Phylum Arthropoda
Crustacea: Crabs, Shrimps, and Their Kin

C rustaceans are one of the most popular invertebrate groups, even among nonbiologists, for they include some of the world's most delectable gourmet fare, such as lobsters, crabs, and shrimps (Figure 21.1). There are an estimated 70,000 described living species of Crustacea, and probably five or ten times that number waiting to be discovered and named. They exhibit an incredible diversity of form, habit, and size. The smallest known crustaceans are less than 100 μm in length and live on the antennules of copepods. The largest are Japanese spider crabs (*Macrocheira kaempferi*), with leg spans of 4 m, and giant Tasmanian crabs (*Pseudocarcinus gigas*) with carapace widths of 46 cm. The heaviest crustaceans are probably American lobsters (*Homarus americanus*), which, before the present era of overfishing, attained weights in excess of 20 kilograms. The world's largest land arthropod by weight (and possibly the largest land invertebrate) is the coconut crab (*Birgus latro*), weighing in at up to 4 kg. Crustaceans are found at all depths in every marine, brackish, and freshwater environment on Earth, including in pools at 6,000 m elevation (fairy shrimp and cladocerans in northern Chile). A few have become successful on land, the most notable being sowbugs and pillbugs (the terrestrial isopods).[1]

Crustaceans are commonly the dominant organisms in aquatic subterranean ecosystems, and new species of these stygobionts continue to be discovered as new caves are explored. They also dominate ephemeral pool habitats, where many undescribed species are known to occur.[2] And crustaceans are the most widespread, diverse, and

Classification of The Animal Kingdom (Metazoa)

Non-Bilateria*
(a.k.a. the diploblasts)
PHYLUM PORIFERA
PHYLUM PLACOZOA
PHYLUM CNIDARIA
PHYLUM CTENOPHORA

Bilateria
(a.k.a. the triploblasts)
PHYLUM XENACOELOMORPHA

Protostomia
PHYLUM CHAETOGNATHA

Spiralia
PHYLUM PLATYHELMINTHES
PHYLUM GASTROTRICHA
PHYLUM RHOMBOZOA
PHYLUM ORTHONECTIDA
PHYLUM NEMERTEA
PHYLUM MOLLUSCA
PHYLUM ANNELIDA
PHYLUM ENTOPROCTA
PHYLUM CYCLIOPHORA

Gnathifera
PHYLUM GNATHOSTOMULIDA
PHYLUM MICROGNATHOZOA
PHYLUM ROTIFERA

Lophophorata
PHYLUM PHORONIDA
PHYLUM BRYOZOA
PHYLUM BRACHIOPODA

Ecdysozoa
Nematoida
PHYLUM NEMATODA
PHYLUM NEMATOMORPHA

Scalidophora
PHYLUM KINORHYNCHA
PHYLUM PRIAPULA
PHYLUM LORICIFERA

Panarthropoda
PHYLUM TARDIGRADA
PHYLUM ONYCHOPHORA
PHYLUM ARTHROPODA
 SUBPHYLUM CRUSTACEA*
  SUBPHYLUM HEXAPODA
  SUBPHYLUM MYRIAPODA
  SUBPHYLUM CHELICERATA

Deuterostomia
PHYLUM ECHINODERMATA
PHYLUM HEMICHORDATA
PHYLUM CHORDATA

*Paraphyletic group

This chapter has been revised by Richard C. Brusca and Joel W. Martin

[1] When most people hear the word "shrimp" they think of edible shrimps, two crustacean groups nested within the order Decapoda (in the suborders Dendrobranchiata and Pleocyemata). However, the term "shrimp" is applied to a number of long-tailed crustaceans, many not closely related at all to decapods. So, in this general sense, there are fairy shrimps, tadpole shrimps, mantis shrimps, etc. In much of the English-speaking world, the word "prawn" is used for the edible shrimps, thus eliminating some of the confusion.

[2] One study of ephemeral pools in northern California discovered 30 probable undescribed and unnamed crustacean species (King et al. 1996).
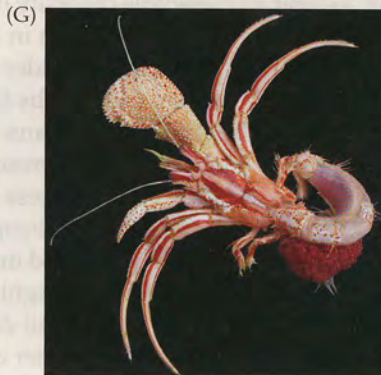
(A)

(B)

