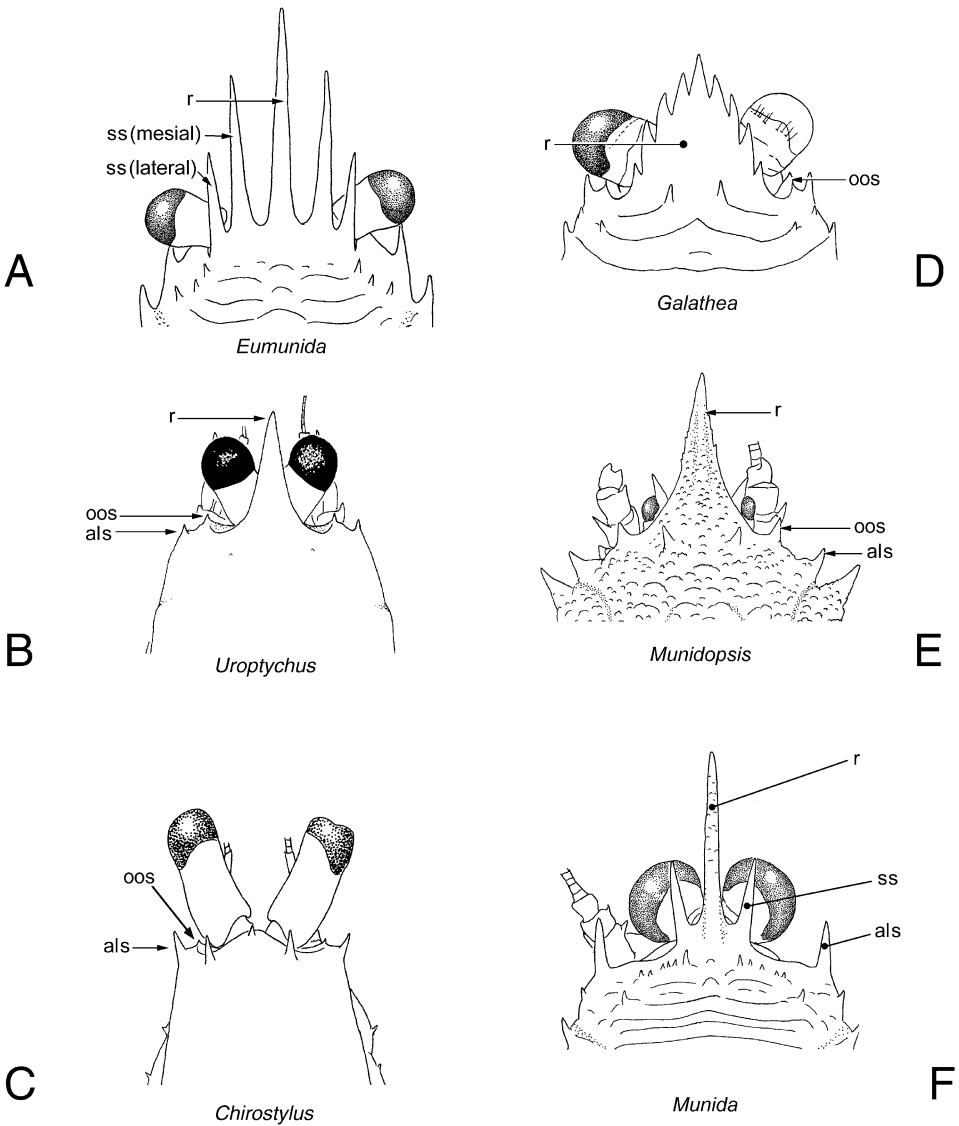
Fig. 70.7. Galatheoidea and Chirostyloidea, anterior carapace forms. A-C, Chirostyloidea; D-F, Galatheoidea. Abbreviations: als, anterolateral spine; r, rostrum; oos, outerorbital spine; ss, supraocular spine. [A, D-F, modified after Baba et al., 2009; B, modified after Ahyong & Poore, 2004; C, modified after Baba, 2009.]

terior carapace lateral lobe or **element** (McLaughlin, 2000) or in *Bythiopagurus* as the **carapace lateral lobe** (McLaughlin, 2003). McLaughlin considers this structure in these three genera as part of the posterior carapace and not as accessory parts of the shield (anterior carapace). Similarly, the calcified plate between the posterior carapace lateral lobes in *Porcellanopagurus* and *Solitariopagurus* is called the **posterior carapace median ele-**

ment (McLaughlin, 2003), and is not part of the linea transversalis but a structure on the posterior carapace, posterior to the linea transversalis.

On the posterior carapace, three distinct pairs of **lines** or **grooves** can usually be distinguished (McLaughlin, 1980, 2003) (fig. 70.6A-C). In the midline we see a pair of elongate sutures, the **cardiac sulcus**; two short lines or grooves slightly lateral to this, the **sulcus cardiobranchialis**; and a **linea anomurica** on each side of the carapace represents the third pair. The area between the two central cardiac sulci is the **postero-median plate**, which is often weakly calcified. A pair of **postero-lateral plates**, found lateral to the postero-median plate, is often weakly calcified and each is bordered laterally by the sulcus cardiobranchialis. The entire posterior carapace is well calcified in several genera, including *Tisea* (Diogenidae), *Birgus* (Coenobitidae), *Ostraconotus* in Paguridae, and *Tylaspis* and *Probeebei* (Parapaguridae).

The lateral branchial regions of the carapace are the **branchiostegites**, separated from the other portion of the carapace by the linea anomurica. The branchiostegites are usually thin and **membranous**, but they are well calcified in *Birgus*. The branchiostegites are anteriorly produced as the **pterygostomial lobes** (Boas, 1880), and the upper portions are sometimes calcified, each forming the **anterodorsal plate** or the **outer pterygostomial plate**. Pilgrim (1973) recognized the **inner pterygostomial plate** between the shield and the outer pterygostomial plate, but this structure is hardly visible externally. The anterodorsal plate is often interrupted by a more or less calcified vertical sulcus, referred to as **sulcus verticalis** (Boas, 1926; Pilgrim, 1973).

Gills of Paguroidea are **phyllobranchiate** (fig. 70.8A-H). In some species of Paguroidea, such as some parapagurid species, the gills were described as **"trichobranchiate"** or "intermediate" between **trichobranchs** and **phyllobranchs** (Lemaitre, 1989). However, McLaughlin & de Saint Laurent (1998) have shown that all those branchs are actually phyllobranchs. In true trichobranchiate gills, the gill elements are tubular and are equal or unequal, but inserted in order or disorder, around the axis. In contrast, the elements of phyllobranchiate gills almost always are inserted biserially in regular pairs along the rachis (fig. 70.8F). The quadriserial appearing gills of certain species of Pylochelidae, Parapaguridae, and Paguridae are inserted biserially on the rachis, but the lamella of each pair is divided, equally or unequally, giving a "trichobranch" or "intermediate" appearance (fig. 70.8G, H). The gill number varies from 9 to 13 pairs. The gills consist of **arthrobranchs**, arising on the arthrodial membrane between the coxa of the pereiopod (thoracic appendages) and the body wall (pleural plate), and **pleurobranchs**, developed from the body wall above the base of the appendages (fig. 70.8A, B, D). Typically, the arthrobranchs are present in pairs on either side of the third maxillipeds, chelipeds, and second through fourth pereiopods, and the 1-3 pleurobranchs.

LITHODOIDEA

The lithodoid crabs differ appreciably in cephalothorax form from the above-mentioned hermit crab families (Macpherson, 1988; Sandberg & McLaughlin, 1998). Most species have the cephalothorax covered by a well-calcified, **vaulted carapace** that is generally pentagonal or pyriform (figs. 70.2, 70.6F). The dorsal face of the carapace is generally
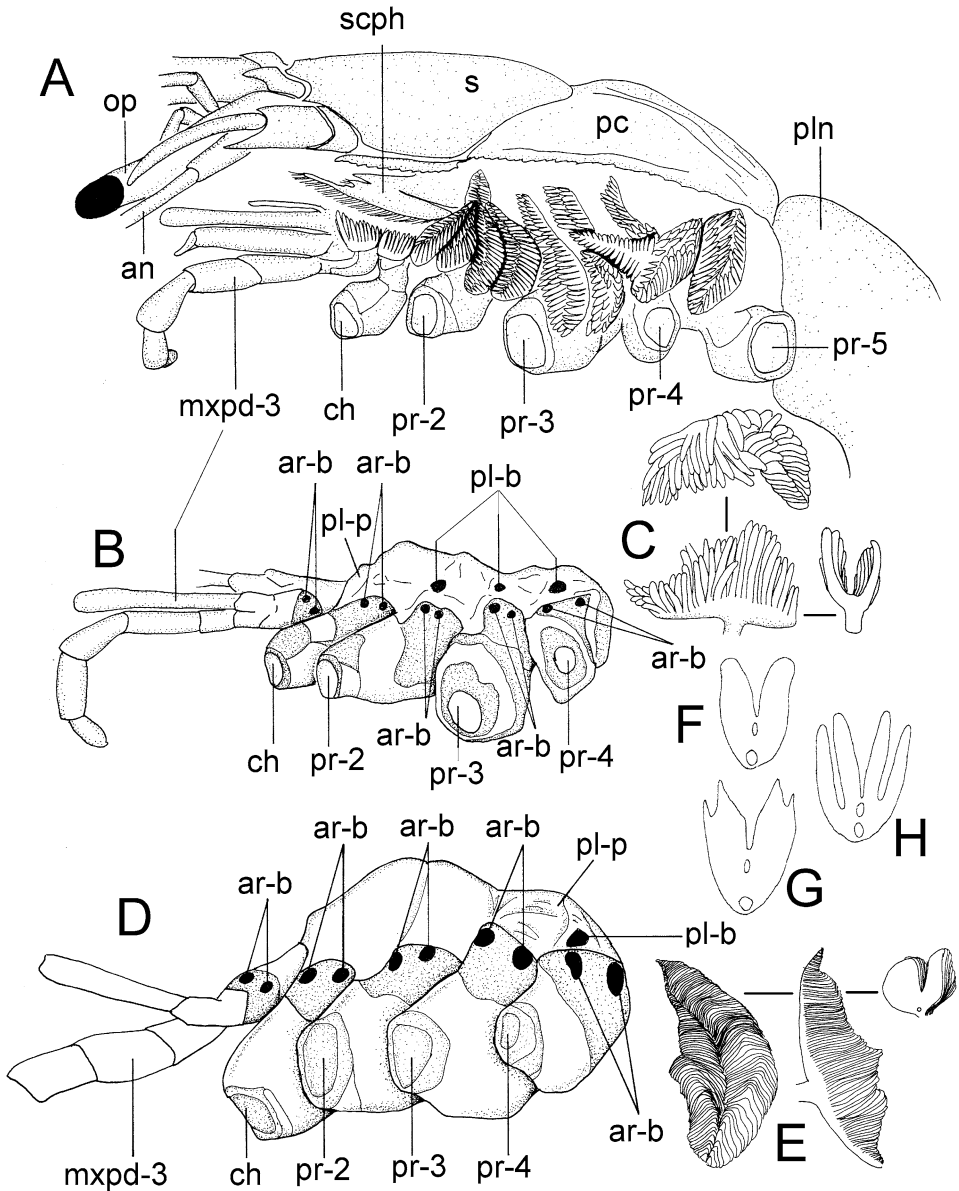
Fig. 70.8. Gills of Paguroidea: diagrammatic pagurid, depicting arrangements of gills. A, left lateral view; B, D, pleural plate and proximal portions of third maxillipeds, chelipeds, and second through fourth pereiopods, indicating position of gills; C, gill with narrow lamellae; E, gill with broad lamellae; F, biserial gill lamella; G, distally divided quadriserial gill lamella; H, deeply divided quadriserial gill lamella. Abbreviations: an, antenna; ar-b, position of arthrobranchiate gill; ch, cheliped; mxpd-3, third maxilliped; op, ocular peduncle; pc, posterior carapace; pl-b, position of pleurobanchiate gill; pln, pleon; pl-p, pleural plate; pr-1 to pr-5, pereiopod 1 through 5; s, shield; scph, scaphocerite. [Illustration by Akira Asakura.]

divisible into a series of regions that are delineated by a series of **carapace grooves**. The small areas posterior to the ocular peduncle and to the antenna are called the **orbital region** and the **antennal region**, respectively. An anteromedian portion of the carapace, including the rostrum and an area immediately posterior, is the **frontal region**. The area posterior to the frontal region is the **gastric region**, and the area posterior to this is the **cardiac region**. A small area posterior to the cardiac region is the **intestinal region**. The lateral portions overlying the **branchiae** are referred to as the **branchial regions**, and areas anterior to these are the **hepatic regions**. An oblique and transverse groove, the **cervical groove**, separates the gastric region from the branchial and cardiac regions, curving anteriorly toward the antennal region. A short groove delineating the posterior edge of the hepatic region is the **hepatic groove**, separating it from the branchial region.

These carapace regions typically bear **spines** or **granules** of various sizes (fig. 70.6F). Spines on the antennal, branchial, cardiac, gastric, and intestinal regions are referred to as antennal, branchial, cardiac, gastric, and intestinal spines, respectively. The **rostrum** is well developed and often very prominent. The **branchiostegites** are well calcified.

As with the Paguroidea, **gills** of lithodoids are **phyllobranchiate**. In comparison to paguroids, the gill numbers are reduced. The third maxillipeds, chelipeds, and second through fourth pereiopod each have paired **arthrobranchs**; the fourth pereiopod also has one **pleurobranch**.

Galatheoidea and Chirostyloidea

The **carapace** in Galatheoidea is generally **dorsoventrally flattened** to somewhat **subcylindrical** (figs. 70.3E, 70.17A). The regions are partially indicated. The **cervical** and **postcervical grooves** are usually well marked. The cervical groove is arcuate and the postcervical groove almost transverse; they coalesce medially. The cardiac and intestinal regions lie posterior to the cervical groove and are demarcated from the branchial regions by a shallow groove. The **rostrum** exhibits a wide range of forms from spiniform, e.g., *Munida*, *Agononida*, *Cervimunida* (Munididae), to broadly triangular, e.g., *Galathea*, *Phylladiorhynchus* (Galatheidae), *Munidopsis* (Munidopsidae), or truncate, e.g., *Heteronida* (Munididae) (figs. 70.7D-F, 70.17A). In Munididae, the rostrum is usually styliform and flanked on either side by a supraocular spine producing a **tridentate** appearance (figs. 70.7F, 70.17A). The **orbits** in galatheoids are shallow and ill-defined (Galatheidae, Porcellanidae, Munididae), or absent in those genera with degenerate **eyes**, such as *Shinkaia*, *Munidopsis*, and *Galacantha* (Munidopsidae). In munidopsids, a spine or projection (**antennal spine**) on the anterior carapace margin flanking the eye (above the antennal peduncle) may be present (Baba, 2005). This 'antennal spine', however, appears to be the remnant of the outer orbit and is probably better termed the **outer orbital spine** (fig. 70.7D, E), as in Brachyura, with which it appears to be homologous. Certainly, the **'antennal spine'** in munidopsids does not appear to be homologous with the antennal spine of carideans and astacideans, for instance, which lies on the anterior carapace margin distal from the outer orbital spine (termed **suborbital** in Caridea and Astacidea). The anterolateral margin of the carapace is typically armed with a spine or tooth, except in some species of *Munidopsis*, in which the anterolateral angle of the carapace can be blunt

or rounded. The dorsal surface of the carapace is variously setose and spiny, and may be transversely grooved or ridged, e.g., Galatheidae, Munididae, some Munidopsidae; or tuberculate, smooth, or scabrous, Munidopsidae. Most galatheoids bear one or more pairs of **epigastric spines**. The lateral margins of the carapace are usually defined by a series of tubercles or spines, most prominent and numerous in the anterior half. The posterior margin of the carapace is defined by a low ridge, which may bear small spines. As in other Anomura, the **linea anomurica** demarcates a well-calcified **branchiostegite**. The lateral surface of the branchiostegite is usually longitudinally carinate or grooved, and the anterior margin usually bears a spine; a shallow **V-shaped notch** between the anterior margin of the branchiostegite and anterolateral corner partially accommodates the lateral margin of the antennal peduncle.

The structure of the carapace in Porcellanidae is in many respects very similar to that of other galatheoids, especially Galatheidae, but the carapace is more distinctly **flattened**, and generally **broadly ovate** (figs. 70.3F, 70.19A) (though it may be elongate as in *Pseudoporcellanella* or *Euceramus*). The regions are very weakly defined, usually with only the position of the cervical groove indicated on the central portion of the carapace. The **rostrum** ranges from absent (*Pachycheles*) to prominent and multilobate (*Lissoporcellana*), but is typically broadly triangular. As in galatheids, the outer margin of the orbit is usually indicated by a small tooth or projection. The carapace surface usually bears weak, arcuate striae and the lateral margins may or may not bear small spines and tubercles. The branchiostegite ranges from a single well-calcified unit to being subdivided into multiple calcified elements. There is usually a deep V-shaped notch between the anterior margin of the branchiostegite and anterolateral corner, through which the antennal peduncle protrudes.

Gills of Galatheoidea and Chirostyloidea are phyllobranchiate in the following combination: **podobranchs** absent, four **pleurobranchs** (one each on the first to fifth thoracomere), 10 **arthrobranchs** (two each on the third maxilliped to the fourth pereiopod). Gills in Porcellanidae are similar in structure and number to those of other galatheoids but differ in the arthrobranch combination (one each on the second and third maxillipeds, two each on the first four pereiopods).

As in Galatheoidea, the **carapace** in Chirostyloidea is well calcified, typically elongate, and flattened to subcylindrical; it is variously ornamented (or not) with setae, transverse grooves, tubercles, scales or spines (figs. 70.3C, 70.18A, B).

In Chirostylidae and Eumunididae, the cervical and postcervical grooves meet medially and are evident to varying degrees in most genera, though they may be near obsolete in the chirostylids, *Uroptychus* and *Uroptychodes*. The cardiac region may be evident in *Gastroptychus* and *Chirostylus*, but is not visible in other genera. Other carapace regions are not indicated. The **rostrum** is well developed (except in *Chirostylus*) and ranges from spiniform, e.g., Eumunididae, *Gastroptychus* (Chirostylidae) and some species of *Uroptychus* (Chirostylidae), to broadly triangular, e.g., many species of *Uroptychus* (figs. 70.7A-C, 70.18A, B). Additionally, in Eumunididae, **supraocular spines** are present (two pairs in *Eumunida* and one pair in *Pseudomunida*). The orbits in chirostylids and eumunidids are shallow and poorly developed (such that the eyes are unable to retract)

or absent as in *Chirostylus* and *Hapaloptyx* (fig. 70.7C). The outer limits of the orbits, when present, are usually defined by a small spine. The anterolateral angle is usually also armed. The dorsal surface of the carapace is variously setose and spiny, and may be transversely striated, tuberculate, smooth, or scabrous. The dorsum is transversely striated in *Eumunida*, and in Chirostylidae spinous, e.g., *Gastroptychus* and *Chirostylus*, or smooth to spinous, e.g., *Uroptychus* and *Uroptychodes*. In most genera of Chirostylidae, one of more pairs of epigastric spines or tubercles may be present on the carapace. The lateral margins of the carapace often are defined by spines or tubercles, and the posterior margin is usually distinctly concave and typically without a low ridge. The posterolateral margin in most chirostylids is rounded to obtusely angular. In *Chirostylus* and *Hapaloptyx*, however, the posterolateral carapace margin is deeply excavated. The **linea anomurica** demarcates a well-calcified **branchiostegite**. The lateral surface of the branchiostegite is usually smooth and the anterior margin usually bears a spine. Unlike the chirostylids and eumunidids, the carapace of kiwaids is longitudinally cordate, well calcified, and flattened (figs. 70.3D, 70.20A). The dorsal surface is smooth and sparsely setose. The cervical and postcervical grooves are shallow but distinct, and do not meet medially as in Chirostylidae and Eumunididae. The cardiac region is small and triangular, demarcated by shallow grooves. The branchial regions meet medially but are separated by a longitudinal groove. The intestinal region is short, wide, triangular, and separated from the branchial regions by shallow grooves. The rostrum is well developed as a broad, triangular plate flanked by a small supraocular spine. The orbits are absent, consistent with the degenerate eyes. The lateral margins of the carapace are cristate and unarmed. The **linea anomurica** demarcates a well-calcified **branchiostegite** that is sparsely granular on its anterior half, and longitudinally carinate posteriorly; the anterior margin is rounded.

Aegloidea

The carapace shape is a unique feature of the aeglids but considerable variation exists between the many species (Martin & Abele, 1988; Bond-Buckup & Buckup, 1994). The **carapace**, which may be smooth, finely granulate, or covered with setal punctuations, is dorso-ventrally depressed and dorsally divided by a distinct **cervical groove** into a narrow anterior region and a wider posterior region (figs. 70.3A, 70.21A). The anterior region has a large, triangular, pointed **rostrum**, which can be carinate or not. Lateral to the rostrum, on each side, is an anteriorly directed **orbital spine** and then a larger **anterolateral spine**, defining the orbital and extraorbital sinus, respectively. The lateral edges of the anterior carapace region have three hepatic lobes, each defined by a short, corneous spine. The ventral part of the anterior carapace region is divided into an anterior subrostral area and a more posterior subhepatic region, and each portion is further subdivided by **sutures** (**lineae**). The posterior carapace region is dorsally separated into seven distinct **regions** by sutures. Laterally there are the interior, anterior, and posterior branchial areas, while in the center is a roughly rectangular cardiac region with a raised, usually punctate, **areola**. There is a prominent spine, the epibranchial tooth, present at the anterior lateral edge of the posterior carapace region. The ventral portion of the posterior carapace region is also similarly subdivided into a series of plates by complex sutures.

The **ocular peduncles** are generally short and broad, with inflated, highly pigmented corneas (fig. 70.21A). One exception to this is the **troglobitic species**, *Aegla cavernicola* Türkay, 1972, where the cornea is reduced and the ocular peduncle tapers distally. Aeglids have 13 pairs of large foliaceous **gills**, which appear to be a **hybrid** condition between **phyllobranch** proximally and **trichobranch** distally.

<div align="center">LOMISOIDEA</div>

The **carapace** is basically triangular in shape with the apex being more rounded near the eyes (figs. 70.3B, 70.22A, B). The entire carapace is covered with dense **setal punctuations**, obscuring most underlying detail. Sometimes the cardiac and branchial sutures can be distinguished. There are no obvious lateral spines and the **rostrum** and **orbital spines** are blunt. The first two **pleonites** are visible dorsally and the second is expanded laterally to be wider than the carapace. The **ocular peduncles** are broad, setose, dorsoventrally flattened, and extended into blunt anterior projections forward of the reduced lateral **corneas**. Ocular acicles are absent. *Lomis* has 14 pairs of **trichobranchiate gills**.

<div align="center">HIPPOIDEA</div>

In Blepharipodidae and Albuneidae, the **carapace** is generally subrectangular, the dorsal face of it is moderately convex, and the regions are only weakly defined (fig. 70.9A). The **setal field**, a broad mat of very short, dense, simple setae, is present on the anterior portion of the carapace (Boyko, 2002). The carapace also possesses numerous transverse, setose grooves (**carapace grooves** or CG), which can be identified as, at least, 11 major grooves (**CG1-CG11**). The median element of CG1 forms the posterior margin of the setal field. The metagastric region contains the short, anterior CG2 and the longer, posterior CG3. CG4 spans the width of the carapace and marks the border of the metagastric and mesogastric regions. CG5 is a fairly short groove that occurs medially in the mesogastric region. CG6 corresponds to the cervical groove in other Anomura. CG7 is usually divided into two well-separated lateral fragments, but in some genera, CG7 merges medially with CG6. CG8 to CG11 are relatively short medial grooves arranged anteriorly to posteriorly in the cardiac region (Boyko, 2002). The **rostrum** is reduced or absent. The lateral projections, or post-antennal spines, vary from absent to strongly developed. Some degree of decalcification is observed in the posterior and/or ventral portions of the **branchiostegites** in *Albunea*, *Lophomastix*, and *Blepharipoda* (cf. McLaughlin & Lemaitre, 1997).

In Hippidae, the carapace is ovate, subcylindrical, and more or less expanded (fig. 70.9F-H). The dorsal surface of the carapace is often covered by very weak, wavy

Fig. 70.9. Carapace and pleon of Hippoidea. A, Carapace, *Albunea microps* Miers, 1878; B, ocular peduncles, *Blepharipoda liberata* Shen, 1949; C, same, *Albunea microps*; D, first-sixth pleomeres, *Lophomastix japonica*; E, telson, *Lophomastix japonica*; F, G, carapace,
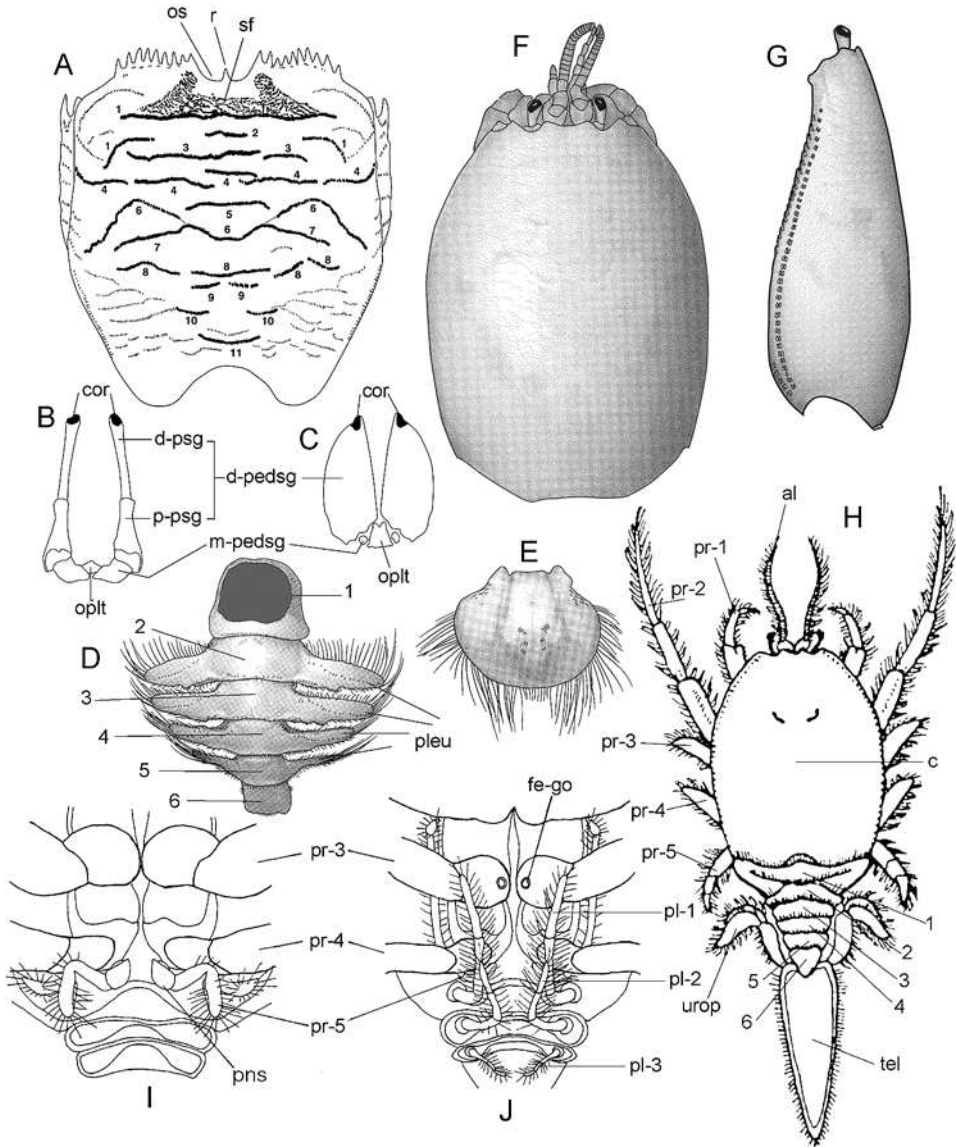
Hippa pacifica; H, *Hippa adactyla* Fabricius, 1787 with pleon fully extended; I, posterior portion of cephalothorax and anterior portion of pleon, male, *Hippa truncatifrons*; J, same, female, *Hippa truncatifrons*. A-F, H, dorsal; G, left lateral; I, J, ventral. Abbreviations: A: os, ocular sinus; r, rostrum; sf, setal field; 1 to 11, carapace grooves 1 to 11. B, C: cor, cornea; d-psg, distal pseudosegment; m-pedsg, medial peduncular segment; oplt, ocular plate; p-psg, proximal pseudosegment. D, H, I, J: 1 to 6, (position of) first to sixth pleomere; fe-go, female gonopore; al, antennule; c, carapace; pl-1 to pl-3, first to third pleopod; pleu, pleura; pns, penis; pr-1 to pr-5, first to fifth pereiopod; tel, telson; urop, uropod. [A-E, after Boyko, 2002; F, G, after Boyko & Harvey, 1999; H, after Miyake, 1982; I, J, after Kato & Suzuki, 1992.]

transverse grooves and its lateral margins sometimes bear a submarginal row of small, setose pits. The rostrum is reduced or absent. Ocular peduncles are short and slender.

According to one definition of gills (McLaughlin & Saint Laurent, 1998), the gills of Albuneidae are phyllobranch, and those of Blepharipodidae are truly trichobranch (Boyko, 2002).

Pleon

The **pleon** consists of six **somites** plus a **telson**. In most literature on anomurans, this structure is often referred to as the "abdomen". However, Schram & Koenemann (2004) recently more clearly defined these terms in crustaceans. The "pleon" is considered the region posterior to the thorax, when differentiated by a structurally distinct set of limbs, and is typically posterior to the gonopores and the postulated anterior-most expression of *Abdominal-B* gene (see Schram & Koenemann, 2004, for the definition). The "pleon" is the region posterior to a trunk that lacks limbs, which is posterior to the expression of the *Abd-B* gene and exhibits no expression of any *Hox* genes. So, the posterior region in all decapods, including anomurans, is more properly termed the pleon.

The telson is generally more or less reduced in anomurans. However, in galatheoids, the telson most often, together with uropods, forms the **tail fan**.

PAGUROIDEA

In the symmetrical hermit crabs, Pylochelidae, the **pleon** is **straight** and all the **tergal** and **sternal plates** are well calcified and clearly distinguishable (Forest, 1987) (figs. 70.1A, B, 70.10A). However, in most species of the families Paguridae, Diogenidae, Coenobitidae, Parapaguridae, and Pylojacquesidae, the pleon is primarily soft and membranous (figs. 70.1C, E, F, 70.10B-D). It is **dextrally twisted**, but exceptions are known, such as in *Discorsopagurus*, *Orthopagurus*, *Enneophyllus*, *Pylopagurus*, and *Xylopagurus* in Paguridae (fig. 70.1D), and *Tsunogaipagurus* in Parapaguridae, which have a straight pleon.

The first **pleomere** is small and its narrow **sternite** may be partially fused with the **last thoracomere**. In the second to fifth pleomeres, rudiments of the plates appear only as faint cuticular thickenings or transverse fibrils of connective tissue (Sandberg & McLaughlin, 1998; Forest et al., 2000). Exceptions include *Birgus* (Coenobitidae) and *Probeebei* (Parapaguridae), both of which have strongly calcified tergal and sternal plates. The tergite of the sixth pleomere is often well calcified and interesting examples are seen in the operculate sixth tergite of *Xylopagurus*, *Discorsopagurus*, and *Orthopagurus* (cf. Lemaitre, 1995).

LITHODOIDEA

The **pleon** is short, broad, more or less calcified, and **folded underneath** the cephalothorax (Sandberg & McLaughlin, 1998) (fig. 70.2A-C). The first pleomere is reduced as in other hermit crab families. The ventral surfaces of the second to fifth pleomeres are also uncalcified. **Tergal development** in these somites differs appreciably, and can be represented by calcified or membranous plates, referred to as **median**, **lateral**, and **marginal plates**. **Supplemental plates** (**median accessory plates**) are sometimes developed adjacent to the
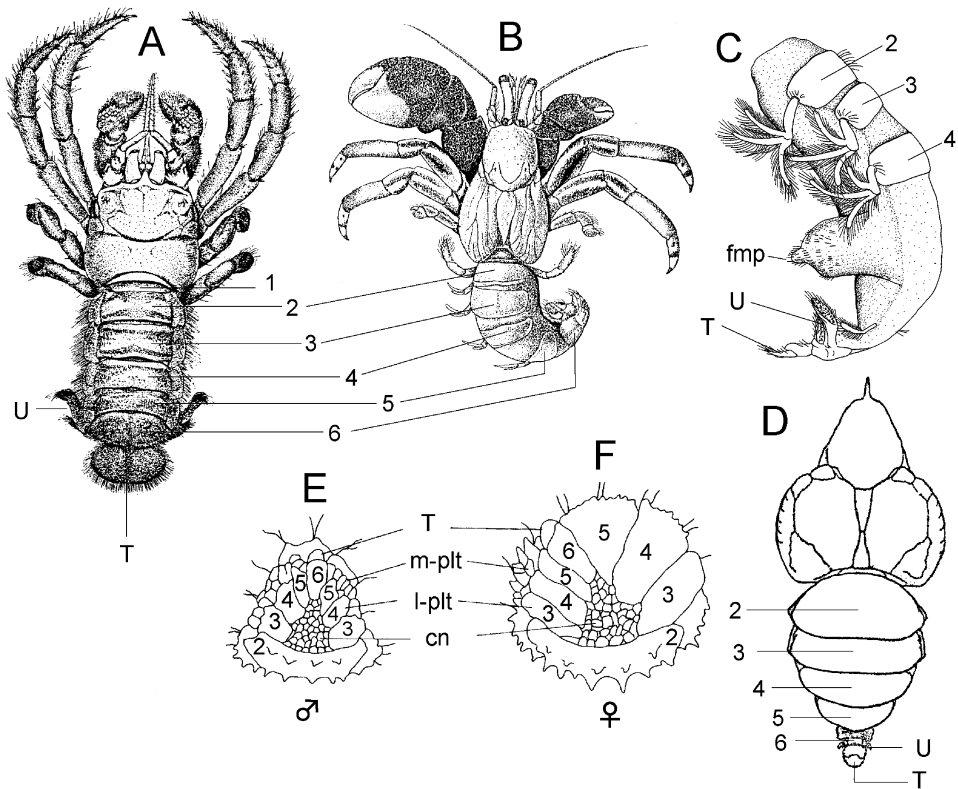
Fig. 70.10. Pleon of Paguroidea and Lithodoidea. A, *Cancellocheles sculptipes* (Miyake, 1978) (Pylochelidae); B, *Calcinus laevimanus* (Randall, 1840) (Diogenidae); C, *Dardanus umbella* Asakura, 2006 (Diogenidae); D, *Birgus latro* (Coenobitidae); E, male of diagrammatic lithodid; F, female of diagrammatic lithodid. A, B, D, dorsal; C, dorsolateral, left; E, F, ventral. Abbreviations: 1 through 6, (position of) first through sixth pleomere; cn, central nodule; fmt, fleshy membraneous protuberance; l-plt, lateral plate; m-plt, marginal plate; T, telson; U, uropod. [A, after Miyake, 1978; B, after Alcock, 1905; C, after Asakura, 2006a; D, after Borradaile, 1916; E, F, after Sandberg & McLaughlin, 1998.]

median plate. In Hapalogastridae, the tergites of the third to fifth somites are entirely uncalcified. In some genera of Lithodidae, the median plates of the tergites of the third to fifth somites are similarly uncalcified. The marginal plates may be **subdivided** into two or more **small plates**. Membranous areas and/or plates may be covered with **calcareous nodules** (Sandberg & McLaughlin, 1998).

In females, the plates on the **right side** are frequently more strongly developed than those on left, resulting in an **asymmetrical pleon** (fig. 70.10F), although this is not always obvious in some genera. In males, these plates are symmetrical (fig. 70.10E).

GALATHEOIDEA AND CHIROSTYLOIDEA

The **pleon** of galatheoids and chirostyloids is symmetrical, and consists of six freely articulating somites and the telson. The **uropods** are well developed, forming, with the

telson, a **tail fan**. The pleon in galatheoids and chirostyloids is typically carried tucked beneath the cephalothorax (figs. 70.3C-F, 70.17A, 70.18A, 70.19A, 70.20A).

Among the galatheoids, members of the Galatheidae, Munididae, and Munidopsidae have a well-developed pleon, generally uniform across the group. The **tergites** are typically strongly convex, being subcylindrical in cross-section for the anterior somites, and becoming flattened for the posterior somites. The first somite is **narrower** than the posterior width of the carapace and markedly shorter than the second somite. The **pleura** are present as an **oblique flange** on each lateral margin of the first somite. These flanges articulate anteriorly with the posterolateral margin of the carapace, and posteriorly with the **pleuron** of the second somite. The second through fifth somites have distinct pleura, of which the second is largest (fig. 70.17A, B). The sixth somite bears a pair of biramous uropods. The **telson** is broad and lamellar, consisting of multiple **calcified elements** separated by **transverse** and **diagonal decalcified lines**. The telson is thus **flexible** in multiple planes. The telson surface is sparsely setose, and the margins are lined with plumose setae and sometimes, small denticles. The dorsal surface of the second through fifth pleomeres is typically transversely striated, ridged, and sparsely setose. The ridges of some pleomeres, particularly of the second and third, usually have spines, the number and arrangement of which are **taxonomically diagnostic**. The pleonal surface in *Shinkaia* (Munidopsidae) is smooth and sparsely setose.

The **pleon** in Porcellanidae is structurally similar to that of other galatheoids, but with somites much shorter and flatter, enabling the pleon to be tucked more fully beneath the cephalothorax (figs. 70.3F, 70.19A, E). Similarly, the pleura of porcellanids are further reduced in comparison to that of other galatheoids. The telson and uropods of porcellanids, like those of other galatheoids, is broad and lamellar, the telson consisting of 5 to 7 calcified elements separated by transverse and diagonal decalcified lines.

As in Galatheoidea, the pleon in Chirostyloidea is held partially tucked under the cephalothorax (fig. 70.18A).

In Chirostylidae, the first pleomere is shorter than the second, and narrower than the posterior width of the carapace. The second through fifth somites have short but distinct pleura, of which the second is largest (fig. 70.18A, F). The pleura are usually rounded to truncate, but may be acutely triangular in *Gastroptychus* and *Chirostylus*. The sixth somite bears a pair of biramous uropods. The dorsal surface of the pleon is smooth in most Chirostylidae, but is often spinous or tuberculate in *Gastroptychus*. The telson is usually broader than long (occasionally as wide as long), membranous, and divided into an anterior and posterior portion by a transverse suture. The posterior portion is usually medially emarginate.

The pleon of Eumunididae is similar to that of Chirostylidae, although the dorsal surface is marked by **transverse striae**, and the second pleonite bears a strong, anterolaterally directed spine on each side (this spine is also present in Aeglidae, although proportionally smaller).

In Kiwaidae, the pleon is smooth, spineless, and sparsely setose (figs. 70.3D, 70.20A). The second through sixth somites have distinct pleura, each with two **longitudinal carinae** near the posterior margins. The sixth somite bears well-developed biramous uropods. The

telson is as long as wide, membranous, and divided into an anterior and posterior portion by a transverse suture (fig. 70.20D). The anterior portion is transversely ovate. The posterior portion is narrower than the anterior portion, and divided by a shallow longitudinal median suture. The posterior margin is distinctly emarginate.

AEGLOIDEA

The **pleon** is well developed with six pleonites and a telson. The fifth and sixth pleonites and the telson and uropods are usually held under the pleon, with only the first four pleonites being visible dorsally (fig. 70.3A). The first pleonite is reduced and largely covered by the posterior edge of the carapace. As in Eumunididae (Chirostyloidea), the second pleonite has a stout, anterolaterally directed spine on each pleuron. Dorsally, the pleonites are heavily calcified and have large, ventrally directed lateral pleura. The ventral surface of each pleonite though, is reduced to a membraneous covering (except for a thin calcified bar on the first pleonite). The telson is a simple, broad plate, usually divided by a central suture (fig. 70.21G).

LOMISOIDEA

The **pleon** in *Lomis* is symmetrical, well developed, and has six pleonites and a telson. The dorsal surface is well calcified in both sexes, but the ventral surface is predominantly membraneous. The first pleonite is reduced to a small, triangular somite about one-third the width of the second pleonite (fig. 70.22A). The second pleonite is the largest (being slightly wider than the posterior carapace) and the third through sixth pleonites are each progressively smaller. This gives the entire pleon a triangular appearance (slightly more rounded in the female) when extended. Pleonites two and six are the longest somites and three through four are approximately equal in length. The telson is a small, semicircular structure and is undivided (fig. 70.22E).

HIPPOIDEA

In Blepharipodidae and Albuneidae, the **pleon** is weakly folded underneath. The first pleomere is trapezoidal or subrectangular. In Blepharipodidae, the second to fifth and, in Albuneidae, the second to fifth or the second to fourth, pleomeres have pleura that are expanded and directed laterally, anterolaterally, or posterolaterally. The sixth pleomere is small and subrectangular. The telson is ovate and its terminal margin is entire (figs. 70.4A, B, 70.9D, E).

In Hippidae, the pleon is folded underneath. The telson is elongate, lanceolate, apically acute, and firmly pressed against the thorax (figs. 70.4C, D, 70.9H-J).

Appendages

CEPHALON

Antennule. – This comprises the first cephalic appendage, when the pre-segmental region, **acron**, is not counted. All crustacean appendages are regarded as **biramous**, each consisting of a basal **protopod** and two terminal **rami**, i.e., an **endopod** and an **exopod**.

In the **antennulae** of **hermit crab** species, two **flagella** commonly arise from a **peduncle**, showing the biramous condition. However, as has been pointed out by McLaughlin (1982), there is considerable doubt as to whether these biramous flagella are homologous with the endopod and exopod of typical biramous appendages (Calman, 1909). In particular, this doubt arises from studies on larval development of primitive decapods and euphausiids (Dobkin, 1961; Lomakina, 1978). Therefore, in most taxonomic studies, these flagella are simply described as "**upper** flagellum", "upper rami of flagella", or "**dorsal** flagellum", and "**lower** flagellum", "lower rami of flagella" or "**ventral** flagellum". However, Ingle (1993) described these structures as "exopod" and "endopod" in his large monograph of North Atlantic and Mediterranean Sea hermit crabs. But, to date, there is no study to answer satisfactorily the question of **homology**.

In **Paguroidea**, the **peduncle** of the antennula is three-segmented, referred to as (from proximal to distal) the basal, penultimate, and ultimate segments, or the first to third peduncular segments (fig. 70.11A). The basal segment is generally short, but noticeably broad in some species of *Dardanus*, and has a prominent **statocyst**, a diminutive organ providing a sense of balance. The ultimate and penultimate segments are generally long and sparsely setose, except in some species of *Pagurixus*, e.g., *Pagurixus boninensis* (Melin, 1939), which bears two rows of tufts of short setae on the ventral face of the ultimate segment (McLaughlin & Haig, 1984), and in *Anapagurus hyndmanni* (Bell, 1845), in which dense, long setae are present on the ventral face of both the ultimate and penultimate segments (Ingle, 1993). In many species, a few to several exceptionally long setae are present at the dorso-distal angle of the ultimate segment. Two multi-segmented flagella arise apically from the ultimate segment. The **upper flagellum** is generally long and its ventral margin bears numerous long **aesthetascs**. In marine species, the flagella terminate in a tapered filament, but in land hermit crabs of the family Coenobitidae, the flagella terminate bluntly, somewhat "stick-like", and distally a few to several segments are fused (fig. 70.11G). The **lower flagellum** is short and small in both marine and terrestrial species. The antennulae are most commonly much shorter than the antennae, but in coenobitids they are much longer than the antennae (fig. 70.11G).

In **Lithodoidea**, this appendage is morphologically quite similar to that of Paguroidea.

In **Galatheoidea** and **Chirostyloidea**, the antennule consists of a 3-segmented **peduncle** and a pair of flagella. The basal segment is generally short and stout, and usually bears distal and lateral spines. The second and third peduncular segments are generally slender, subcylindrical, or subconical in Chirostyloidea and most Galatheoidea (figs. 70.17A, B, 70.18A), and short and shout in Porcellanidae (fig. 70.19A). The basal antennular segment holds numerous important **taxonomic characters**, most notably the distolateral and distomesial spines, and the lateral spines. In Kiwaidae (Chirostyloidea), all segments are unarmed and glabrous apart from some short distolateral setae on the basal segment (fig. 70.20C). Two multi-segmented flagella arise from the apex of the third segment. In Galatheoidea and most Chirostyloidea, the **upper flagellum** is longer and thicker than the lower flagellum, and its ventral margin bears numerous long aesthetascs, and terminates in a tapered filament; the **lower flagellum** is slender and evenly tapered. In Kiwaidae, unlike
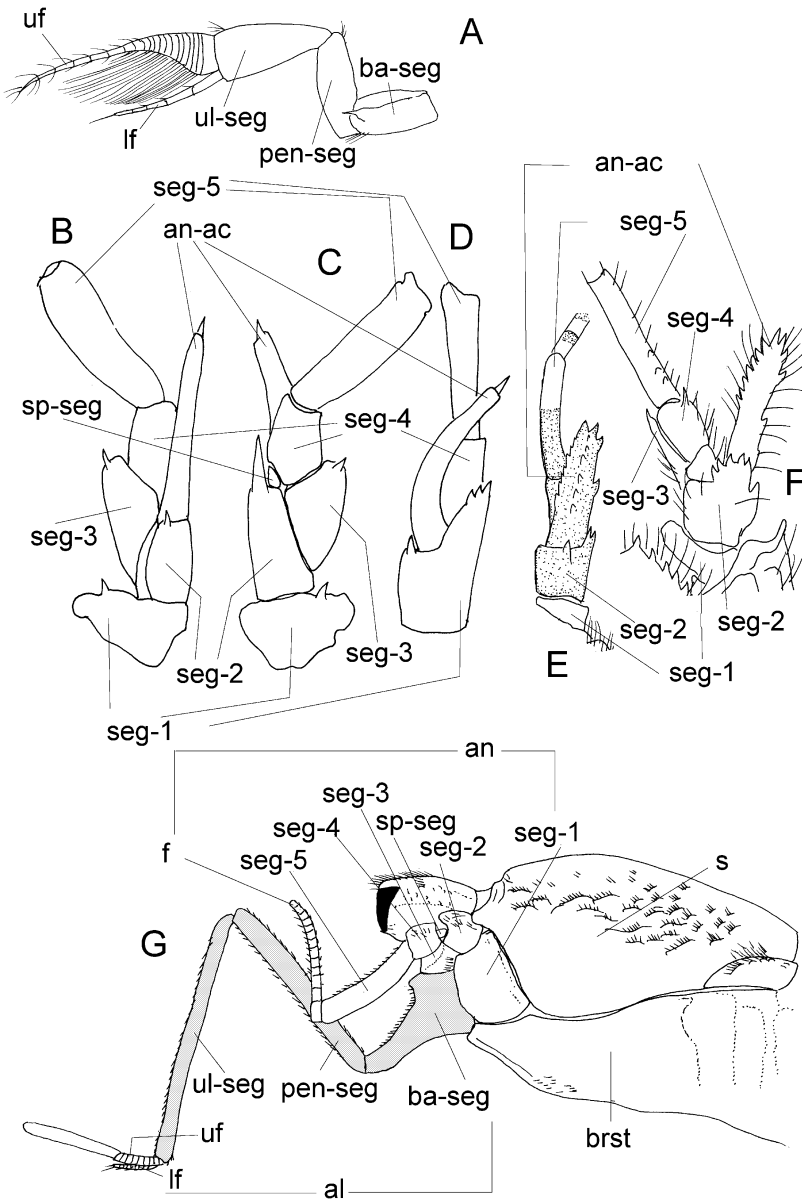
Fig. 70.11. Antennulae and antennae of Paguroidea. A, left antennule, lateral, *Pseudopaguristes bollandi*; B, right antenna, mesial, *Boninpagurus acanthocheles* Asakura & Tachikawa, 2004; C, same, lateral; D, same, dorsal; E, right antenna, dorsal, *Pseudopaguristes shidarai* Asakura, 2004; F, left antenna, lateral, same; G, left lateral view of anterior half of cephalothorax, *Coenobita spinosus* H. Milne Edwards, 1937. Abbreviations: al, antennule; an, antenna; an-ac, antennal acicle; ba-seg, basal segment; brst, branchiostegite; f, flagellum; lf, lower flagellum; pen-seg, penultimate segment; s, shield; seg-1 to seg-5, segments 1 to 5; sp-seg, supernumerary segment; uf, upper flagellum; ul-seg, ultimate segment. [A, after Asakura & McLaughlin, 2003; B-D, after Asakura & Tachikawa, 2004; E, F, after Asakura, 2004a; G, after Asakura, 2004b.]

other chirostyloids, the dorsal and ventral flagella are short and subequal in length and the ventral flagellum has two swollen basal segments followed by a slender terminal portion.