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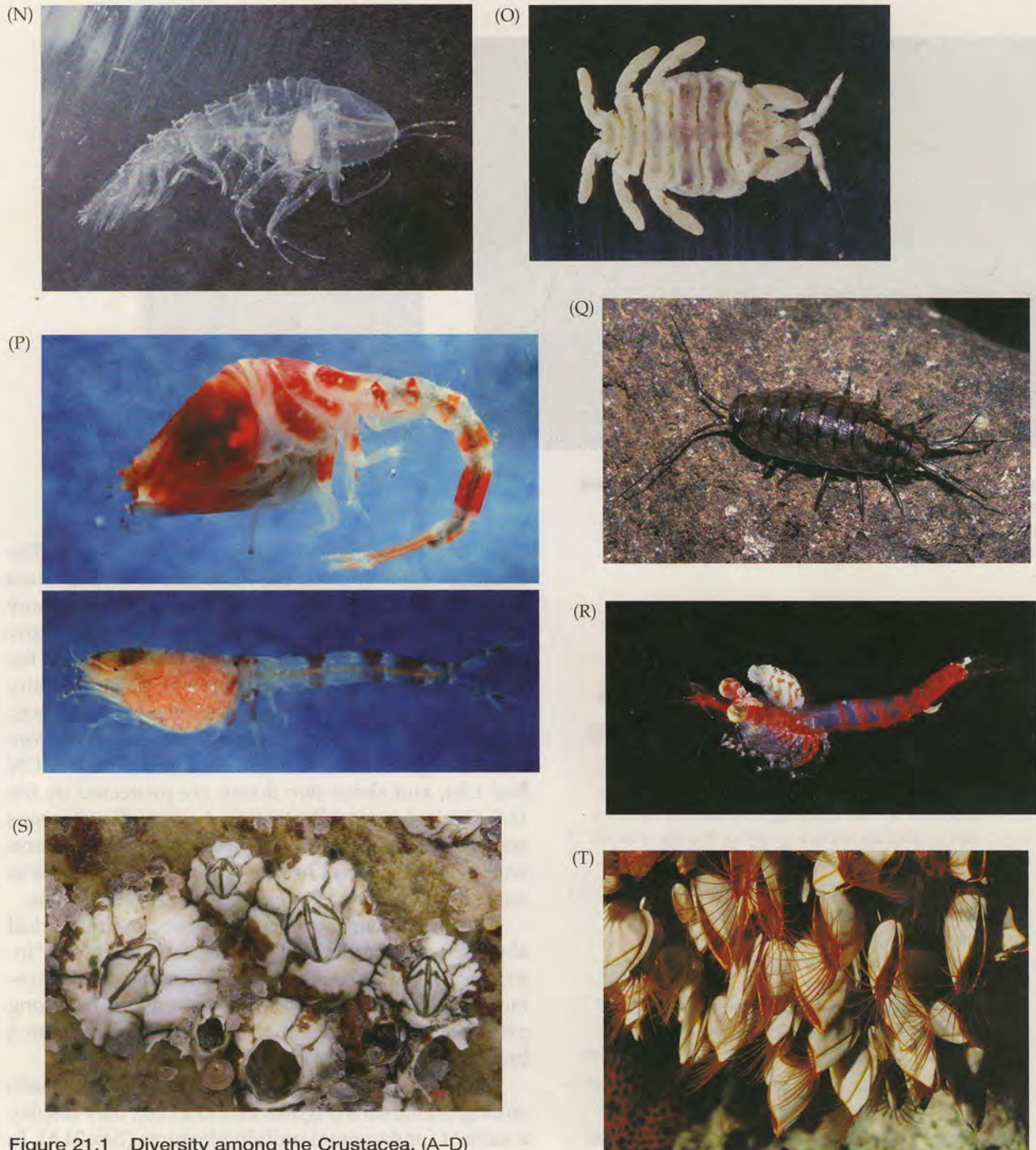(F)

(G)

(H)

(I)

(J)

(K)

(L)

(M)

Figure 21.1   Diversity among the Crustacea. (A–D) Classes Remipedia, Cephalocarida, and Branchiopoda. (A) *Speleonectes ondinae*; note the remarkably homonomous body of this swimming crustacean (Remipedia). (B) A cephalocarid. (C) A tadpole shrimp (Branchiopoda; Notostraca) from an ephemeral pool. (D) A clam shrimp (Branchiopoda: Diplostraca), carrying eggs. (E–Q) Class Malacostraca. (E) The fiddler crab, *Uca princeps* (Decapoda: Brachyura). (F) The giant Caribbean hermit crab, *Petrochirus diogenes* (Decapoda: Anomura). (G) A hermit crab (*Paragiopagurus fasciatus*) removed from its snail shell (Decapoda: Anomura). (H) The coconut crab, *Birgus latro* (Decapoda: Anomura), climbing a tree. (I) *Euceramus praelongus*, the New England olive pit porcelain crab (Decapoda: Anomura). (J) The pelagic lobsterette, *Pleuroncodes planipes* (Decapoda: Anomura). (K) The cleaner shrimp, *Lysmata californica* (Decapoda: Caridea). (L) The unusual rock-boring lobster shrimp, *Axius* *vivesi* (Decapoda: Axiidea). (M) The Hawaiian regal lobster, *Enoplometopus* (Decapoda: Achelata). (N,O) Two unusual amphipods (Peracarida: Amphipoda). (N) *Cystisoma*, a huge (some exceed 10 cm), transparent, pelagic hyperiid amphipod. (O) *Cyamus scammoni*, a parasitic caprellid amphipod that lives on the skin of gray whales. (P) A male and female cumacean; note the eggs in the marsupium of the female (Peracarida: Cumacea). (Q) *Ligia pacifica* (Peracarida: Isopoda), the rock louse; *Ligia* are inhabitants of the high spray zone on rocky shores worldwide. (R) The mysid *Siriella* sp. (Peracarida: Mysida) with a parasitic epicaridean isopod (Peracarida: Isopoda: Dajidae) attached to its carapace (Western Australia). (S,T) Class Thecostraca. (S) Acorn barnacles, *Semibalanus balanoides* (Cirripedia: Thoracica). (T) *Lepas anatifera* (Cirripedia: Thoracica), a pelagic barnacle hanging from a floating timber.

(U)

(V)

Figure 21.1 (continued)   Diversity among the Crustacea.
(U) Class Copepoda; the calanoid copepod *Gaussia*,
a common planktonic genus. (V) Class Tantulocarida,
Deoterthron, parasitic on other crustaceans.

BOX 21A   Characteristics of the Subphylum Crustacea

1. Body composed of a 6-segmented head, or cephalon (plus the acron), and a long postcephalic trunk; trunk divided into two more or less distinct tagmata (e.g., thorax and abdomen) in all but the remipedes and ostracods (Figure 21.2)

2. Cephalon composed of (anterior to posterior): presegmental (indistinguishable) acron, protocerebral segment (lacking appendages), antennular segment, antennal segment, mandibular somite, maxillulary somite, and maxillary somite; one or more anterior thoracomeres may fuse with the head in members of some classes (e.g., Remipedia, and Malacostraca), their appendages forming maxillipeds

3. Cephalic shield or carapace present (highly reduced in anostracans, amphipods, and isopods)

4. Appendages multiarticulate, uniramous or biramous

5. Mandibles usually multiarticulate limbs that function as biting, piercing, or chewing/grinding jaws

6. Gas exchange by aqueous diffusion across specialized branchial surfaces, either gill-like structures or specialized regions of the body surface

7. Excretion by true nephridial structures (e.g., antennal glands, maxillary glands)

8. Both simple ocelli and compound eyes occur in most taxa (not Remipedia), at least at some stage of the life cycle; compound eyes often elevated on stalks

9. Gut with digestive ceca

10. With nauplius larva (unknown from any other arthropod subphylum); development mixed or direct

abundant animals inhabiting the world's oceans. The biomass of one species, the Antarctic krill (*Euphausia superba*), has been estimated at 500 million tons at any given time, probably surpassing the biomass of any other group of marine animals (and rivaling that of the world's ants). The range of morphological diversity among crustaceans far exceeds that of even the insects. Many species of Crustacea are threatened by environmental degradation, over 500 are listed on the IUCN Red List, and about two dozen are protected by the U.S. Environmental Protection Agency. Crustaceans are also the most common invasive invertebrates, and well over 100 species have established themselves in marine and estuarine waters of North America alone.

Because of their taxonomic diversity and numerical abundance, it is often said that crustaceans are the "insects of the sea." We prefer to think of insects as "crustaceans of the land." And indeed, there is now strong phylogenetic evidence that the insects arose from a branch within the Crustacea.

Despite the enormous morphological diversity seen among crustaceans (Figures 21.1 to 21.20), they display a suite of fundamental unifying features (Box 21A). In an effort to introduce both the diversity and the unity of this enormous group of arthropods, we first present a classification and synopses of the major taxa. We then discuss the biology of the group as a whole, drawing examples from its various members. As you read this chapter, we ask that you keep in mind the general account of the arthropods presented in Chapter 20.

Classification of The Crustacea

Crustaceans have been known to humans since ancient times and have provided us with sources of both food and legend. It is somewhat comforting to carcinologists (those who study crustaceans) to note that Can-
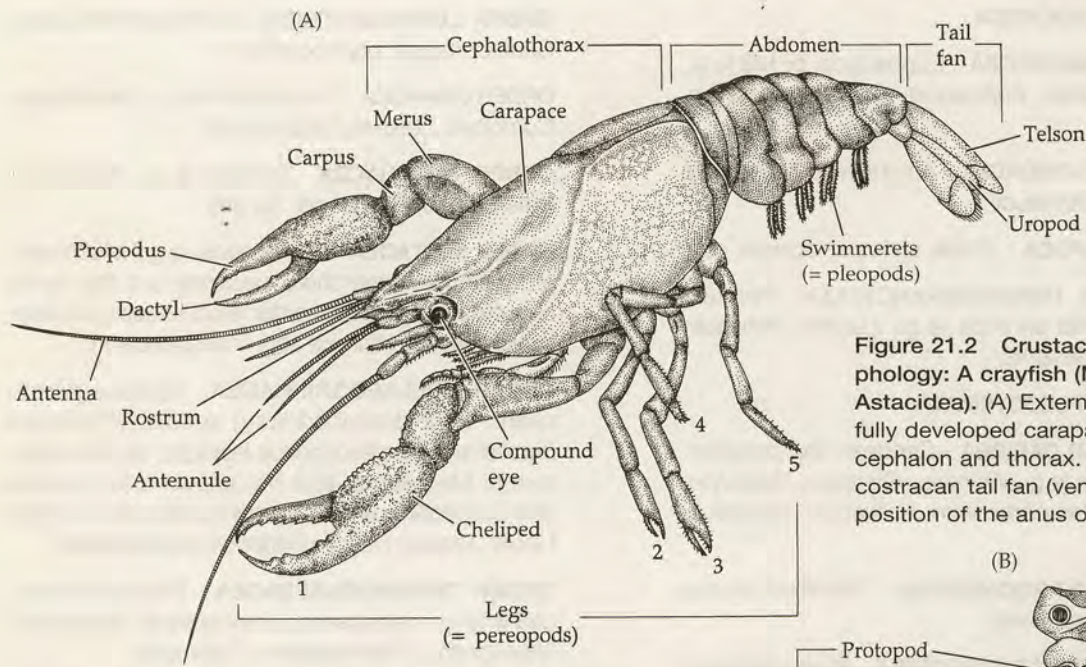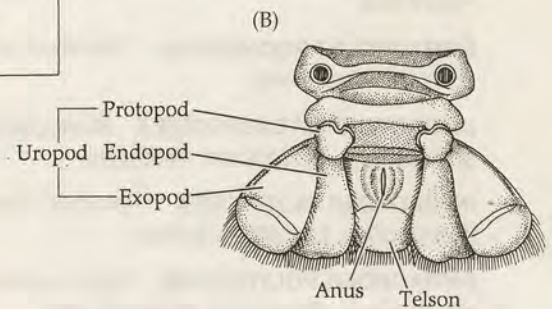
(A)

Figure 21.2 **Crustacean external morphology: A crayfish (Malacostraca, Astacidea).** (A) External form. Note the fully developed carapace covering the cephalon and thorax. (B) The typical malacostracan tail fan (ventral view). Note the position of the anus on the telson.

(B)

cer, one of the two invertebrates represented in the zodiac, is a crab (the other, of course, is Scorpio—another arthropod). Our modern view of Crustacea as a taxon can be traced to Lamarck's scheme in the early nineteenth century. He recognized most crustaceans as such, but placed the barnacles and a few others in separate groups. For many years barnacles were classified with molluscs because of their thick, calcareous outer shell. Crustacean classification as we know it today was more or less established during the second half of the nineteenth century, although internal revisions continue. Martin and Davis (2001) presented an overview of crustacean classification, and readers are referred to that publication for a window into the labyrinthine history of this subphylum. Our classification recognizes 11 classes, following Ahyong et al. (2011) and Martin et al. (2014).