In **Aegloidea**, the antennule is characterized by a **globose basal segment** followed by a **two-segmented stalk**. The distal segment has two short **flagella**, the dorsal one with 10-13 segments and the ventral one with about 10 segments. The basal segment has both simple and plumose setae, while just long simple setae are present proximally on the second peduncular segment.

In **Lomisoidea**, the antennular **peduncle** is three-segmented with the second and third segments being the longest and equal in length. The distal segment has two short **flagella**, the dorsal one larger than the ventral.

Among **Hippoidea**, the antennulae are generally much longer and stouter than the antennae in Blepharipodidae and Albuneidae, but in Hippidae, they are much shorter than the antennae (figs. 70.4A-D, 70.9F). The **peduncle** is three-segmented. The **dorsal flagellum** consists of 18-85 articles in Blepharipodidae and 17-250 in Albuneidae, and the **ventral flagellum** consists of 6-12 articles in Blepharipodidae and 0-7 in Albuneidae. In Hippidae, *Emerita* species have the antennulae about three times the length of the ocular peduncles.

Antenna. – In Paguroidea, the **antenna** is composed of a long, uniramous **flagellum**, an **exopod** referred to as the "antennal acicle" in the six hermit crab families, or as the "scaphocerite" in lithodoids, a **peduncle** consisting of five segments referred to as (proximal to distal) the first to fifth segments, and also very often, a small segment referred to as the "supernumerary segment" between the third and fourth segments dorsolaterally (figs. 70.5A-C, 70.6A, B, 70.11B-F). In marine species, the flagella are generally long and terminate in a tapered filament. Setation of the flagella varies from sparse and short, to moderately long and with numerous setae. Many species of *Diogenes* and several species of *Paguristes* have a double row of very long plumose setae, forming a **setal net** on each flagellum. By rotating these flagella, they filter out organic particles from suspension in the seawater. The antennal acicles are most often armed with short spines in species of Diogenidae and Parapaguridae (fig. 70.5A-C, E). In contrast, the antennal acicles of species in Paguridae are often poorly armed and sometimes long and curved laterally (fig. 70.11B-D). The first segment of the peduncle is sometimes armed with one to a few spines on the ventrodistal margin. In the second segment, the dorsolateral distal angle is often produced anteriorly and terminated acutely, and, similarly, the dorsomesial distal angle is often provided with a spine. The ventrodistal margin of the third segment is generally produced, and sometimes armed with a spine. The fourth segment is short and the fifth is long and slender in most species.

In **Lithodoidea**, this appendage is morphologically quite similar to that of Paguridae, except for the acicle that is sometimes reduced to a small sclerite only.

Whereas the plesiomorphic condition in Anomura is five free segments, in **Galatheoidea** the second and third segments are fused, resulting in a 4-segmented **peduncle** and a long, uniramous **flagellum** (figs. 70.17A, 70.19A). No acicle is present. The immovable basal segment is broad and stout, usually with a distomesial spine or projection, and includes the **antennal gland aperture** (fig. 70.17E). The second segment usually bears

a distomesial and distolateral spine or projection in most galatheoids, but is variously ornamented in Porcellanidae (fig. 70.19C). The third and fourth segments are much smaller than the preceding, and are usually unarmed. The flagellum terminates in a tapered filament. In most Galatheoidea, the antenna is directed anteriorly or anterolaterally, whereas in Porcellanidae, the antenna is directed laterally or posterolaterally (fig. 70.19A, C).

In **Chirostyloidea**, the antenna is composed of a five-segmented **peduncle**, a supernumerary segment as in paguroids, an **acicle** articulating with the second segment, and a long, uniramous **flagellum** (figs. 70.18C, 70.20C). The basal segment is short and stout, and includes the **antennal gland aperture**. The second segment usually bears a distolateral spine or projection and articulates with the acicle (when present). The third segment is similar in size to the second segment, and the fourth and fifth segments are progressively longer, except in Kiwaidae, in which the third through fifth segments are of similar size. Each of the peduncular segments may bear spines or granules. The flagellum terminates in a tapered filament. The acicle is present in Chirostylidae (except *Chirostylus* and *Hapaloptyx*), present in Eumunididae, and absent in Kiwaidae; it is typically lanceolate, but may bear short spines.

In **Aegloidea**, the antenna is longer than the antennule and may be up to twice the length of the body. The **peduncle** is five-segmented but the second and third segments are fused, making it appear superficially four-segmented (fig. 70.21C). The basal segment is globose, the next three segments are basically triangular and interlocking, while the last (fifth) segment is subcylindrical and the longest of all. The **flagellum** is long and multiarticulate.

In **Lomisoidea**, the antennal **peduncle** has six segments and a multi-articulate **flagellum**, that curves towards the mouthparts. The scaphocerite is absent (fig. 70.22B).

In **Hippoidea**, the antenna is composed of a uniramous **flagellum**, an exopod referred to as the **"antennal acicle"**, and a **peduncle** consisting of five segments (fig. 70.23B). The **flagellum** is generally short and composed of 8-44 articles in Blepharipodidae and 1-9 articles in Albuneidae. In Hippidae, the antennae of the species of *Emerita* have the long flagella densely beset laterally with several rows of fringed setae. The antennae of the species of *Hippa* have short flagella composed of one to several articles (figs. 70.9F, 70.23M).

Mandible. – The mandibles are the innermost appendage pair of the mouthparts. In **Paguroidea**, the mandible is well developed. The associated **palp** is three-segmented in the majority of species (fig. 70.12A), but exceptions are *Anapagurus bicorniger* A. Milne-Edwards & Bouvier, 1892 and *Catapaguroides megalops* A. Milne-Edwards & Bouvier, 1892 (both Paguridae), in which only two segments can be recognized (Ingle, 1993). The ultimate segment of the palp is ovate and its margin is invested with numerous stiff setae. The **incisor** and **molar processes** are calcareous and most often unarmed, but 3-5 blunt teeth are sometimes recognized in the incisor processes of species of *Pylopaguropsis* (cf. Asakura, 2000). A notable exception is presented by the species belonging to a recently established family, Pylojacquesidae, whose incisor process is mostly corneous and armed with prominent, acute teeth.

In **Lithodoidea**, this appendage is morphologically quite similar to that of Paguridae.
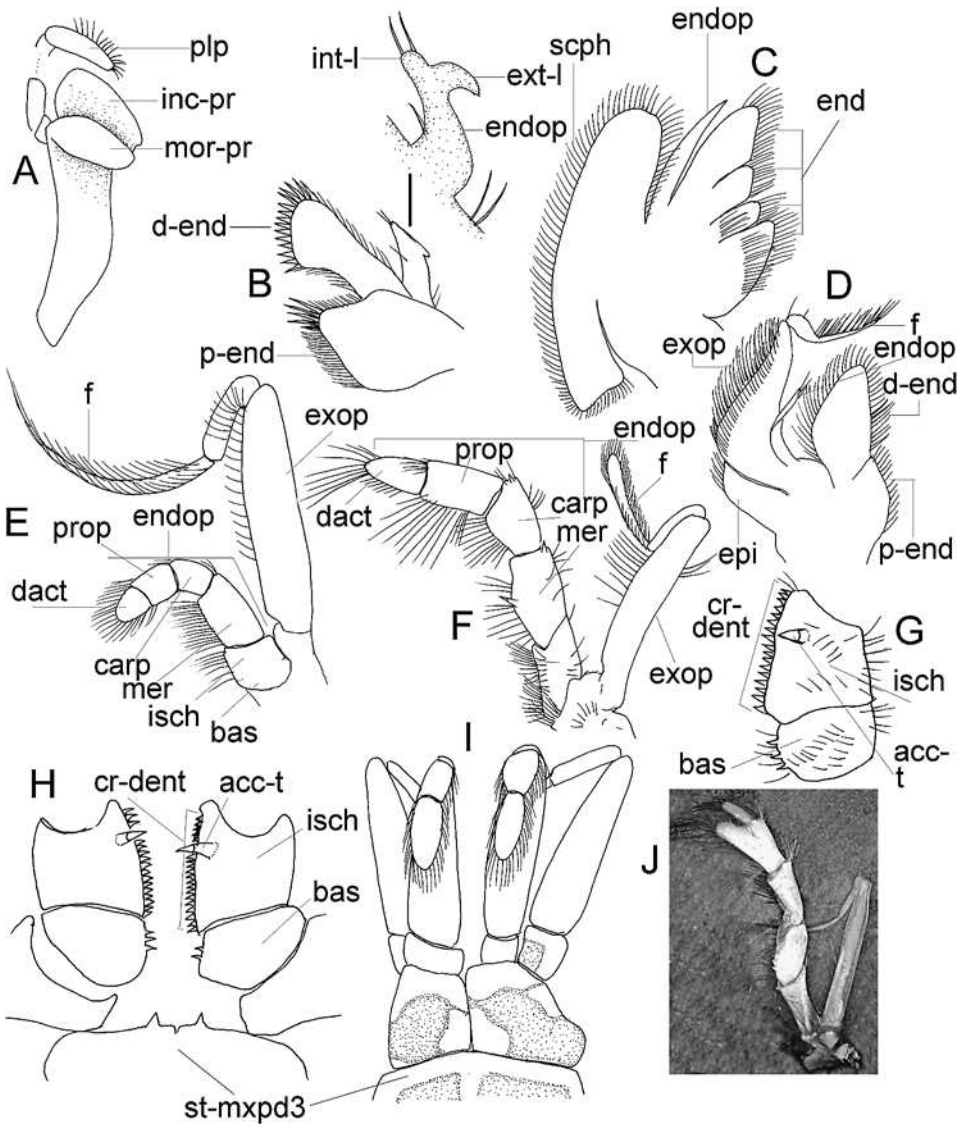
Fig. 70.12. Mouthparts of Paguroidea. A-E, I, *Pseudopaguristes bollandi*; F-H, *Boninpagurus acanthocheles*; J, *Pomatocheles jeffreysii*. A, mandible, left, internal; B, maxillule, left, external; C, maxilla, left, internal; D, first maxilliped, left, internal; E, second maxilliped, left, external; F, third maxilliped, left external; G, same, ischium and basis, internal; H, basal portion of third maxillipeds and its sternite, ventral, setae omitted; I, third maxillipeds and their sternite, ventral; J, third maxilliped, right, mesial. Abbreviations: acc-t, accessory tooth; bas, basis; carp, carpus; cr-dent, crista dentata; dact, dactylus; d-end, distal endite; end, endite; endop, endopod; epi, epipod; exop, exopod; ext-l, external lobe; f, flagellum; inc-pr, incisor process; int-l, internal lobe; isch, ischium; mer, merus; mor-pr, moral process; p-end, proximal endite; plp, palp; prop, propodus; scph, scaphocerite; st-mxpd3, sternite of third maxillipeds. [A-E, I, after Asakura & McLaughlin, 2003; F-H, after Asakura & Tachikawa, 2004; J, photo by Akira Asakura.]

In **Galatheoidea**, the mandible is well developed, though the **molar process** is reduced to a blunt ridge along the posterior margin of the corpus. The occlusal margin of the **incisor process** is calcareous and feebly toothed. The **palp** is three-segmented, of which the third segment is ovate with several simple distal setae. The first and second palp segments are simple, with the second being longer.

As in Galatheoidea, the mandible in **Chirostyloidea** has a reduced **molar process** and a well developed **palp**, being two-segmented in Kiwaidae, and three-segmented in Chirostylidae and Eumunididae. The cutting edge of the **incisor process**, however, is strongly toothed in Chirostylidae and Kiwaidae, being calcareous in the former, chitinous in the latter. In Eumunididae, the cutting edge is tridentate.

In Aegloidea, the mandible has a well developed, strongly sclerotized, and asymmetrical **incisor process**, but a virtually absent **molar process**. The mandibular **palp** is two-segmented (both segments about equal) with the proximal segment bearing simple and plumose setae and the distal segment being flattened, ovate, and bordered with simple, pappose and plumose setae.

In Lomisoidea, the mandible is currently undescribed for *Lomis hirta*.

In Hippoidea, the general morphology of the mandible in Albuneidae and Blepharipodidae is quite similar to that of Paguroidea. The **incisor process** is calcareous and often provided with a few blunt teeth, and the cutting edge is also with or without a tooth. The **palp** is three-segmented (fig. 70.23C).

Maxillule. – The **maxillule** is the second appendage pair of the mouthparts and is composed of an **endopod** and **bilobed endites**, called the **distal** and **proximal endites**, reespectively. In **Paguroidea**, although McLaughlin (1980, 1982) interpreted the "endite" as the mesial protrusion of the margin of the protopod, Ingle (1993) referred these bilobed structures to the basis and coxa of the protopod. Since the protopod is segmented into a coxa and a basis, Ingle (1993) interpreted that these lobed structures are the protopod itself. The **exopod** is considered absent in species of Paguroidea (cf. Jackson, 1913). The endopod is provided, or not, with an **external lobe**, and if present, the shape of the external lobe usually has **taxonomic value** (fig. 70.12B).

In **Lithodoidea**, this appendage is morphologically quite similar to that of Paguridae.

In **Galatheoidea** and **Chirostyloidea**, the exopod is absent. The **endopod** is slender, unsegmented, and setose. The **distal endite** is spatulate, with its mesial margin lined with simple, corneous setae and plumose setae. The **proximal endite** is much broader and lamellar, and the margins are fringed with simple and plumose setae.

In **Aegloidea**, the maxillule is thin, membraneous, and has an **endopod** and a **proximal** and **distal endite**. The endopod has a few simple setae, while both endites are bordered by many long and short, simple and pappose setae and a few spines.

In **Lomisoidea**, the maxillule in *Lomis* is membraneous and has a 2-3 segmented **endopod** (with a prominent **posteriorly directed lobe**) and a **proximal** and **distal endite**. The endopod is bilobed and the two endites are bordered by long setae.

In **Hippoidea**, the exopod is absent in species of Albuneidae and Blepharipodidae (fig. 70.23D).

Maxilla. – The **maxilla** is the third appendage pair of the mouthparts and composed of an **exopod**, an **endopod**, and **endites**. In **Paguroidea**, the exopod is very well developed into a large, lobulate **"scaphognathite"** (fig. 70.12C) and is closely apposed to the lateral, inner surface of the cephalothorax, where it is used to develop a **respiratory current**. The setae on its margin vary in number and size, and the shape of the posterior lobe may be sub-acute, truncate, or sub-oval (Ingle, 1993). The endopod is broadened proximally and thin distally, and usually, four endites are recognized on the mesial margin (McLaughlin, 1974). However, these structures are again interpreted as the bilobed basis and coxa of the protopod by Ingle (1993). This difference in interpretation is still controversial.

In **Lithodoidea**, this appendage is morphologically quite similar to that of Paguridae.

In **Galatheoidea** and **Chirostyloidea**, the **scaphognathite** is large, broadly reniform, and flattened, with margins lined by simple and plumose setae. The maxilla has a slender, setose **endopod**. Two **endites** are typically recognized, each of which, as a result of a marginal incision dividing each endite, is usually bilobed. The margins of both endites bear numerous simple and plumose setae.

In **Aegloidea**, the maxilla is a large, flattened appendage primarily used for pumping water over the anterior branchial surfaces. The **endopod** and the bilobed distal and proximal **endites** project ventrally, while the large paddle-like **scaphognathite** projects dorsally. Both endites are bordered with numerous simple, pappose and plumose setae while the scaphognathite is lined with plumose setae only.

In **Lomisoidea**, the maxilla is composed of a ventral bilobed **endite** and a paddle-like **endopod**, while the dorsal exopod is very well developed into a large, flat **scaphognathite**. The margins of endopods and exopod are all bordered with long setae.

In **Hippoidea**, the general morphology of the maxilla in Albuneidae and Blepharipodidae is similar to that of Paguroidea (fig. 70.23E).

THORAX

First maxilliped. – Being the first thoracic appendage, the first maxilliped also is the fourth appendage pair of the mouthparts and is composed of an **exopod**, an **endopod**, and **endites**. In **Paguroidea**, the exopod is noticeably narrow distally and broadened proximally in the majority of species (fig. 70.12D). The **exopod** bears a multiarticulate flagellum, but the flagellum is lacking in species of Parapaguridae. The **epipod** is difficult to recognize in most species of Paguridae, but it is well developed in Pylochelidae and some genera of Diogenidae, including *Dardanus*, *Paguristes*, and *Pseudopaguristes*. The endopod is short in most species and does not reach to, or beyond, the distal margin of the distal endite ("basis" by Ingle's, 1993, interpretation).

In **Lithodoidea**, this appendage is morphologically quite similar to that of Paguridae.

In **Galatheoidea** and **Chirostyloidea**, the **exopod** is usually two-segmented and bears a setose **pseudo-flagellum**. The distal segment is slender, and together with the pseudo-flagellum, is termed the **'lash'**. In Eumunididae, Kiwaidae, and most galatheoids the flagellum is multiarticulate. Munidopsidae, *Chirostylus*, and *Hapaloptyx*, however, lack the lash, and in other chirostylids, the lash is smooth and undivided (Schnabel & Ahyong, 2010). The endopod is digitiform to crescent-shaped, or spatulate (Kiwaidae). The distal

and proximal endites are well developed, bearing coarse plumose setae, and the distal endite is the larger. The **epipod** is absent in Chirostylidae and present in Eumunididae, Kiwaidae, and all Galatheoidea.

In **Aegloidea**, the first maxilliped is thin, foliose, and only slightly larger than the maxilla. The **exopod** is 2-segmented with the proximal portion produced into a large lamellar lobe and the distal portion terminating in a multi-articulated **flagellum**. The **endopod** has a reduced, palp-like terminal lobe and well-developed distal and proximal endites. The proximal endite is small and ovoid, while the distal endite is larger and subrectangular. All articles of the first maxilliped are lined with a dense border of a variable mixture of simple, pappose, plumose, and a few comb setae.

In **Lomisoidea**, the exopod bears a flagellum in *Lomis*. An epipod is present.

In **Hippoidea**, the two-segmented exopod of Albuneidae and Blepharipodidae lacks a flagellum. The epipod is present (fig. 70.23F).

Second maxilliped. – The second maxilliped constitutes the fifth appendage pair of the mouthparts, and the second thoracic appendage. In **Paguroidea**, the **exopod** bears a long, multiarticulate **flagellum**, and, in addition, at least two segments are recognized in its **peduncular portion** (fig. 70.12E). In the **endopod**, segmentation is well developed and the dactylus, propodus, carpus, merus, and ischiobasis, the latter rarely separated into basis and ischium, can be recognized. In some species of Pylochelidae, the epipod is present.

In **Lithodoidea**, this appendage is morphologically quite similar to that of Paguridae.

In **Galatheoidea** and **Chirostyloidea**, the **exopod** comprises two setose peduncular segments and a multiarticulate flagellum. The **endopod** is setose and consists of the dactylus, propodus, carpus, merus, and ischiobasis. The epipod is absent.

In **Aegloidea**, the second maxilliped is morphologically very similar to that recorded for Paguroidea and Galatheoidea. The **exopod** comprises two peduncular segments (the proximal one setose) and a multiarticulate flagellum. The **endopod** is setose, pediform, and consists of the dactylus, propodus, carpus, merus, and ischiobasis. An epipod is absent.

In **Lomisoidea**, the second maxilliped is morphologically very similar to that recorded for Paguroidea and Galatheoidea.

In **Hippoidea**, the exopod of Albuneidae and Blepharipodidae is two-segmented and the flagellum is composed of only one elongate article (fig. 70.23G). The endopod is similar to that of Paguroidea.

Third maxilliped. – The third maxillipeds comprise the sixth and outermost appendage pair of the mouthparts, and the third pair of appendages of the thoracic region. In **Paguroidea**, the **exopod** bears a long **flagellum**, and, in addition, at least two segments are recognized in its **peduncular portion** (fig. 70.12F). In the **endopod**, segmentation is well developed, and the **dactylus**, **propodus**, **carpus**, **merus**, **basis**, and **ischium** can all be recognized, although the ischium is sometimes incompletely separated from the basis through an only partial suture. In Pylochelidae, the endopod is **chelate** in *Pylocheles* or **subchelate** in *Cheiroplatea*. In all hermit crab families, most species have the ischium bearing a dentate ridge, the **"crista dentata"**, but also one or more accessory teeth may be present in many species of Pylochelidae and Paguridae (fig. 70.12G, H). The crista dentata is reduced to 3 to 5 large, spine-like teeth in *Scopaeopagurus* and some species

of *Catapagurus* in Paguridae, and is lacking in most species of *Diogenes* in Diogenidae. The **basal portion** of the third maxillipeds is **widely separated** by the **sternal plate** in Paguridae (fig. 70.12H) and Parapaguridae, **approximate** in Diogenidae, Coenobitidae, and Pylochelidae (fig. 70.12I, J), and of **intermediate condition** in Pylojacquesidae. In some species of the Pylochelidae, the epipod is present.

In **Lithodoidea**, this appendage is morphologically quite similar to that of Paguridae.

In **Galatheoidea** and **Chirostyloidea**, the **exopod** consists of a two-segmented peduncle, of which the first segment is the largest, and a setose multiarticulate flagellum. The **endopod** is setose and consists of the dactylus, propodus, carpus, merus, and ischiobasis, and each segment is setose, particularly the dactylus and propodus, which are densely covered with plumose setae (figs. 70.17C, D, 70.18D). The demarcation between ischium and basis is evident as a shallow groove. The **spination of the carpus and merus** is considered particularly important in **galatheoid taxonomy**. The mesial margin of the ischium is cristate, of which the proximal half is dentate (**crista dentata**) (fig. 70.17D). In Galatheidae, Munididae, Munidopsidae, and Chirostyloidea, the third maxilliped is **pediform** and is essentially used to hold food items while feeding. In Porcellanidae, however, the third maxillipeds are **operculiform** through mesial expansion of the carpus, merus, and ischium (fig. 70.19D). Moreover, porcellanids use the third maxilliped to strain food particles from the water column in a manner similar to that used by cirripedes. Thus, the distal four segments in porcellanids are typically equipped with **fan-shaped rows** of long, plumose setae. During feeding, porcellanids swing the third maxillipeds laterally, in an alternating folding and unfolding of the setae, which are in turn wiped by the second maxillipeds. The epipod is present in Galatheidae, Munididae, and Munidopsidae, and absent in Porcellanidae and all Chirostyloidea.

In **Aegloidea**, the third maxilliped is well-developed, pediform, and functions in feeding and grooming. It is morphologically very similar to that described in Galatheoidea, except that the epipod is present as a small membraneous bud proximal to the coxa (fig. 70.21D, E).

In **Lomisoidea**, the third maxilliped is well developed, pediform (fig. 70.22C), and very similar to that described in Galatheoidea.

In **Hippoidea**, most species lack the **crista dentata**, but it is well developed in species of Blepharipodidae (fig. 70.23H); a reduced one is found in several species of *Albunea*. In Albuneidae and Blepharipodidae, the exopod is two-segmented. In Hippidae, this appendage is sub-operculiform and the meri are enlarged and broadened.

First pereiopod. – The first to fifth pairs of the **pereiopods** (fourth to eighth thoracic appendages) are **uniramous**, consisting of **coxa** and **basis** plus a 5-segmented **endopod** (dactylus, propodus, carpus, merus, and ischium). In Paguroidea, the first pereiopod is the **cheliped**. The left and right chelipeds are similar in size and morphology in Pylochelidae (figs. 70.1A, 70.10A), but in Paguridae, Parapaguridae, and Lithodoidea, the right is always larger than the left (figs. 70.1C, H, I, 70.2A-C, 70.13A, B), and the shape and armature are often different between the two. The left cheliped is always larger in Coenobitidae (fig. 70.1G), while in Diogenidae, the left is largest in approximately half of the genera (figs. 70.10B, 70.13C-E), including *Calcinus* and *Diogenes*, and the chelipeds are equal
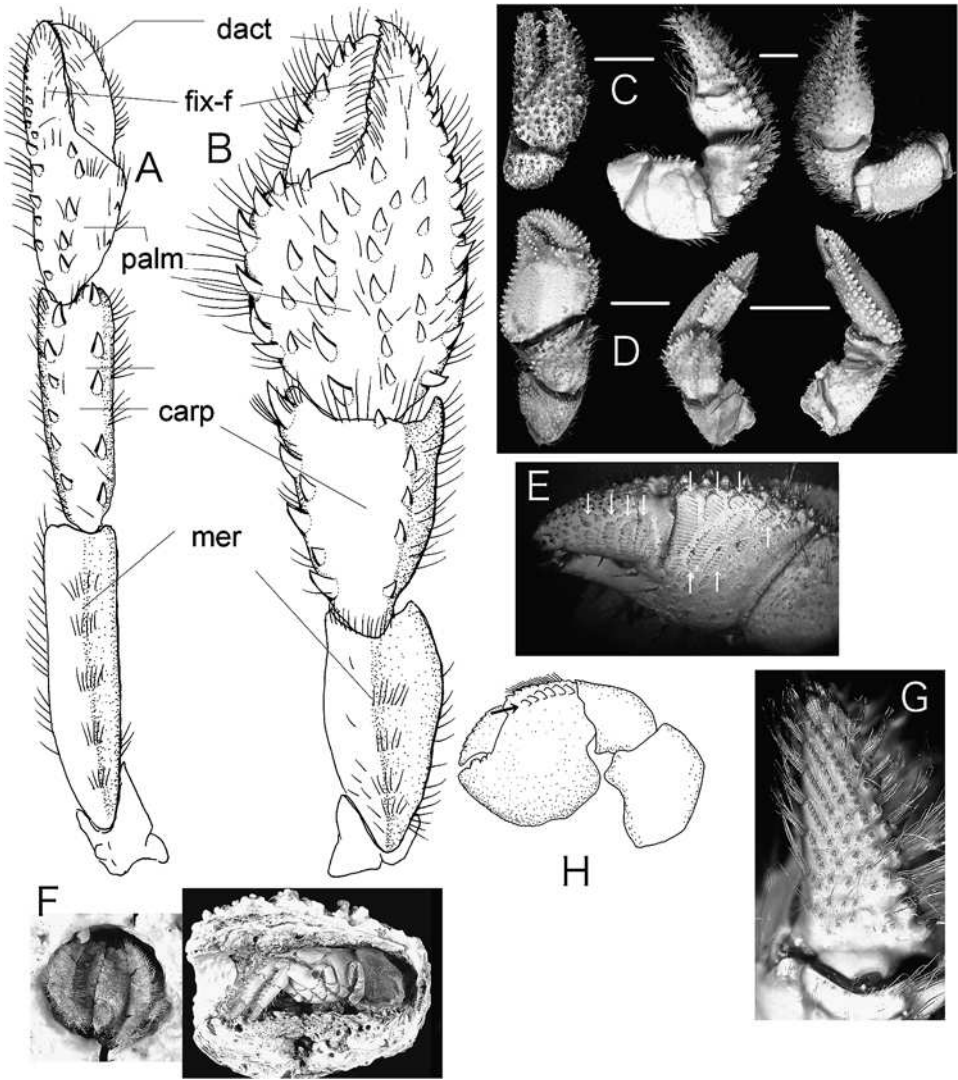
Fig. 70.13. Chelipeds of Paguroidea. A, B, *Micropagurus spinimanus* Asakura, 2005; C, *Stratiotes japonicus* (Miyake, 1961); D, *Diogenes edwardsii* (De Haan, 1849); E, *Strigopagurus strigimanus* (White, 1847); F, *Cancellus typus* H. Milne Edwards, 1836; G, *Paguristes digitalis* Stimpson, 1858; H, diagrammatic *Coenobita*. A, left cheliped, dorsal; B, right cheliped, dorsal; C, left cheliped, dorsal, mesial, lateral (from left to right); D, left cheliped, outer, upper, lower (from left to right); E, right cheliped, arrows indicating stridulatory structures; F, operculate chelipeds and second pereiopod, anterior view (left) and whole body, left lateral view (right); G, dactyl of right cheliped, indicating rows of corneous spines on mesial face; H, left cheliped, outer view, indicating stridulatory structure on outer face. Abbreviations: fix-f, fixed finger; other abbreviations as in fig. 70.12. [A, B, after Asakura, 2005; C, D, G, after Asakura, 2006b; E, photo by Akira Asakura; F, after Asakura, 2003; H, illust. by Akira Asakura.]

or subequal in size and armature in the remaining half of the genera, such as *Paguristes* and *Aniculus* (fig. 70.13G). However, a few exceptions are known in the diogenids, such as *Petrochirus* in which the right is always distinctly larger, and *Pseudopaguristes* and *Clibanarius* in which the size relation between the two chelipeds varies by species. The chelae open horizontally in the majority of species, but in some genera of Diogenidae such as *Dardanus* and *Calcinus*, the propodal-carpal articulations are rotated from the perpendicular plane of the body so that the chelae open in an obliquely vertical plane.

Chelipeds can often be used as an **operculum** for the gastropod shell (or other shelter) inhabited by a hermit crab. Many species in Pylochelidae use both chelipeds to form an operculum (figs. 70.1A), while various species of Diogenidae, Coenobitidae, and Paguridae use the larger cheliped only as an operculum (fig. 70.13H). The morphology of the chelipeds is sometimes different between the sexes and in some species of *Pagurus*, the right cheliped in males is quite large and elongate, e.g., *Pagurus longicarpus* Say, 1817, in comparison to that of the female.

In **Lithodoidea**, this appendage is morphologically quite similar to that of Paguridae.

In **Galatheoidea** and **Chirostyloidea**, the first pereiopods are the obvious **chelipeds**. They are usually longer than the overall body length, and always longer than the carapace, and consist of the dactylus and propodus (which form the chela), carpus, merus, ischiobasis, and coxa (figs. 70.3C, E, F, 70.17A, 70.18A, 70.19A). An epipod is usually present. The chelipeds are usually slightly dissimilar in size in Porcellanidae, but near symmetrical in other Galatheoidea and Chirostyloidea. **Sexual dimorphism**, however, is evident in adult males in which the chelipeds are usually longer and more inflated than in females. Additionally, in some large males of some species of *Munida*, one chela develops a larger gape, between the dactylus and propodus, along with a pronounced tooth on the occlusal margins. This modification is believed to be instrumental in male-to-male competition for mates (Claverie & Smith, 2007). Normally, the occlusal margins of the dactylus and propodus are lined with teeth or nodules, and the apices are calcareous, and usually simple. In Kiwaidae, the cheliped fingers have corneous denticulation distally and corneous scales lining the remaining occlusal margins. In many species of *Munidopsis* and several other galatheoid genera, the cheliped fingers terminate in a series of teeth that interdigitate when the chela is closed. In porcellanids, the chelipeds are dorsoventrally flattened, with a broad chela and carpus. When folded, the chelipeds are held transversely and they typically open horizontally (fig. 70.19A). In Galatheoidea and Chirostyloidea, the chelipeds are typically subcylindrical (broad and flattened in *Shinkaia*), held anteriorly, and the chelae typically open vertically. The chelipeds in all groups may be variously ornamented with spines, tubercles, striae, and setae. In Kiwaidae, the surfaces of the chelipeds are studded with conical spines and tubercles, and are densely covered with plumose setae (fig. 70.3D).

In **Aegloidea**, the first pereiopods are chelate, asymmetrical (almost always larger on the left side), and often larger in males than in females. The **cheliped** is often highly variable in form both between sides in the same individual and within a species. The dactylus is usually short and heavy, dorsally and laterally smooth or finely granulate, with the cutting edge lined with low corneous scales or tubercles. The propodus is large and

inflated (fig. 70.3A), usually with a smooth or finely granulate surface, and the cutting edge may or may not have a large proximal tubercle or tooth. A characteristic of the aeglids is the presence in most species (see Bond-Buckup & Buckup, 1994) of a large **palmar ridge**, **crest**, or **lobe** (armed or unarmed) on the dorsal surface of the propodus. The carpus is short and stout, and dorsally armed with 4-5 large corneous spines. The merus is heavy and triangular, and similarly armed with three rows of corneous spines. The ischium and basis are fused and unarmed, except for the occasional presence of a large ventromesial spine. The coxa is heavy, globose, and generally unarmed.

In **Lomisoidea**, the **chelipeds** are dorsoventrally flattened and inwardly directed in *Lomis*, like in Porcellanidae (fig. 70.3B). All segments are stout, and covered with coarse granulations and punctuations of setae. A significant palmar crest, ridge, or lobe is present, as in aeglids.

In **Hippoidea**, the first pereiopods are similar from left to right. In Hippidae, they are not chelate but simple, and the dactyli are cylindrical or lamellate (figs. 70.4C, 70.9H). The first pereiopods in Albuneidae and Blepharipodidae are large, well calcified chelipeds (fig. 70.23I). The carpus is with (Blepharipodidae) or without a dorsodistal spine (Albuneidae).

Second and third pereiopod. – In **Paguroidea**, these appendages are well developed and used for **walking**, or very rarely **swimming**, such as in the pagurids *Iridopagurus* and *Spiropagurus* (cf. de Saint Laurent-Dechance, 1966; Garcia-Gomez, 1983). Adaptation for swimming among hermit crabs consists primarily of the development of natatory setae on these appendages (McLaughlin, 1982). The appendages at issue are sometimes **asymmetrical**, in particular in Paguridae, Diogenidae, and Coenobitidae. In many species of *Dardanus* (Diogenidae), the dactylus and propodus of the left third pereiopod are much broader and the armature is often more complicated than on those of the right third appendage. Most species of land hermit crab, *Coenobita*, use the left cheliped and left second and third pereiopod as an **operculum** of their gastropod host shell, and consequently the dactylus and propodus are broad and their lateral faces are flattened. Conspicuous dissimilarlity in these appendages is also known in many other genera including *Clibanarius*, *Pylopaguropsis*, and *Pagurodofleinia*. Setation is also different from left to right in some species. For example, *Diogenes patae* Asakura & Godwin, 2006 has dense, plumose setae on the lateral faces of the left second and third pereiopod, but those of the right lack such setation. A wide variety of morphology is seen in the **dactyli** of the second and third pereiopods. Cylindrical or subcylindrical-shaped dactyli are known in many species in Paguridae, Diogenidae, and Lithodoidea, and these are frequently armed with rows of corneous spines, in particular on the ventral faces and sometimes on the mesial faces dorsally (fig. 70.14A-I). In these cases, the dactyli can sometimes be slightly curved ventrally as well. Flattened dactyli are known in *Diogenes* (Diogenidae) and various species in Paguridae, such as *Catapagurus* (fig. 70.14J, K), in which the dactyli are sometimes unarmed but provided with rows of setae. The dactyli of many species of Parapaguridae are slender and slightly curved ventrally (fig. 70.1H, I). The morphology of the **propodi** is varied, but is generally rectangular or subrectangular from lateral view. The armature of the propodi is also varied, as a few corneous spines at the ventrodistal angle, a row of corneous spines on the ventral margin, or a row of
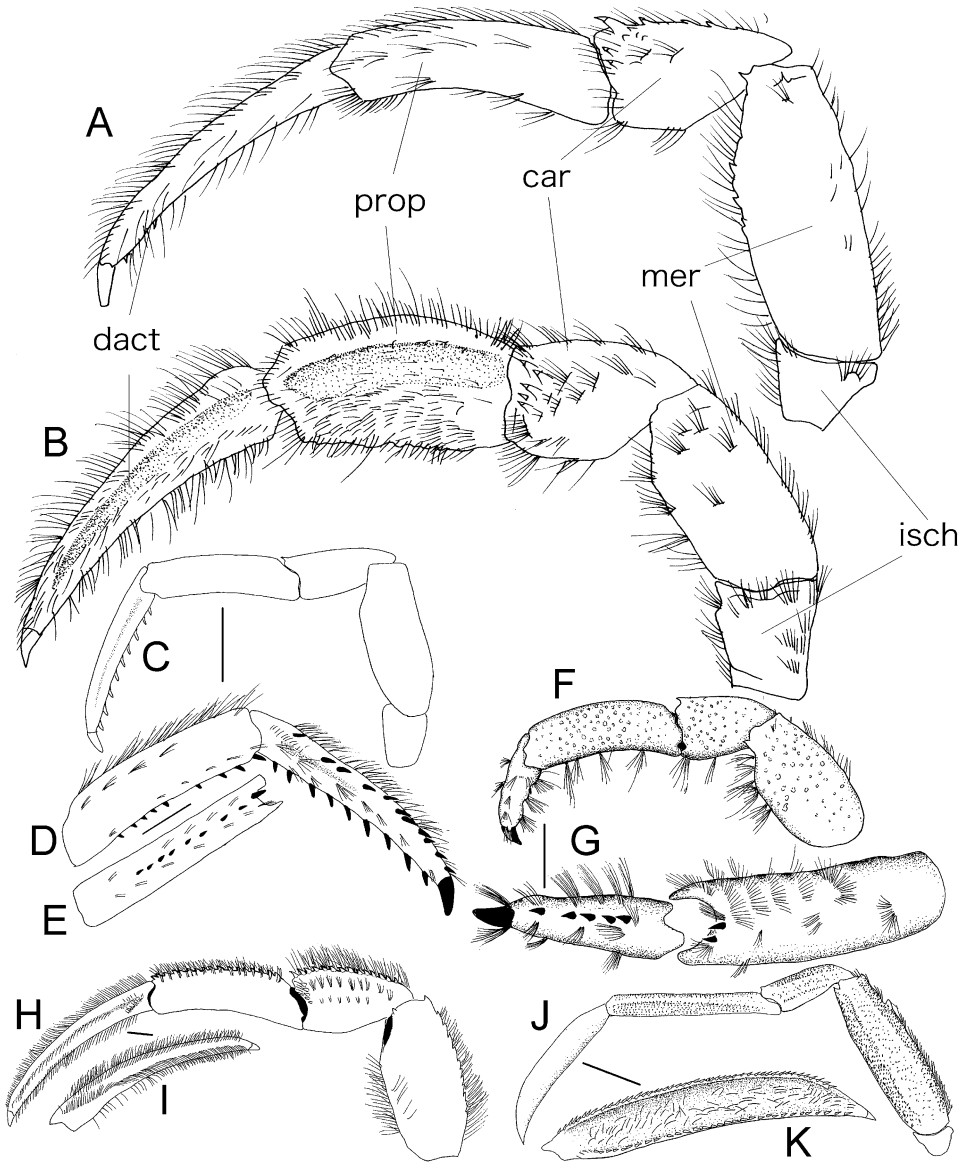
Fig. 70.14. Second and third pereiopods of Paguroidea. A, B, *Dardanus umbella*; C, D, E, *Pylopaguropsis furusei* Asakura, 2000; F, G, *Calcinus elegans* (H. Milne Edwards, 1836); H, I, *Diogenes nitidimanus*; J, K, *Catapagurus tuberculosus* (Asakura, 1999). A, left second pereiopod, lateral; B, left third pereiopod, lateral; C, left second pereiopod, lateral; D, same, dactylus and propodus, mesial; E, same, propodus, ventral; F, left second pereiopod, lateral; G, left third pereiopod, dactylus and propodus, ventral; H, left second pereiopod, lateral; I, same, dactylus, mesial; J, left second pereiopod, same, dactyl, mesial. Abbreviations as in fig. 70.12. [A, B, after Asakura, 2006a; C, D, E, after Asakura, 2000; F, G, after Asakura, 2002; H, I, illust. by Akira Asakura; J, K, after Asakura, 1999.]

calcareous spines may be present. The **carpi** are generally short and very often provided with a dorsodistal spine. The **meri** are generally rectangular or subrectangular from lateral view. In **females**, a **gonopore** opens on one or both **coxae** of the **third pereiopods**. But **males** with small gonopores on these coxae are also reported in some species (see the section on the genital apparatus, herein).

In **Lithodoidea**, the second through third pereiopods are developed as walking legs. They are symmetrical from left to right and composed of dactylus, propodus, carpus, merus, ischiobasis, and coxa (fig. 70.2A-C).

In **Galatheoidea** and **Chirostyloidea**, the second through third pereiopods are walking legs. They are always symmetrical from left to right and are composed of dactylus, propodus, carpus, merus, ischiobasis, and coxa (fig. 70.3C, E, F). Epipods are usually absent, except in the galatheoids *Raymunida*, *Galacantha*, and *Shinkaia* (first to third pereiopods), and some species of *Munidopsis* and *Galathea* (variable). In all galatheoids and almost all chirostyloids, the walking legs are structurally similar, **differing** chiefly in **length** (the second pereiopod is the longest, followed by the third and fourth pereiopod) and in minor details of ornamentation. Only in the chirostylid genus *Uroptychodes* are the walking legs significantly **heteromorphic**; here, the second pereiopod is distinctly more slender than the third and fourth pereiopod.

In **Galatheoidea**, the walking leg segments are usually flattened and variously spinose and setose (figs. 70.17A, 70.19A). *Shinkaia* is exceptional among galatheoids in having dense plumose setae covering the ventral surface of the sternum, and the proximal half of the pereiopod. The dactyli of galatheids and porcellanids are typically armed distally with a corneous **unguis**, followed by a row of fixed or articulated corneous spines on the flexor margin. In addition to other surface spines, the propodus is usually also armed with a series of movable calcareous spines.

The walking legs in **Chirostyloidea** are usually subcylindrical to slightly flattened, and are also variously armed and ornamented (figs. 70.18A, 70.3C, D) (generally smooth in *Uroptychus*, and spinose in other genera). The dactyli and propodi present a wide range of ornamentation, ranging from a corneous **unguis** with rows of fixed or movable flexor spines and setae, to minute denticulation or no armature at all. Similarly, the flexor margin of the propodus may have rows of movable spines, or lack ornamentation. In many species, especially of *Uroptychus*, the dactylus and propodus appear to form a **prehensile limb**, possibly as an adaptation for clinging to branching soft corals. The dactylus is arcuate, and occludes, or almost, with the distal flexor margin of the propodus that bears a series of movable spines set on an expansion of the propodus. Sexes are separate in galatheoids. In females, the gonopore is on the ventral surface of the coxa of the third pereiopod.

In **Aegloidea**, the second through third pereiopods are walking legs, as in galatheoids, and are composed of dactylus, propodus, carpus, merus, ischiobasis, and coxa. They are structurally similar and of approximately the same size (fig. 70.3A). All of the limbs are angled forward, so that the posterior faces of the appendages point upward. All segments are covered with sparse, short simple setae, the merus, carpus, and propodus may bear rows of short spines on the dorsal and ventral edges, and the carpus is usually ornamented with a single distodorsal, corneous spine.

In **Lomisoidea**, the second through third pereiopods are short and stout, and the dactylus ends in a conical claw. Epipods are absent. They are covered with punctuations of setae and fine granulation like the chelipeds (fig. 70.3B).

In **Hippoidea**, these appendages are well developed as walking legs (fig. 70.4A-D). In females, a gonopore opens on both coxae of the third pereiopod (fig. 70.9J), but males with small gonopores on these coxae are also reported in some species of Albuneidae. In Albuneidae and Blepharipodidae, the dactyli are more or less hook-like, laterally compressed, and dorsoventrally expanded. The dorsodistal angle of the carpus is often strongly produced, in particular in the second and third pereiopods (fig. 70.23J-L). In Hippidae, the dactyli are flattened (fig. 70.9H).