CLASSIFICATION OF CRUSTACEA

CLASS REMIPEDIA   Remipedes. One living order, Nectiopoda (e.g., *Cryptocorynectes, Godzillius, Lasionectes, Pleomothra, Speleonectes*)

CLASS CEPHALOCARIDA   Cephalocarids (e.g., *Chiltoniella, Hampsonellus, Hutchinsoniella, Lightiella, Sandersiella*)

CLASS BRANCHIOPODA   Branchiopods

    ORDER ANOSTRACA   Fairy shrimps (e.g., *Artemia, Branchinecta, Branchinella, Streptocephalus*)

    ORDER NOTOSTRACA   Tadpole shrimps (*Lepidurus, Triops*)

    ORDER DIPLOSTRACA   The "bivalved" branchiopods

        SUBORDER LAEVICAUDATA   Flat-tailed clam shrimps (e.g., *Lynceus*)

        SUBORDER ONYCHOCAUDATA   Clam shrimps, cladocerans (water fleas), and cyclestherians

        INFRAORDER SPINICAUDATA   Clam shrimps (e.g., *Cyzicus, Eulimnadia, Imnadia, Metalimnadia*)

        INFRAORDER CLADOCEROMORPHA   Water fleas and cyclestheriids

        TRIBE CYCLESTHERIDA   Monotypic: *Cyclestheria hislopi*

        TRIBE CLADOCERA   Water fleas (e.g., *Anchistropus, Daphnia, Leptodora, Moina, Polyphemus*)

CLASS MALACOSTRACA

    SUBCLASS PHYLLOCARIDA

        ORDER LEPTOSTRACA   Leptostracans or nebaliaceans (e.g., *Dahlella, Levinebalia, Nebalia, Nebaliella, Nebaliopsis, Paranebalia*)

    SUBCLASS HOPLOCARIDA

        ORDER STOMATOPODA   Mantis shrimps (e.g., *Echinosquilla, Gonodactylus, Hemisquilla, Squilla*)

    SUBCLASS EUMALACOSTRACA

        SUPERORDER SYNCARIDA   Syncarids

        ORDER BATHYNELLACEA   (e.g., *Bathynella*)

        ORDER ANASPIDACEA   (e.g., *Anaspides, Psammaspides*)

SUPERORDER EUCARIDA

ORDER EUPHAUSIACEA Euphausids, or krill (e.g., *Bentheuphausia, Euphausia, Meganyctiphanes, Nyctiphanes*)

ORDER AMPHIONIDACEA Amphionids. Monotypic: *Amphionides reynaudii*

ORDER DECAPODA Crabs, shrimps, lobsters, etc.

SUBORDER DENDROBRANCHIATA Penaeid and sergestid shrimps (e.g., *Lucifer, Penaeus, Sergestes, Sicyonia*)

SUBORDER PLEOCYEMATA

INFRAORDER CARIDEA Caridean and procaridean shrimps (e.g., *Alpheus, Crangon, Hippolyte, Lysmata, Macrobrachium, Palaemon, Pandalus, Pasiphaea*)

INFRAORDER PROCARIDOIDA "Primitive" shrimp (*Procaris, Vetericaris*)

INFRAORDER STENOPODIDEA Stenopodidean shrimps (e.g., *Spongicola, Stenopus*)

INFRAORDER GLYPHEIDEA "Primitive" lobsters (*Neoglyphea, Laurentaeglyphea*)

INFRAORDER POLYCHELIDA Deep-sea slipper lobsters (e.g., *Polycheles, Stereomastis*)

INFRAORDER BRACHYURA "True" crabs (e.g., *Actaea, Callinectes, Cancer, Cardisoma, Carcinus, Grapsus, Hemigrapsus, Maja, Menippe, Ocypode, Pachygrapsus, Pinnotheres, Polydectus, Portunus, Scylla, Uca, Xantho*)

INFRAORDER ANOMURA Hermit crabs, galatheid crabs, sand crabs, porcelain crabs, etc. (e.g., *Birgus, Coenobita, Emerita, Galathea, Hippa, Kiwa, Lithodes, Lomis, Paguristes, Pagurus, Petrochirus, Petrolisthes, Pleuroncodes, Pylopagurus*)

INFRAORDER ASTACIDEA Crayfishes and clawed (chelate) lobsters (e.g., *Astacus, Cambarus, Homarus, Nephrops*)

INFRAORDER ACHELATA (formerly Palinura). Palinurid, spiny, and Spanish (slipper) lobsters (e.g., *Enoplometopus, Evibacus, Ibacus, Jassa, Jasus, Palinurus, Panulirus, Scyllarus*)

INFRAORDER AXIIDEA Lobster shrimps (e.g., *Axiopsis, Axius, Calocarides, Calocaris, Callianassa, Neaxius*)

INFRAORDER GEBIIDEA Mud and ghost shrimps (e.g., *Axianassa, Gebiacantha, Thalassina, Upogebia*)

SUPERORDER PERACARIDA

ORDER MYSIDA Mysids or opossum shrimps (e.g., *Acanthomysis, Hemimysis, Mysis, Neomysis*)

ORDER LOPHOGASTRIDA Lophogastrids (e.g., *Gnathophausia, Lophogaster*)

ORDER CUMACEA Cumaceans (e.g., *Campylaspis, Cumopsis, Diastylis, Diastylopsis*)

ORDER TANAIDACEA Tanaids (e.g., *Apseudes, Heterotanais, Paratanais, Tanais*)

ORDER MICTACEA Mictaceans (e.g., *Mictocaris,* etc.). Some researchers separate out the family Hirsutiidae as a distinct order (Bochusacea, containing *Hirsutia, Montucaris* and *Thetispelecaris*).

ORDER SPELAEOGRIPHACEA Spelaeogriphaceans. Four described living species (*Potiicoara brazilienses, Spelaeogriphus lepidops,* and two species of *Mangkurtu*), and two known fossil species (the Carboniferous *Acadiocaris novascotica* and the Upper Jurassic *Liaoningogriphus quadripartitus*)

ORDER THERMOSBAENACEA Thermosbaenaceans (e.g., *Halosbaena, Limnosbaena, Monodella, Theosbaena, Thermosbaena, Tulumella*)

ORDER ISOPODA Isopods (sea slaters, rock lice, pillbugs, sowbugs, roly-polies)

SUBORDER ANTHURIDEA (e.g., *Anthura, Colanthura, Cyathura, Mesanthura*)

SUBORDER ASELLOTA (e.g., *Asellus, Eurycope, Jaera, Janira, Microcerberus, Munna*)

SUBORDER CALABOZOIDEA (*Calabozoa*)

SUBORDER CYMOTHOIDA (e.g., *Aega, Bathynomus, Cymothoa, Cirolana, Rocinela*)

SUBORDER EPICARIDEA (e.g., *Bopyrus, Dajus, Hemiarthrus, Ione, Pseudione*)