Fourth pereiopod. – In **Paguroidea**, this appendage is more or less **reduced** and used **to brace** against the inside of the shell's columella and, assisted by the similarly-reduced fifth pereiopods and uropods, holds the hermit crab within its shell or other housing. McLaughlin (1997, 2003) recognized four types of fourth pereiopod. **Subchelate:** the pereiopod is developed as a prehensile structure by the folding back of the dactylus against the propodus (fig. 70.15A). **Semichelate:** the ventral margin of the propodus is produced beneath the dactylus to such an extent that flexion of the dactylus becomes much more akin to the action of a dactylus against a fixed finger of a chelate appendage (fig. 70.15C). **Chelate:** a complete chela. **Simple:** the dactylus is joined to the distal margin of the propodus so that the dactylus and the propodus do not form any chelate condition (fig. 70.15D-F). Most species have a semichelate fourth pereiopod, some have a subchelate one, and the simple or chelate conditions are seen only infrequently. Among those species, the dactyl is very often provided with a row of corneous spines or teeth, either on the ventral margin or ventrally on the lateral face (fig. 70.15C). In some genera of Paguridae, such as *Solenopagurus*, *Pylopagurus*, *Pagurus*, and the diogenid genus *Pseudopaguristes*, a **preungual process** occurs. This anomalous structure is an oval or circular, blister-like, nodule-like, or finger-like projection found between the terminal claw and the distalmost tooth of the ventral row of corneous spines (fig. 70.15A; see Lemaitre

Fig. 70.15. Fourth and fifth pereiopods of Paguroidea. A, B, *Pseudopaguristes bicolor* Asakura & Kosuge, 2004; C, *Calcinus elegans*; D, *Alainopaguroides lemaitrei* McLaughlin, 1997; E, *Ostraconotus spatulipes* A. Milne-Edwards, 1880; F, *Solitariopagurus tuerkayi* McLaughlin, 1997; G, *Enneophyllus spinirostris* McLaughlin, 1997; H, *Nematopaguroides fagei* Forest & de Saint Laurent, 1968; I, *Anapagurus chiroacanthus* (Lilljeborg, 1856); J, *Decaphyllus barunajaya* McLaughlin, 1997; K, *Micropagurus polynesiensis* (Nobili, 1906); L, *Pagurojacquesia polymorpha* de Saint Laurent & McLaughlin, 2000; M, *Tarrasopagurus rostrodenticulatus* McLaughlin, 1997; N, *Trichopagurus trichophthalmus* (Forest, 1954); O, *Forestopagurus drachi* (Forest, 1966); P, *Catapaguroides japonicus* de Saint Laurent, 1968; Q, *Turleania multispina* McLaughlin, 1997; R, *Michelopagurus limatulus* (Henderson, 1888); S, *Acanthopagurus dubius* (A. Milne-Edwards & Bouvier, 1900); T, *Solenopagurus lineatus* (Wass, 1963); U, *Enneopagurus garciagomezi* McLaughlin, 1997; V, *Pagurodes inarmatus* Henderson, 1888. A, left fourth pereiopod, dactylus through carpus, lateral; B, right fifth pereiopod, lateral; C, left fourth pereiopod, lateral; D, left fourth pereiopod, dactylus and propodus, lateral; E, right fourth pereiopod, lateral; F, left fourth pereiopod, dactylus through carpus,
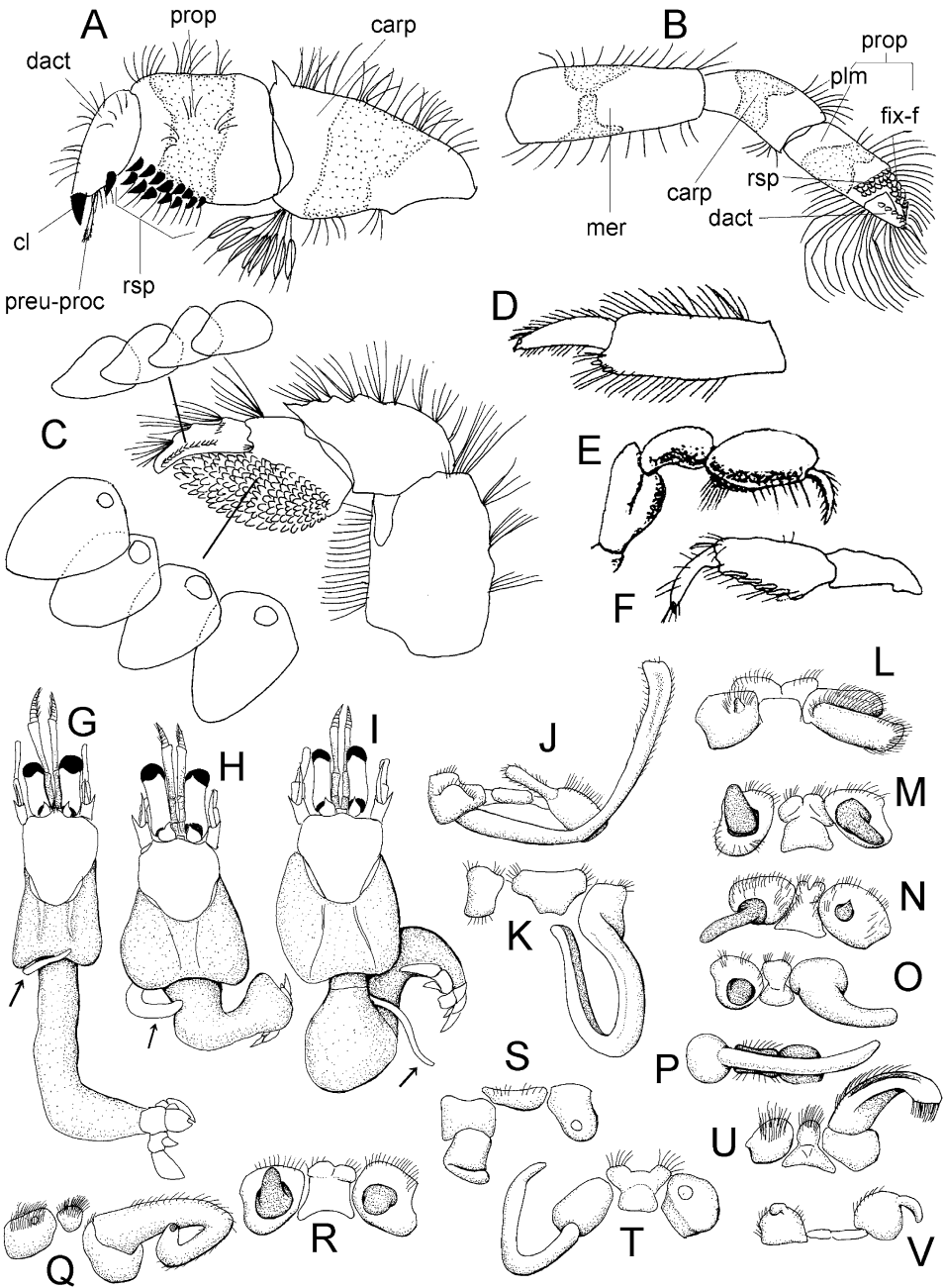
lateral; G-I, dorsal view of whole body, pereiopod excluded, dorsal; J-V, coxae and sternite of fifth pereiopods and sexual tubes. Abbreviations: cl, claw; preu-proc, preungual process; fix-f, fixed finger; other abbreviations as in fig. 70.12. [A, after Asakura & Kosuge, 2004; C, illust. by Akira Asakura; D, after McLaughlin, 1997; E, after A. Milne-Edwards & Bouvier, 1894; F, after McLaughlin, 1997; G-V, after Asakura, 2003.]

et al., 2010). Furthermore, another conspicuous structure, a prominent, circular **"type A" sensory structure** is also known in species of *Elassochirus* (Paguridae) on the lateral faces of the fourth pereiopod. The propodi are usually armed with corneous scales or spines. There may be a row of widely separate spines, a single row of scales, or multiple rows of scales, forming a rasp (fig. 70.15A, C).

In **Lithodoidea**, the fourth pereiopods are also walking legs, and their morphology is similar to that of the preceding two pairs. The same is also the case for **Galatheoidea**, **Chirostyloidea**, **Aegloidea**, **Lomisoidea**, and **Hippoidea** (figs. 70.3A-F, 70.9H, 70.23L).

Fifth pereiopod. – The fifth pereiopods are **reduced** and usually chelate or occasionally subchelate (see definition above). In **Paguroidea**, the dactylus is sometimes provided with a row of tiny corneous spines or teeth on the cutting edge. The dactylus and propodus (including the fixed finger) may have one to a few rows of corneous scales, sometimes forming rasps (fig. 70.15B). In **males**, a **gonopore** generally opens on both **coxae** of this appendage (fig. 70.5G). However, certain species of Coenobitidae possess calcified tubular elongations (**sexual tubes**) on one or both coxae, acting as a sperm delivery tube (see Reproduction, below). Furthermore, males of a number of genera in Paguridae have membranous, chitinous, or weakly calcified sexual tubes on one or both coxae (fig. 70.15G-I). These sexual tubes may be short, long, coiled, bent across the ventral body surface, or with a terminal filament. These structures provide **diagnostic characters** for species identification as well as for generic assignment (fig. 70.15J-V).

In **Lithodoidea**, this appendage is folded underneath the carapace and is morphologically quite similar to that of Paguridae.

In **Galatheoidea** and **Chirostyloidea**, the fifth pereiopod is considerably different from the preceding limbs. It is markedly smaller than the walking legs, lacking spines or ornamentation other than setae, and is typically used in **grooming** (figs. 70.3C, E, F, 70.17A, 70.18A, 70.19A). The limb is composed of dactylus, propodus, carpus, merus, ischiobasis, and coxa, and is held folded against the body along the posterolateral margin of the carapace, or partially concealed beneath the anterior two pleomeres. The densely setose dactylus and propodus form a chela, and they may be provided with minute teeth or scales on the occlusal margins. The setation of the chela is sexually dimorphic in *Bathymunida* and allies (Munididae). In males, the gonopore is present on the ventral surface of the coxa. In Galatheoidea, the fifth pereiopod coxa inserts on sternite 8. In Chirostyloidea, sternite 8 is absent, and the fifth pereiopod coxa inserts on the articular membrane of the eighth thoracomere. In Kiwaidae of the superfamily Chirostyloidea, the fifth pereiopod is unusual in having a strongly flattened propodus with a pronounced semi-circular expansion of the extensor margin, and in having its coxal insertion beneath the seventh sternite, which is not visible externally. When folded, the limb is partially concealed beneath the anterior two pleomeres (fig. 70.3D).

In **Aegloidea**, the fifth pereiopod is reduced and modified, and therefore differs significantly from the other pereiopods. It is carried beneath the posterior part of the carapace and functions in **cleaning** the gills, the posterior dorsal carapace, the third and fourth pereiopod, and pleopods and eggs in the female. The tip of the appendage is chelate, formed by the articulation of a minute dactylus with the propodus. The propodus, carpus,

merus, and ischium are all elongated, cylindrical segments with varying amounts of long simple setae (mostly distally). The basis is not fused with the ischium, but articulates with the globose coxa. In males the coxa is modified to carry a small sexual tube, of sorts. The membraneous vas deferens extends from the gonopore on the coxa, and is supported by a slightly elongate, **spoon-shaped process**.

In **Lomisoidea**, the fifth pereiopod is reduced, slender, and deflected into the branchial chamber. The tip of the dactyl is minutely chelate.

In **Hippoidea**, this appendage is reduced, chelate, and folded underneath the carapace (fig. 70.9H-J). In males, a gonopore opens on both coxae of the fifth pereiopod.

PLEOPODS

First to fifth pleopods. – In **Paguroidea**, the pleopods are highly variable. In Pylochelidae, the pleomeres each have a pair of pleopods: in males, the first and second pleopods are modified as **gonopods**, and the third to fifth pleopods may be uniramous or biramous; in females, the first pleopods are modified as gonopods, and the second to fifth pleopods are usually biramous. In most species of Diogenidae and Paguridae, the first pleopods are absent in both sexes, but unpaired second to fifth, or third to fifth, left pleopods are present in males, and often the second to fifth, or less frequently, second to fourth left pleopods, are present in females (figs. 70.10B, C, 70.16A, B). However, there are some exceptions (fig. 70.16C). For example, males of species of *Paguristes* and *Pseudopaguristes* have paired first and second pleopods (figs. 70.5G, 70.16D-F) and females have a paired first pleopod, all of which are modified as gonopods. Similarly, females of a considerable number of genera in Paguridae including *Agaricochirus*, *Chanopagurus*, *Enallopagurus*, *Lophopagurus*, *Nematopagurus*, and *Pylopagurus* have paired first pleopods modified as gonopods. The first to fifth pleopods are totally absent in males of *Spiropagurus* (Paguridae) and *Cancellus* (Diogenidae). In Coenobitidae, males lack the pleopods, but females have three unpaired left pleopods. In Parapaguridae, males have paired first and second pleopods modified as gonopods, while females have paired second pleopods in which the right is reduced and usually have unpaired left third to fifth pleopods.

In **Lithodoidea**, the males lack the pleopods, but females often have a pair of small first pleopods and uniramous, unpaired second to fifth left pleopods (fig. 70.16G, H).

In **Galatheoidea** and **Chirostyloidea**, most males have paired gonopods on the first two pleomeres, and paired modified uniramous pleopods on the third to fifth pleomeres. Several galatheoids, however, lack the first gonopod in males, e.g., *Agononida*, *Anoplonida*, *Crosnierita*, and *Galathea inflata* Potts, 1915. In female galatheoids, the first pleomere lacks pleopods, the second pleopod is rudimentary or well developed, and the third to fifth pleopods are fully developed. In Porcellanidae, males have a single pair of uniramous pleopods on the second pleomere, and females have a pair of uniramous pleopods on the second to fifth pleomeres. In most Chirostyloidea, males usually have paired gonopods on the first two pleomeres, and females have paired pleopods on the second to fifth pleomeres. In Eumunididae, however, the males lack pleopods altogether (except in some species of *Eumunida* in which a vestigial second pleopod may be present) and females have paired
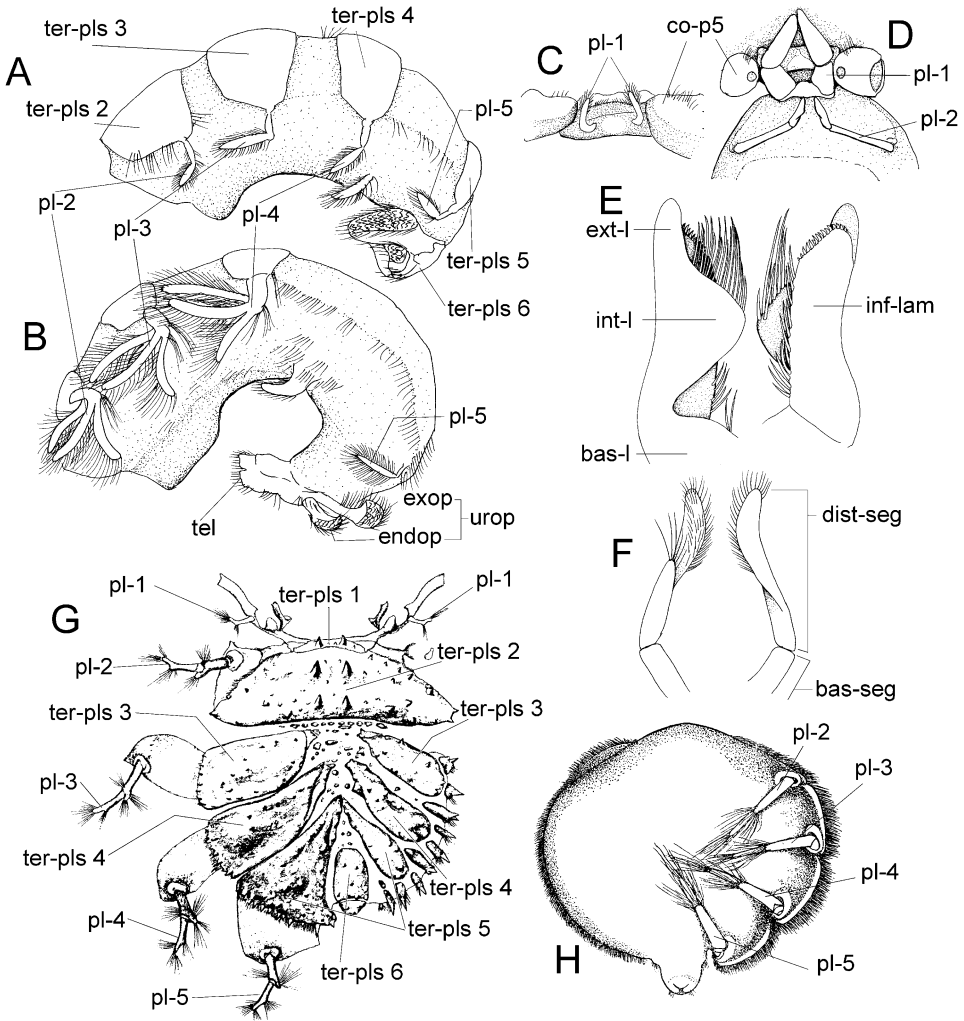
Fig. 70.16. Pleonal appendages of Paguroidea and Lithodoidea. A, B, *Dardanus robustus* Asakura, 2006; C, *Pylopaguropsis furusei*; D-F, *Pseudopaguristes bollandi*; G, *Paralithodes*; H, *Oedignathus inermis* (Stimpson, 1860). A, pleon, dorsolateral, left, male; B, same, female; C, coxae and sternite of fifth pereiopods and first pleopods, ventro-posterior, female; D, coxae and sternite of fifth pereiopods and first and second pleopods, ventral, male; E, distal portion of first pleopod of male, external (left) and internal (right); F, distal portion of second pleopod of male, external (left) and internal (right); G, pleon, outer, female; H, pleon, inner, female. Abbreviations: bas-l, basal lobe; bas-seg, basal segment; co-p5, coxa of fifth pereiopod; dist-seg, distal segment; endop, endopod; exop, exopod; ext-l, external lobe; inf-lam, inferior lamella; int-l, internal lobe; pl-1 to pl-5, first through fifth pleopod; tel, telson; ter-pls 1 to ter-pls 6, tergite of first through sixth pleomere; urop, uropod. [A, B, after Asakura, 2006a; C, after Asakura, 2000; D-F, after Asakura & McLaughlin, 2003; G, after Boas, 1924; H, after Kamita, 1956.]

second to fifth pleopods. In Kiwaidae, both males and females have uniramous second to fifth pleopods, those of males being reduced.

In **Aegloidea**, the female has four pairs of well-developed, subequal, uniramous pleopods that are two-segmented, with the proximal segment being twice the length of the distal segment in the first and second pleopods, but as long as in the third and fourth. The distal segment is terminally rounded, with numerous long, simple setae. The male pleopods are greatly reduced and are represented by minute knobs only on the second through fourth pleomeres.

In **Lomisoidea**, the male has a pair of prominent pleopods on pleonites 1 and 2, and then paired vestigial bumps, representing the pleopods, on pleonites 3 through 5. The first pleopod is uniramous, 3-segmented, with the distal segment oval in shape and setose. The second pleopod is 3-segmented and biramous, with the endopod being oval in shape and setose, and the exopod being digitiform and setose distally. The female has five pairs of symmetrical pleopods. The first pleopod is reduced and digitiform, while pleopods two through five are 2-segmented, biramous, and setose. The exopod and endopod are subequal on each pleopod.

In **Hippoidea**, females of Albuneidae and Blepharipodidae have pairs of well-developed, uniramous, second to fifth pleopods. Males lack pleopods, but an exception is found in species of some genera of Albuneidae, which have rudimentary or small pleopods on the second to fifth pleomeres. In Hippidae, males lack pleopods (fig. 70.9I), and females have paired second to fourth pleopods (*Hippa*) (fig. 70.9J) or second to fifth pleopods (other genera).

Uropods. – In **Paguroidea**, these limbs are paired, well calcified, stout, and bear numerous corneous scales forming rasps on the **endopods** and **exopods** (and occasionally on the **protopods**) (figs. 70.1A, 70.10A-D, 70.16A, B). The exopods are generally larger than the endopods.

In **Lithodoidea**, uropods are absent (figs. 70.10E, F, 70.16G).

In **Galatheoidea** and **Chirostyloidea**, the uropods consist of a short, stout protopod that may or may not bear spines and setae, and a lamellar exopod and endopod. The margins of the exopod and endopod are lined with plumose setae and sometimes also small spines or denticles. Together with the telson, the uropods form a tail fan (figs. 70.3C, E, 70.17B, 70.18F, 70.19E, 70.20D).

In **Aegloidea**, the sixth pleomere bears well-developed, oval, lamellar uropods, the margins of which are lined with dense plumose and simple setae. The outer and inner uropodal rami curve slightly inwards and articulate with the telson to make a functional tail fan (fig. 70.21G).

In **Lomisoidea**, the females have well-developed, slender uropods that do not form a tail fan (fig. 70.22F). The uropods are 2-segmented and the outer rami are three times as long as the inner rami. When the pleon is extended, the uropods point anteriorly, not posteriorly. The uropods are vestigial in males.

In **Hippoidea**, a pair of uropods is present, specialized for **burrowing**, and not provided with rasps. In Hippidae, the uropods are long and lamellar (fig. 70.9H).
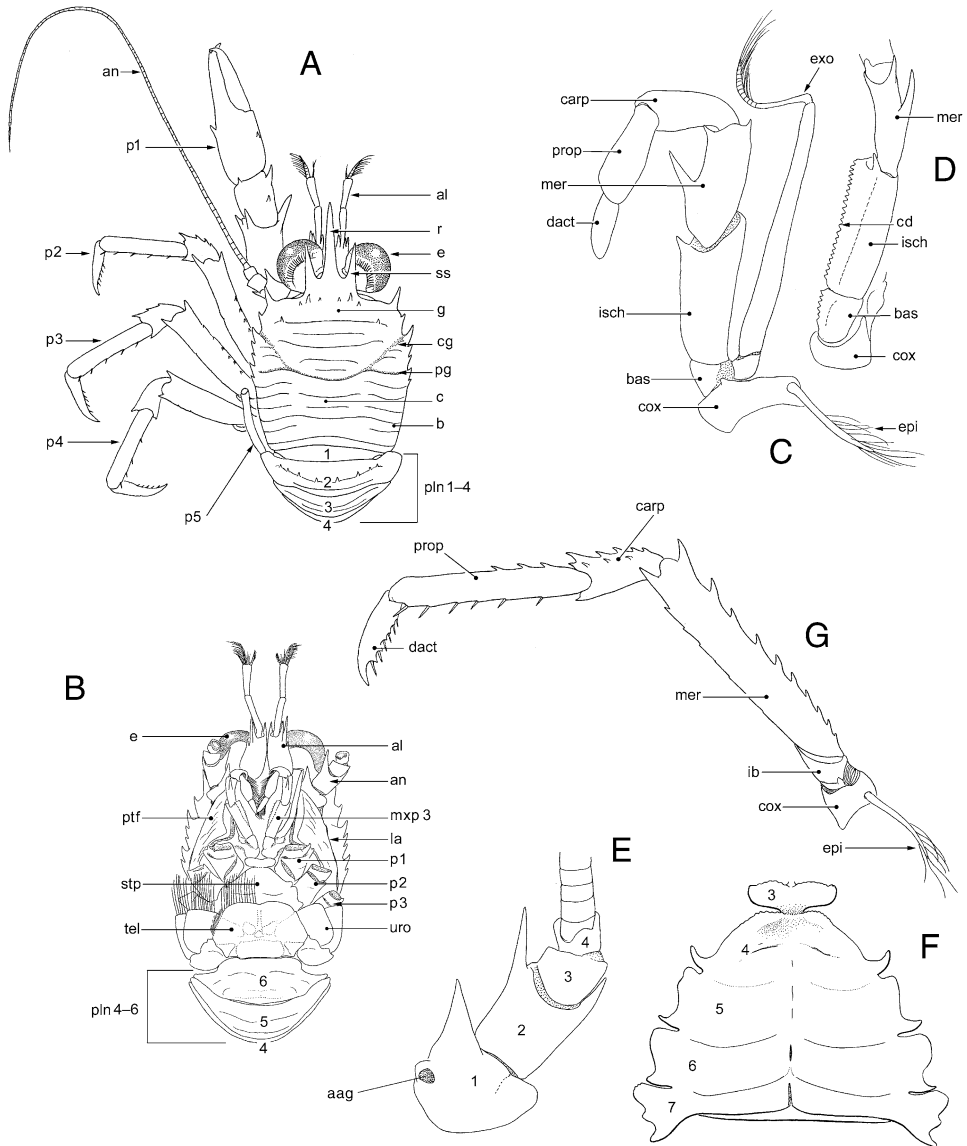
Fig. 70.17. Galatheoidea. A-F, *Munida* (Munididae); G, *Galathea* (Galatheidae). A, dorsal habitus; B, ventral habitus; C, maxilliped 3, lateral view; D, maxilliped 3, mesial view showing crista dentata; E, antenna, segments numbered; F, sternal plastron, segments numbered; G, pereiopod 2. Abbreviations: aag, aperture of antennal gland; an, antenna; al, antennule; b, branchial region; bas, basis; c, cardiac region; carp, carpus; cd, crista dentata; cg, cervical groove; cox, coxa; dact, dactylus; e, eye; epi, epipod; exo, exopod; ib, ischiobasis; isch, ischium; la, linea anomurica; mer, merus; mxp3, maxilliped 3; pg, postcervical groove; p1 through 5, pereiopods 1 through 5; pln 1 through 6, pleonites 1 through 6; r, rostrum; ptf, pterygostomial flap; ss, supraocular spine; stp, sternal plastron; tel, telson; uro, uropod. [Modified after Baba et al., 2009.]
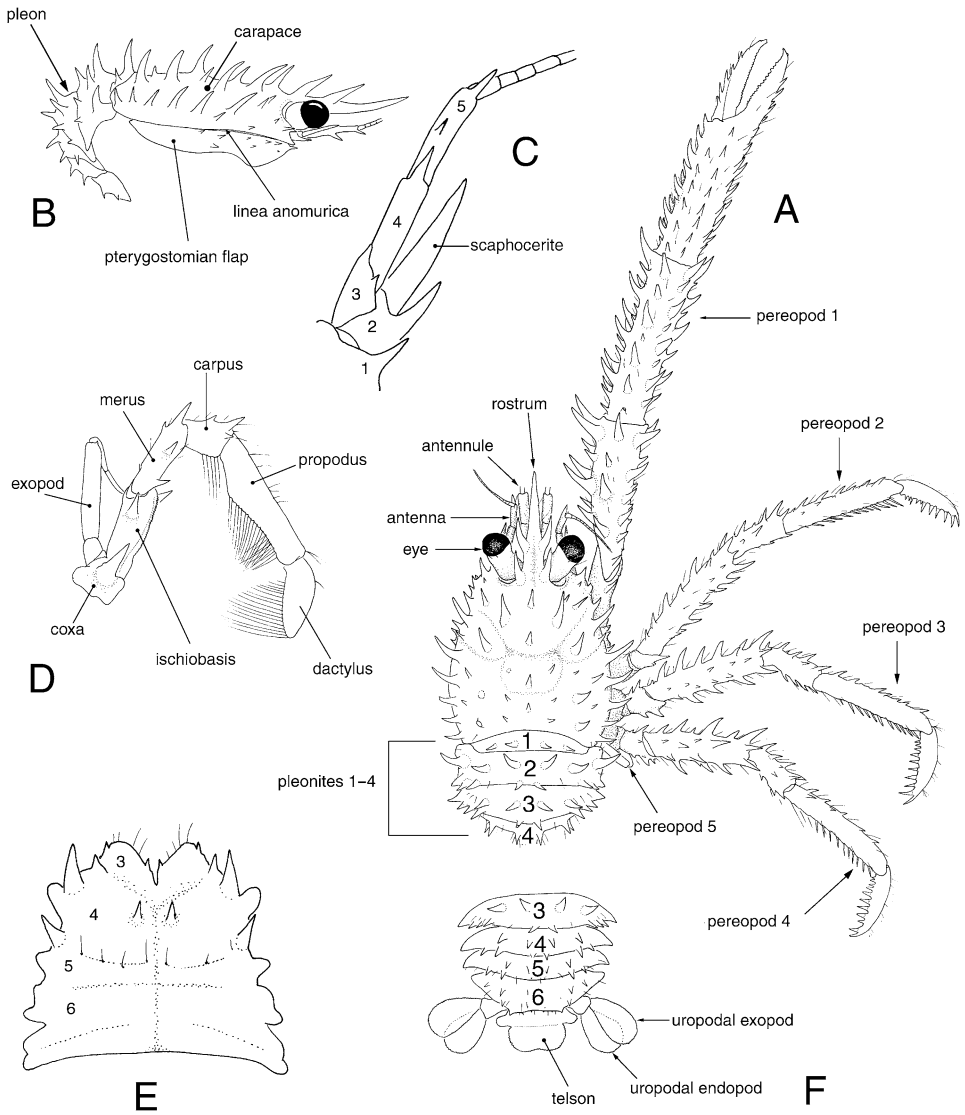
Fig. 70.18. Chirostyloidea, Chirostylidae: *Uroptychus spinirostris* (Ahyong & Poore, 2004). A, dorsal habitus; B, body, right lateral view; C, antenna; D, maxilliped 3, lateral view; E, sternal plastron; F, posterior pleon. [Modified after Ahyong & Poore, 2004.]

INTERNAL MORPHOLOGY

Both McLaughlin (1980, 1983c) and Felgenhauer (1992b) provided excellent reviews of the internal systems of all decapods. Only subsequent, or more detailed, works specific to anomuran internal systems are discussed below.
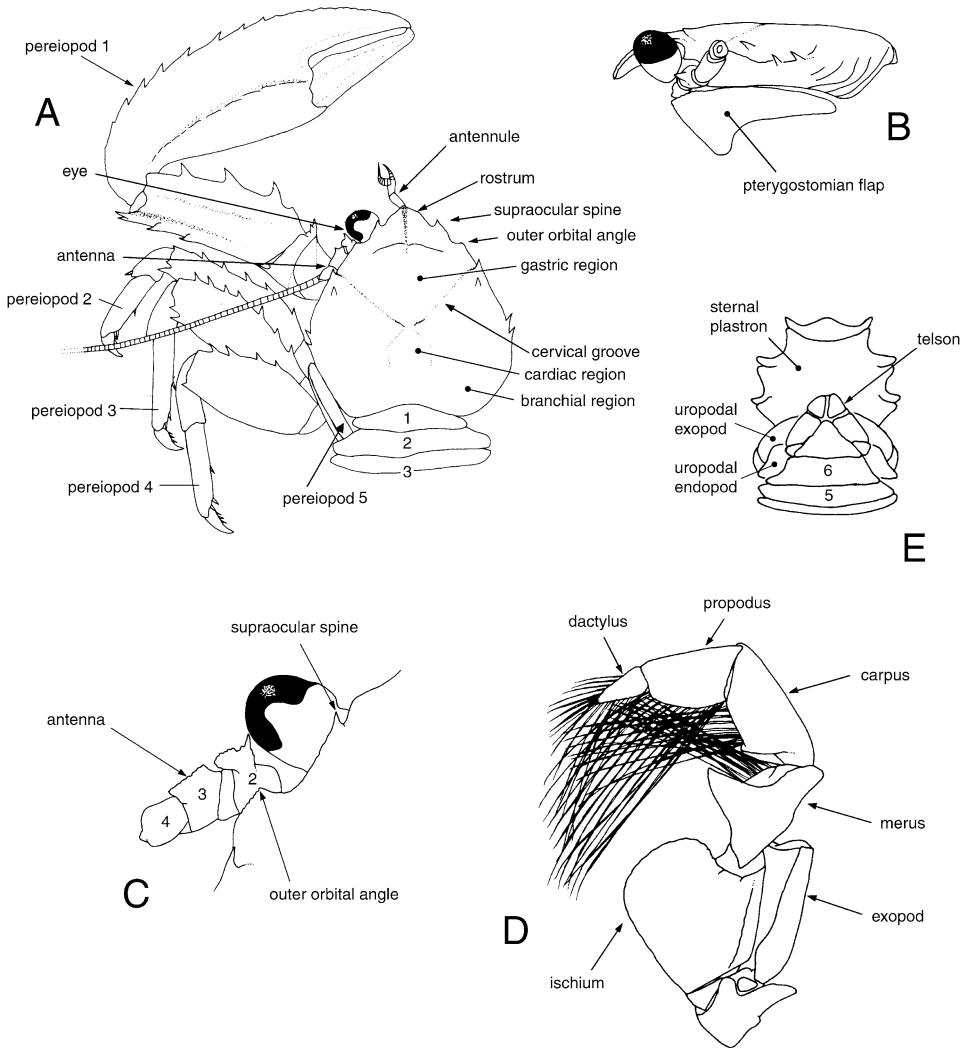
Fig. 70.19. Galatheoidea, Porcellanidae: *Petrolisthes*. A, dorsal habitus; B, carapace, left lateral view; C, orbit and antenna; D, maxilliped 3, lateral view; E, sternal plastron and posterior pleon. [Modified after Osawa et al., 2010.]

Muscles

Mellon (1992) reviewed the ultrastructure of decapod **muscles**, but published work on the specific **musculature** of anomurans is sporadic and limited to just a few taxa. Pilgrim (1973) described the specific musculature in the thorax of the hermit crab *Pagurus longicarpus*, Pike (1947) described the musculature of the squat lobster *Galathea squamifera* Leach, 1814, and Myklebust & Tjonneland (1975) examined the ultrastructure
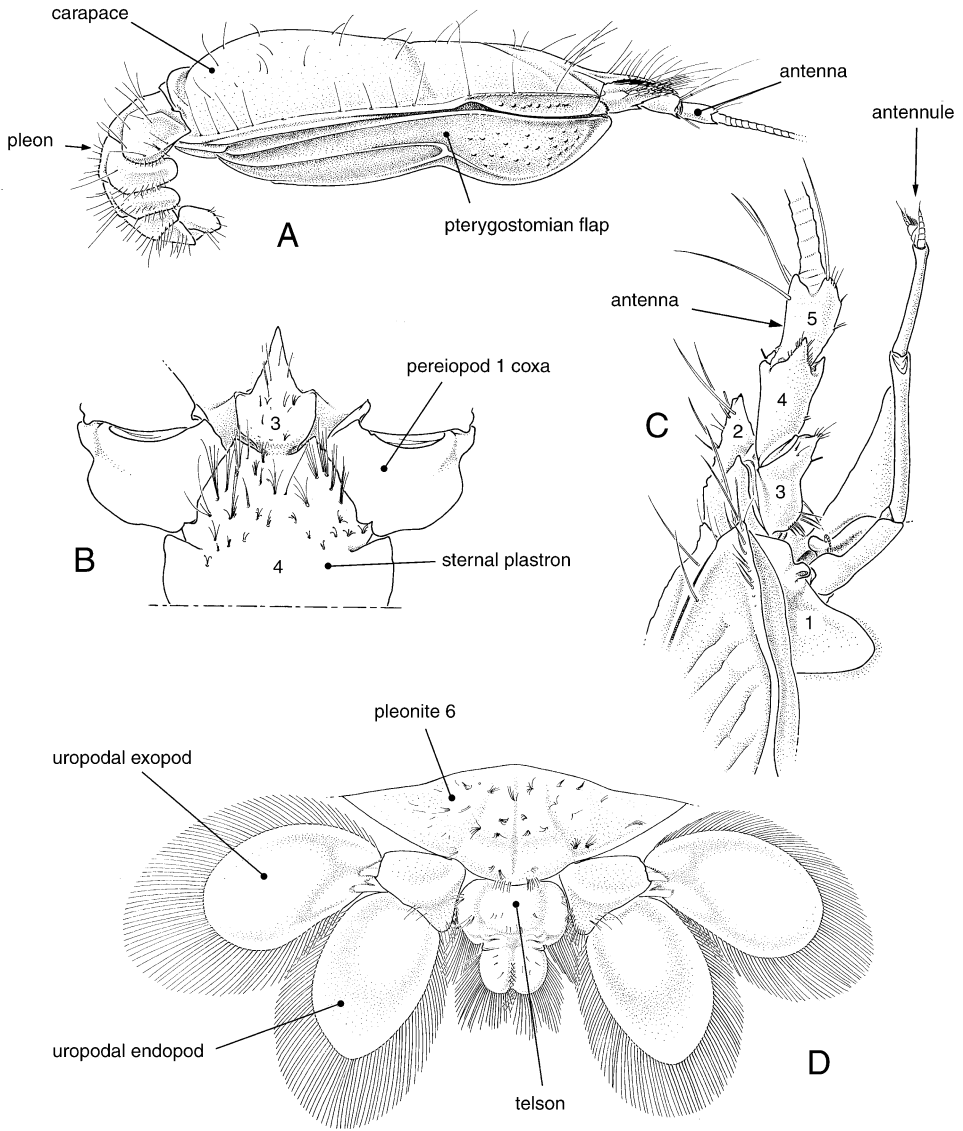
Fig. 70.20. Chirostyloidea, Kiwaidae: *Kiwa hirsuta*. A, body, right lateral view; B, anterior sternal plastron, somites numbered; C, antenna and antennules, segments numbered; D, distal pleon. [Modified after Macpherson et al., 2005.]

of the cardiac muscle cells in the galatheid, *Munida*. Meiss & Norman (1977b) provided an overview of the musculature of the **stomatogastric system** in some anomurans, and similarly Kunze & Anderson (1979) analyzed the muscles in the foregut of *Clibanarius taeniatus* (H. Milne Edwards, 1848) (see digestive system, below). A series of papers by Paul and colleagues on the neuromuscular morphology used for swimming, escape re-
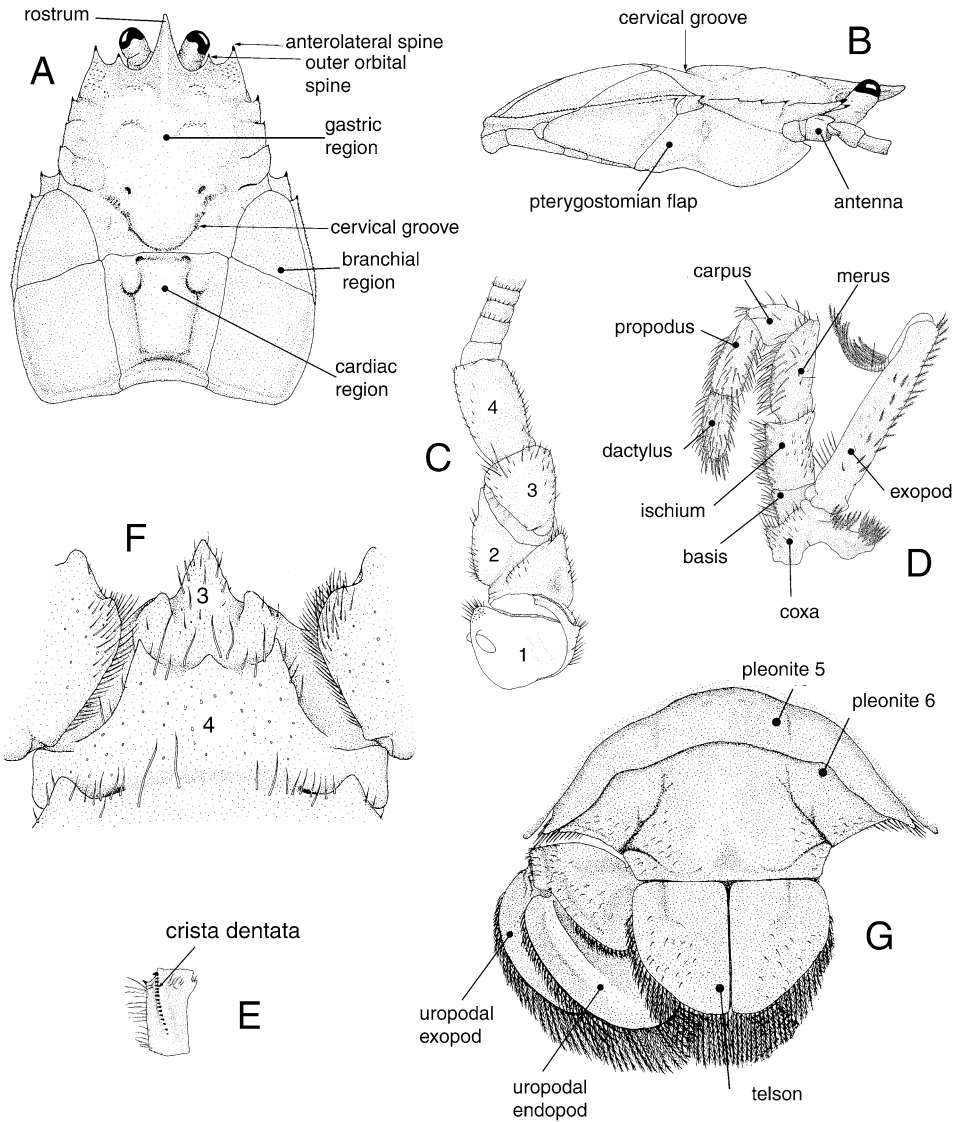
Fig. 70.21. Aegloidea, Aeglidae. A-C, G, *Aegla uruguayana* Schmitt, 1942; D-F, *Aegla platensis*. A, carapace, dorsal view; B, carapace, right lateral view; C, antenna; D, maxilliped 3, lateral view; E, maxilliped 3 ischium, mesial view showing crista dentata; F, anterior sternal plastron, somites numbered; G, posterior pleon. [Modified after Martin & Abele, 1988.]

sponse tail-flipping, or digging in decapods, included several anomurans, e.g., *Munida*, *Blepharipoda*, and *Emerita*, and investigated the evolution of the morphology and behaviors based on comparisons of pleonal musculature and associated neural circuitry (see Paul et al., 1985; Paul, 1989, 1991, 2003).
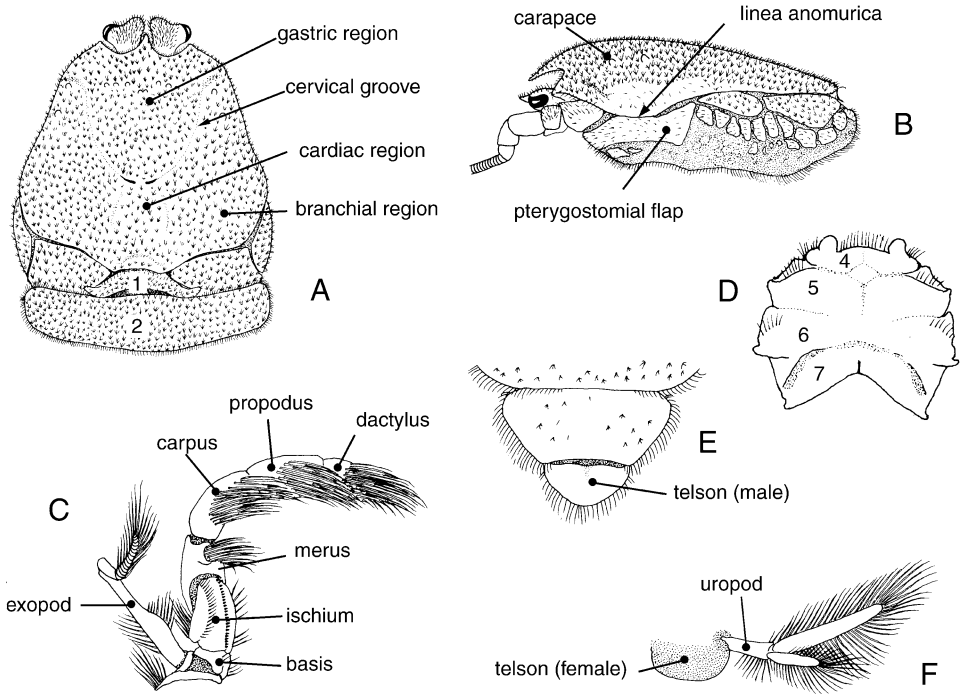
Fig. 70.22. Lomisoidea, Lomisidae: *Lomis hirta*. A, carapace and anterior pleon (pleonites numbered); B, carapace, left lateral view; C, maxilliped 3, mesial view; D, sternal plastron, somites numbered; E, posterior pleon, male; F, telson and left uropod of female, ventral view (right pleopod not shown). [Modified after Martin & Abele, 1986.]

Nervous system

Govind (1992) provided an excellent overview of the decapod **nervous system** from which the anomuran morphology can be basically inferred. As mentioned in the above section on muscles, Paul and colleagues (Paul et al., 1985; Paul, 1989, 1991, 2003) describe the neurobiology of several anomuran species, across two superfamilies, in the context of the evolution of certain behaviors. The morphology and evolution of the **cerebral ganglia** (**brains**) of 13 species of decapods, including three anomurans (*Pagurus*, *Birgus*, and *Petrolisthes*) is also described in Sandeman et al. (1993). In hermit crabs, the **supraesophageal ganglion** (brain) is prominent, and located in the midline between the ocular peduncles and above the epistome. From this ganglion, major **nerves** radiate, including the optic, antennal, antennular, and tegumental nerves (McLaughlin, 1980, 1983c).

Around the esophagus, the **esophageal connective** is located, with the swelling of the **paraesophageal ganglion**. The esophageal connective terminates in a **thoracic ganglionic mass** overlaying the ventral thoracic artery (fig. 70.24A, C). Three masses of fused ganglia, separated by constrictions, comprise this thoracic mass. The third cluster of ganglia, which
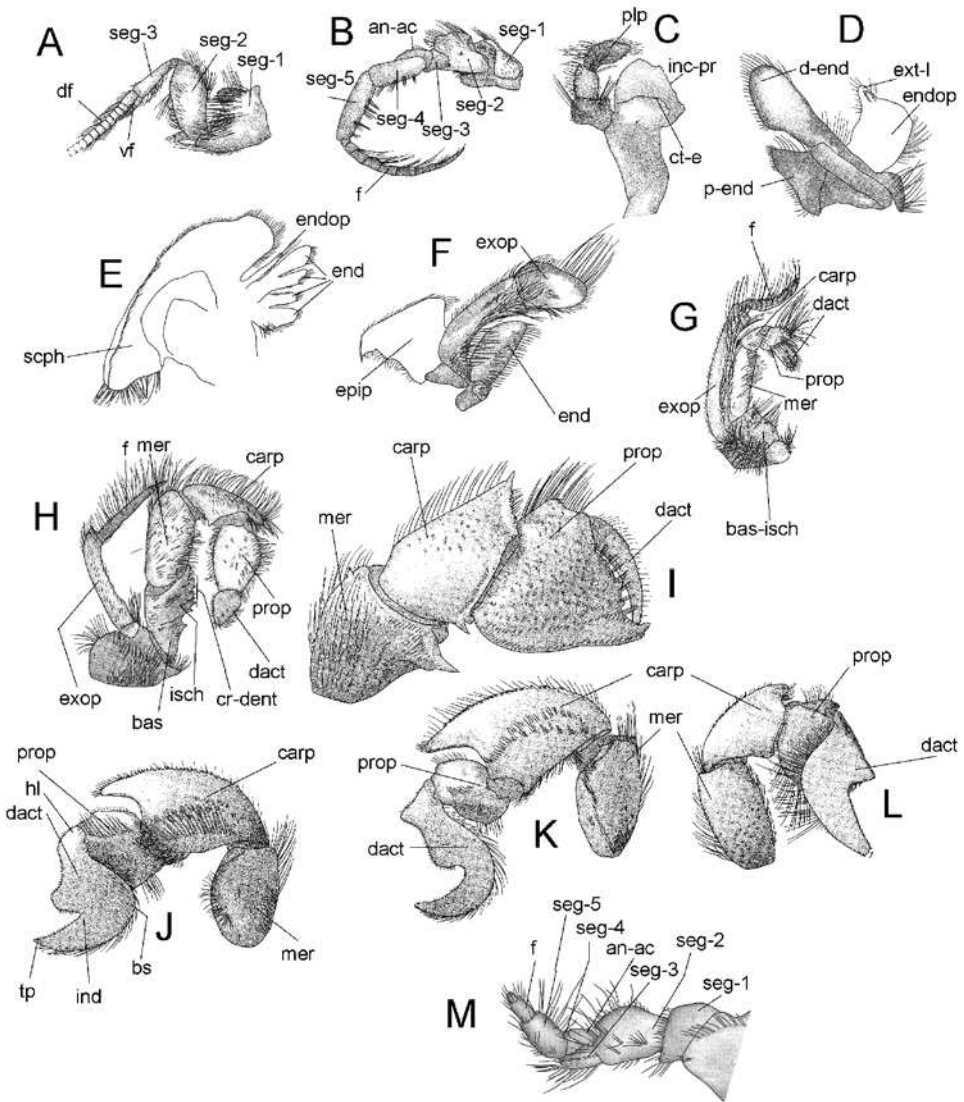
Fig. 70.23. Cephalothoracic appendages of Hippoidea. A-L, *Lophomastix japonica*; M, *Hippa pacifica*. A, left antennule, lateral; B, left antenna, lateral; C, mandible, left, mesial; D, maxillule, left, lateral; E, maxilla, right, lateral; F, first maxilliped, right, lateral; G, second maxilliped, right, lateral; H, third maxilliped, right, lateral; I, first pereiopod, right, lateral; J, second pereiopod, left, lateral; K, third pereiopod, left lateral; L, fourth pereiopod, left, lateral; M, antenna, left lateral.
    Abbreviations as in fig. 70.12. [A-L, after Boyko, 2002; M, after Boyko & Harvey, 1999.]

is pierced by the sternal artery, is composed of the ganglia of the fourth and fifth pereiopod and first pleomere.

    In the pleon, the nerve cord is of the ladder type with five pairs of fused ganglia (fig. 70.24C). As a result of the flexure of the pleon, the nerve cord in hermit crabs is

skewed to the left from the second to fourth pleomeres. The pleonal flexure also results in the atypical development of pleonal musculature.

Sense organs

An overview of **sense organs** in Decapoda can be found in Govind (1992). Compound eyes, antennular aesthetasc sensilla, and statocysts are three organs for which there is some published literature specific to Anomura.

The known types of **eyes** in anomurans include the **apposition eye** (fig. 70.25A), found in the hippoid, *Hippa adactyla* Fabricius, 1787 and the aegloid, *Aegla denticulata* Nicolet, 1849, and the **superposition eye** (fig. 70.25B), of which there are three forms (Gaten, 1998; Richter, 2002; Porter & Cronin, 2009) (fig. 70.25C-H). These are the **reflecting superposition compound eye** (with many mirrors), which is found in the galatheoids, including *Petrolisthes elongatus* (H. Milne Edwards, 1837), *Porcellana platycheles* (Pennant, 1777), *Munida irrasa* A. Milne-Edwards, 1880, and *Munida rugosa* (Fabricius, 1775), the chirostyloids, e.g., *Chirostylus investigatoris* (Alcock & Anderson, 1899) (see Bursey, 1975; Eguchi et al., 1982; Fincham, 1988; Meyer-Rochow et al., 1990; Gaten, 1994, 1998), and also in the lithodoid *Paralomis multispina* (Benedict, 1895) (see Eguchi et al., 1997). Then there is the **refracting superposition eye** (with many lenses) only found so far in Anomura (cf. Nilsson, 1990) in the diogenid hermit crab, *Dardanus megistos* (Herbst, 1804) (fig. 70.25K). And finally the **parabolic superposition compound eye** (with mirror-lens combination) found in the pagurid hermit crab, *Pagurus bernhardus* (Linnaeus, 1758), by Nilsson (1988). All forms of the compound eye contribute to the formation of a single, erect image in the eye, on a layer of contiguous, deep-lying receptors (fig. 70.25I, J). Hermit crabs have compound eyes that are covered by the **cornea**, a transparent version of the general body cuticle, and set on moveable **eyestalks** (the **ocular peduncles**) (figs. 70.1A-I, 70.5A-C, 70.6A, B, 70.8A, 70.10A, B). The **facets** are **square** in outline in galatheoids and some species of the symmetrical hermit crabs Pylochelidae, including *Cheiroplatea laticaudata* Boas, 1926 and *Pylocheles mortensenii* Boas, 1926. **Hexagonal facets** are almost certainly **plesiomorphic**, so the presence of square facets in galatheoids and pylochelids lends support to a close relationship between the two groups as recovered by recent phylogenetic analyses (Ahyong & O'Meally, 2004; Tsang et al., 2008; Ahyong et al., 2009). The ommatidial facets are hexagonal in all other hermit crabs and in Hippidae (cf. Richter, 2002). The cornea is well **pigmented** in almost all anomuran species, but variable in size and shape. Exceptions to strongly pigmented corneas include deep-sea members like *Kiwa* (fig. 70.3D), some galatheoids (Munidopsidae), and Pylochelidae (*Cheiroplatea*, for example) where the cornea can be degenerate (fig. 70.5E). A single hermit crab species, the deep-sea parapagurid *Typhlopagurus foresti* de Saint Laurent, 1972 (fig. 70.5F), was initially reported to completely lack eyes (corneas) (de Saint Laurent, 1972), but Lemaitre (2006) later showed that the corneas were present, but are small, and hidden both distally and ventrally.

The primary **chemosensory organs** of decapods are the antennulae, the dactyls of the walking legs, and the mouthparts. Antennular chemosensitivity is usually ascribed to
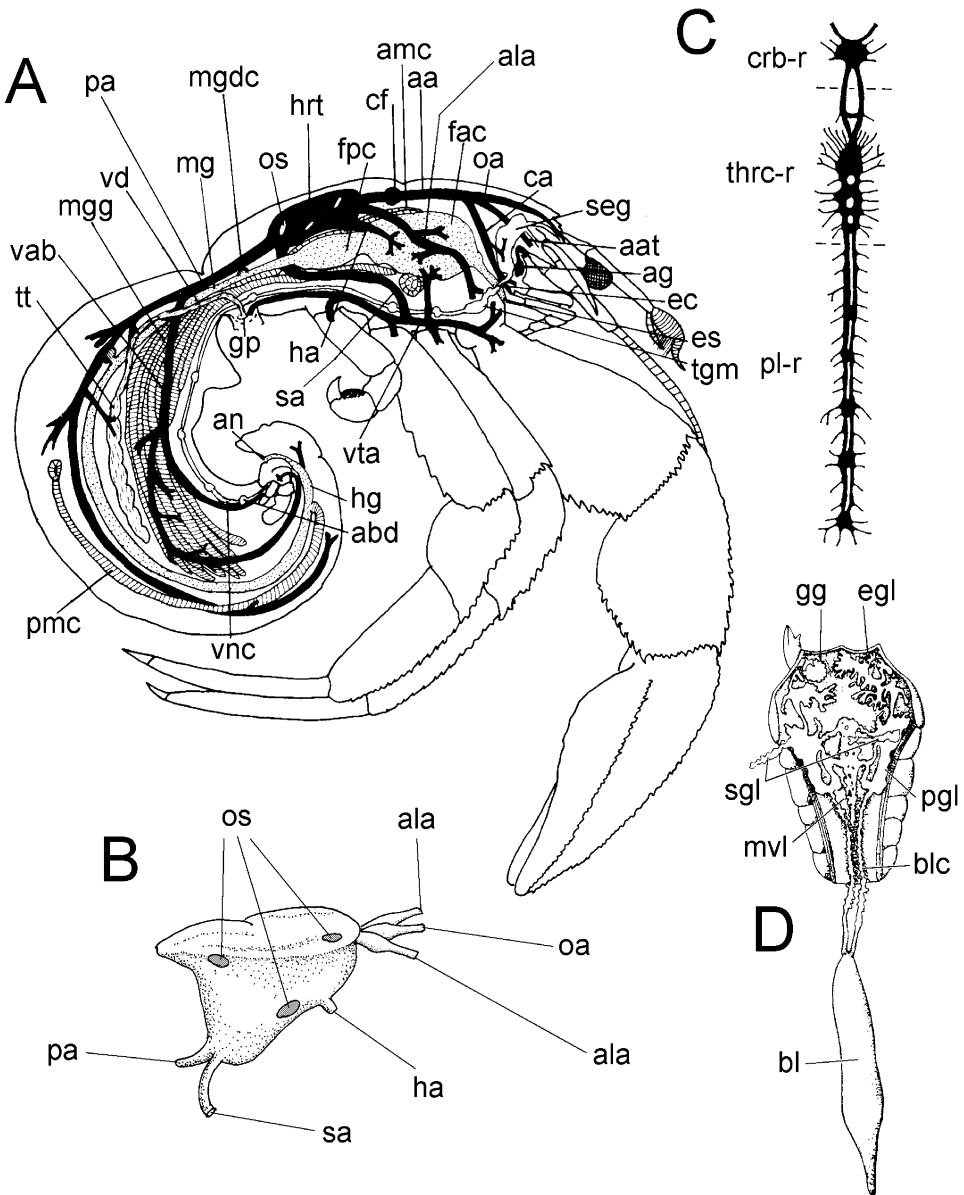
Fig. 70.24. Digestive, nervous, and circulatory systems of a pagurid hermit crab. Abbreviations A, B: aat, antennal artery; abg, pleonal ganglion; ag, antennal gland; ala, anterior lateral arteries; amc, anterior midgut caeca; an, anus; ca, cephalic artery; cf, cor frontale (frontal heart); ec, esophageal connective; es, esophagus; fac, anterior chamber (cardiac stomach) of foregut; fpc, posterior chamber (pyloric stomach) of foregut; gp, gonopore; ha, hepatic arteries; hg, hind gut; hrt, heart; mg, midgut; mgdc, midgut diverticulum; mgg, midgut gland; oa, optic artery; os, ostium; pa, posterior aorta; pmc, posterior midgut caecum; sa, sternal artery; seg, supraesophageal ganglion; tgm, thoracic ganglionic mass; tt, testis; vab, ventral aortic branch; vd, vas deferens; vnc, ventral nerve cord; vta, ventral thoracic artery. Abbreviations C: crb-r, cerebral region; pl-r, pleonal region; thrc-r, thoracic

aesthetascs or **sensilla** borne on the lateral filament of this appendage. In the hermit crab *Pagurus hirsutiusculus* (Dana, 1851), the aesthetascs of the antennulae each have between 300 and 500 receptors, and approximately 6000-8000 **sensory endings** fill the lumen of the aesthetascs. This gives an estimated branching ratio of about 20 distal branches for each **dendrite** in the basal region of a seta. The aesthetasc hairs have also been investigated on the antennulae of the land hermit crab genera *Coenobita* (cf. Ghiradella et al., 1968; Vannini & Ferretti, 1997) and *Birgus* (cf. Stensmyr et al., 2005), where they are adapted for insect-like **olfaction** in the terrestrial/aerial environment (Vannini & Ferretti, 1997; Greenaway, 2003; Stensmyr et al., 2005).

The important **mechanoreceptor** is the **statocyst**, a **gravity receptor** providing balance, located at the base of the first antennular segments.

Digestive system

The **digestive** or **alimentary system** in decapods is particularly well described and illustrated, in the overview of internal anatomy by Felgenhauer (1992b) and then again later in the same volume by Icely & Nott (1992). Apart from those studies, there is only limited literature specific to Anomura.

In anomurans, the principal components of the digestive system include the **esophagus**, the **foregut** (**stomach**), the **midgut**, the **hindgut**, and their accompanying glands (**caeca**) (fig. 70.24A). The esophagus of anomurans is short. The foregut is divisible into the anterior chamber (**cardiac stomach**) and posterior chamber (**pyloric stomach**) (fig. 70.26A-C). The inner walls of these chambers are deeply folded and strengthened by a series of **plates** or **ossicles**. The entrance from the esophagus to the anterior chamber is guarded by the **esophageal valves** that prevent backflow and assist, together with the **lateral accessory teeth** (**pectineal ossicles**), in pushing larger food material towards the **cardiopyloric valve** and **gastric mill** (fig. 70.26D, E, G, H). The gastric mill is located in the anterior chamber and its lateral and dorsal teeth act in **trituration** of this larger material (fig. 70.26F). The cardiopyloric valve lies in the ventral midline at the posterior end of the anterior chamber and separates a large **median food channel** leading to the gastric mill from paired ventrolateral channels leading to the **ampullae**. Setal screens borne on the post-pectineal and anterolateral cardiac ossicles guard the entrances to these **ventrolateral channels**. The **cardiac setal screen** governs the size of particles that pass into the channels and then onto the ampullae. The ampullae themselves contain further setal screens, which separate channels leading to the **digestive glands** from channels leading to the midgut. The midgut is an elongate, thin-walled, smooth tube extending almost the full length of the pleon. The hindgut terminates in a ventrally directed **anus** at the terminal end of the telson (McLaughlin, 1983c).

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region. Abbreviations D: bl, nephrosac; blc, duct between anterior and posterior vesicular masses; egl, epigastric lobe; gg, left antennal gland; mvl, medioventral lobe; pgl, paragastric lobe; sgl, supragastric lobe. [A, after McLaughlin, 1980, 1983c; B, D, after Makarov, 1962; C, after Sandeman, 1982.]
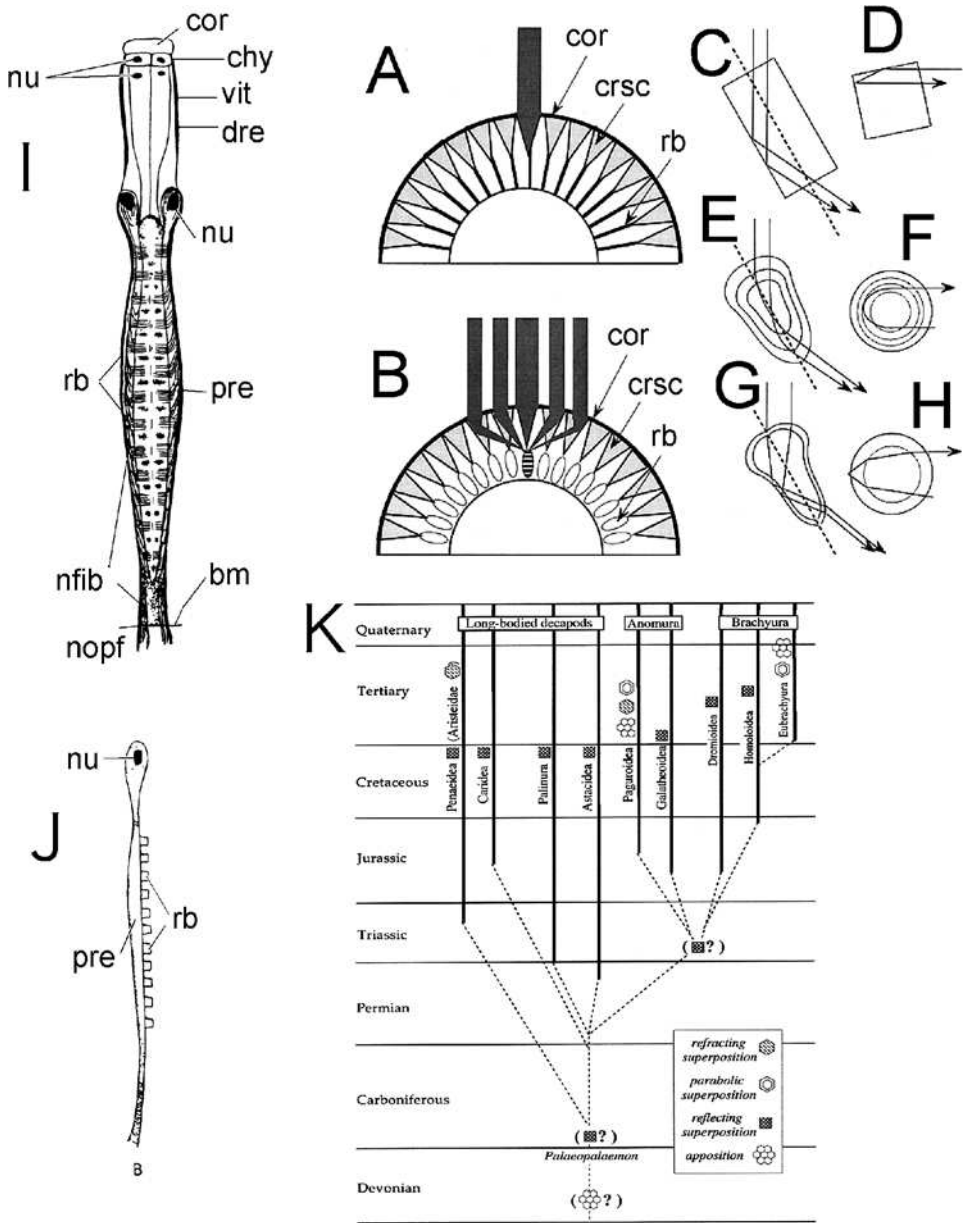
Fig. 70.25. A-H: diagrammatic representation of the main types of anomuran compound eyes. A, apposition eye, showing isolation of the ommatidium; B, superposition eye, showing redirection of light from many facets to the target rhabdom; C-H, light path through the crystalline cones of superposition eyes viewed from the side and from above (the dotted line marks the ommatidial axis); C, D, reflecting superposition; E, F, refracting superposition; G, H, parabolic superposition; I, *Pagurus*, longitudinal section through ommatidium; J, *Pagurus*, proximal retinal cell. Abbreviations A-J: bm, basilar membrane; chy, corneal cell; cor, cornea; crsc, crystalline cone; nfib, unpaired

At the junction of the **anterior** chamber of the foregut and the **posterior** chamber a pair of small, anteriorly directed caeca, the **anterior midgut caeca**, arise dorsally, and ducts of the **hepatopancreas** (**midgut gland**) also enter the midgut at this level. At the junction between the midgut and the hindgut (**rectum**), a prominent, anteriorly directed caecum, the **posterior midgut caecum**, arises (McLaughlin, 1983c).

Other published works on the gastric mill and other parts of the digestive system in anomurans can be found in Patwardhan (1935), Schaefer (1970) [for *Diogenes brevirostris* Stimpson, 1858]; Pike (1947) [for *Galathea squamifera*]; Caine (1975, 1976), Meiss & Norman (1977a, b), and Kunze & Anderson (1979) [for *Clibanarius taeniatus*, *Clibanarius virescens* (Krauss, 1843), *Paguristes squamosus* McCulloch, 1913, and *Dardanus setifer* H. Milne Edwards, 1836]. Morphology and functional anatomy of the foregut, specifically, are provided for the galatheoids *Porcellana platycheles* and *Galathea squamifera*, by Ngoc-Ho (1984) and Pike (1947), and more recently for the aeglid, *Aegla platensis* Schmitt, 1942, by Castro & Bond-Buckup (2003).

Circulatory system

General overviews of the decapod **circulatory/vascular system** (including **blood** or **hemolymph**) can be found in McLaughlin (1980, 1983c), Felgenhauer (1992b), and Martin & Hose (1992). The decapod **cardiovascular system** has a single muscular **ventricle** suspended in the **pericardial sinus** by ligaments (fig. 70.24A, B). The hemolymph (blood) is pumped out into seven arteries: (1) anteriorly is the anterior aorta, (2) and (3) the paired anterolateral arteries, and (4) and (5) the paired hepatic arteries; posteriorly is (6) the posterior aorta and (7) the sternal artery (Wilkens, 1999). The anterior **aorta** supplies blood to the eyestalks, antennae, and supraesophageal ganglion. The anterolateral **arteries** supply blood to the gonads, dorsal hepatopancreas, foregut, and antennal glands. The hepatic arteries branch into the rest of the hepatopancreas. The posterior aorta supplies blood to the pleon, hindgut, and pleopods. Lastly, the sternal artery divides ventrally after it leaves the heart and supplies blood to the limbs and mouthparts. All arteries further branch into arterioles, then into fine capillary-like vessels, and finally dissolve into lacunae. It is at the level of the lacunae that the blood bathes all the tissues, and gas, nutrient, and waste exchange occurs. Decapods lack a true venous system (although there are afferent and efferent branchial **veins** only in the gill lamellae) and rely on a system of lacunae and **sinuses** to collect the blood and transport it back to the heart, via the gills and three pairs of **cardiac ostia** (McLaughlin, 1983c; McGaw, 2005).

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fibrils; nopf, fiber of peduncular lobus opticus; nu, nucleus; pre, proximal retinal cell; rb, rhabdome; re, distal retinal cell (principal pigment cell); vit, vitreous body. K, the stratigraphic ranges of the extant crustaceans (excluding those with reduced or absent eyes) together with the optics used (in brackets where presumed); the dotted lines indicate possible evolutionary relationships. [A-H, after Nilsson, 1990 and Gaten, 1998; I, J, after Makarov, 1962; K, after Gaten, 1998 based on Schram, 1982, Wägele, 1989, and Glaessner, 1969.]
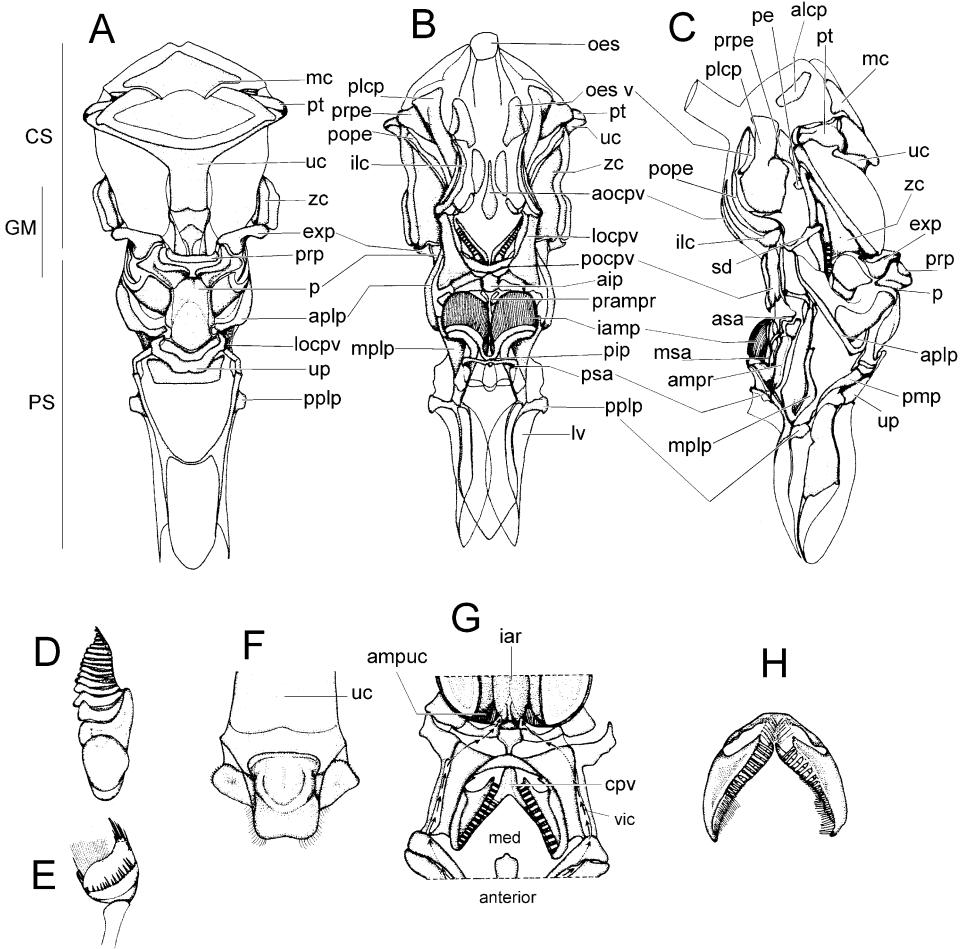
Fig. 70.26. Proventriculus of *Clibanarius taeniatus*. A, proventriculus and its ossicles, dorsal view; B, same, ventral view; C, same, lateral view; D, lateral accessory teeth; E, lateral teeth; F, dorsal tooth of gastric mill, ventral view; G, cardiopyloric region, dorsal view, showing ventrolateral channels leading to ampullae; H, cardiopyloric valve. Abbreviations A-C: aip, anterior inferior pyloric ossicle; alcp, anterior lateral cardiac plate; ampr, ampullary roof ossicle; aocpv, anterior ossicle of cardiopyloric valve; aplp, anterior pleuropyloric ossicle; asa, anterior supra-ampullary ossicle; dv, dorsal valve; exp, exopyloric ossicle; iamp, inferior ampullary ossicle; ilc, inferolateral cardiac ossicle; locpv, lateral ossicle of cardiopyloric valve; lv, lateral valve; mc, mesocardiac ossicle; mplp, middle pleuropyloric ossicle; msa, middle supra-ampullary ossicle; oes, esophagus; oesv, esophageal valve; p, pyloric ossicle; pe, pectineal ossicle; pip, posterior inferior pyloric ossicle; lpcp, posterior lateral cardiac plate; pmp, posterior mesopyloric ossicle; pocpv, posterior ossicle of cardiopyloric valve; pope, postpectineal ossicle; pplp, posterior pleuropyloric ossicle; pramp, pre-ampullary ossicle; prp, propyloric ossicle; prpe, prepectineal ossicle; psa, posterior supra-ampullary ossicle; pt, pterocardiac ossicle; sd, subdentary ossicle; uc, urocardiac ossicle; up, uropyloric ossicle; zc, zygocardiac ossicle. Abbreviation F: uc, urocardiac ossicle. Abbreviations G: ampuc, upper chamber of ampulla; cpv, cardiopyloric valve; fp, filter press; iar, interampullary ridge; med, median channel; vlc, ventrolateral channel. [A-H, after Kunze & Anderson, 1979.]

Paguroidea

In hermit crabs, the **heart** is located in the posterior-dorsal region of the cephalothorax under the carapace. The heart is surrounded by the **pericardium**, which extends from the cervical groove to the eighth thoracomere and blood flows from the gills into the pericardium and into the heart via one anterodorsal pair and two lateral pairs of ostia (fig. 70.24A, B). Each ostium is provided with a set of valves that prevents the blood from flowing back into the pericardial sinus on **systole**.

Emanating from the heart anteriorly are three arteries, the median optic artery and the paired anterior lateral arteries. A **frontal heart** (*cor frontale*) is formed in the optic artery anteriorly from the heart. This structure was first described by Baumann (1917) as a special pulsating structure or an **accessory heart** formed from enlargement of the blood vessel [but see also chapter 9 in volume 2 of the present series]. The optic artery passes over the dorsal surface of the foregut and then turns ventrally and divides into two branches that provide blood to the anterior cephalic area and supraesophageal ganglion. The anterior lateral arteries provide branches to the foregut and musculature. Ventrally from the heart, the small hepatic arteries are located. In hermit crabs, this pair of arteries no longer supplies blood to the hepatopancreas, which now lies almost exclusively in the pleon, but terminate, instead, on the foregut or midgut.

From the posterior margin of the heart, the sternal artery and the posterior aorta emerge; the former is antero-ventrally directed, and the latter is large and posteriorly directed. The sternal artery passes ventrally into the seventh thoracomere and then turns horizontally. At the level of the fifth thoracomere, it turns ventrally again and pierces the central ganglionic mass between the nerves of the second and third pereiopod. Beneath the nerve cord, the vessel divides into anterior and posterior branches. The former, the ventral thoracic artery, provides blood to the chelipeds, mouthparts, renal gland, and ventral region of the foregut; the latter supplies blood to the third through fifth pereiopods, but, in contrast to other anomurans, it does not enter the pleon.

From the posterior aorta, the ventral aortic branch is at the level of the first pleomere, and then it divides further into the submuscular and supramuscular branches at the level of the third pleomere. The submuscular branch passes ventrally along the ventral nerve cord and terminates in the sixth pleomere. The supramuscular branch provides numerous branches to the hepatopancreas and gonads, and terminates with branches to the telson and uropods.

Recent work on the hermit crab cardiovascular system is specific to the **terrestrial** hermit crabs, Coenobitidae (cf. Greenaway, 2003) and has revealed in *Birgus* and *Coenobita* (via intricate corrosion casting) a well-developed and complex network with highly vascularized **branchiostegal lungs** and **pleonal lungs** in addition to gills (Farrelly & Greenaway, 2005).

Lithodoidea

Sophisticated corrosion casting techniques were also recently employed by McGaw & Duff (2008) to reveal the intricate cardiovascular system of the lithodid crabs, *Lopholithodes mandtii* Brandt, 1848 and *Lopholithodes foraminatus* (Stimpson, 1859). The

system is essentially the same as that described above for decapods and hermit crabs, except that differences occur in the pleon because of its shortened and ventrally folded nature in lithodids. Also, the process of **carcinization** in the king crabs means that the cardiovascular morphology is very similar to that described for many brachyuran crabs, but appears to be simpler (McGaw & Duff, 2008).

Excretory system

A general overview of the decapod **excretory system** can be found in Felgenhauer (1992b). A variety of tissues and organs contribute to **metabolic waste excretion**, but the excretion in anomurans is mainly via the **antennal glands**, which arise as **coelomoducts** and remnants of the coelom in the antennal somite. It is composed of a mesodermal **coelomic sacculus** and an ectodermal **nephridial canaliculus**. The proximal part of the canaliculus is very ramified, forming the **labyrinth** (**nephrostome**), and the distal part is broadened to form a **collector bladder** (fig. 70.24D), out of which leads an **efferent duct**, lined with a chitinous cuticle terminating in an opening (**nephropore**) on the mesial side of basal portions of the antenna (McLaughlin, 1980, 1983c) (figs. 70.17E, 70.21C).

In hermit crabs, the **anterior vesicular mass** is found in the cephalothorax, which is connected with anastomoses to the antennal glands. Each anastomosis is broadened to form a mass of ramified tubes, which in turn form the **epigastric lobe**. From this lobe, a narrow canal is extended, which leads to another pair of masses of ramified tubes, the **paragastric lobes**, situated on the lateral sides of the stomach. This paired mass is connected with a small **supragastric lobe**. Beneath the stomach, the single **medioventral lobe** is found, which by means of an anterior and posterior branch is connected with the paragastric lobes. In hermit crabs, a **posterior vesicular mass** is also found. It consists of a pair of ramified tubes leading out of the paragastric lobes, extending along the intestine to the pleon, where they unite to form a single **pleonal bladder** (**nephrosac**) with thin walls that extends for approximately three quarters of the length of the pleon (McLaughlin, 1980, 1983c).

Several papers dealing specifically with the excretory system of the highly modified, terrestrial coconut crab, *Birgus latro* (Linnaeus, 1767) (cf. Greenaway & Morris, 1989; Greenaway et al., 1990; Dillaman et al., 1999; Morris et al., 2000), are reviewed in the paper on terrestrial adaptations of the Anomura by Greenaway (2003).

Genital apparatus and reproduction

Although Anomura are morphologically diverse, the external **genital apparatus** generally consists of small spherical or oval **gonopores** on the ventral **coxal segment** of the **third pereiopod** in females (fig. 70.9J) and the **fifth pereiopod** in males (fig. 70.5G), as has been universally described for the reptant Decapoda (cf. Felgenhauer, 1992a; Krol et al., 1992), and in more detail for *Aegla* (cf. Martin & Abele, 1986, 1988), *Coenobita* (cf. Martin & Abele, 1986; Tudge & Lemaitre, 2006), *Diogenes* (cf. Manjón-Cabeza & Garcia Raso, 2000), *Clibanarius* (cf. Hess & Bauer, 2002), *Galathea* (cf. Kronenberger et al., 2004), and *Isocheles* (cf. Mantelatto et al., 2009a), and *Pagurus* (cf. Scelzo et al., 2010).

Variations on this basic pattern have been described for **intersex** individuals where usually both sets of male and female gonopores are visible externally, although the internal functionality varies, with only rare cases of actual **hermaphroditism** having been reported. Recent papers on intersex hermit crabs include McLaughlin & Lemaitre (1993), Turra (2004, 2005, 2007), Gusev & Zabotin (2007), and Fantucci et al. (2008), while Kronenberger et al. (2004) briefly recorded instances of intersex individuals in *Galathea* (Galatheidae) from the North Sea.

Interestingly, some male anomurans have one or both gonopores extended as tubular structures, generally termed **sexual tubes** (Lemaitre & McLaughlin, 2003), some of which can be very large and elaborate (fig. 70.15G-V). Some sort of sexual tube has been recorded in the aeglids (Martin & Abele, 1988) and hippids (Snodgrass, 1952), but detailed morphological and ultrastructural descriptions are only recently available for the hermit crabs *Micropagurus acantholepis* (Stimpson, 1858) (Paguridae) (Lemaitre & McLaughlin, 2003; Tudge & Lemaitre, 2004), and *Coenobita clypeatus* (Herbst, 1791) and *Coenobita perlatus* H. Milne Edwards, 1837 (Coenobitidae) (Tudge & Lemaitre, 2006). The occurrence and diversity appear greatest in Paguridae (present in some form in more than 60% of the genera), but impressively large and heavily calcified homologues(?) also are apparent in the two genera, *Coenobita* and *Birgus*, of the terrestrial Coenobitidae. In the investigated taxa (above) the function of the sexual tubes as active **spermatophore delivery structures** has been confirmed for representatives in both families, but the evolutionary significance and history of the structures will probably have to wait for better familial and superfamilial phylogenies.

The internal morphology of the male and female reproductive system has been described and illustrated by Felgenhauer (1992b) and Krol et al. (1992), as a general overview of Decapoda.

The **male reproductive system** in Anomura consists of **paired testes**, each leading to an **external gonopore** on the fifth pereiopod (and any of its modifications mentioned above) via a convoluted **vas deferens** and straighter **gonoduct** (fig. 70.24A). The entire tubular system can be divided into discrete functional regions (testis, collecting tubule, proximal, medial, and distal vas deferens, and gonoduct) based on external appearance, diameter, musculature, and glandular activity, with differing numbers of further subregions identified in various taxa (Mouchet, 1930, 1931; Rathnavathy, 1941; Matthews, 1953, 1956a, b; Greenwood, 1972; Subramoniam, 1984; Fingerman, 1992; Manjón-Cabeza & Garcia Raso, 2000; Hess & Bauer, 2002; Kronenberger et al., 2004; Tirelli et al., 2006).

A most voluminous part of the literature on anomuran reproduction is in the area of the microstructure and ultrastructure of male **spermatophores** and contained **spermatozoa**. The anomuran spermatophore is the most complex of the decapod spermatophores (Hinsch, 1991a, b; Subramoniam, 1991; Fingerman, 1992; Krol et al., 1992) and is usually described as a tripartite, **stalked structure** with a foot or **pedestal**, a **stalk** of variable width and length, and a bivalved, **terminal ampulla** full of spermatozoa (Tudge, 1991, 1997, 1999). With a few exceptions, e.g., Aeglidae, Hippoidea, and possibly the Lomisidae and some Lithodoidea, all anomuran representatives investigated for spermatophore structure

have this complex stalked morphology, but with many having distinctive (phylogenetically informative) familial or generic traits (Tudge, 1991, 1999; Tudge & Jamieson, 1996a, b; Scelzo et al., 2004, 2010; Tirelli et al., 2008, 2010; Mantelatto et al., 2009a). To date, the male spermatophore morphology is known (through light microscopy, scanning or transmission electron microscopy) for 84 species, in 41 genera, from 12 of the 17 currently recognized anomuran families (McLaughlin et al., 2007a). The five families for which the spermatophore morphology is currently un-documented are Blepharipodidae, Chirostylidae, Hapalogastridae, Kiwaidae, and Pylojacquesidae.

The spermatozoa show similar diversity within Anomura (see fig. 4 in Tudge & Scheltinga, 2002, for representatives of 13 anomuran families) but with some consistent characteristic suites of traits (Tudge, 1997). Anomuran spermatozoa vary from long, **pseudo-flagellate cells** with multiple arms formed into a **rope-like tail** (the porcellanid genera *Pisidia* and *Aliaporcellana*), through depressed **ovoid cells** with barely discernible vertices for arms (*Pylocheles* and *Lomis*), to the commonest form where an ovoid to elongate, complexly zoned, **acrosome vesicle** sits superiorly on a meager cytoplasm with usually three **microtubular arms** and a posterior **nucleus** (see the hermit crabs *Birgus*, *Clibanarius*, and *Pagurus*). Three important review papers exhaustively summarize and/or list all the previous anomuran spermatozoal literature from the early 1900's to the present, in the context of reviewing the more diverse and larger crustacean and decapod spermatozoal morphology. These review papers are Jamieson (1991), Jamieson & Tudge (2000), and most recently Tudge (2009), the latter two being chapters in books on decapod reproduction and phylogeny, respectively. When collated, the spermatozoal morphology is currently known (at the LM, SEM, and TEM level) for 74 species in 39 genera, representing 14 of the 17 current anomuran families. The remaining anomuran families for which we have no data on spermatozoal morphology are Blepharipodidae, Kiwaidae, and Pylojacquesidae.

Some publications dealing exclusively with aspects of **female reproductive biology** in anomurans (see review in Krol et al., 1992), a galatheid (Kronenberger et al., 2004), and then specifically in hermit crabs, are available and include descriptions of **ovaries**, **oogenesis**, and/or **eggs** (Subramaniam, 1935; Carayon, 1941; Kamalevani, 1949; Komm & Hinsch, 1987), **egg fixation** to pleopods (Matthews, 1959), **egg incubation** (Torati & Mantelatto, 2008), and **egg volume** and **fecundity** (Terossi et al., 2010). A review of the literature on female life history traits (including brood size, egg diameter, and eclosion date) for the families Hapalogastridae and Lithodidae can be found in Zaklan (2002).

Endocrine system

Decapod **glands** can be divided into **endocrine** and **exocrine**. The endocrine system is further subdivided into **neuroendocrine** glands (**sinus glands**, **postcommissural organs**, and **pericardial organs**) and **non-neural** or **epithelial** endocrine glands (**Y-organs**, **mandibular organs**, and **androgenic glands**). The exocrine glands include **dermal tegumental glands**, **antennal glands** (usually treated as part of the excretory system), and **midgut glands** (usually treated as part of the digestive system) (Fingerman, 1992).

Hanström (1939) and Kurup (1964) addressed the presence and structure of the **sinus gland** in Anomura, with the latter paper specifically on the porcellanid, *Petrolisthes cinctipes* (Randall, 1839). Similarly, the **pericardial organ** is described in the hermit crab, *Pagurus bernhardus* (Paguridae) by Alexandrowicz (1953) and the lithodid crab, *Paralithodes brevipes* (H. Milne Edwards & Lucas, 1841) by Miyawaki (1955).

The existence of the **Y-organ**, which functions in controlling aspects of **molting**, is reported in *Diogenes*, *Clibanarius*, and *Paguristes* in Diogenidae; *Pagurus* and *Anapagurus* in Paguridae; *Galathea* in Galatheidae; and *Porcellana* and *Pisidia* in Porcellanidae (cf. Gabe, 1953; Le Roux, 1974, 1982). The Y-organs are situated in the maxillary somite in *Pagurus* and in the maxillulary somite in zoeae of *Clibanarius*, *Pagurus*, and *Pisidia*.

The existence of the **mandibular organs**, which might well be involved in various metabolic processes including the controlling of molting, reproduction, and processes of development and metamorphosis, is reported in *Clibanarius* in Diogenidae; *Pagurus* and *Anapagurus* in Paguridae; and *Porcellana* and *Pisidia* in Porcellanidae (cf. Le Roux, 1968, 1974). This organ is located in the vicinity of the insertion of the mandibles, i.e., near their articulation with the sclerites of the cephalothorax.

The **androgenic glands** are only found in male malacostracans where they are involved in sexual differentiation (Fingerman, 1992). Charniaux-Cotton (1955) named the "androgenic gland" in the anatomy of an amphipod and, in a later paper with colleagues, described the ultrastructure of this organ from the diogenid hermit crab *Clibanarius erythropus* (Latreille, 1818) (see Charniaux-Cotton et al., 1966).

Tegumental glands are scattered throughout the decapod cuticle and may be uni-, tri-, or multi-cellular (Felgenhauer, 1992a; Fingerman, 1992), the latter often referred to as **rosette glands**. These typical tegumental rosette glands have recently been recorded in the base of the fifth pereiopod of the land hermit crab genus *Coenobita* (cf. Tudge & Lemaitre, 2006) and scattered along the fifth pereiopod in species of the freshwater anomuran genus *Aegla* (cf. Almerão et al., 2007). Anomura were also the source for the recently characterized **crustacean hyperglycaemic hormone** by Montagne et al. (2008). It was also recently discovered that the neuroendocrine system is involved in regulating salt and water balance in the terrestrial hermit crab, *Birgus latro* as well as in the terrestrial gecarcinid brachyuran crabs (Morris, 2001). These terrestrial decapods have evolved a filtration and reabsorption system that is analogous, in many respects, to the vertebrate **kidney**.

DEVELOPMENT AND LARVAE

Larval development in Anomura is **metamorphic**. A general review of events within the constituent groups follows here.

Paguroidea and Lithodoidea

The **first post-embryonic stage** is a **zoea** (fig. 70.27A, E-H, J, K). The zoeal stage is followed by **metamorphosis** to a **megalopa** (fig. 70.27I, L), often referred to as
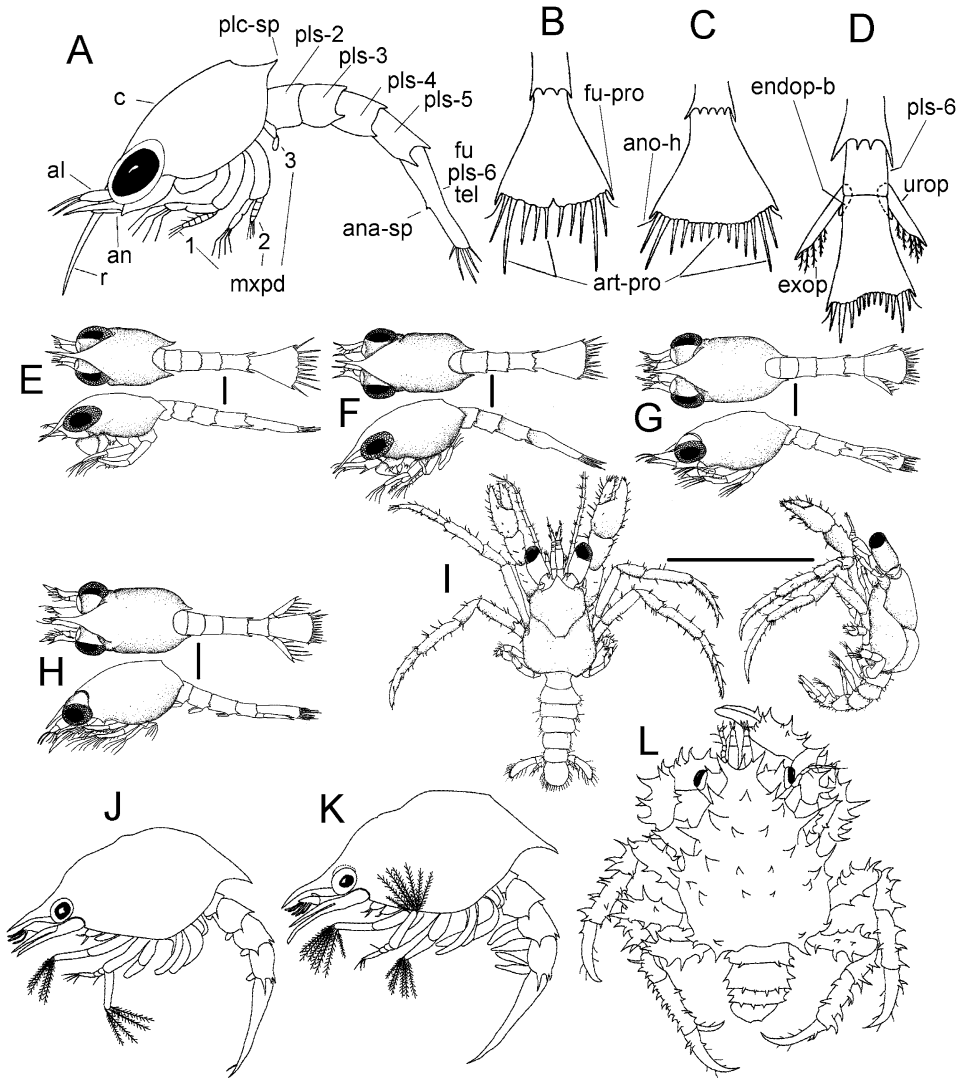
Fig. 70.27. Larvae of Paguroidea and Lithodoidea: A, diagrammatic pagurid; B, C, *Pagurus*; D, *Lithodes*; E-I, *Pagurus constans* (Stimpson, 1858); J-L, *Paralomis hystrix* (De Haan, 1846). A, first stage zoea, lateral; B, posterior margin of fifth pleomere, sixth somite, and telson of third stage zoea; C, posterior margin of fifth pleomere and telson of first stage zoea; D, same; E-H, first through fourth zoeas, dorsal and lateral views; I, megalopa, same; J, first stage zoea, lateral; K, second stage zoea, same; L, megalopa, dorsal. Abbreviations: ana-sp, anal spine; ano-h, anomuran hair; art-pro, articulated process; endop-b, endopod bud; fu-pro, fused process; fu pls-6 tel, fused sixth somite and telson; plc-sp, posterolateral carapace spine. [A-D, after Sandberg & McLaughlin, 1998; E-I, after Hong & Kim, 2002; J-L, after Konishi & Taishaku, 1994.]

a **glaucothoe**. The **number of zoeal stages** varies among the taxa, with 2 to 7 in Coenobitidae and Diogenidae, 4 to 6 in Parapaguridae, 4 (rarely 3) in Paguridae, and 2 to 5 in Lithodoidea (generally 2 to 4 in Lithodidae; 4 to 5 in Hapalogastridae; cf. Crain & McLaughlin, 2000). The **duration of the zoeal stage** is also highly variable among the taxa. For example, in Coenobitidae, *Coenobita variabilis* McCulloch, 1909 undergoes **abbreviated development** and reaches the megalopa stage in only six days after only two non-feeding zoeal stages (Harvey, 1992). On the other hand, the zoeal life span of *Coenobita scaevola* (Forskål, 1775) ranges from 54 to 80 days with seven zoeal stages (Al-Aidaroos & Williamson, 1989). The larval development of the coconut crab, *Birgus latro* (also in Coenobitidae); was first described by Reese & Kinzie (1968), was later reviewed by Schiller et al. (1991) in their chapter on reproduction, early life history, and recruitment; and then later again for both *Birgus* and *Coenobita* in the paper on terrestrial adaptations in Anomura by Greenaway (2003).

In the **zoeal stages** of Coenobitidae, the carapace is smoothly rounded and provided with a narrow, dagger-like rostrum but no posterolateral spine nor pterygostomial spine. However, in Diogenidae, pterygostomial spines (*Paguristes*) or submarginal posterior spines (*Calcinus*) do occur. In Parapaguridae, the carapace is equipped with a dorsal carina, an elongate rostrum, and no posterolateral spine, but with or without pterygostomial spines. In Paguridae, the carapace is smoothly rounded, with or without the dorsal carina or spine, and provided with a narrow rostrum and usually a posterolateral spine.

In most species, five pleomeres are differentiated in the first zoeal stage, and six in either the second or third zoeal stage (fig. 70.27A-D). None of the endopods of the pereiopods become functional in the zoeal stage. In the first zoeal stage, functional exopods are confined to the first and second maxillipeds, and each exopod ends in four setae. More setae are always added at the second zoeal molt and subsequent molts. In the second zoeal stage, a further pair of exopods (on the third maxillipeds) usually becomes functional. The endopod of the third maxilliped in the zoeal stages arises from the side of the basis, usually in the proximal half, while the exopod arises terminally.

Abbreviated development was reported in some species including *Calcinus* sp. (cf. Calado et al., 2006) and *Cancellus* (cf. Mayo, 1973), in which the larvae hatch at the megalopa stage. Calado et al. (2006) reported in an undescribed species of *Calcinus* from shallow water in Portugal, that 23 observed specimens of ovigerous females had only one to six very large eggs inside the gastropod shell, that one female was recorded with a single megalopa inside the gastropod shell, and six females had one or two fully-developed juveniles associated with them in their shells. This is an interesting example of **brood care** in hermit crabs.