SUBORDER GNATHIIDEA (e.g., *Gnathia, Paragnathia*)

SUBORDER LIMNORIDEA (e.g., *Limnoria, Keuphylia, Hadromastax*)

SUBORDER MICROCERBERIDEA (e.g, *Atlantasellus, Microcerberus*)

SUBORDER ONISCIDEA (e.g., *Armadillidium, Ligia, Oniscus, Porcellio, Trichoniscus, Tylos, Venezillo*)

SUBORDER PHREATOICIDEA (e.g., *Mesamphisopus, Phreatoicopis, Phreatoicus*)

SUBORDER PHORATOPIDEA (*Phoratopus*)

SUBORDER SPHAEROMATIDEA (e.g., *Ancinus, Bathycopea, Paracerceis, Paradella, Sphaeroma, Serolis, Tecticeps*)

SUBORDER TAINISOPIDEA (*Pygolabis, Tainisopus*)

SUBORDER VALVIFERA (e.g., *Arcturus, Idotea, Saduria*)

ORDER AMPHIPODA   Amphipods—beach hoppers, sand fleas, scuds, skeleton shrimps, whale lice, etc.

SUBORDER GAMMARIDEA   (e.g., *Ampithoe, Anisogammarus, Corophium, Eurythenes, Gammarus, Niphargus, Orchestia, Phoxocephalus, Talitrus*)

SUBORDER HYPERIIDEA   (e.g., *Cystisoma, Hyperia, Phronima, Primno, Rhabdosoma, Scina, Streetsia, Vibilia*)

SUBORDER CAPRELLIDEA   (e.g., *Caprella, Cyamus, Metacaprella, Phtisica, Syncyamus*)

SUBORDER INGOLFIELLIDEA   (e.g., *Ingolfiella, Metaingolfiella*)

CLASS THECOSTRACA   Barnacles and their kin

SUBCLASS FACETOTECTA   Monogeneric (*Hansenocaris*): the mysterious "y-larvae," a group of marine nauplii and cyprids for which adults are unknown

SUBCLASS ASCOTHORACIDA   Two orders (Laurida, Dendrogastrida) of parasitic thecostracans (e.g., *Ascothorax, Dendrogaster, Laura, Synagoga, Zoanthoecus*)

SUBCLASS CIRRIPEDIA   Cirripedes, the barnacles, and their kin

SUPERORDER THORACICA   True barnacles. Four orders, Lepadiformes (pedunculate or goose barnacles: e.g., *Lepas*), Ibliformes, Scalpelliformes (*Pollicipes, Scalpellum)*, and Sessilia (sessile or acorn barnacles: e.g., *Balanus, Chthamalus, Conchoderma, Coronula, Tetraclita, Verruca*)

SUPERORDER ACROTHORACICA   Burrowing "barnacles." Two orders, Cryptophialida and Lythoglyptida (e.g., *Cryptophialus, Trypetesa*)

SUPERORDER RHIZOCEPHALA   Parasitic "barnacles." Two orders, Kentrogonida and Akentrogonida (e.g., *Heterosaccus, Lernaeodiscus, Mycetomorpha, Peltogaster, Sacculina, Sylon*)

CLASS TANTULOCARIDA   Deep water, marine parasites (e.g., *Basipodella, Deoterthron, Microdajus*)

CLASS BRANCHIURA   Fish lice, or argulids. A single family (Argulidae) (e.g., *Argulus, Chonopeltis, Dipteropeltis, Dolops*)

CLASS PENTASTOMIDA   Tongueworms. Two orders, numerous families (e.g., *Cephalobaena, Linguatula, Pentastoma, Waddycephalus*)

CLASS MYSTACOCARIDA   Mystacocarids, with a single family (Derocheilocarididae), and 13 species (e.g., *Ctenocheilocaris, Derocheilocaris*)

CLASS COPEPODA

SUBCLASS PROGYMNOPLEA

ORDER PLATYCOPIOIDA   Platycopioids (e.g., *Antrisocopia, Platycopia*)

SUBCLASS NEOCOPEPODA

SUPERORDER GYMNOPLEA

ORDER CALANOIDA   Calanoids (e.g., *Bathycalanus, Calanus, Diaptomus, Eucalanus, Euchaeta*)

SUPERORDER PODOPLEA

ORDER CYCLOPOIDA   Cyclopoids (e.g., *Cyclopina, Cyclops, Eucyclops, Lernaea, Mesocyclops, Notodelphys*)

ORDER GELYELLOIDA   Gelyelloids (e.g., *Gelyella*)

ORDER HARPACTICOIDA   Harpacticoids (e.g., *Harpacticus, Longipedia, Peltidium, Porcellidium, Psammus, Sunaristes, Tisbe*)

ORDER MISOPHRIOIDA   Misophriods (e.g., *Boxshallia, Misophria*)

ORDER MONSTRILLOIDA   Monstrilloids (e.g., *Monstrilla, Stilloma*)

ORDER MORMONILLOIDA   Mormonilloids. Monogeneric: *Mormonilla*

ORDER POECILOSTOMATOIDA   Poecilostomatoids (e.g., *Chondracanthus, Erebonaster, Ergasilus, Pseudanthessius*)

ORDER SIPHONOSTOMATOIDA   Siphonostomatoids (e.g., *Clavella, Nemesis, Penella, Pontoeciella, Trebius*)

CLASS OSTRACODA   Ostracods

SUBCLASS MYODOCOPA

ORDER MYODOCOPIDA   (e.g., *Cypridina, Euphilomedes, Eusarsiella, Gigantocypris, Skogsbergia, Vargula*)

ORDER HALOCYPRIDA   (e.g., *Conchoecia, Polycope*)

SUBCLASS PODOCOPA

ORDER PODOCOPIDA   (e.g., *Cypris, Candona, Celtia, Darwinula, Limnocythre*)

ORDER PLATYCOPIDA   (e.g., *Cytherella, Sclerocypris*)

ORDER PALAEOCOPIDA   (e.g., *Manawa*)

Synopses of Crustacean Taxa

The following descriptions of major crustacean taxa will give you an idea of the range of diversity within the group and the variety of ways in which these successful animals have exploited the basic crustacean body plan.