Galatheoidea and Chirostyloidea

A **variable number of zoeal stages** is usually followed by a **single megalopa stage** followed by the **first juvenile stage**. The number of zoeal stages varies between taxa. Two to five zoeal stages precede the megalopa in Porcellanidae. Four or five zoeal stages are usually present in Galatheidae and Munididae (cf. Fujita & Shokita, 2005, and references

therein), and at least some species of *Munidopsis* (Munidopsidae) undergo **abbreviated development**. For instance, *Munidopsis serricornis* (Loven, 1852) has three zoeal stages of which the third stage is the equivalent of the fourth zoea of other galatheids (Samuelsen, 1972; as *Munidopsis tridentatus* Ortmann, 1892). *Munidopsis polymorpha* Koelbel, 1892 has only two zoeal stages followed directly by a crab stage rather than a megalopa (Gore, 1979; Wilkens et al., 1990).

Full larval development has not been studied in Chirostyloidea, though the number of zoeal stages is believed to vary. In the chirostylids, the genera *Uroptychus*, *Gastroptychus*, and *Chirostylus*, appear to have abbreviated development, with the first zoea hatching at a stage resembling fourth or fifth stage galatheids (Pike & Wear, 1969; Clark & Ng, 2008). Additionally, Clark & Ng (2008) observed that the first zoea of *Chirostylus* is **lecithotrophic**, a feature associated with abbreviated development. In contrast, larval development in Eumunididae, exemplified by *Eumunida annulosa* de Saint Laurent & Macpherson, 1990 and *Eumunida capillata* de Saint Laurent & Macpherson, 1990, do not show abbreviated development, with the first zoea equivalent to the first zoea of galatheids (Guerao et al., 2006). Moreover, Guerao et al. (2006) found that in many respects, *Eumunida* larvae are typically pagurid, having two terminal plumose setae on the antennal endopod, a three-segmented endopod on the maxillule, absence of posterolateral carapace spines, and a scaphognathite with 5 plumose setae and without a posterior lobe. Clark & Ng (2008) also observed the absence of posterolateral spines on the carapace for larval *Chirostylus*, questioning the original galatheoid placement of Chirostylidae. These larval anomalies, aligning chirostylids with paguroids instead of galatheids, are consistent with spermatozoal morphology (Tudge, 1997) and recent phyogenetic analyses that similarly suggest polyphyly among the major squat lobster clades, and more specifically, involving a close relationship between chirostyloids and paguroids (Ahyong et al., 2009; Chu et al., 2009). Nothing is currently known of development in kiwaids.

Aegloidea

Significantly abbreviated development is also found in aeglids from South America. Development is **direct**, from **large yolky eggs**, there are no free-swimming larval forms and a **juvenile**, resembling the adult, hatches directly from the egg (Bond-Buckup et al., 1996, 1999; Bueno & Bond-Buckup, 1996; Lizardo-Daudt & Bond-Buckup, 2003; Bueno et al., 2000).

Hippoidea

Larval development was studied in several species of hippids from the genera *Emerita* and *Hippa* (cf. Johnson & Lewis, 1942; Rees, 1959; Knight, 1966; Kato & Suzuki, 1992), and in albuneids and blepharipodids (Knight, 1970; Sandifer & van Engle, 1972; Stuck & Truesdale, 1986; Seridji, 1988; Konishi, 1987). The first post-embryonic stage is a zoea, and it bears a remarkable, but superficial, resemblance to larvae of brachyuran crabs in that the carapace is spherical and the lateral and rostral spines are distinctly deflected ventrally (fig. 70.28A-E, G). This is consistent with many phylogenetic analyses of Decapoda,
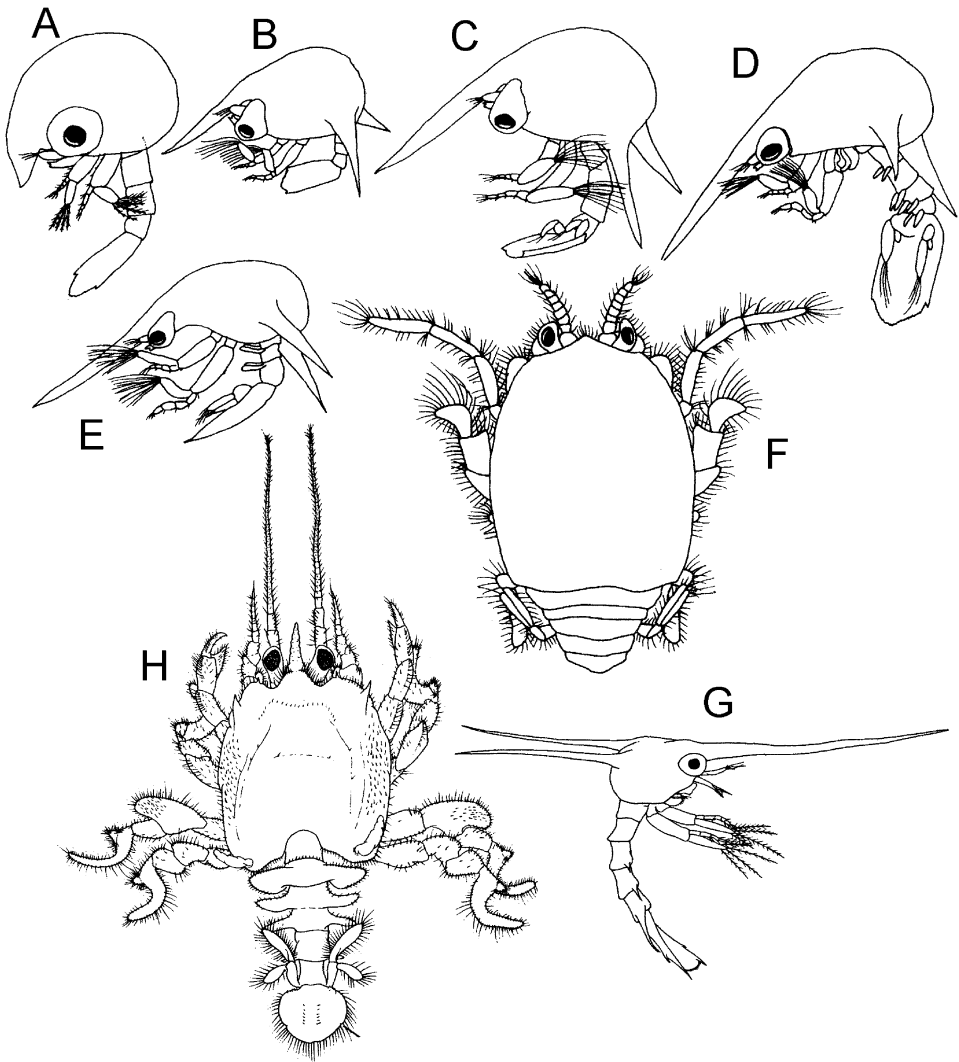
Fig. 70.28. Larvae of Hippoidea: A-F, *Hippa truncatifrons*; G, H, *Lepidopa benedicti*. A-E, first through fifth stage zoeas, lateral; F, megalopa, dorsal; G, first stage zoea, lateral; H, megalopa, dorsal. [A-F, after Kato & Suzuki, 1992; G, H, after Stuck & Truesdale, 1986.]

finding hippoids to be basal in Anomura, which is itself sister to Brachyura (Ahyong & O'Meally, 2004; Tsang et al., 2008; Ahyong et al., 2009; Chu et al., 2009). The **zoeal stage** is followed by metamorphosis to a **megalopa** (fig. 70.28F, H). The number and duration of the zoeal stages is variable. For example, there are 7 stages in 23-33 (average 28) days in *Emerita talpoida* (Say, 1817) (see Rees, 1989), 6 stages in 52 days in *Emerita holthuisi* Sankolli, 1965 (see Siddiqi, 2006), 5 stages in about 60 days in *Hippa truncatifrons* (Miers, 1878) (see Kato & Suzuki, 1992), and 4 stages in 14-17 days in *Lepidopa benedicti* Schmitt, 1935 (see Stuck & Truesdale, 1986).

ECOLOGY AND ETHOLOGY

Ecological distribution

Paguroidea

Hermit crabs are mostly **aquatic** and occur in all of the world's oceans at depths ranging **from intertidal** zones and the continental shelf to **deep-sea bottoms**. In temperate to boreal waters, various species of *Pagurus* are found in intertidal and shallow water zones, and *Elassochirus*, *Labidochirus*, and lithodids are seen from shallow waters to continental slopes. **Seasonal migration** is known in several species; *Pagurus minutus* Hess, 1865 and *Diogenes nitidimanus* Terao, 1913 migrate offshore in winter and summer, respectively, for reproduction.

In tropical waters, coral reefs are inhabited mainly by species of *Calcinus*, *Clibanarius*, and *Dardanus*. In mangrove swamps, species of *Clibanarius* are often found, some of which are known to adapt to diluted seawater. Only one species has been known to inhabit a truly freshwater environment, *Clibanarius fonticola*, from Vanuatu in the South Pacific (McLaughlin & Murray, 1990). The land hermit crabs of the genus *Coenobita* and the coconut crab *Birgus* live an essentially **terrestrial** life, except for reproductive periods when they release zoeae into the sea.

Species of Parapaguridae are deepwater inhabitants, ranging from depths of 55 m to 5000 m, but mainly occur at 200-3000 m (Lemaitre, 1989).

Lithodoidea

Information concerning the ecological distribution of this superfamily can be found in the Biogeography section (p. 300 ff.).

Galatheoidea and Chirostyloidea

Galatheoids and chirostyloids are **marine** (or **anchialine** as in the case of *Munidopsis polymorpha*), and live on hard or coarse substrates from the intertidal zone to about 5000 m depth (Baba, 2005). Porcellanids are most abundant and diverse on shallow tropical reefs down to depths of about 100 m. They live in crevices under rocks, amongst coral, and *Neopetrolisthes* species are commensal with sea anemones. Some squat lobsters live in shallow, nearshore, and coral reef waters, as in the majority of species of *Galathea*, or are sometimes pelagic, e.g., *Munida gregaria* (Fabricius, 1793), but most galatheoids and chirostyloids are most speciose and abundant at continental shelf and slope depths. In general, deepwater galatheoids occur on all types of substrate, whether deepwater reef or soft muddy habitats. Some, such as *Munidopsis serricornis* in the North Altantic are strongly associated with soft coral (Samuelsen, 1972), but most galatheoids do not appear to form strong **associations**. Chirostyloids, on the other hand, are often associated with deepwater corals, especially antipatharians, alcyonaceans, and gorgonaceans (Baba et al., 2008; Kilgour & Shirley, 2008; Le Guilloux et al., 2010). At present, kiwaids are known only from **hydrothermal vents** in the southeastern Pacific (Baba et al., 2008).

Species of Hippidae inhabit the surf zone or shallow subtidal zones of the temperate and tropical sandy beaches of the world. Similarly, the albuneid and blepharipodid species live buried in sandy sediments from the low intertidal to offshore in the temperate and tropical waters world-wide.

AEGLOIDEA AND LOMISOIDEA

Information of the ecological distribution of these endemic superfamilies can be found in the Biogeography section (p. 300 ff.).

Shell and other object use

Hermit crabs are known to **carry vacant gastropod shells** or other material as **portable shelters**. Members of Pylochelidae, having a symmetrical pleon, are **tusk-shell** inhabitants, or may be **xylicolous** or **petricolous** (fig. 70.29G, H). Species of Diogenidae, Paguridae, and Coenobitidae, most frequently utilize gastropod shells that are **dextrally coiled** (fig. 70.29A, B, D, E), but exceptions are also known to use **bivalve shells** (fig. 70.29C), polychaete worm tubes, bryozoan skeleton tubes, vermetid shell tubes, cavities in corals, pieces of wood or bamboo (fig. 70.29I, J), and sponges. Striking **symbiotic relationships** are known between many species of Parapaguridae and colonies of anthozoans, especially zoanthids, as portable shelters (fig. 70.29F).

Symbiotic association

Many examples of **symbiotic associations** between anomurans (principally hermit crabs) and other invertebrates are known. According to the comprehensive worldwide review by Williams & McDermott (2004), they can be ecologically divided into: (1) species found on the shells occupied by hermit crabs (epibiotic species), e.g., cnidarians, bryozoans, and sponges; (2) species boring into these shells (endolithic species), e.g., polychaetes, small arthropods, sponges, and bryozoans; (3) species living within the lumen of the shell (either free-living or attached to the shell), e.g., small crustaceans, flatworms, and polychaetes; or (4) species attached to the hermit crabs themselves, and hypersymbionts (fig. 70.30A-C). In total, over 550 invertebrates from 16 phyla are known associates of over 180 species of hermit crab. Of these, 114 appear to be **obligate commensals** of hermit crabs, 215 are **facultative commensals**, and 232 are **incidental associates**. The taxa exhibiting the highest number of associates are arthropods (126), polychaetes (105), and cnidarians (100). Several lithodids (*Lithodes*, *Lopholithodes*, *Neolithodes*, *Paralomis*, *Paralithodes*) are known as hosts to snailfish (Liparidae: *Careproctus* spp.), which use the crabs' spiny exterior as mobile shelter, and the branchial chamber to incubate their eggs (Yau et al., 2000; Batson, 2003). The lithodid-*Careproctus* association is possibly better regarded as parasitic rather than commensal, because the host-crab experiences some compression or localized gill necrosis (Love & Shirley, 1993; Somerton & Donaldson, 1998).
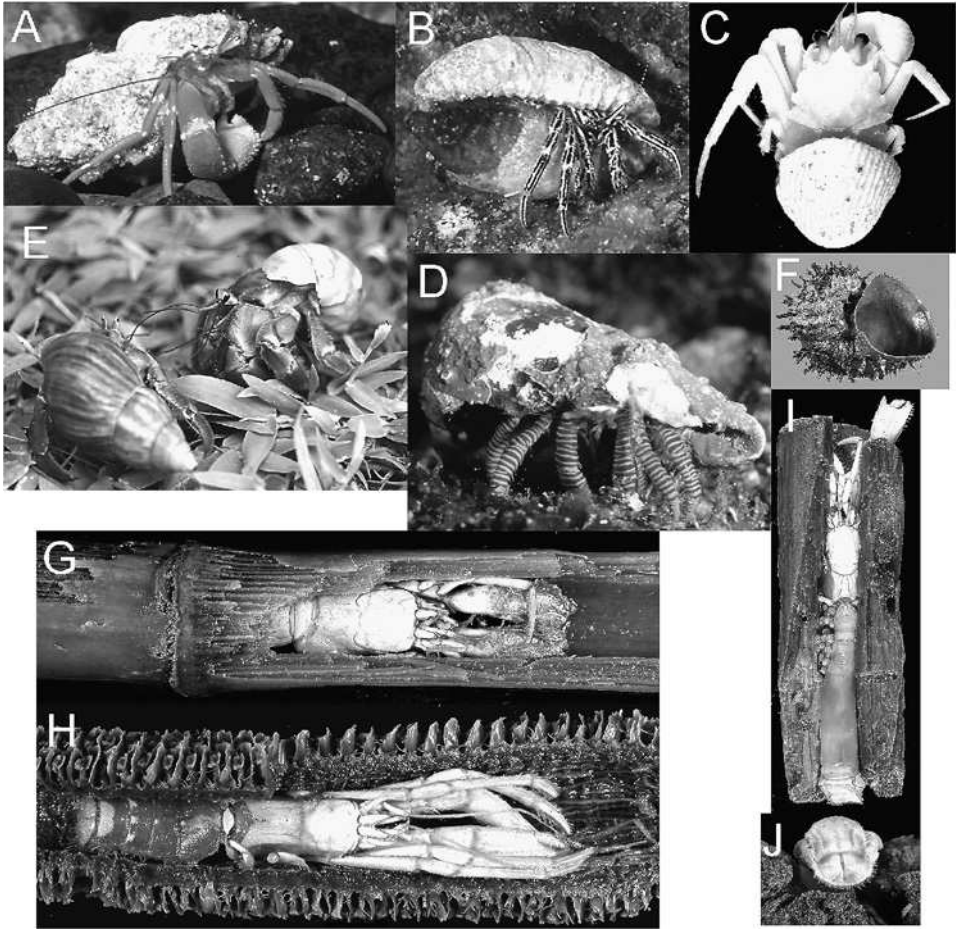
Fig. 70.29. Shell and other object use of hermit crabs. A, *Pylopaguropsis furusei* in normal dextral gastropod shell; B, *Clibanarius eurysternus* (Hilgendorf, 1879) in cypraeid shell; C, *Porcellanopagurus tridentatus* Whitelegge, 1900 bearing bivalve shell; D, *Ciliopagurus strigatus* (Herbst, 1804) in conid shell; E, *Coenobita purpureus* Stimpson, 1858 in land snail shell; F, "pseudoshell" (colony of the hydroid *Hydractinia sodalis* Stimpson, 1858) used by *Pagurus constans*; G, *Bathycheles incisus* (Forest, 1987) in bamboo; H, *Parapylocheles scorpio* (Alcock, 1894) in corn; I, *Xylopagurus caledonicus* Forest, 1997 in wood; J, same, telson. [Photos: A, B, by Koji Furuse; C-J, by Akira Asakura.]

Parasites

Two major taxonomic groups of **parasites** on species of Anomura are well known; **Bopyridae** (Isopoda) (fig. 70.31C-G) and **Rhizocephala** (Cirripedia) (fig. 70.31A, B).

Fig. 70.30. Communities of hermit crab associates [after Williams & McDermott, 2004]. A, symbionts associated with the gastropod shell, *Aporrhais* sp., inhabited by *Paguristes eremita* (Linnaeus, 1767) and *Pagurus cuanensis* Bell, 1845, scales = 2 mm [modified from Stachowitsch,
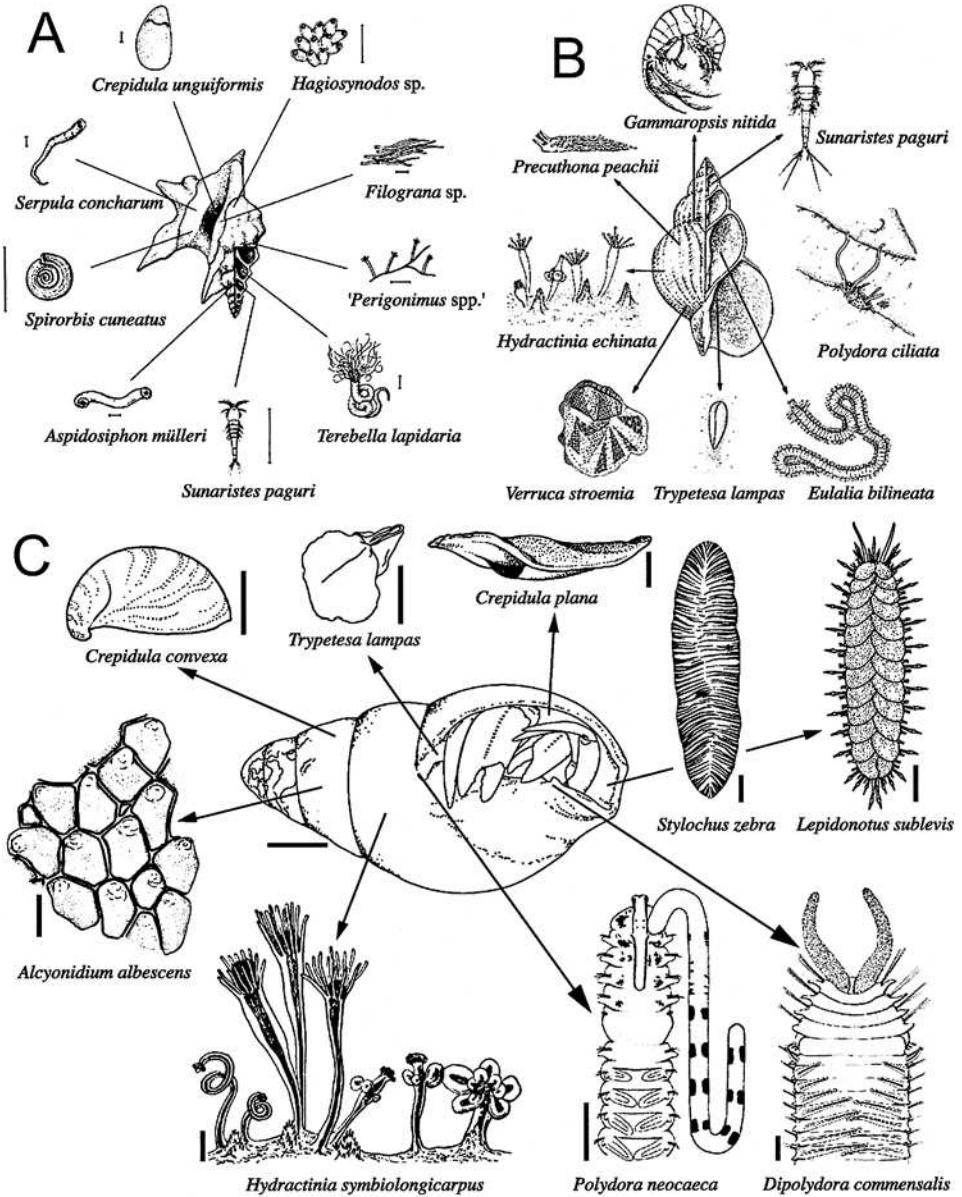
1980, fig. 2]; B, symbionts associated with shells inhabited by *Pagurus bernhardus* [modified from Jensen & Bender, 1973, fig. 3]; C, symbionts associated with *Pagurus longicarpus*: center of figure shows shell of *Ilyanassa obsoleta* (Say, 1822) inhabited by *Pagurus longicarpus*; vertical scales on left of associates = 0.5 mm, vertical scales to right of associates = 5 mm; horizontal scale for center figure = 2.5 mm [inset figures modified from: Pettibone, 1963, fig. 3A; Blake, 1971, fig. 11a; Baluk & Radwan'ski, 1991, fig. 8A; Weiss, 1995, figs. 7.01C, D, 4.06A, 6.05B; Williams & Radashevsky, 1999, fig. 1A].
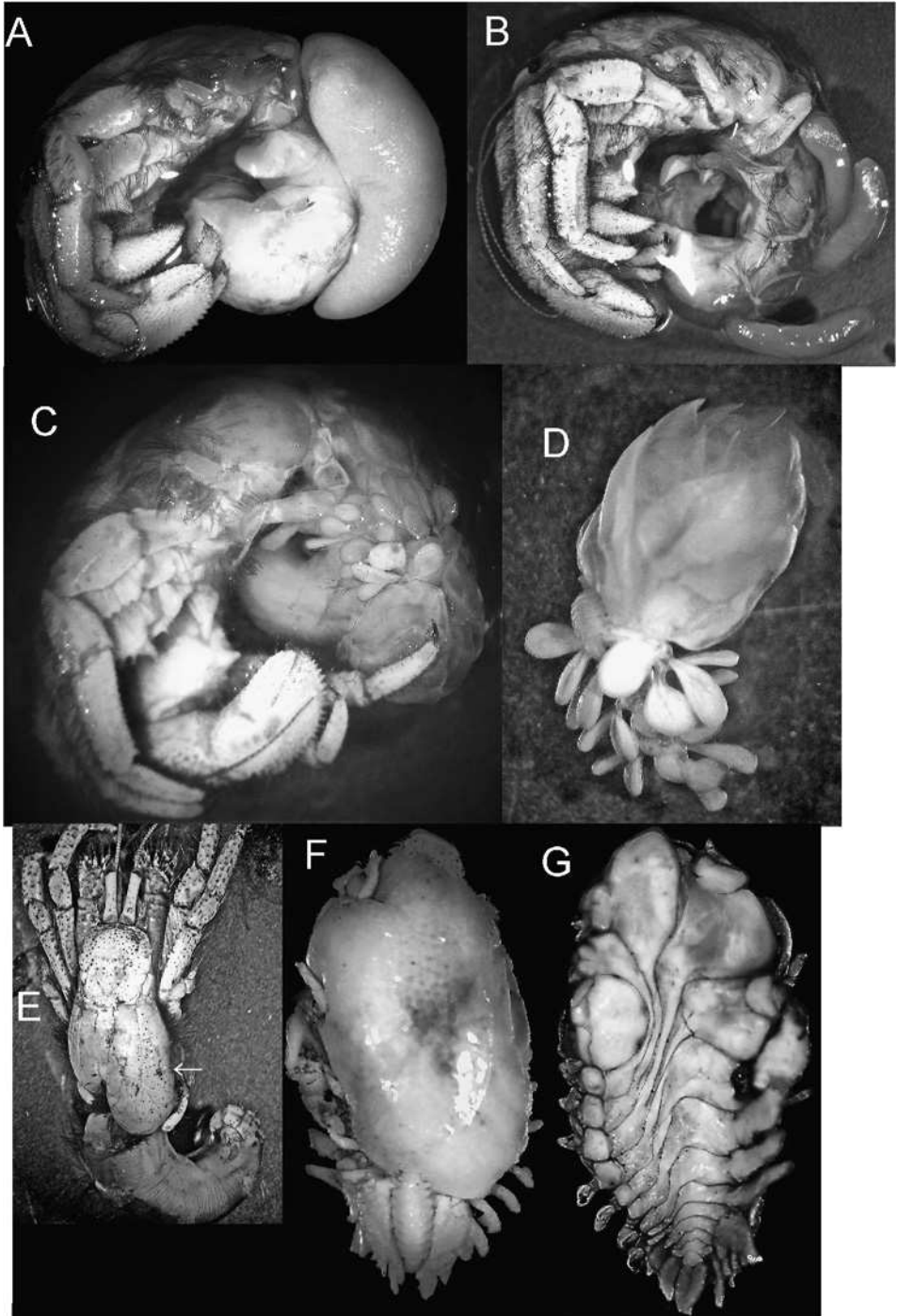
Bopyridae is known to contain over 500 described species, all of which are **obligate parasites** of decapod crustaceans, and more than 185 species among them infest paguroids, galatheoids, and chirostyloids. Species in the subfamily Pseudioninae are found in the branchial chamber, while species in the subfamily Athelginae are found attached to the dorsal face of the pleon.

Species of **Peltogastridae** in Rhizocephala are parasitic in hermit and king crabs (Lörz et al., 2008). The body of this parasite consists of a **network of threads** penetrating the body, and only the **externa** (the reproductive organ of adult females) is recognized externally, attached to the pleon. *Briarosaccus callosus* Boschma, 1930 is a common rhizocephalan parasite of lithodids. The rhizocephalan itself is also known to sometimes be parasitized by cryptoniscid isopods (Watters, 1998).

Epizoonts of aeglids include flatworms (*Temnocephala* sp.), the 'anchor worm', a parasitic copepod (*Lernaea*), and the polychaete worm, *Stratiodrilus* sp. (cf. Dioni, 1972; Viozzi et al., 2005). Whether temnocephalans and *Stratiodrilus* are truly parasitic on *Aegla* remains to be determined.

Predators

Known **predators** on hermit crabs include birds and small mammals in case of land and intertidal hermit crab species, and fish, octopus, and brachyuran crabs in marine species. Lithodids, especially as juveniles, may be prey to demersal fish (Ahyong & Dawson, 2006), as are galatheoids. When swarming, galatheoids, such as *Munida gregaria*, can be a significant prey item for pelagic fish, whales, and seabirds (Zeldis, 1985; Schnabel & Connell, 2007).

Ethology

Hermit crabs have a very complex behavioral repertoire, including elaborate **shell investigation behaviors** to assess shell quality, and social behavior. The **social behavior**, defined as behavior seen among individuals, is divisible into **ritualized agonistic display** or direct **aggressive behavior** when two individuals are encountered, **shell fighting behavior**, **male-male fighting** for mature females, **pre-copulatory guarding** of a mature female by a male, and elaborate behavioral interaction before and after **copulation**. These social behaviors are shown in fig. 70.32A-Q, and defined in table I.

ECONOMIC IMPORTANCE

Unlike the brachyurans, chelate and achelate lobsters, and caridean and penaeoid shrimps, there are very few of the heterogeneous anomuran taxa that are of significant

Fig. 70.31. Parasites of hermit crabs. A, *Peltogaster* sp. (Rhizocephala, Kentrogonida) on *Pagurus filholi* (De Man, 1887); B, *Peltogasterella* sp. (Rhizocephala, Kentrogonida) on *Pagurus filholi*; C, *Athelges takanoshimensis* Ishii, 1914 (Isopoda, Bopyridae) on *Pagurus filholi*; D, same, female attached by small male posterolaterally, dorsal; E, *Clibanarius virescens* parasitized by *Asymmetrione asymmetrica* (Shiino, 1933) (Isopoda, Bopyridae); F, female of *Asymmetrione asymmetrica* attached by small male posteriorly, dorsal; G, same, ventral. [Photos by Akira Asakura.]
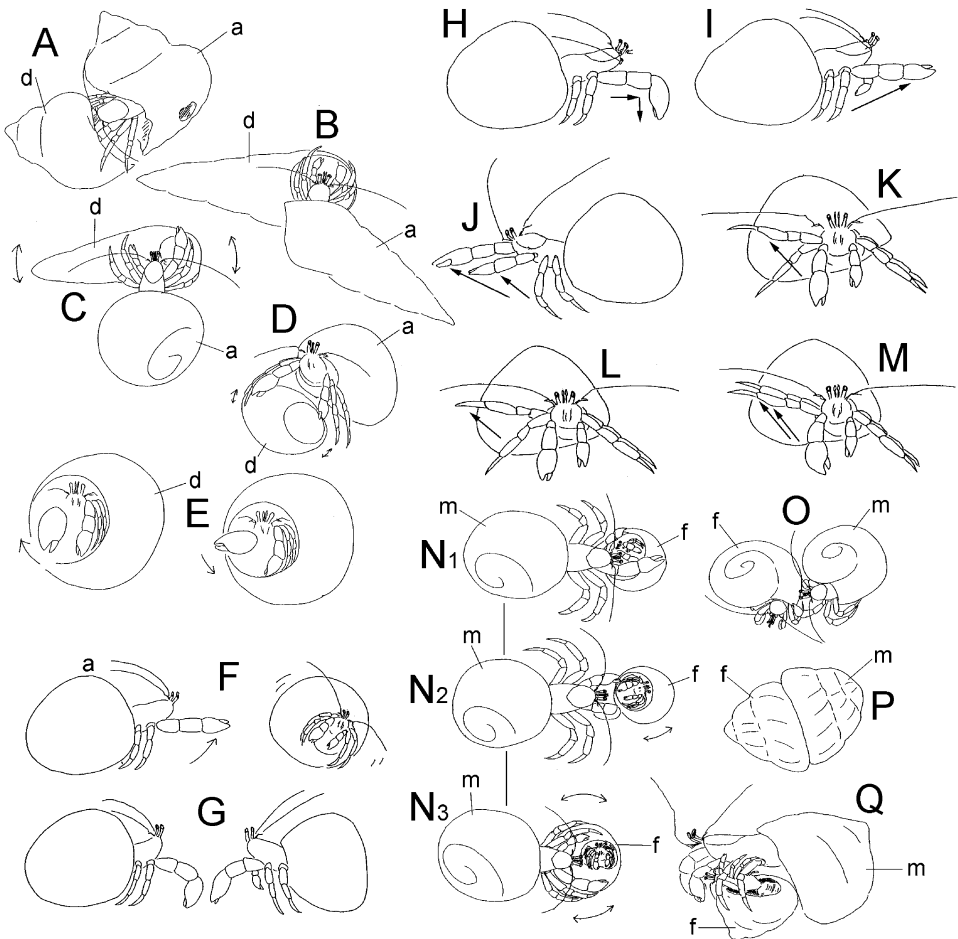
Fig. 70.32. Hermit crab behavior. A-E, shell fighting and defensive behavior: A-C, *Pagurus filholi*; D, E, *Pagurus gracilipes* (Stimpson, 1858). A, B, position of shell fighting; C, rocking behavior during shell fighting; D, spasmodic shaking; E, cheliped flicking; a, attacker; b, defender. F-G, direct aggressive behavior: F, thrusting, *Pagurus filholi*; G, cheliped match, *Pagurus gracilipes*. H-M, agonistic display: H, cheliped presentation; I, cheliped extension; J, same, double; K, ambulatory raise (second pereiopod); L, ambulatory raise (third pereiopod); M, double ambulatory raise. N-Q, precopulatory guarding and copulation: N1-N3, Q, *Pagurus filholi*; O, *Pagurus gracilipes*; P, *Clibanarius virescens*; m, male; f, female; N1, O, P, basic position of precopulatory guarding; N2, male gently moving shell of female back and forth with his minor cheliped around axis perpendicular to plane of female shell aperture; N3, male rocking shell of female using chelipeds and ambulatory legs; Q, positions of copulation. [All illustrations from Imazu & Asakura, 2006.]

economic importance. Exceptions are the lithodid or **stone crabs** (Lithodidae), the Indo-West Pacific **coconut crab**, *Birgus latro* (Coenobitidae), and to a lesser extent, the **squat lobster** *Cervimunida johni* Porter, 1903 (Munididae), which is frequently sold in Chilean fish markets as 'langostino armaillo'.

TABLE I
Behavioral terminology used in this chapter [after Hazlett, 1966, with slight modifications]

AGONISTIC DISPLAY

Cheliped presentation: crab moves its larger cheliped forward until dactyl perpendicular to substratum (fig. 70.25H)

Cheliped extension: crab moves its chelipeds forward until dactyls parallel to substratum (fig. 70.25I, J)

Ambulatory raise: crab moves usually one, or occasionally two to four, ambulatory leg(s) rapidly away from body and holds that position for a short time (fig. 70.25K-M)

DIRECT AGGRESSIVE BEHAVIOR

Thrusting: attacker aggressively inserts its major cheliped into underside of shell of opponent, quickly moves upward, and thrusts opponent off (fig. 70.25F)

Pushing: crab aggressively pushes opponent by cheliped(s) and/or one, or occasionally two to four, ambulatory leg(s)

Cheliped match: when two crabs encounter, each pushes the other with dorsal face of larger cheliped in cheliped presentation position (fig. 70.25G)

ESCAPE OR DEFENSIVE BEHAVIOR

Jumping: crab lifts its body by larger cheliped using lever principle and jumps quickly backward

Dislodging shaking: when crawled upon by another, crab rapidly moves up and down and/or side to side to cause the other to fall off

Cheliped flicking: defender flicks its chela in withdrawing position (fig. 70.25E)

SHELL FIGHTING BEHAVIOR

Rapping: attacker brings its shell forward, into contact with defender's shell through a movement of abdomen, in which this physical striking produces a clearly audible click (fig. 70.25A, B); attacker strikes shell several times, then rests shortly, and then repeats action

Spasmodic shaking: attacker rapidly shakes defender's shell back and forth along horizontal plane (fig. 70.25D)

Rocking: attacker rocks defender's shell back and forth using both chelipeds and ambulatory legs (fig. 70.25C)

Rotating: attacker revolves defender's shell through 360° between series of rapping, by movements of chelipeds and ambulatory legs

Paguroidea

The coconut or robber crab, *Birgus latro*, is the largest land crab (growing to 4 kg or nearly 9 pounds) and is the most highly terrestrialized decapod (Greenaway, 2003). It is distributed on oceanic islands (primarily restricted to islands with few predators) and small offshore islets adjacent to large continental islands across a broad geographical range in the tropical Indo-Pacific region, with reports stretching from the Aldabras Islands in the Indian Ocean to the Pitcairn group and Easter Island in the Pacific Ocean. They are excellent eating and have been part of the indigenous diet in their natural ranges for a long time. The crabs are cooked like other large decapod crustaceans by boiling or steaming and often sold as a luxury food item. Recently, economic pressure has increased the exploitation of this species (in some cases leading to localized extirpation) and investigations of their **"farming" potential** have been made (see Brown & Fielder, 1991, and papers therein).

There have also been **conservation management** strategies effected in some regions, such as **minimum legal size** limit restrictions in Guam and Vanuatu, and the capture of ovigerous females has been banned in Guam and the Federated States of Micronesia.

Lithodoidea

There are very **significant fisheries** for various lithodid species in polar and sub-polar waters in both the northern and southern hemispheres, with the northern Pacific and the southern Pacific and southern Atlantic oceans being focal points. Zaklan (2002, table 8) provided a summary of worldwide lithodid fisheries, with respective references, and more recently Otto (2006) and Otto & MacIntosh (2006) gave such overviews.

Commercial fisheries for lithodid crabs are almost entirely made up from landings of three genera: *Paralithodes*, *Lithodes*, and *Paralomis*. Lithodid crab fisheries began before 1900 in Japan and spread across the northern Pacific Ocean by 1940. Fisheries targeted **red king crab**, *Paralithodes camtschaticus* (Tilesius, 1815), with lesser amounts of **blue king crab**, *Paralithodes platypus* (Brandt, 1850) and **brown king crab**, *Paralithodes brevipes*. *Paralithodes* spp., especially red king crabs, have always dominated lithodid fisheries. **Golden king crab**, *Lithodes aequispinus* Benedict, 1895, became important in northern Pacific Ocean waters after major declines in red king crab fisheries in the early 1980's. **Southern king crabs**, *Lithodes santolla* (Molina, 1782), are fished in southern South America along with **softshell red crab**, *Paralomis granulosa* (Jacquinot, 1847). These five species accounted for more than 89% of lithodid landings for 1984-2003. World lithodid landings peaked at 150 100 metric tons in 1966 (fig. 70.33A) after development in pre-World War II Asia and rapid post-1950 expansion in Alaska and Asia. The world lithodid landings fell to 60 540 tons in 1973 but rebounded to 104 970 tons in 1980, owing to abundant eastern Bering Sea red king crab stocks. Eastern Bering Sea and Gulf of Alaska red king crab stocks soon collapsed, and landings fell to a low of 40 920 tons in 1983. The world lithodid landings reached 81 390 tons in 1997 with increased Russian landings, but have declined sharply to only 32 610 tons. In the 1960's, Russian scientists successfully introduced red king crabs to the northern Atlantic Ocean and resultant fisheries currently provide 9% of world lithodid landings. Elsewhere, landings of *Paralithodes* spp. trend downward, while other lithodid species are stable or increasing (fig. 70.33B).

Until 1975, almost all worldwide lithodid landings were taken in **tangle nets**. Now virtually all landings are taken with **pots** or **traps**. Pots are considered less destructive to untargeted portions of the catch such as females or juveniles. Other **conservation measures** usually include a **legal minimum size**, a prohibition against harvesting females, **seasonal closures**, and **catch quota**. Enforcement of conservation measures varies widely among countries and fisheries.

Galatheoidea

To date, porcellanids and chirostyloids have not been commercially exploited to any great extent, except occasionally for the **ornamental aquarium trade**, e.g., the anemone
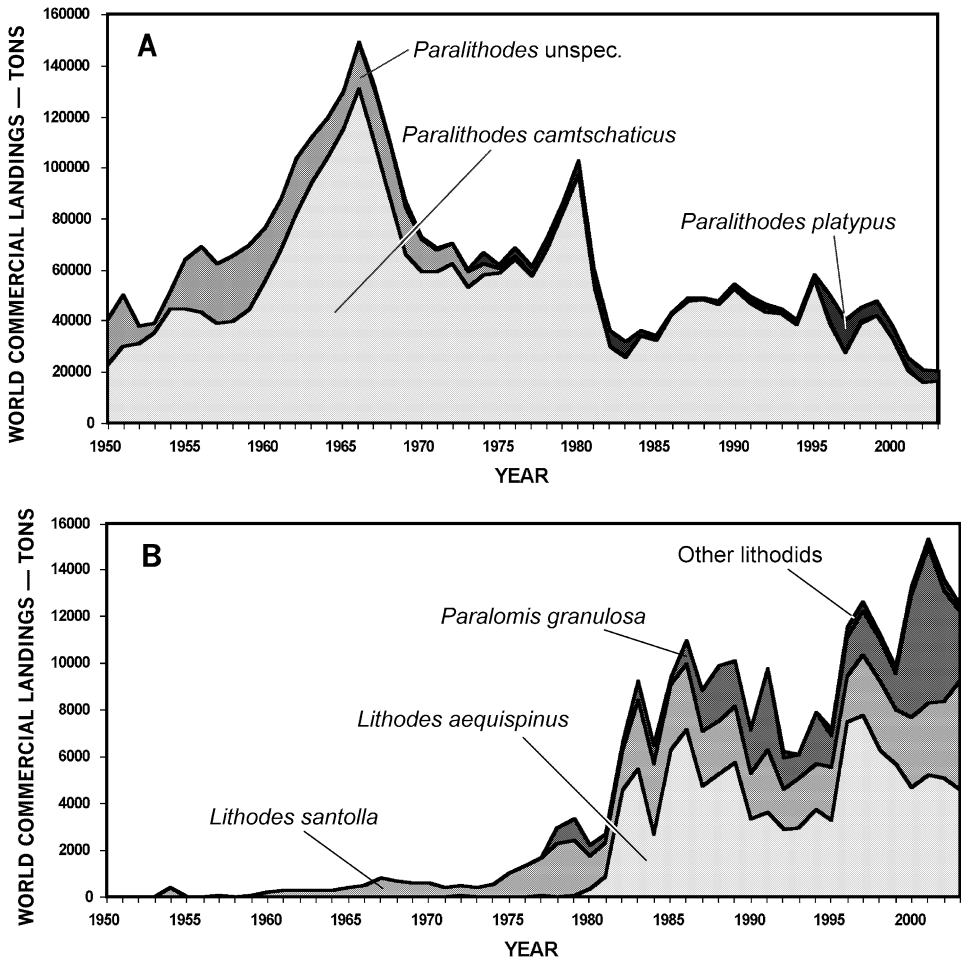
Fig. 70.33. Indicators of economic importance of various anomurans. A, world commercial landings of *Paralithodes* spp. based on FAO statistical data adjusted for the species composition of king crab landings from Alaska waters; B, world commercial landings of *Lithodes* spp. and *Paralomis granulosa* based on FAO statistical data adjusted for the species composition of king crab landings from Alaska waters. [A, B, from Otto, 2006.]

crabs, *Neopetrolisthes* spp. In contrast, galatheids are commercially harvested, chiefly as tailmeat for human consumption and as meal for fish and poultry feed (Aurioles-Gamboa & Balart, 1995; Lovrich et al., 1998; Tapella & Lovrich, 2006; Vinuesa, 2007). *Pleuroncodes monodon* (H. Milne Edwards, 1837) and *Cervimunida johni* are commercially fished off Chile, with landings peaking at around 50 000 tons in 1977, thereafter falling to around 8000 tons annually following **over-fishing** (Roa & Bahamonde, 1993). Elsewhere, fisheries have been unsuccessfully explored for *Pleuroncodes planipes* Stimpson, 1860 (off the Pacific coast of Mexico: Aurioles-Gamboa & Balart, 1995), *Munida quadrispinosa* Benedict, 1902 (Pacific coast of North America: Burd & Jamieson, 1988), and *Munida*

gregaria (New Zealand: Zeldis, 1985, 1989). One or more of the aforementioned species have also been explored as a source of amino- and fatty acids for human dietary supplements; as a source of proteases useful in cheese manufacture; and even as a source of pigment for enhancement of farmed salmonids and poultry (Burd & Jamieson, 1988; Zeldis, 1989; Kashkina & Kashkin, 1993; García-Carreño & Hernández-Cortés, 1995).

PHYLOGENY AND BIOGEOGRAPHY

Phylogeny

HISTORY AND MORPHOLOGICAL ANALYSES

The **relationships** among the diverse families in Anomura, and among representatives within families, have now been the subject of many investigations at the morphological and molecular level (Ahyong et al., 2009; Lemaitre & McLaughlin, 2009). Most of the literature prior to 1997 dealing with the **evolutionary history** of Anomura and various constituent families is adequately reviewed in the morphological papers of Richter & Scholtz (1994), Scholtz & Richter (1995), McLaughlin & Lemaitre (1997), Tudge (1997), and Lemaitre & McLaughlin (2009). Of note are the phylogenetic analyses of the constituent families of Anomura using adult and larval somatic morphology (MacDonald et al., 1957; McLaughlin, 1983b; Martin & Abele, 1986).

MacDonald et al. (1957) produced an **intuitive evolutionary scheme** for the relationships of the hermit crabs and allies based on larval characters alone and divided the seven families into two groups with separate evolutionary histories from common ancestral anomuran stock. The two groups (superfamilies) were Coenobitoidea (Coenobitidae, Diogenidae, Lomisidae, and Pylochelidae) and Paguroidea (Lithodidae, Paguridae, and Parapaguridae). McLaughlin (1983b) produced the first **cladistic analysis** of Anomura with 30 morphological characters mapped onto her resultant **cladogram**. She abandoned Coenobitoidea and reunited six anomuran families under the monophyletic Paguroidea (Coenobitidae, Diogenidae, Lithodidae, Paguridae, Parapaguridae, and Pylochelidae) and included representatives of Hippoidea, Lomisoidea (as Lomoidea), and Galatheoidea. McLaughlin's (1983b) analysis was soon followed by another **phylogenetic analysis** of the Anomura from Martin & Abele (1986), who analyzed, while investigating the placement of the enigmatic freshwater aeglids from South America, the 13 anomuran families (in four superfamilies) using 54 morphological characters. They found the aeglids to be primitive galatheoids, that the lithodids grouped with *Lomis* rather than the other paguroids, and also that Anomura was indeed monophyletic. As with McLaughlin's study, they found no support for the two independent hermit crab lineages of MacDonald and colleagues (MacDonald et al., 1957).

The year 1997 saw two papers dealing with **anomuran phylogeny** (McLaughlin & Lemaitre, 1997; Tudge, 1997), but each dealt with a different **morphological dataset**. McLaughlin & Lemaitre (1997) used **adult morphology** to investigate the process of carcinization (obtaining a crab-like form) within Anomura, in direct response to Cunningham et al. (1992) who proposed that the symmetrical king crabs were derived from

within the asymmetrical hermit crab ancestors. McLaughlin & Lemaitre's (1997) clado-
gram (based on 59 taxa and 37 characters) clearly separates the asymmetrical hermit crabs
(Coenobitidae, Diogenidae, Paguridae, and Parapaguridae) from the lithodoids (Lithodi-
dae and Hapalogastridae) as sister clades. The symmetrical hermit crabs, Pylochelidae, are
sister to the remaining anomurans. Tudge (1997), on the other hand, used a novel dataset
of **spermatozoal characters** to infer anomuran phylogenetic relationships. His "sperm
tree" had representatives of nine anomuran families with some out-group decapods from
Thalassinidea, Astacidea, and Brachyura (among others) and, apart from some basal incon-
sistency associated with incomplete morphological data (*Thalassina* and *Lomis*), basically
produced a monophyletic Anomura with most constituent families monophyletic, too.