Subphylum Crustacea

Body composed of a 6-segmented cephalon (plus presegmental acron), or head, and multisegmented post-

cephalic trunk; trunk divided into thorax and abdomen (except in remipedes and ostracods); segments of cephalon bear first antennae (antennules), second antennae, mandibles, maxillules, and maxillae (see Table 20.2); one or more anterior thoracomeres may fuse with the head (e.g., Remipedia and Malacostraca), their appendages forming maxillipeds (secondarily modified for feeding); cephalic shield or carapace present (secondarily lost in some groups); with antennal glands or maxillary glands (excretory nephridia); both simple ocelli and compound eyes in most groups, at least at some stage of the life cycle; compound eyes stalked in many groups; with nauplius larval stage (suppressed or bypassed in some groups), and often a series of additional larval stages. There are an estimated 70,000 living species, in over 1,000 families.[3]

Class Remipedia

Body of two regions, a cephalon and an elongate homonomous trunk of up to 32 segments, each with a pair of flattened limbs. Cephalon with a pair of sensory preantennular frontal processes; first antennae biramous; trunk limbs laterally directed, biramous, paddle-like, but without large epipods; rami of trunk limbs (exopod and endopod) each of three or more articles; without a carapace, but with cephalic shield covering head; midgut with serially arranged digestive ceca; first trunk segment fused with head and bearing one pair of prehensile maxillipeds; labrum very large, forming a chamber (atrium oris) in which reside the "internalized" mandibles; maxillules function as hypodermic fangs; last trunk segment partly fused dorsally with telson; telson with caudal rami; segmental double ventral nerve cord; eyes absent in living species; male gonopore on trunk limb 15, female on 8; up to 45 mm in length. The above diagnosis is for the 24 known living remipedes (order Nectiopoda); the fossil record is currently based on a single poorly preserved specimen (order Enantiopoda) (Figures 21.1A 21.3D–F, 21.21D, 21.22F, and 21.31E,F).

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[3]Segments of the thorax are called thoracomeres (regardless of whether or not any of these segments are fused to the head), whereas appendages of the thorax are called thoracopods. The term "pereon" refers to that portion of the thorax not fused to the head (when such fusion occurs), and the terms "pereonites" (= pereomeres) and "pereopods" are used for the segments and appendages, respectively, of the pereon. Hence, on a crustacean with the first thoracic segment (thoracomere 1) fused to the head, thoracomere 2 is typically called pereonite 1, the first pair of pereopods represents the second pair of thoracopods, and so on. Be assured that we are trying to simplify, not confuse, this issue. Also, we caution you that the homology of the thorax and abdomen among the major crustacean lineages is probably more reverie than reality; the segmental homologies of the thorax and abdomen have not yet been unraveled among the crustacean classes. For summaries of naupliar development across the group and larval features in all crustaceans, see Martin et al. (2014). In most crustacean species the number of body segments is fixed, but in at least two groups (notostracans and remipedes) the segment number can vary within a given species.

The discovery of living remipedes in 1981 by Jill Yager, strange vermiform crustaceans first collected from a cavern in the Bahamas, gave the carcinological world a turn. The combination of features distinguishing these creatures is puzzling, for they possess characteristics that are certainly very primitive (e.g., long, homonomous trunk; double ventral nerve cord; segmental digestive ceca; cephalic shield) as well as some attributes traditionally recognized as advanced (e.g., maxillipeds; nonphyllopodous [though flattened], biramous limbs). They swim about on their backs as a result of metachronal beating of the trunk appendages, similar to anostracans. The remipedes are thus reminiscent of two other primitive classes, the branchiopods and cephalocarids. However, the laterally directed limbs are unlike those of any other crustacean, and the "internalized" mandibles and the poison-injecting hypodermic maxillules are unique (the complex venom contains neurotoxins, peptidases, and chitinases). The presence of the preantennular processes is also puzzling, although similar structures are known to occur in a few other crustaceans. Some phylogenetic analyses based on morphological data suggest that remipedes may be the most primitive living crustaceans, whereas molecular data remain ambiguous on the subject or, in some cases, ally them with cephalocarids and/or the Hexapoda.

All of the living remipedes discovered thus far are found in caves (usually with connections to the sea) in the Caribbean Basin, Indian Ocean, Canary Islands, and Australia. The water in these caves is often distinctly stratified, with a layer of fresh water overlying the denser salt water in which the remipedes swim. Remipedes hatch as lecithotrophic naupliar larvae, which is also unusual given their habitat (most cave crustaceans have direct development). Postnaupliar development is largely anamorphic; juveniles have fewer trunk segments than do the adults. Based on the three pairs of raptorial, prehensile cephalic limbs (and direct observations), it was long thought that remipedes were strictly predators. However, studies by Stefan Koenemann and his colleagues have suggested they might also be capable of suspension feeding.

Class Cephalocarida

Head followed by 8-segmented thorax with each segment bearing limbs, a 11-segmented limbless abdomen, and a telson with caudal rami; common gonopore on protopods of sixth thoracopods; carapace absent but head covered by cephalic shield; thoracopods 1–7 biramous and phyllopodous, with large flattened exopods and epipods (exites) and stenopodous endopods; thoracopods 8 reduced or absent; maxillae resemble thoracopods; no maxillipeds; eyes absent; nauplii with antennal glands, adults with maxillary glands and (vestigial) antennal glands (Figures 21.1T, 21.3A–C, and 21.21A).