Morphology-based phylogenies of Anomura published since 1997 include Schram
(2001), Dixon et al. (2003), and Ahyong & O'Meally (2004), these three within the context
of broader decapod phylogeny; and McLaughlin et al. (2007a). Schram (2001) reviewed
the status of decapod phylogenetics to date and briefly covered the principal papers dealing
with Anomura (outlined above). Dixon et al. (2003) analyzed decapod phylogeny based on
external morphology of 60 taxa including 14 anomuran representatives from 13 families
and 6 superfamilies. The main findings were: *Aegla* (Aegloidea) is outside of Galatheoidea
and basal to the anomurans; Hippoidea and Lithodoidea are sister taxa (in some analyses);
Paguroidea is monophyletic and sister to *Lomis* (Lomisoidea); and Anomura (as Anomala)
and Brachyura are reciprocally monophyletic sister clades, forming the **Meiura clade** of
Richter & Scholtz (1995). Ahyong & O'Meally (2004) built on the Dixon et al. (2003)
dataset, and analyzed the decapod phylogeny in combination with **molecular sequences**
from three genes for all the reptant Decapoda. The 13 representative anomuran genera
(each representing one family) were analyzed using 105 morphological characters: both
alone and in combination with the molecular data. As expected, with respect to the
positions of Anomura and Brachyura, the **morphological cladogram** is similar to that
of Dixon et al. (2003), with a monophyletic Meiura, Hippoidea, and Paguroidea, but with
both Lithodoidea and *Lomis* basal to the paguroids, and a polyphyletic Galatheoidea. The
combined analysis maintained some of these relationships except galatheoids are returned
to **monophyly** (minus *Aegla*, which groups with *Lomis*) and polyphyletic Paguroidea with
lithodoids sister to *Pagurus*, and *Pylocheles* sister to the galatheoids.

With all of this renewed interest in decapod and anomuran phylogeny, McLaughlin and
colleagues (McLaughlin et al., 2007a) revisited (and upgraded) the landmark 1983 analysis
of hermit crab relationships (McLaughlin, 1983b), but with more data (79 morphological
characters) and more taxa (representatives of 17 families). The resulting cladogram
produced few surprising results apart from wide separation of lithodoids from paguroids,
but did lead to a new classification of seven superfamilies (three of them new) and elevation
of Lithodinae and Hapalogastrinae to family status.

Most recently, three papers have investigated relationships within families of Anomura.
Relationships of the few investigated Diogenidae for which spermatozoal and sper-
matophore morphology are known were analyzed by Tirelli et al. (2008, 2010) for these
reproductive characters alone. Not surprisingly, these limited datasets found some genera
monophyletic (*Calcinus* and *Clibanarius*) but others not so (*Dardanus* and *Diogenes*), and
limited biogeographic subclades were also apparent. The recent external morphological

analysis of Pylochelidae (cf. Lemaitre et al., 2009) using 41 of 45 recognized species and 78 characters, revealed some poorly resolved cladograms, but did recover, under certain conditions, robust monophyletic clades for all seven genera and established some interesting and useful subfamilial clades.

Anomuran representatives have also been included in phylogenetic analyses (or intuitive evolutionary trees) of other decapods based on morphological characters as diverse as spermatozoa (Koltzoff, 1906; Tudge, 1997), neural and brain morphology (Sandeman et al., 1993; Paul, 2003), and eye morphology (Gaten, 1998; Richter, 2002).

Phylogenetic analyses of members of Anomura based on **molecular sequence data** only started 20 years ago but now exceed morphological analyses in number. These molecular phylogenetic contributions fall into two categories of analysis: those dealing exclusively with members of Anomura, and those including anomuran representatives as part of a larger, usually decapod-wide, analysis. Each category will be dealt with separately below in chronological order.

Including molecular data: inside Anomura

Cladistic analyses of Anomura started with the pioneering **18S rRNA nucleotide sequence analysis** of four selected anomurans by Spears & Abele (1988) (abstract only) and was followed a few years later by the **16S rRNA** analysis of pagurid-lithodid relationships by Cunningham et al. (1992). The paper by Cunningham and colleagues was a seminal contribution to the field for several reasons, not only because it thrust anomuran evolutionary relationships onto the front cover of the prestigious journal "Nature", but also because it corroborated the thesis that symmetrical king crabs (*Lithodes* and *Paralithodes*) are derived from asymmetrical hermit crabs, possibly from within the genus *Pagurus*: the **'hermit to king' hypothesis**. This controversial result sparked immediate responses from evolutionary biologists (see Gould, 1992) and carcinologists alike (see Richter & Scholtz, 1994 and McLaughlin & Lemaitre, 1997) and sparked a small renaissance in anomuran phylogenetic analysis that continues today.

The **internal relationships** of the anomuran sand crab genus, *Emerita*, were the focus of the next molecular contribution by Tam et al. (1996). They used both 16S rRNA and **cytochrome oxidase I** genes to determine the divergence times and zoogeography of some American species of this common beach crustacean. Partial sequences of four mitochondrial genes (12S, 16S, COI, and COII) and a nuclear gene (28S) were used by Zaklan (2002) to investigate the internal relationships of the then family Lithodidae (now Lithodoidea, see McLaughlin et al., 2007a). Zaklan (2002) found support for two sister clades, corresponding to Hapalogastrinae and Lithodinae (now Hapalogastridae and Lithodidae) and that the lithodoids were the sister to the pagurid hermit crabs. Pérez-Losada et al. (2002) used 18S rDNA sequences to examine anomuran relationships of a small set of 12 taxa from five superfamilies (Aegloidea, Chirostyloidea, Galatheoidea, Paguroidea, and Hippoidea). They were primarily testing the systematic position of Aeglidae (then considered to be in Galatheoidea) in the analysis and found the two species of *Aegla* they sequenced to be outside of the clade containing the rest of the sequenced chirostyloids and galatheoids. They also found the paguroids to be the sister taxon to the

chirostyloids and galatheoids, Aeglidae to be basal to them, and the hippoids basal to all the sequenced anomurans. Most of the same authors later investigated the biogeography of 64 species of *Aegla* (cf. Pérez-Losada et al., 2004) using the nuclear 28S rDNA gene and four mitochondrial genes (12S and 16S rDNA, COI, and COII). They found five **monophyletic clades** of species that correspond to five **biogeographic regions** on both the Pacific coast (2 clades) and Atlantic coast (3 clades), and using **molecular clock** methodologies confirmed the **"Pacific-Origin" hypothesis** for the group.

Macpherson et al. (2005) also included a brief phylogenetic analysis of select anomurans (just 13 species) using 18S rRNA in their description of a new family (Kiwaidae), genus, and species (*Kiwa hirsuta* Macpherson, Jones & Segonzac, 2005) of galatheoid from Pacific-Antarctic hydrothermal vents. Their cladogram inferred that *Kiwa* was a basal galatheoid (but McLaughlin et al., 2007a, later elevated it to separate superfamily status). Mantelatto et al. (2006) analyzed selected diogenid hermit crabs using 16S rDNA sequences as part of an investigation into the taxonomic status of *Loxopagurus* and *Isocheles*. Mantelatto et al. (2009b) later used the same partial 16S rDNA gene, and many similar diogenid taxa, to re-examine the taxonomic status of two species of hermit crabs, *Pagurus forceps* H. Milne Edwards, 1836 and *Pagurus comptus* White, 1847. Their resultant cladograms show a monophyletic Diogenidae, with the same three subclades of genera as in Mantelatto et al. (2006), as a sister clade to the monophyletic Paguridae. The much-expanded taxon sampling in the genus *Pagurus*, including the two species in question (above) revealed three subclades or groups roughly corresponding to three biogeographic regions.

The most recent **molecular phylogeny** of Anomura (Ahyong et al., 2009) used sequences from one mitochondrial (16S) gene and two nuclear (18S and 28S) genes to investigate 44 taxa from 16 of the then recognized 17 extant families (fig. 70.34) (currently 20 families, see Classification, below). This is the largest anomuran dataset analyzed so far, and both Maximum Parsimony and Bayesian Inference methods were employed to generate the cladograms. The topologies differ quite radically from many previous molecular or morphological analyses and indicate significant **poly-** and **paraphyly** of the major superfamilies. Some notable differences from previous proposals (Martin & Davis, 2001; McLaughlin et al., 2007a) include **polyphyly** of Pylochelidae (although, see McLaughlin & Lemaitre, 2008, 2009, and Lemaitre & McLaughlin, 2009 for recent support for divisions within this family), polyphyly of Galatheoidea *sensu lato* (including possible inclusion of *Kiwa* in Chirostylidae), paraphyly of Galatheidae, and polyphyly of Paguroidea.

Including molecular data: Anomura inside Decapoda

As mentioned above, molecular analyses with anomurans as part of a larger **decapod dataset** started with the 18S rRNA analysis of brachyuran relationships (Spears et al., 1992), which included one anomuran, *Clibanarius*. The most intriguing result from Spears et al. (1992) was the finding that the primitive brachyuran crab, *Hypoconcha*, was apparently an anomuran rather than a brachyuran. That result remained controversial for more than a decade but was subsequently shown to be the result of a sequencing error
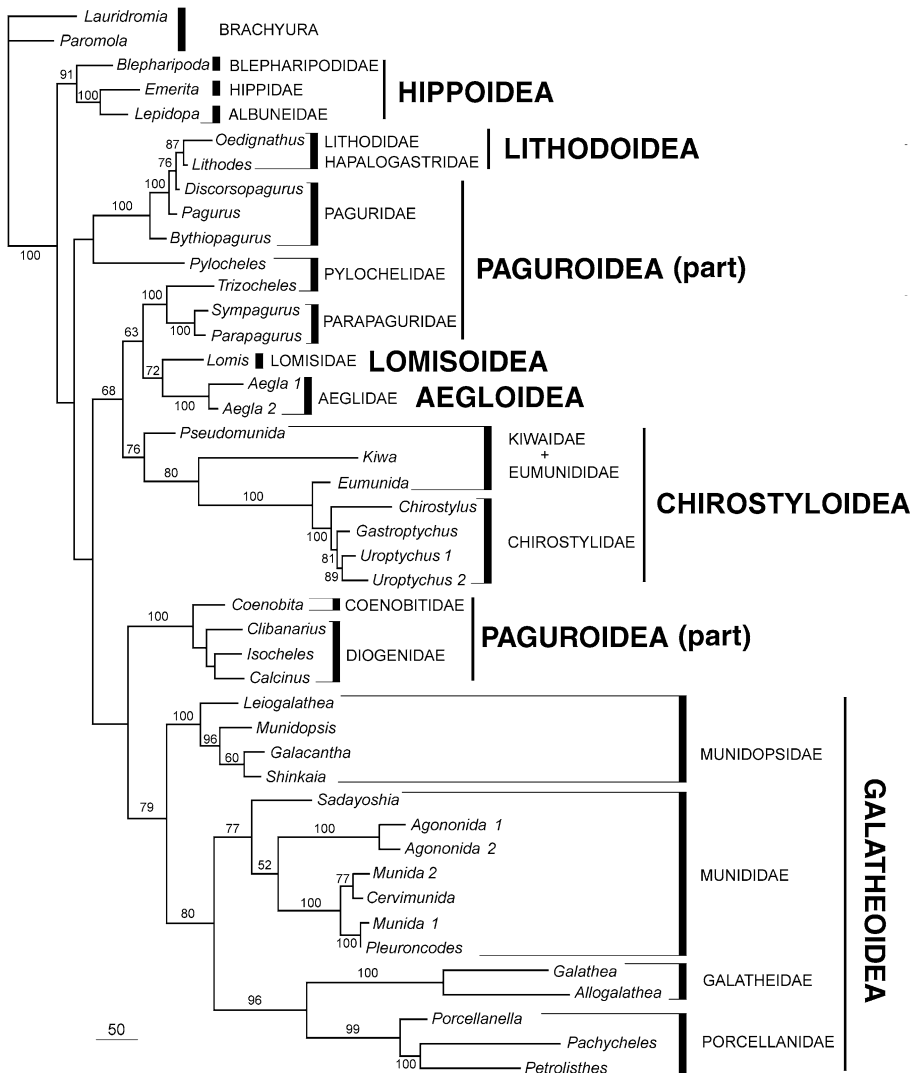
Fig. 70.34. Molecular phylogeny of Anomura based on mitochondrial 16S and nuclear 18S and 28S sequences. Single most parsimonious topology derived from maximum parsimony analysis under equal weights (TL = 3836, CI = 0.4726, RI = 0.6184). Jackknife proportions indicated at nodes. Superfamilies as recognized by McLaughlin et al. (2007). [Modified from Ahyong et al., 2009.]

(Ahyong et al., 2007). Morrison et al. (2002) analyzed a much larger taxon sample (26 decapods, including 18 anomurans) using four mitochondrial genes (18S, 28S, COII, and 16S) to investigate the multiple independent **carcinization events** in Anomura. The study found a monophyletic Anomura with four independent carcinization events therein (present in Porcellanidae, Lomisidae, Lithodoidea, and Coenobitidae). In the last five years, there has been a veritable explosion of molecular phylogenetic analyses of Decapoda, all including various subsets of anomuran crabs for comparison.

The phylogenetic analysis of Ahyong & O'Meally (2004), mentioned already, also included simultaneous analysis of 16S, 18S, and 28S rRNA sequences in combination with morphological characters. Porter et al. (2005) used 16S, 18S, 28S, and the **histone H3 gene** to investigate geological divergence times on a large decapod dataset (only six anomurans were included, though) and found a monophyletic Anomura between the slightly older Brachyura and the younger achelate lobsters. Anomura, according to this analysis, apparently radiated from common **reptant ancestors** at the **Carboniferous/Permian boundary** about 300 million year ago. Similarly, Tsang et al. (2008) used two nuclear **protein-coding genes** to investigate the origin and evolution of reptant decapods (64 taxa). Their resulting cladogram inferred no great differences within Anomura, but recovered a monophyletic Meiura (Anomura + Brachyura). Within Anomura, Hippoidea are basal, followed by Lomisoidea, then Galatheoidea (with the interesting inclusion of a paguroid, *Pylocheles*), and finally two sister clades comprised of the remaining Paguroidea and Lithodoidea.

Two decapod-wide molecular analyses appeared simultaneously (Toon et al., 2009; Chu et al., 2009). Both papers deal with the utility of multiple and different molecular markers to elucidate **decapod phylogeny**; they vary only in the number of genes and taxa used. Toon et al.'s (2009) results were based on eight genes (both mitochondrial and nuclear), included only six anomurans, and found them monophyletic with respect to the rest of the decapods. Their small taxon sampling across very disparate superfamilies provides little useful information on relationships within Anomura. Chu et al. (2009) analyzed two protein-coding genes in their taxon-rich (135 species) analysis. Their 23 anomuran species form a clade (as sister to a monophyletic Brachyura, as usual) and reveal basal Hippoidea, followed by a galatheid, porcellanid, and pylochelid clade sister to two large clades, comprising the parapagurids, chirostylids, kiwaids, lomisids, and aeglids in one, and the diogenids, pagurids, and lithodids in the other. Chu et al.'s (2009) results thus parallel those of Ahyong et al. (2009) in recovering a basal Hippoidea as well as polyphyly among the hermit crabs and squat lobsters. The multi-gene phylogeny of Decapoda by Bracken et al. (2009) analyzed sequences from three **ribosomal genes** and one nuclear protein coding gene (16S, 18S, 28S, H3) from 17 anomuran taxa (out of a total of 128 decapod species). The representatives from 12 anomuran families are monophyletic, but are not shown to be the sister group to Brachyura, instead being placed between the Thalassinidea and the remainder of the reptant decapod infraorders (albeit with weak statistical support).

The most recent multi-gene analyses of the Anomura (Schnabel et al., 2011; Tsang et al., 2011) found evidence for polyphyly among the hermit crabs and polyphyly among the marine squat lobsters, which are distributed in two widely separate clades, Galatheoidea and Chirostyloidea. Schnabel et al. (2011) combined sequences of three ribosomal genes (16S, 18S, 28S) and morphology, and Tsang et al. (2011) combined sequences of five nuclear protein coding genes. Of note is that Tsang et al. (2011) found strong support for derivation of the two main squat lobster clades from within separate hermit crab clades.

After 114 years (see the evolutionary tree of relationships in Bouvier's, 1895, work on *Lomis*, lithodids, and the hermit crabs), the field has not converged on a **definitive phylogeny** of the constituent families in Anomura (cf. McLaughlin et al., 2007a) and

many conflicting views abound (Ahyong et al., 2009; Bracken et al., 2009; Lemaitre & McLaughlin, 2009). It is widely agreed that **Anomura is monophyletic** (see Martin & Abele, 1986; Scholtz & Richter, 1995; Schram, 2001; Dixon et al., 2003; Ahyong & O'Meally, 2004; Tsang et al., 2008; Bracken et al., 2009) and that it is the **sister clade to Brachyura** (the clade of **Meiura** of Scholtz & Richter, 1995). However, consensus has not yet been found at the superfamily and family level. Despite the high level of discordance among studies, some **patterns** are emerging among **molecular studies**: (1) that Hippoidea appears to be sister to the remaining anomurans; (2) that marine squat lobsters belong to two widely separate clades, Galatheoidea and Chirostyloidea; (3) that Aegloidea and Lomisoidea are sister taxa and closely related to Chirostyloidea; (4) that Paguroidea are probably paraphyletic, especially with respect to Pylochelidae and Parapaguridae; (5) that lithodoids are consistently found to be closely related to the paguroids.

Biogeography

The diverse nature of Anomura has meant that no single work exists that summarizes the **biogeography** of the entire infraorder. Each family is dealt with in turn by different authors, while in some cases a zoogeographic text is not available and the **distributional data** from systematic accounts are all that have been published. Thus, the 17 families of McLaughlin et al. (2007a) are each dealt with separately below.

For a few of the anomuran families, the only known representatives are monotypic and/or endemic, and often the only information about their distribution is in the original systematic account. These monotypic families are: Lomisidae (cf. Hale, 1927; Pilgrim, 1965; McLaughlin, 1983a), Pylojacquesidae (cf. McLaughlin & Lemaitre, 2001), and Kiwaidae (cf. Macpherson et al., 2005).

Coenobitidae

Limited biogeographic information is published on the tropical, terrestrial hermit crabs in the genera *Birgus* and *Coenobita*. Papers by Hartnoll (1988) and Nakasone (1988) and a book on *Birgus* by Brown & Fielder (1991) provide much of the early literature where distributional data can be found.

Diogenidae

The hermit crab family Diogenidae is a large and diverse group with a worldwide distribution. There are no comprehensive review papers dealing with the biogeography of the family as a whole, so one is forced to consult a large selection of the taxonomic literature to glean this information. A non-exhaustive set of examples follows. A comparison of the Atlantic coast of South America diogenid fauna with that of the Atlantic coast of North America was done by Forest & de Saint Laurent (1967), while other regional distributions of diogenids are also provided for the northeastern Atlantic Ocean and Mediterranean Sea (Ingle, 1993), the Seychelles in the northern Indian Ocean (McLaughlin & Hogarth, 1998), the South China Sea (Rahayu, 2000), New Zealand (Forest et al., 2000), the Andaman Sea in the northern Indian Ocean (McLaughlin, 2002), and the Gulf of Oman (Moradmand &

Sari, 2007). There is also a set of literature that deals with regional or worldwide reviews of a particular genus within the family, and examples of these include the genera *Aniculus* (cf. Forest, 1984), *Calcinus* (cf. Poupin, 1997; Poupin & McLaughlin, 1998; Poupin & Lemaitre, 2003; Poupin et al., 2003), *Clibanarius* (cf. Rahayu & Forest, 1992), *Diogenes* (cf. Rahayu & Forest, 1994; Siddiqui et al., 2004), and *Trizopagurus* (cf. Forest, 1995).

PAGURIDAE

Paguridae is also a large and diverse family with a worldwide distribution. As with the diogenids, there are no comprehensive review papers dealing with their biogeography, and so a selection of the taxonomic literature must be consulted. A brief zoogeographic outline of the pagurids of the northern Pacific, and boreal Soviet waters is provided in Makarov (1962); comparisons of the Atlantic coast of South America pagurid fauna with that of the corresponding coast of North America have been made by Forest & de Saint Laurent (1967); while other regional distributions of pagurids are also provided for northwestern North America (McLaughlin, 1974), the northeastern Atlantic Ocean and Mediterranean Sea (Ingle, 1993), the Seychelles in the northern Indian Ocean (McLaughlin & Hogarth, 1998), the South China Sea (Rahayu, 2000), New Zealand (Forest et al., 2000), the Andaman Sea in the northern Indian Ocean (McLaughlin, 2002), and the Gulf of Oman (Moradmand & Sari, 2007). The set of literature that deals with regional or worldwide reviews of pagurid genera includes: *Pagurus* (cf. Ingle, 1985; McLaughlin & Forest, 1999), *Paguritta* (cf. McLaughlin & Lemaitre, 1993), *Pagurixus* (cf. McLaughlin & Haig, 1984), and *Xylopagurus* (cf. Lemaitre, 1995).

PARAPAGURIDAE

This family of deepwater (generally between 100 and 2000 m) hermit crabs has a worldwide distribution and several papers have dealt with regional distributions of the family, or particular genera, often including bathymetric data. These include reviews of species in the waters of the eastern Atlantic (Lemaitre, 1990), Antarctic and Subantarctic waters (Lemaitre & McLaughlin, 1992), French Polynesian waters (Lemaitre, 1994), Australian waters (Lemaitre, 1996), Indonesian waters (Lemaitre, 1997), and New Zealand waters (Lemaitre, 2000), as well as reviews of the genus *Parapagurus* in the western Atlantic (Lemaitre, 1989) and Pacific and Indian oceans (Lemaitre, 1999), and a worldwide review of the genus *Sympagurus* (cf. Lemaitre, 2004).

PYLOCHELIDAE

Two papers by Forest (1987a, b) provide the bulk of the available information regarding the depth distributions and biogeography of all valid members of this family of deepwater, symmetrical hermit crabs. Very recently, papers dealing with larval development (McLaughlin & Lemaitre, 2008) and morphological phylogeny (Lemaitre et al., 2009) have allowed a reassessment of the family and its constituent subfamilies (McLaughlin & Lemaitre, 2009).

Hapalogastridae and Lithodidae

One of the first contributions to understanding the zoogeographic distribution of lithodoids (among other Anomura) in northern Pacific waters was that of Makarov (1962; an English translation of the original 1938 Russian text). As well as suggesting distinct zoogeographic zones for lithodoids, Makarov also postulated a North Pacific **center of origin** and mapped **dispersal routes** to the other oceans of the world. Dawson (1989) provided a comprehensive bibliography of the lithodoid literature including early works on depth distributions and biogeography; Zaklan (2002) later reviewed the distribution, biology, and fisheries of the world's lithodoids. Since Zaklan's synopsis, various studies have extended the ranges of some lithodids into polar, Antarctic waters (Thatje & Arntz, 2004; Thatje & Lörz, 2005; Thatje et al., 2005, 2008; Ahyong & Dawson, 2006) and have increased our knowledge of regional faunas (Macpherson & Chan, 2008; Hall & Thatje, 2009b; Ahyong, 2010a, b; Ahyong & Chan, 2010; Ahyong et al., 2010). Otto (2006) reviewed worldwide lithodid fisheries and Hall & Thatje (2009a) provided a detailed review of lithodoid biogeography in the context of temperature contraints. The chief patterns to be observed in lithodoids are as follows: their greatest generic diversity is found in the northern Pacific, in which 10 of 15 genera exclusively occur (including all 5 genera of the Hapalogastridae). These 10 genera are principally shallow water forms requiring low temperatures for survival of early life-history stages, so their ranges are largely constrained by sea surface temperature. Deepwater lineages escaped seasonal temperature fluctuations, and underwent at least three radiations into water bodies outside the North Pacific. The largest lithodid genera (*Lithodes*, *Neolithodes*, and *Paralomis*) are cosmopolitan and range from Arctic to subantarctic (*Lithodes*) or Antarctic waters (*Neolithodes*, *Paralomis*). Moreover, the species from the deepwater lineages currently live close to the threshold of their temperature tolerance in the Southern Ocean, and their future distribution may be affected by increases in ocean temperature. Thus, lithodoids apparently originated in the northern Pacific, from where the group has expanded worldwide, but with ranges constrained by water temperature.

Chirostyloidea and Galatheoidea

Historically, these two squat lobster superfamilies have been dealt with together, and this convention will continue here for convenience. The earliest discussions of zoogeography in these families were in Milne-Edwards & Bouvier (1894) and Doflein & Balss (1913), although their taxonomy is now outdated. Biogeographical and bathymetric data are now provided in the more recent systematic works of Baba (2005) and Baba et al. (2008). The bulk of chirostyloid and galatheoid diversity is in the western Pacific at continental shelf and slope depths. Although this partly reflects sampling effort, the phenomenon nevertheless appears to be real, with Munididae, at least, having experienced significant, recent **radiation** in the southwestern Pacific (Machordom & Macpherson, 2004). Of the 35 galatheoid genera, 6 are represented in both the Indo-West Pacific and Atlanto-East Pacific regions, and *Anomeomunida* occurs only in the Atlantic Ocean. The remaining 29 genera are restricted to the Indo-West Pacific. The two largest galatheoid genera, *Munida* and *Munidopsis*, each with well over 200 species, are cosmopolitan. Of

the eight recognized chirostyloid genera, four are represented in both the Indo-West Pacific and Atlanto-East Pacific regions, including the largest genus, *Uroptychus* (with more than 200 known species). Species of *Pseudomunida* and *Uroptychodes* occur only in the Pacific Ocean, and *Hapaloptyx* is only found in the Indian Ocean. Species level studies of squat lobster biogeography are currently underway, and a recent study of deep-sea galatheoids (Macpherson et al., 2009) from the Pacific Ocean revealed a general increase in species richness from high to low latitudes, and a longitudinal decrease in species richness from the western to central Pacific. Thus, the tropical western Pacific contains the highest **species richness** for Galatheidae. Moreover, there is a tendency towards smaller body size and **endemism**, differentiating the Coral Sea, Indo-Malay Archipelago, New Zealand, and French Polynesia as 'independent' **centers of diversity**.

Species composition in relation to **habitat** is subject to ongoing studies. Recently, Rowden et al. (2010) found that among southwestern Pacific squat lobsters, **seamount community** composition was not distinct from that of other habitats at comparable depth, such as **slopes** and **canyons**. However, communities on seamounts on **ridges** may be distinct from those found elsewhere on ridges, these differences being more pronounced with geographic distance.

Porcellanidae

This large, highly carcinized anomuran family has only recently been dealt with in any biogeographic perspective, and often then only regionally, even though the systematic literature has a long history. Harvey (1991) provided an in-depth look at the biogeography of the reasonably limited porcellanid fauna from the Galapagos Islands, while the biogeography and depth distributions of western Atlantic porcellanids are covered in publications from Werding et al. (2003) and Rodriguez et al. (2006). The latter paper provides the information in the context of a molecular phylogeny. Porcellanids are most common in shallow tropical and sub-tropical waters of the world (often in **commensal relationships** with invertebrates, such as corals or echinoderms), but they also occur at high latitudes in subpolar waters. As with the galatheids and chirostylids, the bulk of porcellanid diversity occurs in the tropical Indo-West Pacific region. Of the 29 extant genera, one-third is represented only in the Atlanto-East Pacific, one fifth are cosmopolitan, and the remaining genera occur only in the Indo-West Pacific region. The largest genus, *Petrolisthes*, is cosmopolitan and contains about 100 species.

Aeglidae

Notes on the distribution and biogeography of these unique freshwater, endemic South American anomurans span a more than 100-year period in the literature. In his work on freshwater decapods Ortmann (1902) made brief mention of the distribution of the only species known at the time, *Aegla laevis* Leach, 1820, but 40 years later the number of described species had risen to 20 and Schmitt (1942) made zoogeographic and distributional remarks on all of them. Later Feldmann (1986) used living distributions, fossil occurrence, and **continental drift theory** to postulate on the **paleobiogeography** of the family. It is known from a few fossil **aeglids in New Zealand** (Feldmann, 1984)

and Mexico (Feldmann et al., 1998) that aeglids arose in marine environments in the southern Pacific Ocean and this strengthens the argument of Ortmann (1902) that aeglids invaded South America from this ocean and extended their range to the east and the north into freshwater systems. Schmitt (1942) and Morrone & Lopretto (1994, 1995) suggested dispersal in the opposite direction, i.e., east to west (see below), based on the premise that the least ornamented morphology seen in Atlantic species is plesiomorphic. The fact that the New Zealand Cretaceous marine fossil is heavily ornamented (Feldmann, 1984) contradicts this argument. A monograph of all 59 known species with distribution maps was published by Bond-Buckup & Buckup (1994), and this was followed by two papers by Morrone & Lopretto (1994, 1995) dealing with analyses of historical pan-biogeography and southern **South American endemicity** of Aeglidae (along with two other South American freshwater decapod families, Parastacidae and Trichodactylidae). More recent contributions by Pérez-Losada et al. (2002, 2004) provide a molecular systematic account of Aeglidae in the context of Anomura, and molecular divergence times and zoogeography for 64 recognized species of *Aegla*, respectively (see phylogeny section above).

ALBUNEIDAE AND BLEPHARIPODIDAE

Boyko & Harvey (2009) studied the phylogeny and biogeography of these two families. Until recently, however, Blepharipodidae was considered part of Albuneidae, and the little published discussion of biogeography of these groups treated them together. Ortmann (1896) suggested that the albuneids originated in the western Atlantic and dispersed westward to the eastern Pacific and continued on through the Indo-West Pacific and then to the Mediterranean Sea. Efford (1971) examined the distribution of species of *Lepidopa*, *sensu lato*, and on the basis of several **geminate species pairs** on either side of the **Isthmus of Panama**, suggested significant **diversification** prior to the Pliocene closure of the **Panamanian seaway**. Coehlo & Calado (1987) attempted to examine albuneid and blepharipodid distributions, but their work was unfortunately compromised by errors introduced by a limited literature survey and inaccurate older literature records. On the basis of phylogenetic analysis following Boyko's (2002) comprehensive taxonomic revision, Boyko & Harvey (2009) concluded that Albuneidae had a shallow water Indo-Pacific origin rather than Atlantic as suggested by Ortmann (1896). Basal and successive genera in the Recent Lepidopinae, *Leucolepidopa* and *Austrolepidopa*, and in Albuneinae, *Stemonopa*, are restricted to the Indo-Pacific. This suggests that rather than originating from a broad **Tethyan distribution**, Albuneidae originated in the shallow Indo-Pacific region and later dispersed eastward into the Atlantic. In contrast, blepharipodids appear to have originated in the eastern Pacific, from which different lineages colonized the Indo-West Pacific and western Atlantic.

HIPPIDAE

Distributional data and zoogeographic studies in this family can be found in Tam et al. (1996), for the American species of *Emerita* only, and along with Albuneidae in Boyko & Harvey (1999). This latter, most recent contribution is primarily a systematic paper but

has distributional information for the two valid Indo-West Pacific species. Both range from east Africa, through the Red Sea and Asia to New Caledonia in the western Pacific Ocean, and north to China and south to tropical Australia. The one species *Hippa pacifica* (Dana, 1852) also occurs in the eastern Pacific Ocean from California to Panama and westward to the Galápagos Islands.

SYSTEMATICS

Classification

Infraorder ANOMURA MacLeay, 1838

PAGUROIDEA Latreille, 1802

Body asymmetrical (rarely symmetrical); ocular scales well-developed or secondarily reduced; 6 antennal articles; 11 pairs of gills; first pereiopods are chelipeds; second and third pereiopod ambulatory, dactyli with claw; fourth pereiopod reduced, simple, chelate or subchelate; fifth pereiopod reduced; third through fifth pleopods paired, unpaired, or absent; uropodal rami not forming a tail fan, with rasps, or absent. [After Poore, 2004.]

COENOBITIDAE Dana, 1851

Carapace and body mostly paguroid in form (*Coenobita*) or with pleon calcified and tucked under (*Birgus*); carapace well calcified; eyestalks laterally flattened, subparallel to each other; antennular peduncles prominently elongate, first segment deflexed, distal two segments slender and cylindrical, dorsal flagellum compressed with tip truncate; antennae short, laterally compressed, acicle small and fused to second peduncular segment; third maxillipeds approximated basally; ischium with well-developed crista dentata, accessory tooth absent; first pereiopod unequal (left larger than right), massive; second and third pereiopod ambulatory, stout, longer than chelipeds; fourth pereiopod chelate or subchelate, fifth pereiopod chelate; pleon asymmetrical, segmentation not clear; male pleopods absent; female with three unpaired pleopods; uropods bear rasp to grasp gastropod shell (except *Birgus*). [After Davie, 2002.]

DIOGENIDAE Ortmann, 1892

Carapace and body paguroid in form; eyestalks cylindrical; antennae long and subcylindrical; antennular flagellum elongate; third maxillipeds usually adjacent at base, ischium with well developed crista dentata, accessory tooth present or absent; 13 or 14 pairs of gills; first pereiopods unequal (generally left larger) or sometimes equal or subequal; male fifth pereiopod with paired (sometimes single) gonopores on coxae, sexual tube absent; first pleopod (or first and second) sometimes paired; second through fifth pleopod unpaired, on left side only, sometimes absent in male; pleon well-developed, asymmetrical, terga weakly calcified, integument membranous; first pleomere distinct from last thoracomere. [After Forest & McLaughlin, 2000; Davie, 2002; Poore, 2004.]

PAGURIDAE Latreille, 1802

Carapace and body paguroid in form; carapace narrow, posterior part usually membranous and soft; antennular flagellum elongate, ends in filament; first maxilliped with distinct flagellum; third maxillipeds widely separated at base (broad sternal plate), ischium with well developed crista dentata, accessory tooth present or absent; usually 11 (sometimes fewer), occasionally 13 pairs of gills; first pereiopods chelate, unequal (right larger) or subequal; second and third pereiopod ambulatory, cylindrical; fourth and fifth pereiopod reduced, one or both chelate or subchelate (rarely simple); male fifth pereiopod with paired gonopores on coxae, sometimes long sexual tube (sometimes paired) present; usually 3 (male) or 4 (female) biramous pleopods on left side only, sometimes first pleopod paired in male or female, rarely first and second pleopod paired in male; pleon soft, well-developed, asymmetrical (rarely symmetrical), integument membranous; first pleomere distinct from last thoracomere; uropods present, usually asymmetrical, modified as holdfasts (with rasps); telson usually with median constriction, lateral terminal margins usually with median cleft. [After de Saint Laurent & McLaughlin, 2000; Davie, 2002; Poore, 2004.]

PARAPAGURIDAE Smith, 1882

Carapace and body paguroid in form; cephalothoracic shield broadly rounded, not narrowing posteriorly, sometimes weakly calcified dorsally; epistome with 0-2 median spines (epistomial spine); labral spine present; third maxillipeds separated at base, ischium with well developed crista dentata, accessory tooth absent; 11 pairs of gills, sometimes with twelfth pair of vestigial pleurobranchs on last thoracomere, gill lamellae divided into two lobes, entire or subdivided; first pereiopods chelate, very unequal (right much larger and often operculate); second and third pereiopod simple, ambulatory, unarmed, long and slender; fourth pereiopod subchelate, with pleurobranch only (rarely rudimentary on fifth pereiopod); fifth pereiopod chelate; first or second pleopod, or both, sometimes paired in male, modified as gonopods; third through fifth pleopods (second through fourth or second through fifth in females) on left only, biramous, exopod short; pleon well developed, asymmetrical, tergites entire, integument membranous; telson entire, without transverse suture. [After Lemaitre, 2000; Davie, 2002; Poore, 2004.]

PYLOCHELIDAE Bate, 1888

Carapace pagurid-like, divided by complete or incomplete linea transversalis; rostrum present or absent; eyestalks normal or reduced, corneas large, reduced, or absent; antennular and antennal peduncles well developed, flagella and acicles present; first maxilliped with well developed epipod, flagellated exopod; third maxillipeds adjacent at base, ischium with well developed crista dentata, accessory teeth present or absent; 14 pairs of gills; first pereiopods chelate, equal, sometimes operculiform; second and third pereiopod simple, ambulatory; fourth and fifth pereiopod more or less subcheliform with propodal

rasp (may be reduced to a line of modified setae); pleon straight (asymmetrical only in *Mixtopagurus*), somites calcified, distinct, articulated; first through fifth pleopod paired; male first and second pleopod and female first pleopod modified as gonopods; telson well developed, with or without transverse suture. [After Forest & McLaughlin, 2000; Davie, 2002; Poore, 2004.]

PYLOJACQUESIDAE McLaughlin & Lemaitre, 2001

Linea transversalis and cervical groove distinct; eyestalks well developed; corneas pigmented or not; ocular acicles elongate; antennular and antennal peduncles well developed, antennal peduncle with supernumerary segmentation; mandible with prominent corneous teeth; first maxilliped with multiarticulate flagellum; third maxillipeds basally separated by narrow protrusion of sternal plate; crista dentata moderately developed, without accessory tooth; thoracic sternites 9-11 fused but with sutures apparent, sternites 12-14 well separated; first pleomere contiguous with last thoracomere, but suture clearly discernible; pleomeres membranous except for partially calcified first tergite and sternite and calcified sixth tergite; third through fifth pleopod developed on left side only; uropods well developed. [After McLaughlin & Lemaitre, 2001; Davie, 2002.]

LITHODOIDEA Samouelle, 1819

Body crab-like, pleon folded underneath; carapace calcified, dorsal regions well defined, typically bearing a variable number and size of granules or spines; rostrum present, variable size and shape; eyes with pigmented terminal corneas; first maxilliped exopod with flagellum; third maxillipeds widely separated at base; scaphocerite present or reduced to small sclerite; epistome spine absent; first pereiopods chelate, equal or subequal (right larger than left); second through fourth pereiopod ambulatory; fifth pereiopod subchelate, folded under carapace; pleon asymmetrical in females, symmetrical in males, short, broad, calcified, pleonal terga with supplemental calcified plates lateral to paired plates; first pleomere fused to last thoracomere; pleopods absent in males; female first pleopod paired, small; female second through fifth pleopod simple, uniramous, unpaired; uropods absent. [After Davie, 2002; Poore, 2004.]

HAPALOGASTRIDAE McLaughlin, Lemaitre & Sorhannus, 2007

Rostrum flat, triangular, usually shorter that eyestalks; third maxillipeds widely separated basally; ischium with well-developed crista dentata; with one or two accessory teeth; pleon with second and terminal two somites ill-calcified; second abdominal somite composed of one median, two lateral, and two marginal plates; pleopods lacking in males; in females first abdominal somite with rudimentary paired pleopods; second through fifth somites each with unpaired uniramous pleopods on left side. [After Miyake, 1978.]

LITHODIDAE Samouelle, 1819

Body crab-like, pleon folded underneath; carapace calcified, dorsal regions well defined, typically bearing a variable number and size of granules or

spines; rostrum present, variable size and shape; eyes with pigmented terminal corneas; first maxilliped exopod with flagellum; third maxillipeds widely separated at base; scaphocerite present or reduced to small granule; epistome spine absent; first pereiopods chelate, equal or subequal (right larger than left); second through fourth pereiopod ambulatory; fifth pereiopod subchelate, folded under carapace; pleon asymmetrical in females, symmetrical in males, short, broad, calcified, pleonal terga with supplemental calcified plates lateral to paired plates; first pleomere fused to last thoracomere; pleopods absent in males; female first pleopod paired, small; female second through fifth pleopod simple, uniramous, unpaired; uropods absent. [After Davie, 2002; Poore, 2004.]

GALATHEOIDEA Samouelle, 1819

Rostrum well-developed or obsolete; cephalothorax and abdomen symmetrical; all abdominal somites distinct, freely articulating, sclerotized; eighth thoracomere with well-developed sternite; ocular acicles absent; antennal peduncle 4-segmented (segments 2 and 3 of five segments fused); acicle absent; mandible incisor margin entire; third maxilliped with or without epipod; first pereiopods chelate; second to fourth pereiopods as walking legs; telson and uropods laminar, forming tailfan, not folded against preceding somite; telson distinctly or indistinctly subdivided into plates; gills phyllobranchiate. [Modified after Ahyong et al., 2010.]

GALATHEIDAE Samouelle, 1819

Carapace longer than wide; dorsally with transverse striae or tubercles; rostrum well-developed, broad, flattened, usually subtriangular; supraocular spines present or absent; eyes with well-developed cornea; antennal peduncle directed anteriorly or anterolaterally; first maxilliped exopod flagellum well-developed; third maxilliped pediform, ischium and merus elongate, not expanded mesially; epipod present; chelipeds subcylindrical to ovate in cross-section. [After Baba et al., 2009; Ahyong et al., 2010.]

MUNIDIDAE Ahyong, Baba, Macpherson & Poore, 2010

Carapace longer than wide; dorsally with transverse striae; rostrum slender, dorsally ridged, usually styliform; supraocular spines present; telson distinctly or indistinctly subdivided into multiple plates; eyes with well-developed cornea; antennal peduncle directed anteriorly or anterolaterally; mandible having incisor edge entire; first maxilliped exopod flagellum well-developed; third maxilliped pediform, ischium and merus elongate, not expanded mesially; epipod present; chelipeds subcylindical to ovate in cross-section. [After Baba et al., 2009; Ahyong et al., 2010.]

MUNIDOPSIDAE Ortmann, 1898

Carapace dorsally with or without few transverse striae; rostrum well developed, subtriangular or spiniform, supraocular spines absent; telson distinctly or indistinctly subdivided into several plates; eyes reduced or with well-

developed corneae; mandible having incisor edge entire; first maxilliped exopod without lash or with reduced lash; third maxilliped with epipod. [After Ahyong et al., 2010.]

PORCELLANIDAE Haworth, 1825

Rostrum well developed to obsolete, if well-developed, broad, subtriangular, flattened; supraocular spines present or absent; carapace (excluding rostrum) longer than wide to wider than long; dorsal surface smooth or variously ornamented with faint striae or tubercles; tailfan well developed, folded against preceding somite, telson distinctly subdivided into 5 or 7 plates; eyes with well-developed cornea; antennal peduncle directed laterally or posteriorly; first maxilliped exopod flagellum well developed; third maxilliped operculiform; ischium and merus elongate, broad, expanded mesially; epipod absent; chelipeds flattened. [After Ahyong et al., 2010.]

CHIROSTYLOIDEA Ortmann, 1892

Body symmetrical, carapace with or without transverse striae; rostrum variously developed, usually prominent; supraocular spines present or absent; sternal plastron consisting of sternites 3-7; eighth thoracomere without sternal plate; abdomen well-developed, all somites sclerotized, articulating; tailfan well-developed, folded beneath preceding somite; telson and uropods laminar; telson transversely divided by suture; antennal peduncle consisting of 5 segments; acicle present or absent; mandible with toothed cutting edge; first maxilliped with or without epipod; first pereiopod always chelate; second to fourth pereiopods as walking legs; third maxilliped and pereiopods without epipods; gills phyllobranchiate. [After Schnabel & Ahyong, 2010.]

CHIROSTYLIDAE Ortmann, 1892

Carapace without transverse setiferous striae; supraocular spines absent; regions usually ill-defined; branchial regions medially separated by cardiac and intestinal regions; pleuron of second pleonite without spine on anterolateral margin; tailfan folded beneath preceding abdominal somite, telson transversely divided into 2 lobes; third sternite not strongly produced anteriorly; eyes well developed; antennal acicle present or absent; mandibular cutting edge calcified, strongly serrated along its length (except possibly *Hapaloptyx*); first maxilliped without epipod; exopodal flagellum present or absent, not annulated; two arthrobranchs on third maxilliped to fourth pereiopod, 1 arthrobranch on fifth pereiopod; pleurobranch on second to fourth pereiopod; male first and second gonopods present. [Modified after Schnabel & Ahyong, 2010.]

EUMUNIDIDAE A. Milne-Edwards & Bouvier, 1900

Carapace cordiform, elongate, with transverse setiferous striae; posterolateral margin entire, not excavated; rostrum styliform, flanked by 1 or 2 supraocular spines; cervical groove distinct; branchial regions medially separated by cardiac and intestinal regions; second pleonite with pleural margin anterolaterally produced into strong spine; tailfan folded beneath preceding abdominal

somite, telson transversely divided into 2 lobes; third sternite anterior margin transversely sinuous or irregular, not strongly produced anteriorly; eyes well developed; antennal acicle present; mandible incisor ridge with 3 small teeth; first maxilliped with well-developed epipod; exopodal flagellum annulated in distal portion; two arthrobranchs on third maxilliped to fourth pereiopod (vestigial on third maxilliped), 1 arthrobranch on fifth pereiopod; pleurobranch on second to fourth pereiopods; male first gonopod absent, second gonopod vestigial or absent. [Modified after Schnabel & Ahyong, 2010.]

KIWAIDAE Macpherson, Jones & Segonzac, 2005

Carapace elongate, smooth, without transverse setiferous striae; posterolateral margin entire, not excavated; rostrum triangular, flanked by small supraocular spines; cervical groove distinct; branchial regions meeting in midline; second pleonite without pleural spine; tailfan folded beneath preceding abdominal somite, telson transversely divided into 2 lobes; third sternite anterior margin strongly produced anteriorly; eyes strongy reduced, soft, not calcified, movable, unpigmented; antennal acicle absent; mandible incisor ridge strongly serrated along its length, corneous; first maxilliped with well-developed epipod; exopodal flagellum annulated in distal portion; two arthrobranchs on third maxilliped to fourth pereiopod (vestigial on third maxilliped); fifth pereiopod without arthrobranch; pleurobranchs absent; male pleopods 2-5 present. [Modified after Schnabel & Ahyong, 2010.]

AEGLOIDEA Dana, 1852

Carapace widest near posterolateral corners, traversed by prominent cervical groove; thoracic region subdivided into prominent cardiac region axially, and lateral branchial regions subdivided by one or more transverse or longitudinal linae; terminal thoracic sternal element present; rostrum prominent, typically carinate, extending well beyond anterolateral spines; first pereiopods with stout chelae, typically with flabellate projection developed on inner part of hand near articulation with dactylus, inner margin of carpus spinose; telson usually divided by longitudinal suture. [After Feldmann, 1984.]

AEGLIDAE Dana, 1852

As per superfamily diagnosis.

LOMISOIDEA Bouvier, 1895

Body crab-like, symmetrical, flattened, triangular; eyestalks broad and flat; cornea inserted laterally; ocular scales absent; antennal peduncle with 6 articles; epistome with spine; third maxillipeds separated at base; 14 pairs of gills; first pereiopod chelate, short, broad, flat; second through fourth pereiopod ambulatory, dactyli with claw; fifth pereiopod vestigial, carried in branchial chamber; pleon folded under body; first pleomere visible dorsally; third through fifth pleopod paired; male gonopods present; female first pleopod present; female uropods non-spatulate, male uropods vestigial; telson undivided. [After Davie, 2002; Poore, 2004.]

Lᴏᴍɪsɪᴅᴀᴇ Bouvier, 1895
>   As per superfamily diagnosis.

Hɪᴘᴘᴏɪᴅᴇᴀ Latreille, 1825
>   Body symmetrical; ocular scales absent; second through fourth pereiopod dactyli
>   similar; uropodal rami not forming a tail-fan, without rasps. [After Poore, 2004.]

Aʟʙᴜɴᴇɪᴅᴀᴇ Stimpson, 1858
>   Carapace subrectangular, flattened, without lateral expansions covering pereio-
>   pods, dorsal surface moderately convex, broad mat of short, dense, simple se-
>   tae just behind front (setal field), numerous transverse setose grooves; ros-
>   trum reduced or absent; epibranchial spine absent; eyestalks short to markedly
>   elongate; cornea distinct, atrophied, or absent; antennule with 3 segments,
>   dorsal flagellum with 17-250 articles, ventral flagellum with 0-7 articles; an-
>   tenna 5-segmented, acicle present, flagellum with 1-9 articles; mandible well
>   developed, with 3-segmented palp; first maxilliped with epipod; third max-
>   illiped with epipod, merus unarmed, crista dentata absent or weak, exopod
>   slender or lamellar; gills phyllobranchiate; first pereiopods subchelate, dactyli
>   dorsal margin smooth or crenulate, propodus cutting edge smooth or with
>   blunt teeth; second through fourth pereiopod dactyli laterally compressed
>   and dorsoventrally expanded (sickle-shaped); fifth pereiopod reduced, chelate;
>   pleopods absent or rudimentary in males, present on female second through
>   fifth pleomere, uniramous; pleon with pleura on second through fourth somite,
>   or fifth; uropods present, long and lamellar; telson entire, ovoid. [After Boyko,
>   2002; Davie, 2002; Poore, 2004.]

Bʟᴇᴘʜᴀʀɪᴘᴏᴅɪᴅᴀᴇ Boyko, 2002
>   Carapace longer than wide, broadly keeled axially, front narrow; outer ocu-
>   lar spines long, spinose; one or two hepatic anterolateral spines present; epi-
>   branchial spine present; branchiostegite weakly spinose; rostrum triangular,
>   spinose; gills trichobranchiate; eyestalks cylindrical, corneas large; first anten-
>   nular segment unarmed, dorsal flagellum with 18-85 articles, ventral flagel-
>   lum with 6-21 articles; antennal segment unarmed dorsally, acicle short, flag-
>   ellum with 8-44 articles; first maxilliped with epipod; second maxilliped ex-
>   opod with multiarticulate flagellum; third maxilliped carpal projection short,
>   merus armed, strong crista dentata present, exopod slender with flagellum;
>   first pereiopod dactylus subchelate, disto-dorsal carpal spine present, cutting
>   edge spinose; second through fourth pereiopod dactyli laterally compressed
>   and dorsoventrally expanded, dorsal margins of carpi spinose; fifth pereiopod
>   reduced, chelate; pleon with pleura on second through fifth somite; females
>   with uniramous, paired pleopods on second through fifth somite; males with-
>   out pleopods; uropods present; telson entire, ovate, laterally expanded, some-
>   times weakly sexually dimorphic. [After Boyko, 2002.]

Hɪᴘᴘɪᴅᴀᴇ Latreille, 1825
>   Carapace oval, strongly convex, more or less expanded laterally, with lateral

extensions covering all except first pereiopod; rostrum reduced or absent; eyestalks short or long; cornea distinct; mandible reduced; third maxilliped without exopod, suboperculiform with enlarged, broadened merus; first pereiopod simple, dactyli cylindrical or lamellate; second and third pereiopod dactyli curved and flattened, fourth pereiopod dactyli less curved and flattened; female with three pairs of pleopods on second through fourth pleomere; uropodal exopod and endopod long, lamellar; telson strongly elongate, lanceolate, apically acute. [After Haig, 1974; Davie, 2002; Poore, 2004.]

APPENDIX

Taxa at species level (and occasionally at genus level), mentioned in this chapter, with authorities and dates of their description

Acanthopagurus dubius (A. Milne-Edwards & Bouvier, 1900)
Aegla cavernicola Türkay, 1972
Aegla platensis Schmitt, 1942
Aegla schmitti Hobbs, 1979
Aegla uruguayana Schmitt, 1942
Alainopaguroides lemaitrei McLaughlin, 1997
Albunea microps Miers, 1878
Albunea symmysta (Linnaeus, 1758)
Anapagurus bicorniger A. Milne-Edwards & Bouvier, 1892
Anapagurus chiroacanthus (Lilljeborg, 1856)
Asymmetrione asymmetrica (Shiino, 1933)
Athelges takanoshimensis Ishii, 1914

Bathycheles incisus (Forest, 1987)
Birgus latro (Linnaeus, 1767)
Blepharipoda liberata Shen, 1949
Boninpagurus acanthocheles Asakura & Tachikawa, 2004
Briarosaccus callosus Boschma, 1930

Calcinus elegans (H. Milne Edwards, 1836)
Calcinus laevimanus (Randall, 1840)
Cancellocheles sculptipes (Miyake, 1978)
Cancellus typus H. Milne Edwards, 1836
Catapaguroides japonicus de Saint Laurent, 1968
Catapaguroides megalops A. Milne-Edwards & Bouvier, 1892
Catapagurus tuberculosus (Asakura, 1999)
Cervimunida johni Porter, 1903
Cheiroplatea laticaudata Boas, 1926
Chirostylus investigatoris (Alcock & Anderson, 1899)
Ciliopagurus strigatus (Herbst, 1804)
Clibanarius eurysternus (Hilgendorf, 1879)
Clibanarius erythropus (Latreille, 1818)
Clibanarius fonticola McLaughlin & Murray, 1990
Clibanarius taeniatus (H. Milne Edwards, 1848)
Clibanarius virescens (Krauss, 1843)
Coenobita clypeatus (Herbst, 1791)
Coenobita perlatus H. Milne Edwards, 1837

Coenobita purpureus Stimpson, 1858
Coenobita scaevola (Forskål, 1775)
Coenobita variabilis McCulloch, 1909
Cryptolithodes expansus Miers, 1879

Dardanus megistos (Herbst, 1804)
Dardanus robustus Asakura, 2006
Dardanus setifer H. Milne Edwards, 1836
Dardanus umbella Asakura, 2006
Decaphyllus barunajaya McLaughlin, 1997
Diogenes brevirostris Stimpson, 1858
Diogenes edwardsii (De Haan, 1849)
Diogenes nitidimanus Terao, 1913
Diogenes patae Asakura & Godwin, 2006

Enneopagurus garciagomezi McLaughlin, 1997
Enneophyllus spinirostris McLaughlin, 1997
Eumunida annulosa de Saint Laurent & Macpherson, 1990
Eumunida capillata de Saint Laurent & Macpherson, 1990
Emerita benedicti Schmitt, 1935
Emerita holthuisi Sankolli, 1965
Emerita talpoida (Say, 1817)

Forestopagurus drachi (Forest, 1966)

Galathea inflata Potts, 1915
Galathea squamifera Leach, 1814
Gastroptychus affinis (Chace, 1942)

Hapalogaster dentata (De Haan, 1849)
Hippa adactyla Fabricius, 1787
Hippa pacifica (Dana, 1852)
Hippa truncatifrons (Miers, 1878)
Hydractinia sodalis Stimpson, 1858

Ilyanassa obsoleta (Say, 1822)

Kiwa hirsuta Macpherson, Jones & Segonzac, 2005

Lepidopa benedicti Schmitt, 1935
Lithodes aequispinus Benedict, 1895
Lithodes santolla (Molina, 1782)
Lomis hirta (Lamarck, 1818)
Lopholithodes mandtii Brandt, 1848
Lopholithodes foraminatus (Stimpson, 1859)
Lophomastix japonica (Duruflé, 1889)

Michelopagurus limatulus (Henderson, 1888)
Micropagurus acantholepis (Stimpson, 1858)
Micropagurus polynesiensis (Nobili, 1906)
Micropagurus spinimanus Asakura, 2005
Munida gregaria (Fabricius, 1793)
Munida irrasa A. Milne-Edwards, 1880
Munida quadrispinosa Benedict, 1902
Munida rugosa (Fabricius, 1775)
Munidopsis polymorpha Koelbel, 1892

Munidopsis serricornis (Lovén, 1852)
Munidopsis tridentatus Esmark, 1857

Nematopaguroides fagei Forest & de Saint Laurent, 1968

Oedignathus inermis (Stimpson, 1860)
Ostraconotus spatulipes A. Milne-Edwards, 1880

Paralomis hystrix (De Haan, 1846)
Paguristes digitalis Stimpson, 1858
Paguristes eremita (Linnaeus, 1767)
Paguristes squamosus McCulloch, 1913
Pagurixus boninensis (Melin, 1939)
Pagurodes inarmatus Henderson, 1888
Pagurojacquesia polymorpha de Saint Laurent & McLaughlin, 2000
Pagurus bernhardus (Linnaeus, 1758)
Pagurus constans (Stimpson, 1858)
Pagurus cuanensis Bell, 1845
Pagurus filholi (De Man, 1887)
Pagurus gracilipes (Stimpson, 1858)
Pagurus hirsutiusculus (Dana, 1851)
Pagurus insulae Asakura, 1991
Pagurus longicarpus Say, 1817
Pagurus minutus Hess, 1865
Paralithodes brevipes (H. Milne Edwards & Lucas, 1841)
Paralithodes camtschaticus (Tilesius, 1815)
Paralithodes platypus (Brandt, 1850)
Paralomis granulosa (Jacquinot, 1847)
Parapylocheles scorpio (Alcock, 1894)
Petrolisthes elongatus (H. Milne Edwards, 1837)
Pisidia inequalis (Heller, 1861)
Pleuroncodes monodon (H. Milne Edwards, 1837)
Pleuroncodes planipes Stimpson, 1860
Pomatocheles jeffreysii Miers, 1879
Porcellana platycheles (Pennant, 1777)
Porcellanopagurus tridentatus Whitelegge, 1900
Probeebei mirabilis Boone, 1926
Pseudopaguristes bicolor Asakura & Kosuge, 2004
Pseudopaguristes bollandi Asakura & McLaughlin, 2003
Pseudopaguristes shidarai Asakura, 2004
Pylocheles mortensenii Boas, 1926
Pylopaguropsis furusei Asakura, 2000

Solenopagurus lineatus (Wass, 1963)
Solitariopagurus triprobolus Poupin & McLaughlin, 1996
Solitariopagurus tuerkayi McLaughlin, 1997
Strigopagurus strigimanus (White, 1847)

Tarrasopagurus rostrodenticulatus McLaughlin, 1997
Tisea grandis Forest & Morgan, 1991
Trizocheles caledonicus Forest, 1987
Trichopagurus trichophthalmus (Forest, 1954)
Turleania multispina McLaughlin, 1997

Tylaspis anomala Henderson, 1885
Typhlopagurus foresti de Saint Laurent, 1972

Uroptychus spinirostris (Ahyong & Poore, 2004)

Xylopagurus caledonicus Forest, 1997
Xylopagurus rectus A. Milne-Edwards, 1880

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BIBLIOGRAPHY

AHYONG, S. T., 2010a. *Neolithodes flindersi*, a new species of king crab from southeastern Australia (Crustacea: Decapoda: Lithodidae). — Zootaxa, **2362**: 55-62.

— —, 2010b. The marine fauna of New Zealand: king crabs of New Zealand, Australia and the Ross Sea (Crustacea: Decapoda: Lithodidae). — NIWA Biodiv. Mem., **123**: 1-196.

AHYONG, S. T., K. BABA, E. MACPHERSON & G. C. B. POORE, 2010. A new classification of the Galatheoidea (Crustacea: Decapoda: Anomura). — Zootaxa, **2676**: 57-68.

AHYONG, S. T. & T.-Y. CHAN, 2010. *Lithodes formosae*, a new species of king crab from Taiwan (Crustacea: Decapoda: Lithodidae). — Zootaxa, **2332**: 61-68.

AHYONG, S. T. & E. W. DAWSON, 2006. Lithodidae from the Ross Sea, Antarctica, with descriptions of two new species (Crustacea: Decapoda: Anomura). — Zootaxa, **1303**: 45-68.

AHYONG, S. T., J. C. Y. LAI, D. SHARKEY, D. J. COLGAN & P. K. L. NG, 2007. Phylogenetics of the brachyuran crabs (Crustacea: Decapoda) part I: the status of Podotremata based on small subunit nuclear ribosomal RNA. — Mol. Phylogenet. Evol., **45**: 576-586.

AHYONG, S. T., E. MACPHERSON & T. Y. CHAN, 2010. Lithodoidea (king crabs). — In: T. Y. CHAN (ed.), Crustacean fauna of Taiwan: crab-like anomurans (Hippoidea, Lithodoidea, Porcellanidae), pp. 42-66. (National Taiwan Ocean University, Keelung.)

AHYONG, S. T. & D. O'MEALLY, 2004. Phylogeny of the Decapoda Reptantia: resolution using three molecular loci and morphology. — Raffles Bull. Zool., **52**: 673-693.

AHYONG, S. T. & G. C. B. POORE, 2004. The Chirostylidae of southern Australia (Crustacea: Decapoda: Anomura). — Zootaxa, **436**: 1-88.

AHYONG, S. T., K. E. SCHNABEL & E. W. MAAS, 2009. Anomuran phylogeny: new insights from molecular data. — In: J. W. MARTIN, K. A. CRANDALL & D. L. FELDER (eds.), Decapod crustacean phylogenetics. Crust. Iss., **18**: 399-414. (CRC Press, Taylor & Francis Group, Boca Raton, Florida.)

AL-AIDAROOS, A. & D. I. WILLIAMSON, 1989. Larval development of the land crab *Coenobita scaevola* (Forskål, 1775) (Crustacea: Anomura: Coenobitidae) reared in the laboratory. — J. nat. Hist., Lond., **23**: 111-128.

ALCOCK, A., 1905. Catalogue of the Indian decapod Crustacea in the collection of the Indian Museum. Part II. Anomura. — Pp. 1-197. (Trustees of the Indian Museum, Calcutta.)

ALEXANDROWICZ, J. S., 1953. Nervous organs in the pericardial cavity of the decapod Crustacea. — J. mar. biol. Ass. U.K., **31**: 563-580.

ALMERÃO, M. P., M. C. FACCIONI-HEUSER & G. BOND-BUCKUP, 2007. An ultrastructural study of tegumental glands of the fifth pereiopod of *Aegla platensis* (Anomura: Aeglidae). — J. Crust. Biol., **27**: 529-533.

ASAKURA, A., 1999. *Icelopagurus tuberculosus*, a distinct new hermit crab species (Crustacea: Decapoda: Paguridae) from Japan. — Proc. biol. Soc. Wash., **112**: 381-395.

— —, 2000. A review of Japanese species of *Pylopaguropsis* Alcock, 1905 (Decapoda: Anomura: Paguridae). — Crust. Res., **29**: 70-108.

— —, 2002. Hermit crabs of the genus *Calcinus* Dana, 1851 (Crustacea Decapoda Anomura Diogenidae) with a brush of setae on the third pereiopod, from Japan and adjacent waters. — Trop. Zool., **15**: 27-70.

— —, 2003. Biology of crustaceans – recent topics. — Pp. 1-291. (Tokai University Press, Kanagawa.)

— —, 2004a. *Pseudopaguristes shidarai*, a new species of hermit crab (Crustacea: Decapoda: Diogenidae) from Japan, the fourth species of the genus. — Proc. biol. Soc. Wash., **117**: 153-168.

— —, 2004b. Recent topics on taxonomy of hermit crabs from Japanese waters – family Coenobitidae. — Aquabiol. [Kaiyou tow Seibutsu], **150**: 83-89.

— —, 2005. A review of the genus *Micropagurus* (Crustacea Decapoda Anomura Paguridae). — Zootaxa, **1090**: 1-34.

— —, 2006a. *Dardanus sanguinocarpus* Degener, 1925 (Crustacea: Decapoda: Anomura: Diogenidae) species complex: a redescription of *D. sanguinocarpus* and descriptions of three new species. — Zootaxa, **1230**: 1-54.

— —, 2006b. Shallow water hermit crabs of the families Pylochelidae, Diogenidae and Paguridae (Crustacea: Decapoda: Anomura) from the Sea of Japan, with a description of a new species of *Diogenes*. — Bull. Toyama Sci. Mus., **29**: 23-103.

ASAKURA, A. & T. KOSUGE, 2004. *Pseudopaguristes bicolor*, a new specis of hermit crab (Crustacea: Decapoda: Diogenidae) from Japan, the third species of the genus. — Proc. biol. Soc. Wash., **117**: 57-67.

ASAKURA, A. & P. A. MCLAUGHLIN, 2003. A new species of *Pseudopaguristes* McLaughlin, 2002 (Crustacea: Decapoda: Diogenidae) from Japan. — Proc. biol. Soc. Wash., **116**: 453-463.

ASAKURA, A. & H. TACHIKAWA, 2004. *Boninpagurus acanthocheles*, a new genus and species of hermit crab (Decapoda: Anomura: Paguridae) from shallow waters of the Ogasawara Islands, Japan. — J. Crust. Biol., **24**: 157-167.

AURIOLES GAMBOA, D. & E. F. BALART, 1995. La langostilla: biologia ecologia y aprovechamiento. — (Centro de Investigaciones Biologicas del Noroeste, S. C., La Paz, Baja California.)

BABA, K., 2005. Deep-sea chirostylid and galatheid crustaceans (Decapoda: Anomura) from the Indo-Pacific, with a list of species. — Galathea Rep., **20**: 1-317.

— —, 2009. A new species of squat lobster (Decapoda, Anomura, Chirostylidae) from the Philippines and Indonesia. — Crustaceana, **82**: 795-802.

BABA, K., E. MACPHERSON, C.-W. LIN & T.-Y. CHAN, 2009. Crustacean fauna of Taiwan: squat lobsters (Chirostylidae and Galatheidae). — Pp. 1-312. (National Taiwan Ocean University, Keelung.)

BABA, K., E. MACPHERSON, G. C. B. POORE, S. T. AHYONG, A. BERMUDEZ, P. CABEZAS, C.-W. LIN, M. NIZINSKI, C. RODRIGUES & K. E. SCHNABEL, 2008. Catalogue of squat lobsters of the world (Crustacea: Decapoda: Anomura – families Chirostylidae, Galatheidae, Kiwaidae). — Zootaxa, **1905**: 1-220.

BAKEL, B. W. M. VAN, R. H. B. FRAAIJE, J. W. M. JAGT & P. ARTAL, 2008. An unexpected diversity in Late Jurassic hermit crabs (Crustacea, Decapoda, Anomura) in Central Europe. — Jahrb. Geol. Paläont. Abh., **250**: 137-156.

BALUK, W. & A. RADWAN'SKI, 1991. A new occurrence of fossil acrothoracican cirripedes: *Trypetesa polonica* sp. n. in hermitted gastropod shells from the Korytnica Basin (Middle Miocene; Holy Cross Mountains, central Poland), and its bearing on behavioral evolution of the genus *Trypetesa*. — Acta geol. Pol., **41**: 1-36.

BATSON, P., 2003. Deep New Zealand. — Pp. 1-239. (Canterbury University Press, Christchurch.)

BAUMANN, H. VON, 1917. Das cor frontale bei decapoden Krebsen. — Zool. Anz., **49**: 137-144.

BENEDICT, J. E., 1902. Description of a new genus and forty six new species of crustaceans of the family Galatheidae with a list of the known marine species. — Proc. biol. Soc. Wash., **26**: 243-334.

BLAKE, J. A., 1971. Revision of the genus *Polydora* from the east coast of North America (Polychaeta: Spionidae). — Smithson. Contrib. Zool., **75**: 1-32.

BOAS, J. E. V., 1880. II. Wissenschaftliche Mittheilungen. I. *Lithodes* und *Pagurus*. — Zool. Anz., **3**: 349-352.

— —, 1924. Die verwandtschaftliche Stellung der Gattung *Lithodes*. — K. Danske Vidensk. Selsk. Skr biol. Medd., **4**: 1-34.

BOND-BUCKUP, G. & L. BUCKUP, 1994. A família Aeglidae (Crustacea, Decapoda, Anomura). — Arq. Zool., S. Paulo, **32**: 159-346.

BOND-BUCKUP, G., A. P. BUENO & K. A. KEUNECKE, 1996. Primeiro estágio juvenil de *Aegla prado* Schmitt (Crustacea, Decapoda, Anomura, Aeglidae). — Revta. Bras. Zool., **13**: 1049-1061.

— —, — — & — —, 1999. Morphological characteristics of juvenile specimens of *Aegla* (Decapoda, Anomura, Aeglidae). — In: F. R. SCHRAM & J. C. VON VAUPEL KLEIN (eds.), Crustaceans and the biodiversity crisis. Proceedings of the Fourth International Crustacean Congress, Amsterdam, The Netherlands, July 20-24, 1998, **1**: 371-381. (Brill, Leiden.)

BORRADAILE, L. A., 1916. Crustacea Part II. *Porcellanopagurus*: an instance of carcinization. — British Antarct. ("Terra Nova") Exped., 1910, nat. Hist. Rep., **3**: 111-126.

BOUVIER, E. L., 1895. Recherches sur les affinités des *Lithodes* et des *Lomis* avec les paguridés. — Ann. Sci. nat., (Zool.) (7) **18**: 157-213.

BOYKO, C. B., 2002. A worldwide revision of the recent and fossil sand crabs of the Albuneidae Stimpson and Blepharipodidae, new family (Crustacea: Decapoda: Anomura: Hippoidea). — Bull. Am. Mus. nat. Hist., **272**: 1-396.

BOYKO, C. B. & A. W. HARVEY, 1999. Crustacea Decapoda: Albuneidae and Hippidae of the tropical Indo-West Pacific region. — In: A. CROSNIER (ed.), Résultats des campagnes MUSORSTOM, **20**. Mém. Mus. natn. Hist. nat., Paris, **180**: 379-406.

— — & — —, 2009. Phylogenetic systematics and biogeography of the sand crab families Albuneidae and Blepharipodidae (Crustacea: Anomura: Hippoidea). — Invert. Syst., **23**: 1-18.

BRACKEN, H. D., A. TOON, D. L. FELDER, J. W. MARTIN, M. FINLEY, J. RASMUSSEN, F. PALERO & K. A. CRANDALL, 2009. The decapod tree of life: compiling the data and moving toward a consensus of decapod evolution. — Arthrop. Syst. Phyl., **67**: 99-116.

BROWN, I. W. & D. R. FIELDER, 1991. The coconut crab: aspects of the biology and ecology of *Birgus latro* in the Republic of Vanuatu. — ACIAR Monogr., **8**: 1-136.

BUENO, A. P. & G. BOND-BUCKUP, 1996. Os estágios juvenis iniciais de *Aegla violacea* Bond-Buckup & Buckup (Crustacea, Anomura, Aeglidae). — Nauplius, **4**: 39-47.

BUENO, A. P., G. BOND-BUCKUP & L. BUCKUP, 2000. Cresimento de *Aegla platensis* Schmitt em ambiente natural (Crustacea, Decapoda, Aeglidae). — Revta. Bras. Zool., **17**: 51-60.

BURD, B. J. & G. JAMIESON, 1988. Biology and commercial potential of galatheid crabs in British Columbia. — J. Shellfish Res., **7**: 112-113.

BURKENROAD, M. D., 1963. The evolution of the Eucarida (Crustacea, Eumalacostraca), in relation to the fossil record. — Tulane Stud. Geol., **2**: 3-16.

BURSEY, C. R., 1975. The microanatomy of the compound eye of *Munida irrasa* (Decapoda: Galatheidae). — Cell Tiss. Res., **160**: 505-514.

CAINE, E. A., 1975. Feeding and masticatory structures of selected Anomura (Crustacea). — J. exp. mar. Biol. Ecol., **18**: 277-301.

— —, 1976. Relationship between diet and the gland filter of the gastric mill in hermit crabs (Decapoda: Paguridea). — Crustaceana, **31**: 312-313.

CALADO, R., N. NOGUEIRA & A. DOS SANTOS, 2006. Extended parental care in a hermit crab of the genus *Calcinus* (Anomura: Diogenidae). — J. mar. biol. Ass. U.K., **86**: 121-123.

CALMAN, W. T., 1909. Decapoda. Crustacea. [Part VII. Appendiculata. (Third fascicule Crustacea.)] — In: R. LANKASTER (ed.), A treatise on zoology, **7** (3): 253-263. (Adam & Charles Black, London.)

CARAYON, J., 1941. Morphologie et structure de l'appareil génital femelle chez quelques Pagures. — Bull. Soc. zool. France, **66**: 95-122.

CASTRO, T. S. & G. BOND-BUCKUP, 2003. The morphology of cardiac and pyloric foregut of *Aegla platensis* Schmitt (Crustacea: Anomura: Aeglidae). — In: R. LEMAITRE & C. C. TUDGE (eds.), Biology of the Anomura. Proceedings of a symposium at the Fifth International Crustacean Congress, Melbourne, Australia, 9-13 July 2001. Mem. Mus. Vict., **60**: 53-57.

CHABLAIS, J., R. M. FELDMANN & C. E. SCHWEITZER, 2011. A new Triassic decapod, *Platykotta akaina*, from the Arabian shelf of the northern United Arab Emirates: earliest occurrence of the Anomura. — Paläontol. Zeitschr., **85**: 93-102.

CHACE, F. A., 1942. The Anomura Crustacea. I. Galatheidea. Reports of the scientific results of the Atlantis Expeditions to the West Indies, under the joint auspices of the University of Havana and Harvard University. — Torreia, **11**: 1-106.

CHARNIAUX-COTTON, H., 1955. Le déterminisme hormonal des caractères sexuels d'*Orchestia gammarella* (Crustacé amphipode). — C. R. Acad. Sci., Paris, **240**: 1487-1489.

CHARNIAUX-COTTON, H., C. ZERBIB & J. J. MEUSY, 1966. Monographie de la glande androgène des Crustacés Supérieurs. — Crustaceana, **10**: 113-136.

CHU, K. H., L. M. TSANG, K. Y. MA, T. Y. CHAN & P. K. L. NG, 2009. Decapod phylogeny: what can protein-coding genes tell us? — In: J. W. MARTIN, K. A. CRANDALL & D. L. FELDER (eds.), Decapod crustacean phylogenetics. Crust. Iss., **18**: 89-99. (CRC Press, Taylor & Francis Group, Boca Raton, Florida.)

CLARK, P. F. & P. K. L. NG, 2008. The lecithotrophic zoea of *Chirostylus ortmanni* Miyake & Baba, 1968 (Crustacea: Anomura: Galatheoidea: Chirostylidae) described from laboratory hatched material. — Raffl. Bull. Zool., **56**: 85-94.

CLAVERIE, T. & I. P. SMITH, 2007. Functional significance of an unusual chela dimorphism in a marine decapod: specialization as a weapon. — Proc. Roy. Soc. Lond., (B) **274**: 3033-3038.

COELHO, P. A. & T. C. CALADO, 1987. Família Albuneidae: distribuicão geográfica. — Anais Soc. Nord. Zool., **2**: 39-51.

CRAIN, J. A. & P. A. MCLAUGHLIN, 2000. Larval and early juvenile development in the Lithodidae (Decapoda: Anomura: Paguroidea) reared under laboratory conditions. — Invert. Repr. Dev., **37**: 113-127.

CUNNINGHAM, C. W., N. W. BLACKSTONE & L. W. BUSS, 1992. Evolution of king crabs from hermit crab ancestors. — Nature, Lond., **355**: 539-542.

DAVIE, P. J. F., 2002. Crustacea: Malacostraca: Eucarida (Part 2): Decapoda – Anomura, Brachyura. — In: A. WELLS & W. W. K. HOUSTON (eds.), Zoological Catalogue of Australia, **19** (3) (B): 1-641. (CSIRO Publishing, Melbourne.)

DAWSON, E. W., 1989. King crabs of the world (Crustacea: Lithodidae) and their fisheries: a comprehensive bibliography. — N.Z. oceanogr. Inst. misc. Publ., **101**: 1-338. (Wellington.)

DE ANGELI, A. & A. GARASSINO, 2002. Galatheid, chirostylid and porcellanid decapods (Crustacea, Decapoda, Anomura) from the Eocene and Oligocene of Vicenza (N Italy). — Mem. Soc. Ital. Mus. civ. Storia nat. Milano, **30** (3): 1-40.

DILLAMAN, R. M., P. GREENAWAY & S. M. LINTON, 1999. Role of the midgut gland in purine excretion in the robber crab, *Birgus latro* (Anomura: Coenobitidae). — J. Morph., **241**: 227-235.

DIONI, W., 1972. *Didymorchis*, *Temnocephala* (Platyhelmintha) y *Stratiodrilus* (Annelida) vermes epizoicos sobre *Aegla* y *Parastacus* (Crustacea: Decapoda) de lagos andino-patagonicos. Notas taxinomicas y biogeograficas. — Acta zool. Lilloana, Tucumán, **29**: 167-179.

DIXON, C. J., S. T. AHYONG & F. R. SCHRAM, 2003. A new hypothesis of decapod phylogeny. — Crustaceana, **76**: 935-975.

DOFLEIN, F. & H. BALSS, 1913. Die Galatheiden der Deutschen Tiefsee-Expedition. — Deutsche Tiefsee-Exped. 1898-1899, **20**: 125-184, pls. 12-17.

EFFORD, I. E., 1971. The species of sand crabs in the genus *Lepidopa* (Decapoda: Albuneidae). — Zool. Anz., **186**: 59-102.

EGUCHI, E., M. DEZAWA & V. B. MEYER-ROCHOW, 1997. Compound eye fine structure in *Paralomis multispina* Benedict, an anomuran half-crab from 1200 m depth (Crustacea; Decapoda; Anomura). — Biol. Bull., Woods Hole, **192**: 300-308.

EGUCHI, E., T. GOTO & T. H. WATERMAN, 1982. Unorthodox pattern of microvilli and intercellular junctions in regular retinular cells of the porcellanid crab *Petrolisthes*. — Cell Tiss. Res., **222**: 493-513.

FANTUCCI, M. Z., R. BIAGI & F. L. MANTELATTO, 2008. Intersexuality in the western Atlantic hermit *Isocheles sawayai* (Anomura, Diogenidae). — Mar. Biodivers. Rec., **1**: e68. [DOI: 10.1017/S175526720700735X]

FARRELLY, C. & P. GREENAWAY, 2005. The morphology and vasculature of the respiratory organs of terrestrial hermit crabs (*Coenobita* and *Birgus*): gills, branchiostegal lungs and abdominal lungs. — Arthrop. Struct. Dev., **34**: 63-87.

FELDMANN, R. M., 1984. *Haumuriaegla glaessneri* n. gen., and sp. (Decapoda; Anomura; Aeglidae) from Haumurian (Late Cretaceous) rocks near Cheviot, New Zealand. — N.Z. Jl Geol. Geophys., **27**: 379-385.

— —, 1986. Paleobiogeography of two decapod crustacean taxa in the Southern Hemisphere: global conclusions with sparse data. — In: R. H. GORE & K. L. HECK (eds.), Crustacean biogeography. Crust. Iss., **4**: 5-19. (Balkema, Rotterdam.)

— —, 1998. *Paralomis debodeorum*, a new species of decapod crustacean from the Miocene of New Zealand: first notice of the Lithodidae in the fossil record. — N.Z. Jl Geol. Geophys., **41**: 35-38.

FELDMANN, R. M. & I. W. KEYES, 1992. Systematic and stratigraphic review with catalogue and locality index of the Mesozoic and Cenozoic decapod Crustacea of New Zealand. — N.Z. geol. Surv. Rec., **45**: 1-73.

FELDMANN, R. M., F. J. VEGA, S. P. APPLEGATE & G. A. BISHOP. 1998. Early Cretaceous arthropods from the Tlayúa Formation at Tepexi de Rodríguez, Puebla, México. — J. Paleontol., **72**: 79-90.

FELGENHAUER, B. E., 1992a. External anatomy and integumentary structures. — In: F. W. HARRISON & A. G. HUMES (eds.), Microscopic anatomy of invertebrates, **10**: 7-43. (Wiley-Liss, New York.)

— —, 1992b. Internal anatomy of the Decapoda: an overview. — In: F. W. HARRISON & A. G. HUMES (eds.), Microscopic anatomy of invertebrates, **10**: 45-75. (Wiley-Liss, New York.)

FINCHAM, A. A., 1988. Ontogeny of anomuran eyes. — Symp. zool. Soc. Lond., **59**: 123-155.

FINGERMAN, M., 1992. Glands and secretion. — In: F. W. HARRISON & A. G. HUMES (eds.), Microscopic anatomy of invertebrates, **10**: 345-394. (Wiley-Liss, New York.)

FOREST, J., 1984. Révision du genre *Aniculus* Decapoda Diogenidae. — Crustaceana, (Suppl.) **8**: 1-91.

— —, 1987a. Les Pylochelidae ou "Pagures symétriques" (Crustacea Coenobitoidea). — Mém. Mus. natn. Hist. nat., Paris, (A, Zool.) **137**: 1-274.

— —, 1987b. Ethology and distribution of Pylochelidae (Crustacea Decapoda Coenobitoidea). — Bull. mar. Sci., **41**: 309-321.

— —, 1995. Crustacea Decapoda Anomura: révision du genre *Trizopagurus* Forest, 1952 (Diogenidae), avec l'éstablissement de deux genres nouveaux. — In: A. CROSNIER (ed.), Résultats des campagnes MUSORSTOM, **13**. Mém. Mus. natn. Hist. nat., Paris, **163**: 9-149.

FOREST, J. & P. A. MCLAUGHLIN, 2000. Superfamily Coenobitoidea, families Pylochelidae, Diogenidae. — In: J. FOREST, M. DE SAINT LAURENT, P. A. MCLAUGHLIN & R. LEMAITRE (eds.), The marine fauna of New Zealand: Paguridea (Decapoda: Anomura), exclusive of the Lithodidae. NIWA Biodiv. Mem., **114**: 31-103.

FOREST, J. & M. DE SAINT LAURENT, 1967. Crustacés Décapodes: Pagurides. Campagne de la Calypso au large des côtes Atlantiques de l'Amérique du Sud (1961-1962). I. — Rés. scient. Camp. Calypso, **8**: 47-169.

FOREST, J., M. DE SAINT LAURENT, P. A. MCLAUGHLIN & R. LEMAITRE, 2000. The marine fauna of New Zealand: Paguridea (Decapoda: Anomura), exclusive of the Lithodidae. — NIWA Biodiv. Mem., **114**: 1-250.

FRAAIJE, R., 2003. The oldest in situ hermit crab from the Lower Cretaceous of Speeton, UK. — Paleontol., **46**: 53-57.

FUJITA, Y. & S. SHOKITA, 2005. The complete larval development of *Sadayoshia edwardsii* (Miers, 1884) (Decapoda: Anomura: Galatheidae) described from laboratory-reared material. — J. nat. Hist., Lond., **39**: 865-886.

GABE, M., 1953. Sur l'existence, chez quelques Crustacés Malacostracés, d'un organe comparable à la glande de la mue des Insectes. — C. R. Acad. Sci., Paris, **237**: 1111-1113.

GARCÍA-CARREÑO, F. L. & M. P. HERNÁNDEZ-CORTÉS, 1995. Proteasas digestives de la langostilla. — In: D. AURIOLES-GAMBOA & E. F. BALART (eds.), La langostilla: biología, ecología y aprovechamiento, pp. 207-219. (Centro de Investigaciones Biológicas del Noroeste, S.C., La Paz, Baja California.)

GARCÍA-GÓMEZ, J., 1983. Revision of *Iridopagurus* (Crustacea: Decapoda: Paguridae) with the descriptions of new species from American waters. — Bull. mar. Sci., **33**: 10-54.

GATEN, E., 1994. Geometrical optics of a galatheid compound eye. — J. comp. Physiol., (A) **175**: 749-759.

— —, 1998. Optics and phylogeny: is there an insight? The evolution of superposition eyes in the Decapoda (Crustacea). — Contrib. Zool., Amst., **67**: 223-235.

GHIRADELLA, H., J. CASE & J. CRONSHAW, 1968. Fine structure of the aesthetasc hairs of *Coenobita compressus* Edwards. — J. Morph., **124**: 361-386.

GLAESSNER, M. F., 1969. Decapoda. — In: R. C. MOORE (ed.), Treatise on Invertebrate Paleontology, Arthropoda (4), **R** (2): R399-R533. (Geological Society of America and University of Kansas Press, Lawrence.)

GORE, R. H., 1979. Larval development of *Galathea rostrata* under laboratory conditions, with a discussion of larval development in the Galatheidae (Crustacea Anomura). — Fish. Bull., U.S., **76**: 781-806.

GOULD, S. J., 1992. We are all monkeys' uncles. — Nat. Hist., **6**: 14-21.

GOVIND, C. K., 1992. Nervous system. — In: F. W. HARRISON & A. G. HUMES (eds.), Microscopic anatomy of invertebrates, **10**: 395-438. (Wiley-Liss, New York.)

GREENAWAY, P., 2003. Terrestrial adaptations in the Anomura (Crustacea: Decapoda). — In: R. LEMAITRE & C. C. TUDGE (eds.), Biology of the Anomura. Proceedings of a symposium at the Fifth International Crustacean Congress, Melbourne, Australia, 9-13 July 2001. Mem. Mus. Vict., **60**: 13-26.

GREENAWAY, P. & S. MORRIS, 1989. Adaptations to a terrestrial existence by the robber crab *Birgus latro*. III. Nitrogenous excretion. — J. exp. Biol., **143**: 333-346.

GREENAWAY, P., H. H. TAYLOR & S. MORRIS, 1990. Adaptations to a terrestrial existence by the robber crab *Birgus latro*. VI. The role of the excretory system in fluid balance. — J. exp. Biol., **152**: 505-519.

GREENWOOD, J. G., 1972. The male reproductive system and spermatophore formation in *Pagurus novae-zealandiae* (Dana) (Anomura: Paguridea). — J. nat. Hist., Lond., **6**: 561-574.

GUERAO, G., E. MACPHERSON, S. SAMADI, B. RICHER DE FORGES & M.-C. BOISSELIER, 2006. First stage zoeal descriptions of five Galatheoidea species from western Pacific (Crustacea: Decapoda: Anomura). — Zootaxa, **1227**: 1-29.

GUSEV, O. & Y. ZABOTIN, 2007. Observation of intersexuality in land hermit crabs (Anomura: Coenobitidae). — J. mar. biol. Ass. U.K., **87**: 1-4.

HAIG, J., 1974. A review of the Australian crabs of family Hippidae (Crustacea, Decapoda, Anomura). — Mus. Qld Mem., **17**: 175-189.

HALE, H. M., 1927-1929. The crustaceans of South Australia, parts I and II. — Pp. 1-380. (A. B. James, South Australia.)

HALL, S. & S. THATJE, 2009a. Global bottlenecks in the distribution of marine Crustacea: temperature constraints in the family Lithodidae. — J. Biogeogr., **36**: 2125-2135.

— — & — —, 2009b. Four new species of the family Lithodidae (Decapoda: Anomura) from the collections of the National Museum of Natural History, Smithsonian Institution. — Zootaxa, **2302**: 31-47.

HANSTRÖM, B., 1939. Hormones in invertebrates. — Pp. 1-198. (Oxford University Press, New York.)

HARTNOLL, R. G., 1988. Evolution, systematics, and geographical distribution. — In: W. W. BURGGREN & B. R. MCMAHON (eds.), Biology of the land crabs: 6-54. (Cambridge University Press, Cambridge.)

HARVEY, A. W., 1991. Biogeographic patterns of the Galápagos porcelain crab fauna. — In: M. J. JAMES (ed.), Galápagos marine invertebrates: taxonomy, biogeography and evolution in Darwin's islands, pp. 157-172. (Plenum Press, New York.)

— —, 1992. Abbreviated larval development in the Australian terrestrial hermit crab *Coenobita variabilis* McCulloch (Anomura: Coenobitidae). — J. Crust. Biol., **12**: 196-209.

HAZLETT, B. A., 1966. Social behavior of the Paguridae and Diogenidae of Curaçao. — Stud. Fauna Curaçao Caribb. Isl., **23**: 1-143.

HESS, G. S. & R. T. BAUER, 2002. Spermatophore transfer in the hermit crab *Clibanarius vittatus* (Crustacea, Anomura, Diogenidae). — J. Morph., **253**: 166-175.

HINSCH, G. W., 1991a. Ultrastructure of the sperm and spermatophores of the anomuran crab *Pleuroncodes planipes*. — J. Crust. Biol., **11**: 17-22.

— —, 1991b. Structure and chemical content of the spermatophores and seminal fluid of reptantian decapods. — In: R. T. BAUER & J. W. MARTIN (eds.), Crustacean sexual biology, pp. 290-307. (Columbia University Press, New York.)

HONG, S. Y. & M. H. KIM, 2002. Larval development of *Parapagurodes constans* (Decapoda: Anomura: Paguridae) reared in the laboratory. — J. Crust. Biol., **22**: 882-893.

ICELY, J. D. & J. A. NOTT, 1992. Digestion and absorption: digestive system and associated organs. — In: F. W. HARRISON & A. G. HUMES (eds.), Microscopic anatomy of invertebrates, **10**: 147-201. (Wiley-Liss, New York.)

IMAZU, M. & A. ASAKURA, 2006. Descriptions of agonistic, aggressive and sexual behaviors of five species of hermit crabs from Japan (Decapoda: Anomura: Paguridae and Diogenidae). — Crust. Res., (Spec. No.) **6**: 95-107.

INGLE, R. W., 1985. Northeastern Atlantic and Mediterranean hermit crabs (Crustacea: Anomura: Paguroidea: Paguridae). I. The genus *Pagurus* Fabricius, 1775. — J. nat. Hist., Lond., **19**: 745-769.

— —, 1993. Hermit crabs of the northeastern Atlantic Ocean and Mediterranean Sea: an illustrated key. — Pp. 1-495. (Chapman & Hall, London.)

JACKSON, H. G., 1913. *Eupagurus*. — Proc. Trans. L'pool biol. Soc., **27**: 493-573. [LMBC Memoirs, **21**.]

JAGT, J. W. M., B. W. M. VAN BAKEL, R. H. B. FRAAIJE & C. NEUMANN, 2006. In situ fossil hermit crabs (Paguroidea) from northeast Europe and Russia. Preliminary data on new records. — Rev. Mexic. Cien. geol., **23**: 364-369.

JAMIESON, B. G. M., 1991. Ultrastructure and phylogeny of crustacean spermatozoa. — Mem. Qld Mus., **31**: 109-142.

JAMIESON, B. G. M. & C. C. TUDGE, 2000. Crustacea – Decapoda. — In: B. G. M. JAMIESON (ed.), Reproductive biology of invertebrates, **10** (C, Progress in male gamete ultrastructure and phylogeny), pp. 1-95. (John Wiley & Sons, Chichester.)

KAMALAVENI, S., 1949. On the ovaries, copulation and egg formation in the hermit-crab, *Clibanarius olivaceus* Henderson (Crustacea, Decapoda). — J. zool. Soc. India, **1**: 120-128.

KAMITA, T., 1956. Studies on the decapod crustaceans of Corea, Part II. Hermit-crabs. (3). — Rep. Shimane Univ., **6**: 58-76.

KARASAWA, H., 2002. Fossil uncinidean and anomalan Decapoda (Crustacea) in the Kitakyushu Museum and Institute of Natural History. — Bull. Kitakyushu Mus. nat. Hist., **21**: 13-16.

KASHKINA, A. A. & N. I. KASHKIN, 1993. The Mexican red crab *Pleuroncodes planipes* Stimpson, 1860 (Galatheidae) as an intermediate trophic link in the upwelling ecosystem off California Peninsula. — Okeanol., **33**: 579-586.

KATO, T. & H. SUZUKI, 1992. Some biological observations of the mole crabs (Hippidae, Anomura, Decapoda, Crustacea) in Sagami Bay and the complete larval development of *Hippa truncatifrons* (Miers). — Rep. Manazuru mar. Lab. Sci. Ed., Fac. Ed., Yokohama natn. Univ., **8**: 77-97.

KILGOUR, M. & T. SHIRLEY, 2008. *Eumunida picta* S. I. Smith, 1883, and *Lophelia pertusa* (Linnaeus, 1758): a relationship or just good friends? — Crustaceana, **81** (5): 587-593.

KOLTZOFF, N. K., 1906. Studien über die Gestalt der Zelle. I. Untersuchungen über die Spermien der Decapoden, als Einleitung in das Problem der Zellengestalt. — Arch. mikroskop. anat. Entwickl., **67**: 364-572.

KONISHI, K. & H. TAISHAKU, 1994. Larval development of *Paralomis hystrix* (De Haan, 1846) (Crustacea, Anomura, Lithodidae) under laboratory conditions. — Bull. natn. Res. Inst. Aquacult., **22**: 43-54.

KROL, R. M., W. E. HAWKINS & R. M. OVERSTREET, 1992. Reproductive components. — In: F. W. HARRISON & A. G. HUMES (eds.), Microscopic anatomy of invertebrates, **10**: 295-343. (Wiley-Liss, New York.)

KRONENBERGER, K., D. BRANDIS, M. TÜRKAY & V. STORCH, 2004. Functional morphology of the reproductive system of *Galathea intermedia* (Decapoda: Anomura). — J. Morph., **262**: 500-516.

KUNZE, J. & D. T. ANDERSON, 1979. Functional morphology of the mouthparts and gastric mill in the hermit crabs *Clibanarius taeniatus* (Milne Edwards), *C. virescens* (Krauss), *Paguristes squamosus* McCulloch and *Dardanus setifer* (Milne Edwards) (Anomura: Paguridae). — Aust. J. mar. freshw. Res., **30**: 683-722.

KURUP, N. G., 1964. Incretory organs of the eyestalk and brain of the porcelain crab, *Petrolisthes cinctipes* Randall (Reptantia-Anomura). — Gen. comp. Endocrin., **4**: 99-112.

LE GUILLOUX, J., M. HALL-SPENCER, M. K. SÖFFKER & K. OLU, 2010. Association between the squat lobster *Gastroptychus formosus* and cold-water corals in the North Atlantic. — J. mar. biol. Ass. U.K., **90** (7): 1363-1369.

LEMAITRE, R., 1989. Revision of the genus *Parapagurus* (Anomura: Paguroidea: Parapaguridae), including redescriptions of the western Atlantic species. — Zool. Verh., Leiden, **253**: 1-106.

— —, 1990. A review of eastern Atlantic species of the family Parapaguridae (Decapoda, Anomura, Paguroidea). — J. nat. Hist., Lond., **24**: 219-240.

— —, 1994. Crustacea Decapoda: deep-water hermit crabs (Parapaguridae) from French Polynesia with descriptions of four new species. — In: A. CROSNIER (ed.), Résultats des campagnes MUSORSTOM, **12**. Mém. Mus. natn. Hist. nat., Paris, **161**: 375-419.

— —, 1995. A review of hermit crabs of the genus *Xylopagurus* A. Milne Edwards, 1880 (Crustacea: Decapoda: Paguridae), including descriptions of two new species. — Smithson. Contrib. Zool., **570**: 1-27.

— —, 1996. Hermit crabs of the family Parapaguridae (Crustacea: Decapoda: Anomura) from Australia: species of *Strobopagurus* Lemaitre, 1989, *Sympagurus* Smith, 1883 and two new genera. — Rec. Aust. Mus., **48**: 163-221.