Cephalocarids are tiny, elongate crustaceans ranging in length from 2 to 4 mm. There are 12 species in
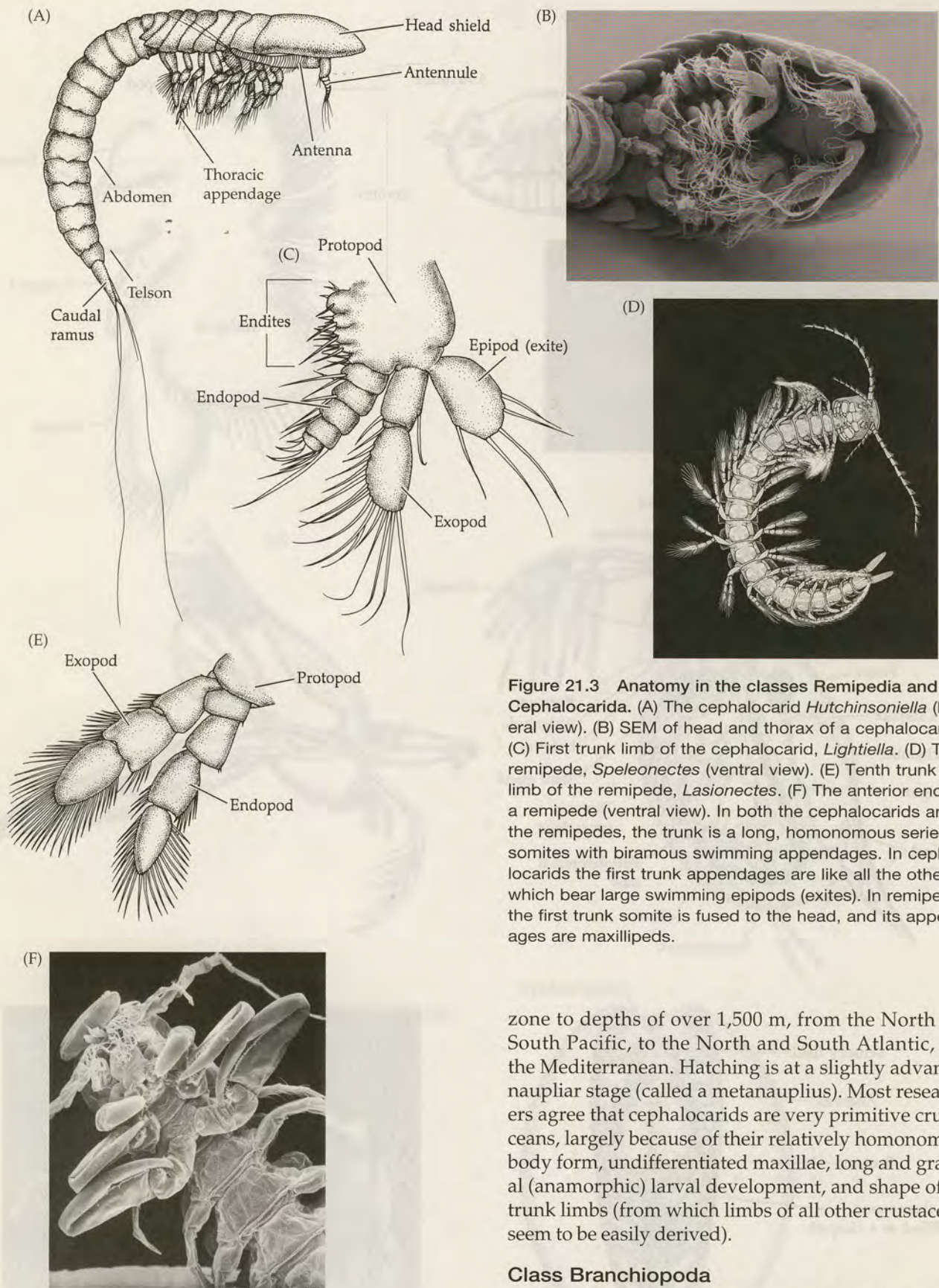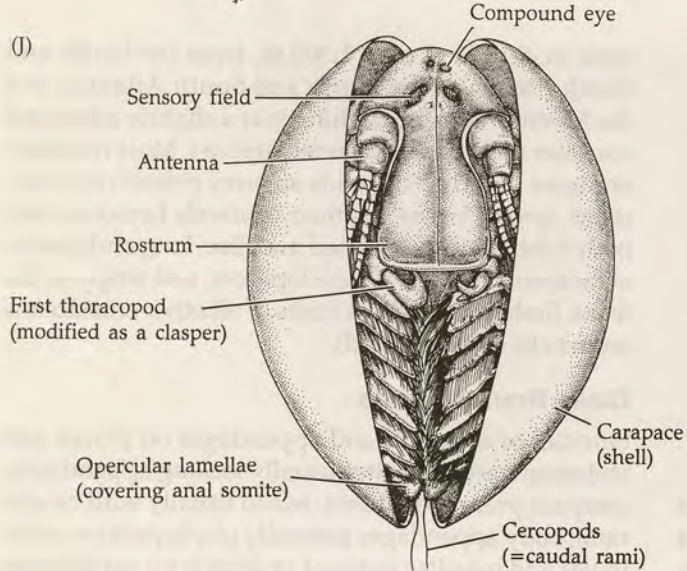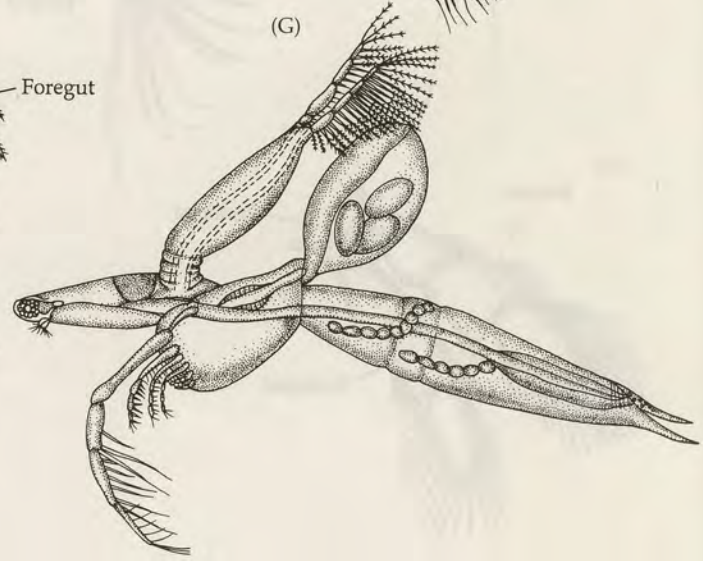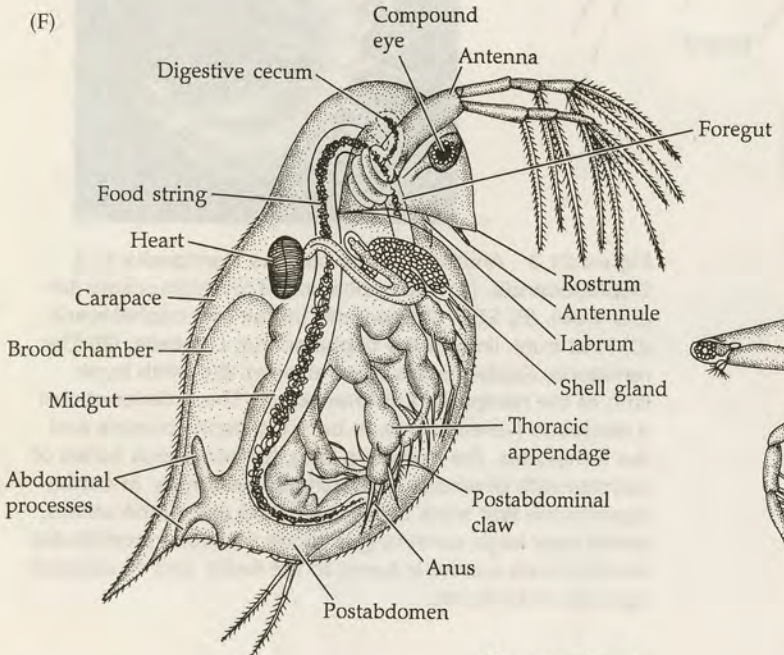
(A) The cephalocarid *Hutchinsoniella* (lateral view) — labels: Head shield, Antennule, Antenna, Thoracic appendage, Abdomen, Telson, Caudal ramus