— —, 1997. Crustacea Decapoda: Parapaguridae from the KARUBAR Cruise in Indonesia, with descriptions of two new species. — In: A. CROSNIER & P. BOUCHET (eds.), Résultats des campagnes MUSORSTOM, **16**. Mém. Mus. natn. Hist. nat., Paris, **172**: 573-596.

— —, 1999. Crustacea Decapoda: a review of the species of the genus *Parapagurus* Smith, 1879 (Parapaguridae) from the Pacific and Indian Oceans. — In: A. CROSNIER (ed.), Résultats des campagnes MUSORSTOM, **20**. Mém. Mus. natn. Hist. nat., Paris, **180**: 303-378.

— —, 2000. Superfamily Paguroidea, family Parapaguridae. — In: J. FOREST, M. DE SAINT LAURENT, P. A. MCLAUGHLIN & R. LEMAITRE (eds.), The marine fauna of New Zealand: Paguridea (Decapoda: Anomura), exclusive of the Lithodidae. NIWA Biodiv. Mem., **114**: 210-245.

— —, 2004. A worldwide review of hermit crab species of the genus *Sympagurus* Smith, 1883 (Crustacea: Decapoda: Parapaguridae). — In: B. MARSHALL & B. RICHER DE FORGES (eds.), Tropical deep-sea benthos, **23**. Mém. Mus. natn. Hist. nat., Paris, **191**: 85-149.

— —, 2006. Two new species of Parapaguridae (Crustacea, Decapoda, Anomura, Paguroidea) with subconical corneas, and new data on biology of some rare species. — Zoosystema, **28**: 517-532.

LEMAITRE, R. & P. A. MCLAUGHLIN, 1992. Descriptions of megalopa and juveniles of *Sympagurus dimorphus* (Studer, 1883), with an account of the Parapaguridae (Crustacea: Anomura: Paguroidea) from Antarctic and Subantarctic waters. — J. nat. Hist., Lond., **26**: 745-768.

— — & — —, 2003. New species of *Goreopagurus* (Decapoda: Anomura: Paguridae) from Tasmania and reevaluation of sexual tubes in hermit crab systematics. — Mem. Mus. Vict., **60**: 221-227.

— — & — —, 2009. Recent advances and conflicts in concepts of anomuran phylogeny (Crustacea: Malacostraca). — Arthrop. Syst. Phylog., **67**: 119-135.

LEMAITRE, R., P. A. MCLAUGHLIN & U. SORHANNUS, 2009. Phylogenetic relationships within the Pylochelidae (Decapoda: Anomura: Paguroidea): a cladistic analysis based on morphological characters. — Zootaxa, **2022**: 1-14.

LEMAITRE, R., C. C. TUDGE & P. A. MCLAUGHLIN, 2010. Preliminary study of the preungual process in the Paguroidea, with emphasis on the Paguridae (Crustacea: Decapoda: Anomura). — Nauplius, **18**: 13-23.

LE ROUX, A., 1968. Description d'organes mandibulaires nouveaux chez les Crustacés Décapodes. — C. R. Acad. Sci., Paris, (D) **266**: 1414-1417.

— —, 1974. Mise au point à propos de la distinction entre l'organe Y et l'organe mandibulaire chez les Crustacés eucarides. — C. R. Acad. Sci., Paris, (D) **278**: 1261-1264.

LIZARDO-DAUDT, H. M. & G. BOND-BUCKUP, 2003. Morphological aspects of the embryonic development of *Aegla platensis* (Decapoda, Aeglidae). — Crustaceana, **76**: 13-25.

LÖRZ, A.-N., H. GLENNER & J. LÜTZEN, 2008. New records of Rhizocephala (Cirripedia) from New Zealand, including the first rhizocephalan records from hot vents and cold seeps. — Crustaceana, **81**: 1013-1019.

LOVE, D. C. & T. C. SHIRLEY, 1993. Parasitism of the golden king crab, *Lithodes aequispinus* Benedict, 1895 (Decapoda, Anomura, Lithodidae) by a liparid fish. — Crustaceana, **65**: 97-104.

LOVRICH, G. A., M. A. CASALINUOVO, S. I. MOLINA, C. CÁRCAMO & R. PIEROTTI, 1998. Las langostillas *Munida subrugosa* y *M. gregaria* (Decapoda, Anomura) como potencial recurso económico patagónico. — Naturalia Patagónica, (Biol.) (Comodoro Rivadavia) **6**: 89-92.

MACDONALD, J. D., R. B. PIKE & D. I. WILLIAMSON, 1957. Larvae of the British species of *Diogenes*, *Pagurus*, *Anapagurus* and *Lithodes* (Crustacea, Decapoda). — Proc. zool. Soc., Lond., **128**: 209-257.

MACHORDOM, A. & E. MACPHERSON, 2004. Rapid radiation and cryptic speciation in squat lobsters of the genus *Munida* (Crustacea, Decapoda) and related genera in the south west Pacific: molecular and morphological evidence. — Mol. Phylogen. Evol., **33**: 259-279.

MACLEAY, W. S., 1838. Illustrations of the Annulosa of South Africa; being a portion of the objects of natural history chiefly collected during an expedition into the interior of South Africa, under the direction of Dr. Andrew Smith, in the years 1834, 1835, and 1836; fitted out by "The Cape of Good Hope Association for exploring Central Africa". — In: A. SMITH, Illustrations of the zoology of South Africa (Invertebrates), pp. 1-75. (Smith, Elder & Co., London.)

MACPHERSON, E., 1988. Revision of the family Lithodidae Samouelle, 1819 (Crustacea, Decapoda, Anomura) in the Atlantic Ocean. — Monogr. Zool. mar., **2**: 9-153.

MACPHERSON, E. & T.-Y. CHAN, 2008. Some lithodid crabs (Crustacea: Decapoda: Lithodidae) from Taiwan and adjacent waters, with the description of one new species from Guam. — Zootaxa, **1924**: 43-52.

MACPHERSON, E., W. JONES & M. SEGONZAC, 2005. A new squat lobster family of Galatheoidea (Crustacea, Decapoda, Anomura) from the hydrothermal vents of the Pacific-Antarctic Ridge. — Zoosystema, **27**: 709-723.

MACPHERSON, E., B. RICHER DE FORGES, K. SCHNABEL, K., S. SAMADI, M. C. BOISSELIER & A. GARCIA-RUBIES, 2009. Biogeography of the deep-sea galatheid squat lobsters of the Pacific Ocean. — Deep-Sea Res., (I) **57**: 228-238.

MAKAROV, V. V., 1938. Crustacea, Anomura. — Fauna SSSR, (n.s.) **16** (10): i-x, 1-324. (Zoologicheskii Institut Akademii Nauk SSSR, Leningrad [now St. Petersburg].) [In Russian.]

— —, 1962. Anomura. — Fauna of U.S.S.R., (Crustacea) **10** (3): 1-283. (Israel Program for Scientific Translations, Jerusalem.) [English translation of the original Russian version of V. V. Makarov, 1938.]

MANJÒN-CABEZA, M. E. & J. E. GARCIA RASO, 2000. Morphological reproductive aspects of males of *Diogenes pugilator* (Roux, 1829) (Crustacea, Decapoda, Anomura) from southern Spain. — Sarsia, **85**: 195-202.

MANTELATTO, F. L. M., L. M. PARDO, L. G. PILEGGI & D. L. FELDER, 2009 (cf. b). Taxonomic re-examination of the hermit crab species *Pagurus forceps* and *Pagurus comptus* (Decapoda: Paguridae) by molecular analysis. — Zootaxa, **2133**: 20-32.

MANTELATTO, F. L. M., R. ROBLES, R. BIAGI & D. L. FELDER, 2006. Molecular analysis of the taxonomic and distributional status for the hermit crab genera *Loxopagurus* Forest, 1964 and *Isocheles* Stimpson, 1858 (Decapoda, Anomura, Diogenidae). — Zoosystema, **28**: 495-506.

MANTELATTO, F. L. M., M. A. SCELZO & C. C. TUDGE, 2009 (cf. a). Morphological and morphometric appraisal of the spermatophore of the southern hermit crab *Isocheles sawayai* Forest & Saint Laurent, 1968 (Anomura: Diogenidae), with comments on gonopores in both sexes. — Zool. Anz., **248**: 1-8.

MARTIN, G. G. & J. E. HOSE, 1992. Vascular elements and blood (hemolymph). — In: F. W. HARRISON & A. G. HUMES (eds.), Microscopic anatomy of invertebrates, **10**: 295-343. (Wiley-Liss, New York.)

MARTIN, J. W. & L. G. ABELE, 1986. Phylogenetic relationships of the genus *Aegla* (Decapoda: Anomura: Aeglidae), with comments on anomuran phylogeny. — J. Crust. Biol., **6**: 576-616.

— — & — —, 1988. External morphology of the genus *Aegla* (Crustacea: Anomura: Aeglidae). — Smithson. Contrib. Zool., **453**: 1-46.

MARTIN, J. W. & G. E. DAVIS, 2001. An updated classification of the Recent Crustacea. — Nat. Hist. Mus. LA County, (Sci. Ser.) **39**: 1-124.

MATTHEWS, D. C., 1953. The development of the pedunculate spermatophore of a hermit crab, *Dardanus asper* (De Haan). — Pacif. Sci., **7**: 255-266.

— —, 1956a. The origin of the spermatophoric mass of the sand crab, *Hippa pacifica*. — Q. J. microsc. Sci., **97**: 257-268.

— —, 1956b. The probable method of fertilization in terrestrial hermit crabs based on a comparative study of spermatophores. — Pacif. Sci., **10**: 303-309.

— —, 1959. Observations on ova fixation in the hermit crab *Eupagurus prideauxii*. — Pubbl. Staz. zool. Napoli, **31**: 248-263.

MCGAW, I. J., 2005. The decapod crustacean circulatory system. A case that is neither open nor closed. — Microsc. Microanal., **11**: 18-36.

MCGAW, I. J. & S. D. DUFF, 2008. Cardiovascular system of anomuran crabs, genus *Lopholithodes*. — J. Morph., **269**: 1295-1307.

MCLAUGHLIN, P. A., 1974. The hermit crabs (Crustacea, Decapoda, Paguridea) of northwestern North America. — Zool. Verh., Leiden, **130**: 1-396.

— —, 1980. Comparative morphology of recent Crustacea. — Pp. i-xiv, 1-177. (W. H. Freeman & Cy, San Francisco.)

— —, 1982. Revision of *Pylopagurus* and *Tomopagurus* (Crustacea: Decapoda: Paguridae), with the description of new genera and species: part III. *Agaricochirus* McLaughlin, *Enallopagurus* McLaughlin, and *Enallopaguropsis* McLaughlin. — Bull. mar. Sci., **32**: 823-855.

— —, 1983a. A review of the phylogenetic position of the Lomidae (Crustacea: Decapoda: Anomala). — J. Crust Biol., **3**: 431-437.

— —, 1983b. Hermit crabs – are they really polyphyletic? — J. Crust. Biol., **3**: 608-621.

— —, 1983c. Internal anatomy. — In: L. H. MANTEL (ed.), The biology of Crustacea, **5**, Internal anatomy and physiological regulation, pp. 1-52. (Academic Press, New York.)

— —, 1997. Crustacea Decapoda: hermit crabs of the family Paguridae from the KARUBAR cruise in Indonesia. — In: A. CROSNIER & P. BOUCHET (eds.), Résultats des campagnes MUSORSTOM, 16. Mem. Mus. natn. Hist. nat., Paris, **172**: 433-572.

— —, 2000. Crustacea: Decapoda: species of *Porcellanopagurus* Filhol and *Solitariopagurus* Türkay (Paguridae), from the New Caledonia area, Vanuatu, and the Marquesas: new records, new species. — In: A. CROSNIER (ed.), Résultats des campagnes MUSORSTOM, 21. Mem. Mus. natn. Hist. nat., Paris, **184**: 389-414.

— —, 2002. A review of the hermit-crab (Decapoda: Anomura: Paguridea) fauna of southern Thailand, with particular emphasis on the Andaman Sea, and descriptions of three new species. — Phuket mar. Biol. Centr. spec. Publ., **23**: 385-460.

— —, 2003. Illustrated keys to families and genera of the superfamily Paguroidea (Crustacea: Decapoda: Anomura), with diagnoses of genera of Paguridae. — In: R. LEMAITRE & C. C. TUDGE (eds.), Biology of the Anomura. Proceedings of a symposium at the Fifth International Crustacean Congress, Melbourne, Australia, 9-13 July 2001. Mem. Mus. Vict., **60**: 111-144.

MCLAUGHLIN, P. A. & J. FOREST, 1999. Hermit crabs of the genus *Pagurus* Fabricius (Crustacea, Decapoda, Paguridae) from south-eastern South Africa. — Ann. S. Afr. Mus., **105**: 297-344.

MCLAUGHLIN, P. A. & J. HAIG, 1984. A review of *Pagurixus* (Decapoda, Anomura, Paguridae) and descriptions of new species. — Crustaceana, **47**: 121-148.

MCLAUGHLIN, P. A. & P. J. HOGARTH, 1998. Hermit crabs (Decapoda: Anomura: Paguridea) from the Seychelles. — Zool. Verh., Leiden, **318**: 1-48.

MCLAUGHLIN, P. A. & L. B. HOLTHIUS, 1985. Anomura versus Anomala. — Crustaceana, **49**: 204-209.

MCLAUGHLIN, P. A. & R. LEMAITRE, 1993. A review of the hermit crab genus *Paguritta* (Decapoda: Anomura: Paguridae) with descriptions of three new species. — Raffl. Bull. Zool., **41**: 1-29.

— — & — —, 1997. Carcinization – fact or fiction? I. Evidence from adult morphology. — Contrib. Zool., Amst., **67**: 79-123.

— — & — —, 2001. A new family for a new genus and new species of hermit crab of the superfamily Paguroidea (Decapoda: Anomura) and its phylogenetic implications. — J. Crust. Biol., **21**: 1062-1076.

— — & — —, 2008. Larvae of two species of *Trizocheles* (Decapoda: Anomura: Paguroidea: Pylochelidae: Trizochelinae), description of the adult of one, and preliminary implications of development on pylochelid phylogeny. — Zootaxa, **1911**: 52-68.

— — & — —, 2009. A new classification of the Pylochelidae (Decapoda: Anomura: Paguroidea) and descriptions of new taxa. — Raffl. Bull. Zool., (Suppl.) **20**: 159-231.

MCLAUGHLIN, P. A., R. LEMAITRE & U. SORHANNUS, 2007 (cf. a). Hermit crab phylogeny: a reappraisal and its "fall-out". — J. Crust. Biol., **27**: 97-115.

MCLAUGHLIN, P. A. & T. MURRAY, 1990. *Clibanarius fonticola*, new species (Anomura, Paguridea: Diogenidae), from a freshwater pool on Espiritu Santo, Vanuatu (South Pacific Ocean). — J. Crust. Biol., **10**: 695-702.

MCLAUGHLIN, P. A., D. L. RAHAYU, T. KOMAI & T. Y. CHAN, 2007 (cf. b). A catalog of the hermit crabs (Paguroidea) of Taiwan. — Pp. 1-365. (National Taiwan Ocean University, Keelung.)

MCLAUGHLIN, P. A. & M. DE SAINT LAURENT, 1998. A new genus for four species of hermit crabs formerly assigned to the genus *Pagurus* Fabricius (Decapoda: Anomura: Paguridae). — Proc. biol. Soc. Wash., **111**: 158-187.

MEISS, D. E. & R. S. NORMAN, 1977a. A comparative study of the stomatogastric system of several decapod Crustacea. I. Skeleton. — J. Morph., **152**: 21-54.

— — & — —, 1977b. A comparative study of the stomatogastric system of several decapod Crustacea. II. Musculature. — J. Morph., **152**: 55-75.

MELLON, D., JR., 1992. Connective tissue and supporting structures. — In: F. W. HARRISON & A. G. HUMES (eds.), Microscopic anatomy of invertebrates, **10**: 77-116. (Wiley-Liss, New York.)

MEYER-ROCHOW, V. B., D. TOWERS & I. ZIEDINS, 1990. Growth patterns in the eye of *Petrolisthes elongatus* (Crustacea; Decapoda; Anomura). — Exp. Biol., **48**: 329-340.

MILNE-EDWARDS, A. & E.-L. BOUVIER, 1894. La famille des Galathéidés. — Ann. Sci. nat., (Zool., 7) **26**: 191-327.

MIYAKE, S., 1978. The crustacean Anomura of Sagami Bay. — Pp. 1-201. (Biol. Lab. Imperial Household, Tokyo.)

— —, 1982. Anomura. — In: T. UCHIDA (ed.), New illustrated encyclopedia of the fauna of Japan, pp. 630-652. (Hokuryukan, Tokyo.)

MIYAWAKI, M., 1955. Observations on the pericardial organ in two kinds of crabs, *Paralithodes brevipes* Brandt and *Telmessus cheiragonus* Tilesius. — Zool. Mag., Tokyo, **64**: 137-140.

MONTAGNE, N., D. SOYEZ, D. GALLOIS, L. OLLIVAUX & J.-Y. TOULLEC, 2008. New insights into evolution of crustacean hyperglycaemic hormone in decapods – first characterization in Anomura. — FEBS [Fed. Soc. Biochem. mol. Biol.] J., **275**: 1039-1052.

MORADMAND, M. & A. SARI, 2007. Littoral hermit crabs (Decapoda: Anomura: Paguroidea) from the Gulf of Oman, Iran. — Iranian J. Anim. Biosyst., **3**: 25-36.

MORRIS, S., 2001. Neuroendocrine regulation of osmoregulation and evolution of air-breathing in decapod crustaceans. — J. exp. Biol., **204**: 979-989.

MORRIS, S., P. GREENAWAY, A. M. ADAMCZEWSKA & M. D. AHERN, 2000. Adaptations to a terrestrial existence by the robber crab *Birgus latro*. IX. Hormonal control of post-renal urine reprocessing and salt balance in the branchial chamber. — J. exp. Biol., **203**: 389-396.

MORRISON, C. L., A. W. HARVEY, S. LAVERY, K. TIEU, Y. HUANG & C. W. CUNNINGHAM, 2002. Mitochondrial gene rearrangements confirm the parallel evolution of the crab-like body form. — Proc. Roy. Soc., Lond., **269**: 345-350.

MORRONE, J. J. & E. C. LOPRETTO, 1994. Distributional patterns of freshwater Decapoda (Crustacea: Malacostraca) in southern South America: a panbiogeographic approach. — J. Biogeogr., **21**: 97-109.

— — & — —, 1995. Parsimony analysis of freshwater Decapoda (Crustacea: Malacostraca) from southern South America. — Neotrópica, **41**: 3-8.

MOUCHET, S., 1930. Mode de formation des spermatophores chez quelques Pagures. — C. R. Acad. Sci., Paris, **190**: 691-692.

— —, 1931. Spermatophores des Crustacés Décapodes Anomoures et Brachyoures et castration parasitaire chez quelques Pagures. — Stat. océanogr. Salammbô, Ann., **6**: 1-203.

MYKLEBUST, R. & A. TJONNELAND, 1975. The membrane system of the cardiac muscle cell in *Munida tenuimana* G. O. Sars (Crustacea, Decapoda). — Cell Tiss. Res., **159**: 339-349.

NAKASONE, Y., 1988. Land hermit crabs from the Ryukyus, Japan, with a description of a new species from the Philippines (Crustacea, Decapoda, Coenobitidae). — Zool. Sci., **5**: 165-178.

NGOC-HO, N., 1984. The functional anatomy of the foregut of *Porcellana platycheles* and a comparison with *Galathea squamifera* and *Upogebia deltaura* (Crustacea: Decapoda). — J. Zool., Lond., **203**: 511-535.

NILSSON, D.-E., 1988. A new type of imaging optics in compound eyes. — Nature, Lond., **332**: 161-165.

— —, 1990. Three unexpected cases of refracting superposition eyes in crustaceans. — J. comp. Physiol., (A) **167**: 71-78.

ORTMANN, A. E., 1896. Die geographische Verbreitung der Decapodengruppe der Hippidea. — Zool. Jahrb., (Syst. Geogr. Biol. Tier.) **9**: 219-243.

— —, 1902. The geographical distribution of freshwater decapods and its bearing upon ancient geography. — Proc. Am. Philos. Soc., Philadelphia, **41**: 267-400.

OSAWA, M. & T.-Y. CHAN, 2010. Part III. Porcellanidae (porcelain crabs). — In: T.-Y. CHAN, (ed.), Crustacean fauna of Taiwan: crab-like anomurans (Hippoidea, Lithodoidea, Porcellanidae), pp. 67-181. (National Taiwan Ocean University, Keelung.)

OTTO, R. S., 2006. A review of worldwide fisheries for lithodid crabs (Decapoda: Anomura: Lithodidae) and their fluctuations. — In: A. ASAKURA (ed.), Biology of the Anomura II. Crust. Res., (Spec. Nr.) **6**: 167-185.

OTTO, R. S. & R. A. MACINTOSH, 2006. Biology of the deep-water crab *Paralomis spinosissima* (Decapoda: Anomura: Lithodidae) near South Georgia Island, South Atlantic. — In: A. ASAKURA (ed.), Biology of the Anomura II. Crust. Res., (Spec. Nr.) **6**: 187-197.

PATWARDHAN, S. S., 1935. On the structure and mechanism of the gastric mill in Decapoda. III. Structure of the gastric mill in Anomura. — Proc. Indian Acad. Sci., (B) **1**: 405-413.

PAUL, D. H., 1989. A neurophylogenist's view of decapod Crustacea. — Bull. mar. Sci., **45**: 487-504.

— —, 1991. Pedigrees of neurobehavioral circuits: tracing the evolution of novel behaviors by comparing motor patterns, muscles, and neurons in members of related taxa. — Brain Behav. Evol., **38**: 226-239.

— —, 2003. Neurobiology of the Anomura: Paguroidea, Galatheoidea and Hippoidea. — In: R. LEMAITRE & C. C. TUDGE (eds.), Biology of the Anomura. Proceedings of a symposium at the Fifth International Crustacean Congress, Melbourne, Australia, 9-13 July 2001. Mem. Mus. Vict., **60**: 3-11.

PAUL, D. H., A. M. THEN & D. S. MAGNUSON, 1985. Evolution of the telson neuromusculature in decapod Crustacea. — Biol. Bull., Woods Hole, **168**: 106-124.

PÉREZ-LOSADA, M., G. BOND-BUCKUP, C. G. JARA & K. A. CRANDALL, 2004. Molecular systematics and biogeography of the southern South American freshwater "crabs" *Aegla* (Decapoda: Anomura: Aeglidae) using multiple heuristic tree search approaches. — Syst. Biol., **53**: 767-780.

PÉREZ-LOSADA, M., C. G. JARA, G. BOND-BUCKUP, M. L. PORTER & K. A. CRANDALL, 2002. Phylogenetic position of the freshwater anomuran family Aeglidae. — J. Crust. Biol., **22**: 670-676.

PETTIBONE, M. H., 1963. Marine polychaete worms of the New England region: I. Families Aphroditidae through Trochochaetidae. — Bull. U.S. natl. Mus., **227** (1): 1-356.

PIKE, B. R., 1947. *Galathea*. Memoirs on Typical British Marine Plants and Animals. — L'pool mar. biol. Cttee, **34**: 1-138.

PILGRIM, R. L. C., 1965. Some features in the morphology of *Lomis hirta* (Lamarck) (Crustacea: Decapoda) and a discussion of its systematic position and phylogeny. — Aust. J. Zool., **13**: 545-557.

— —, 1973. Axial skeleton and musculature in the thorax of the hermit crab, *Pagurus bernhardus* (Anomura: Paguridae). — J. mar. biol. Assoc. U.K., **53**: 363-396.

POORE, G. C. B., 2004. Marine decapod Crustacea of southern Australia: a guide to identification. — Pp. 1-574. (CSIRO Publishing, Collingwood.)

PORTER, M. L. & T. W. CRONIN, 2009. A shrimp's eye view of evolution: how useful are visual characters in decapod phylogenetics? — In: J. W. MARTIN, K. A. CRANDALL & D. L. FELDER (eds.), Decapod crustacean phylogenetics. Crust. Iss., **18**: 181-195. (CRC Press, Taylor & Francis Group, Boca Raton, Florida.)

PORTER, M. L., M. PÉREZ-LOSADA & K. A. CRANDALL, 2005. Model-based multi-locus estimation of decapod phylogeny and divergence times. — Mol. Phylog. Evol., **37**: 355-369.

POUPIN, J., 1997. Les pagures du genre *Calcinus* en Polynésie française avec la description de trois nouvelles espèces (Decapoda, Anomura, Diogenidae). — Zoosystema, **19**: 683-719.

POUPIN, J., C. B. BOYKO & G. L. GUZMÁN, 2003. *Calcinus* hermit crabs from Easter Island, with biogeographic considerations (Crustacea: Anomura: Diogenidae). — In: R. LEMAITRE & C. C. TUDGE (eds.), Biology of the Anomura. Proceedings of a symposium at the Fifth International Crustacean Congress, Melbourne, Australia, 9-13 July 2001. Mem. Mus. Vict., **60**: 91-97.

POUPIN, J. & R. LEMAITRE, 2003. Hermit crabs of the genus *Calcinus* Dana, 1851 (Decapoda: Anomura: Diogenidae) from the Austral Islands, French Polynesia, with description of a new species. — Zootaxa, **391**: 1-20.

POUPIN, J. & P. A. MCLAUGHLIN, 1998. Additional records of *Calcinus* species (Decapoda: Anomura: Diogenidae) from French Polynesia with description of three new species and a key to Indo-West Pacific species of the genus. — Crust. Res., **27**: 9-27.

RAHAYU, D. L., 2000. Hermit crabs from the South China Sea (Crustacea: Decapoda: Anomura: Diogenidae, Paguridae, Parapaguridae). — Raffl. Bull. Zool., (Suppl.) **8**: 377-404.

RAHAYU, D. L. & J. FOREST, 1992. Le genre *Clibanarius* (Crustacea, Decapoda, Diogenidae) en Indonésie, avec la description de six espèces nouvelles. — Bull. Mus. natl. Hist. nat., Paris, (4) **14**: 539-552.

— — & — —, 1994 [1995]. Le genre *Diogenes* (Decapoda, Anomura, Diogenidae) en Indonésie, avec la description de six espèces nouvelles. — Bull. Mus. natl. Hist. nat., Paris, (4) **16**: 383-415.

RATHNAVATHY, C. K., 1941. The spermatogenesis of *Clibanarius olivaceus* Henderson. — Proc. Indian Acad. Sci., (B) **13**: 379-421.

REESE, E. S. & R. A. KINZIE, 1968. The larval development of the coconut or robber crab *Birgus latro* (L.) in the laboratory (Anomura, Paguridae). — Crustaceana, (Suppl.) **2**: 117-144.

RICHTER, S., 2002. Evolution of optical design in the Malacostraca (Crustacea). — In: K. WIESE (ed.), The crustacean nervous system, pp. 512-524. (Springer Verlag, Heidelberg, Berlin, etc.)

RICHTER, S. & G. SCHOLTZ, 1994. Morphological evidence for a hermit crab ancestry of lithodids (Crustacea, Decapoda, Anomala, Paguroidea). — Zool. Anz., **223**: 187-219.

ROA, R. & R. BAHAMONDE, 1993. Growth and expansion of an exploited population of the squat lobster (*Pleuroncodes monodon*) after 3 years without harvesting. — Fish. Res., **18**: 305-319.

RODRÍGUEZ, I. T., G. HERNÁNDEZ & D. L. FELDER, 2006. Phylogenetic relationships among western Atlantic Porcellanidae (Decapoda: Anomura), based on partial sequences of the mitochondrial 16S rRNA gene, with comments on morphology. — In: A. ASAKURA (ed.), Biology of the Anomura II. Crust. Res., (Spec. Nr.) **6**: 151-166.

ROWDEN, A. A., K. E. SCHNABEL, T. A. SCHLACHER, E. MACPHERSON, S. T. AHYONG & B. RICHER DE FORGES, 2010. Squat lobster assemblages on seamounts differ from some, but not all, deep-sea habitats of comparable depth. — Mar. Ecol., **31**: 63-83.

SAINT LAURENT, M. DE, 1972. Sur la famille des Parapaguridae Smith, 1882. Description de *Typhlopagurus foresti* gen. nov., sp. nov., et de quinze espèces ou sous-espèces nouvelles de *Parapagurus* Smith (Crustacea, Decapoda). — Bijdr. Dierk., Amst., **42**: 97-123.

SAINT LAURENT, M. DE & P. A. MCLAUGHLIN, 2000. Superfamily Paguroidea, family Paguridae. — In: J. FOREST, M. DE SAINT LAURENT, P. A. MCLAUGHLIN & R. LEMAITRE (eds.), The marine fauna of New Zealand: Paguridea (Decapoda: Anomura), exclusive of the Lithodidae. NIWA Biodiv. Mem., **114**: 104-209.

SAINT LAURENT-DECHANCE, M. DE, 1966. Remarques sur la classification de la famille des Paguridae et sur la position systématique d'*Iridopagurus* de Saint Laurent. Diagnose d'*Anapagurides* gen. nov. — Bull. Mus. natn. Hist. nat., Paris, (2) **38**: 257-265.

SAMUELSEN, T. J., 1972. Larvae of *Munidopsis tridentata* (Esmark) (Decapoda, Anomura) reared in the laboratory. — Sarsia, **48**: 91-98.

SANDBERG, L. & P. A. MCLAUGHLIN, 1998. Crustacea, Decapoda, Paguridea. — Mar. Invert. Scandinavia, **10**: 1-115. (Universitetsforlaget, Oslo.)

SANDEMAN, D. C., 1982. Organization of the central nervous system. — In: H. L. ATWOOD & D. C. SANDEMAN (eds.), The biology of Crustacea, **3**: 1-61. (Academic Press, New York.)

SANDEMAN, D. C., G. SCHOLTZ & R. E. SANDEMAN, 1993. Brain evolution in decapod Crustacea. — J. exp. Zool., **265**: 112-133.

SCELZO, M. A., M. Z. FANTUCCI & F. L. MANTELATTO, 2010. Spermatophore and gonopore morphology of the southwestern-Atlantic hermit crab *Pagurus exilis* (Benedict, 1892) (Anomura, Paguridae). — Zool. Stud., **49**: 421-433.

SCELZO, M. A., F. L. MANTELATTO & C. C. TUDGE, 2004. Spermatophore morphology of the endemic hermit crab *Loxopagurus loxochelis* (Anomura, Diogenidae) from southwestern Atlantic – Brazil and Argentina. — Invert. Repr. Dev., **46**: 1-9.

SCHAEFER, N., 1970. The functional morphology of the foregut of three species of decapod Crustacea: *Cyclograpsus punctatus* Milne Edwards, *Diogenes brevirostris* Stimpson, and *Upogebia africana* (Ortmann). — Zool. Soc. S. Afr., **5**: 309-326.

SCHILLER, C., D. R. FIELDER, I. W. BROWN & A. OBED, 1991. Reproduction, early life-history and recruitment. — In: I. W. BROWN & D. R. FIELDER (eds.), The coconut crab: aspects of the biology and ecology of *Birgus latro* in the Republic of Vanuatu, pp. 13-33. (ACIAR, Canberra.)

SCHMITT, W., 1942. The species of *Aegla*, endemic South American fresh-water crustaceans. — Proc. U.S. natn. Mus., **91**: 431-520.

SCHNABEL, K. E. & S. T. AHYONG, 2010. A new classification of the Chirostyloidea (Crustacea: Decapoda: Anomura). — Zootaxa, **2687**: 56-64.

SCHNABEL, K. E., S. T. AHYONG & E. W. MAAS, 2011. Galatheoidea are not monophyletic – molecular and morphological phylogeny of the squat lobsters (Decapoda: Anomura) with recognition of a new superfamily. — Mol. Phylog. Evol., **58**: 157-168.

SCHNABEL, K. [E.] & A. CONNELL, 2007. Lobster à la carte. — Water Atmosph., **15** (4): 16-17.

SCHOLTZ, G. & S. RICHTER, 1995. Phylogenetic systematics of the reptantian Decapoda (Crustacea, Malacostraca). — Zool. J. Linn. Soc. Lond., **113**: 289-328.

SCHRAM, F. R., 1982. The fossil record and evolution of Crustacea. — In: L. G. ABELE (ed.), The biology of Crustacea, **1**: 93-147. (Academic Press, New York.)

— —, 2001. Phylogeny of decapods: moving towards a consensus. — Hydrobiologia, **449**: 1-20.

SCHWEITZER, C. E. & R. M. FELDMANN, 2000. First notice of the Chirostylidae (Decapoda) in the fossil record and new Tertiary Galatheidae (Decapoda) from the Americas. — Bull. Mizunami Foss. Mus., **27**: 147-165.

— — & — —, 2005. Decapod crustaceans, the K/P event, and Palaeocene recovery. — In: J. KOENEMANN & R. A. JENNER (eds.), Crustacea and arthropod relationships. Crust. Iss., **16**: 17-53. (CRC Press, Taylor & Francis Group, Boca Raton, Florida.)

SCHWEITZER, C. E., G. GONZÁLEZ-BARBA, R. M. FELDMANN & D. A. WAUGH, 2005. Decapoda (Thalassinidea and Paguroidea) from the Eocene Bateque and Tepetate formations, Baja California Sur, México: systematics, cuticle microstructure, and paleoecology. — Ann. Carnegie Mus., **74**: 275-293.

SIDDIQUI, F. A., Q. B. KAZMI & P. A. MCLAUGHLIN, 2004. Review of the Pakistani species of *Diogenes* Dana, 1851 (Decapoda Anomura Paguroidea Diogenidae). — Trop. Zool., **17**: 155-200.

SNODGRASS, R. E., 1952. The sand crab *Emerita talpoida* (Say) and some of its relatives. — Smithson. misc. Coll., **117**: 1-34.

SOMERTON, D. S. & W. DONALDSON, 1998. Parasitism of the golden king crab, *Lithodes aequispinus*, by two species of snailfish, genus *Careproctus*. — Fish. Bull., U.S., **96**: 871-884.

SPEARS, T. & L. G. ABELE, 1988. Phylogenetic relationships of crustacean anomurans based on partial 18s rRNA nucleotide sequences. — Am. Zool., **29**: 25A.

SPEARS, T., L. G. ABELE & W. KIM, 1992. The monophyly of brachyuran crabs: a phylogenetic study based on 18S rRNA. — Syst. Biol., **41**: 446-461.

STACHOWITSCH, M., 1980. The epibiotic and endolithic species associated with the gastropod shells inhabited by the hermit crabs *Paguristes oculatus* and *Pagurus cuanensis*. — Pubbl. Staz. zool. Napoli, (I, Mar. Ecol.) **1**: 73-101.

STENSMYR, M. C., S. ERLAND, E. HALLBERG, R. WALLÉN, P. GREENAWAY & B. S. HANSSON, 2005. Insect-like olfactory adaptations in the terrestrial giant robber crab. — Curr. Biol., **15**: 116-121.

STUCK, K. C. & F. M. TRUESDALE, 1986. Larval and early postlarval development of *Lepidopa benedicti* Schmitt, 1935 (Anomura: Albuneidae) reared in the laboratory. — J. Crust. Biol., **6**: 89-110.

SUBRAMANIAM, M. K., 1935. Oogenesis of *Clibanarius olivaceus* (Henderson), with special reference to a seasonal variation in the cytoplasmic inclusions. — J. Roy. microsc. Soc. Lond., **55**: 12-27.

SUBRAMONIAM, T., 1984. Spermatophore formation in two intertidal crabs *Albunea symnista* and *Emerita asiatica* (Decapoda: Anomura). — Biol. Bull., Woods Hole, **166**: 78-95.

— —, 1991. Chemical composition of spermatophores in decapod crustaceans. — In: R. T. BAUER & J. W. MARTIN (eds.), Crustacean sexual biology, pp. 308-321. (Columbia University Press.)

TAM, Y. K., I. KORNFIELD & F. P. OJEDA, 1996. Divergence and zoogeography of mole crabs, *Emerita* spp. (Decapoda: Hippidae), in the Americas. — Mar. Biol., Berl., **125**: 489-497.

TAPELLA, F. & G. A. LOVRICH, 2006. Morphological differences between '*subrugosa*' and '*gregaria*' morphs of adult *Munida* (Decapoda: Anomura: Galatheidae) from the Beagle Channel, southern South America. — J. mar. biol. Ass. U.K., **86**: 1149-1155.

TEROSSI, M., L. S. TORATI, I. MIRANDA, M. A. SCELZO & F. L. MANTELATTO, 2010. Comparative reproductive biology of two southwestern Atlantic populations of the hermit crab *Pagurus exilis* (Crustacea: Anomura: Paguridae). — Mar. Ecol., **2010**: 1-8.

THATJE, S., K. ANGER, J. A. CALCAGNO, G. A. LOVRICH, H.-O. PORTNER & W. E. ARNTZ, 2005. Challenging the cold: crabs reconquer the Antarctic. — Ecol., **86**: 619-625.

THATJE, S. & W. E. ARNTZ, 2004. Antarctic reptant decapods: more than a myth? — Polar Biol., **27**: 195-201.

THATJE, S., S. HALL, C. HAUTON, C. HELD & P. TYLER, 2008. Encounter of lithodid crab *Paralomis birsteini* on the continental slope of Antarctica. — Polar Biol., **31**: 1143-1148.

THATJE, S. & A.-N. LÖRZ, 2005. First record of lithodid crabs from Antarctic waters off the Balleny Islands. — Polar Biol., **28**: 334-337.

TIRELLI, T., E. CAMPANTICO, D. PESSANI & C. C. TUDGE, 2006. Description of the male reproductive apparatus of the hermit crab *Calcinus tubularis* (Decapoda: Anomura: Diogenidae). — In: A. ASAKURA (ed.), Biology of the Anomura II. Crust. Res., (Spec. Nr.) **6**: 13-21.

TIRELLI, T. & D. PESSANI, 2007. Multivariate analysis: a useful tool in separating spermatophores produced by the diogenids, *Clibanarius erythropus*, *Diogenes pugilator*, and *Calcinus tubularis* (Decapoda, Anomura, Diogenidae). — Crustaceana, **80**: 999-1011.

TIRELLI, T., D. PESSANI, D. SILVESTRO & C. C. TUDGE, 2008. Reproductive biology of Mediterranean hermit crabs: fine structure of spermatophores and spermatozoa of *Diogenes pugilator* (Decapoda: Anomura) and its bearing on a sperm phylogeny of Diogenidae. — J. Crust. Biol., **28**: 535-543.

TIRELLI, T., D. SILVESTRO, D. PESSANI & C. C. TUDGE, 2010. Description of the male reproductive system of *Paguristes eremita* (Anomura, Diogenidae) and its placement in a phylogeny of diogenid species based on spermatozoa and spermatophore ultrastructure. — Zool. Anz., **248**: 299-312.

TOON, A., M. FINLEY, J. STAPLES & K. A. CRANDALL, 2009. Decapod phylogenetics and molecular evolution. — In: J. W. MARTIN, K. A. CRANDALL & D. L. FELDER (eds.), Decapod crustacean phylogenetics. Crust. Iss., **18**: 15-29. (CRC Press, Taylor, & Francis Group, Boca Raton, Florida.)

TORATI, L. S. & F. L. [M.] MANTELATTO, 2008. Uncommon mechanism of egg incubation in the endemic southern hermit crab *Loxopagurus loxochelis*: how is this phenomenon related to egg production? — Acta Zool., Stockh., **89**: 79-85.

TSANG, L. M., T. Y. CHAN, S. T. AHYONG & K. H. CHU, 2011. Hermit to king, or hermit to all: multiple transitions to crab-like forms from hermit crab ancestors. — Syst. Biol., **60**: 616-629.

TSANG, L. M., K. Y. MA, S. T. AHYONG, T.-Y. CHAN & K. H. CHU, 2008. Phylogeny of Decapoda using two nuclear protein-coding genes: origin and evolution of the Reptantia. — Mol. Phylog. Evol., **48**: 359-368.

TUDGE, C. C., 1991. Spermatophore diversity within and among the hermit crab families, Coenobitidae, Diogenidae and Paguridae (Paguroidea, Anomura, Decapoda). — Biol. Bull., Woods Hole, **181**: 238-247.

— —, 1997. Phylogeny of the Anomura (Decapoda, Crustacea): spermatozoa and spermatophore morphological evidence. — Contrib. Zool., Amst., **67**: 125-141.

— —, 1999. Spermatophore morphology in the hermit crab families Paguridae and Parapaguridae (Paguroidea, Anomura, Decapoda). — Invert. Repr. Dev., **35**: 203-214.

— —, 2009. Spermatozoal morphology and its bearing on decapod phylogeny. — In: J. W. MARTIN, K. A. CRANDALL & D. L. FELDER (eds.), Decapod crustacean phylogenetics. Crust. Iss., **18**: 101-119. (CRC Press, Taylor & Francis Group, Boca Raton, Florida.)

TUDGE, C. C. & B. G. M. JAMIESON, 1996a. Spermatophore and spermatozoal morphology in the Porcellanidae. I. *Aliaporcellana suluensis* and *Pisidia longicornis* (Decapoda, Anomura, Porcellanidae). — Crust. Res., **25**: 73-85.

— — & — —, 1996b. Spermatophore and spermatozoal morphology in the Porcellanidae. II. The genera *Petrolisthes* and *Polyonyx* (Decapoda, Anomura, Porcellanidae). — J. Crust. Biol., **16**: 535-546.

TUDGE, C. C. & R. LEMAITRE, 2004. Studies of male sexual tubes in hermit crabs (Crustacea, Decapoda, Anomura, Paguroidea). I. Morphology of the sexual tube in *Micropagurus acantholepis* (Stimpson, 1858), with comments on function and evolution. — J. Morph., **259**: 106-118.

— — & — —, 2006. Studies of male sexual tubes in hermit crabs (Crustacea, Decapoda, Anomura, Paguroidea). II. Morphology of the sexual tube in the land hermit crabs, *Coenobita perlatus* and *C. clypeatus* (Coenobitidae). — In: A. ASAKURA (ed.), Biology of the Anomura II. Crust. Res., (Spec. Nr.) **6**: 121-131.

TUDGE, C. C. & D. M. SCHELTINGA, 2002. Spermatozoal morphology of the freshwater anomuran *Aegla longirostris* Bond-Buckup & Buckup, 1994 (Crustacea: Decapoda: Aeglidae) from South America. — Proc. biol. Soc. Wash., **115**: 118-128.

TURRA, A., 2004. Intersexuality in hermit crabs: reproductive role and fate of gonopores in intersex individuals. — J. mar. biol. Ass. U.K., **84**: 757-759.

— —, 2005. Reproductive behavior of intertidal hermit crabs (Decapoda, Anomura) in southeastern Brazil. — Rev. Bras. Zool., **22**: 313-319.

— —, 2007. Reproductive role of intersex hermit crabs. — Crustaceana, **80**: 491-494.

VANNINI, M. & J. FERRETTI, 1997. Chemoreception in two species of terrestrial hermit crabs (Decapoda: Coenobitidae). — J. Crust. Biol. **17**: 33-37.

VINUESA, J. H., 2007. Reproduction of *Munida gregaria* (Decapoda: Galatheidae) in San Jorge Gulf, southwest Atlantic Ocean. — J. Crust. Biol., **27**: 437-444.

VIOZZI, G., V. FLORES & C. RAUQUE, 2005. An ectosymbiotic flatworm, *Temnocephala chilensis*, as second intermediate host for *Echinoparyphium megacirrus* (Digenea: Echinostomatidae) in Patagonia (Argentina). — J. Parasit., **91**: 229-231.

WÄGELE, J. W., 1989. On the influence of fishes on the evolution of benthic crustaceans. — Z. zool. Syst. Evolut.-forsch., **27**: 297-309.

WATTERS, G., 1998. Prevalences of parasitized and hyperparasitized crabs near South Georgia. — Mar. Ecol. Prog. Ser., **170**: 215-229.

WEISS, H. M., 1995. Marine animals of southern New England and New York. — Pp. 1-303. (State Geological and Natural History Survey of Connecticut, Hartford.)

WERDING, B. & A. HILLER, 2007. The Porcellanidae (Crustacea: Decapoda: Anomura) of the Red Sea with description of a new species of *Petrolisthes*. — Zootaxa, **1460**: 1-24.

WERDING, B., A. HILLER & R. LEMAITRE, 2003. Geographic and depth distributional patterns of western Atlantic Porcellanidae (Crustacea: Decapoda: Anomura), with an updated list of species. — In: R. LEMAITRE & C. C. TUDGE (eds.), Biology of the Anomura. Proceedings of a symposium at the Fifth International Crustacean Congress, Melbourne, Australia, 9-13 July 2001. Mem. Mus. Vict., **60**: 79-85.

WILKENS, H., J. PARZEFALL & A. RIBOWSKI, 1990. Population biology and larvae of the anchialine crab *Munidopsis polymorpha* (Galatheidae) from Lanzarote (Canary Islands). — J. Crust. Biol., **10**: 667-675.

WILKENS, J. L., 1999. Evolution of the cardiovascular system in Crustacea. — Am. Zool., **39**: 199-214.

WILLIAMS, A. B., 1984. Shrimps, lobsters, and crabs of the Atlantic coast of the eastern United States, Maine to Florida. — Pp. 1-550. (Smithsonian Institution Press, Washington, D.C.)

WILLIAMS, J. D. & J. J. McDERMOTT, 2004. Hermit crab biocoenoses: a worldwide review of the diversity and natural history of hermit crab associates. — J. exp. mar. Biol. Ecol., **305**: 1-128.

WILLIAMS, J. D. & V. I. RADASHEVSKY, 1999. Morphology, ecology, and reproduction of a new *Polydora* species (Polychaeta: Spionidae) from the east coast of North America. — Ophelia, **51**: 115-127.

YAU, C., M. A. COLLINS & I. EVERSON, 2000. Commensalism between a liparid fish (*Careproctus* sp.) and stone crabs (Lithodidae) photographed in situ using a baited camera. — J. mar. biol. Ass. U.K., **80**: 379-380.

ZAKLAN, S. D., 2002. Review of the family Lithodidae (Crustacea: Anomura: Paguroidea): distribution, biology, and fisheries. — In: A. J. PAUL, E. G. DAWE, R. ELNER, G. S. JAMIESON, G. H. KRUSE, R. S. OTTO, B. SAINTE-MARIE, T. C. SHIRLEY & D. WOODBY (eds.), Crabs in cold water regions: biology, management, and economics, pp. 751-843. (Alaska Sea Grant College Program, AK-SG-02-01.)

ZELDIS, J. R., 1985. Ecology of *Munida gregaria* (Decapoda, Anomura): distribution and abundance, population dynamics and fisheries. — Mar. Ecol. Prog. Ser., **22**: 77-99.

— —, 1989. A fishery for *Munida gregaria* in New Zealand and ecological considerations. — N.Z. Fish. techn. Rep., **14**: 1-11.