(C) labels: Protopod, Endites, Endopod, Epipod (exite), Exopod
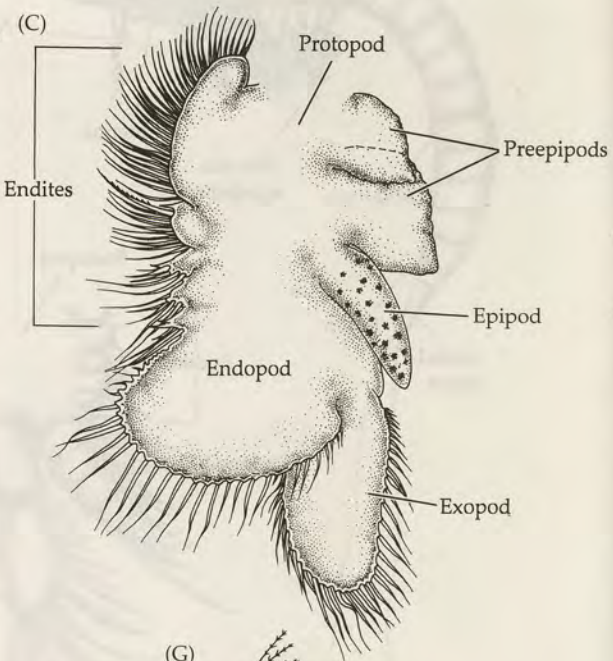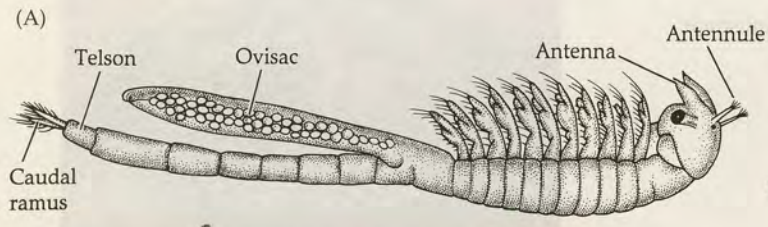
(E) labels: Exopod, Protopod, Endopod

Figure 21.3   Anatomy in the classes Remipedia and Cephalocarida. (A) The cephalocarid *Hutchinsoniella* (lateral view). (B) SEM of head and thorax of a cephalocarid. (C) First trunk limb of the cephalocarid, *Lightiella*. (D) The remipede, *Speleonectes* (ventral view). (E) Tenth trunk limb of the remipede, *Lasionectes*. (F) The anterior end of a remipede (ventral view). In both the cephalocarids and the remipedes, the trunk is a long, homonomous series of somites with biramous swimming appendages. In cephalocarids the first trunk appendages are like all the others, which bear large swimming epipods (exites). In remipedes the first trunk somite is fused to the head, and its appendages are maxillipeds.

zone to depths of over 1,500 m, from the North and South Pacific, to the North and South Atlantic, and the Mediterranean. Hatching is at a slightly advanced naupliar stage (called a metanauplius). Most researchers agree that cephalocarids are very primitive crustaceans, largely because of their relatively homonomous body form, undifferentiated maxillae, long and gradual (anamorphic) larval development, and shape of the trunk limbs (from which limbs of all other crustaceans seem to be easily derived).

Class Branchiopoda

Number of segments and appendages on thorax and abdomen vary, the latter usually lacking appendages; carapace present or absent; telson usually with caudal rami; body appendages generally phyllopodous; maxillules and maxillae reduced or absent; no maxillipeds (Figures 21.1C,D, 21.4, 21.21B, 21.31C, and 21.35B).

5 genera. All are benthic marine detritus feeders. Most are associated with sediments covered by a layer of flocculent organic detritus, although some have been found in clean sands. They occur from the intertidal

(A)

Telson · Ovisac · Antenna · Antennule

Caudal ramus

(B)

(C)

Protopod

Preepipods

Endites

Epipod

Endopod

Exopod

(F)

Compound eye

Digestive cecum · Antenna

Foregut

Food string

Heart

Carapace

Brood chamber

Midgut

Abdominal processes

Rostrum
Antennule
Labrum

Shell gland

Thoracic appendage

Postabdominal claw

Anus

Postabdomen

(G)

(J)

Compound eye

Sensory field

Antenna

Rostrum

First thoracopod (modified as a clasper)

Opercular lamellae (covering anal somite)

Carapace (shell)
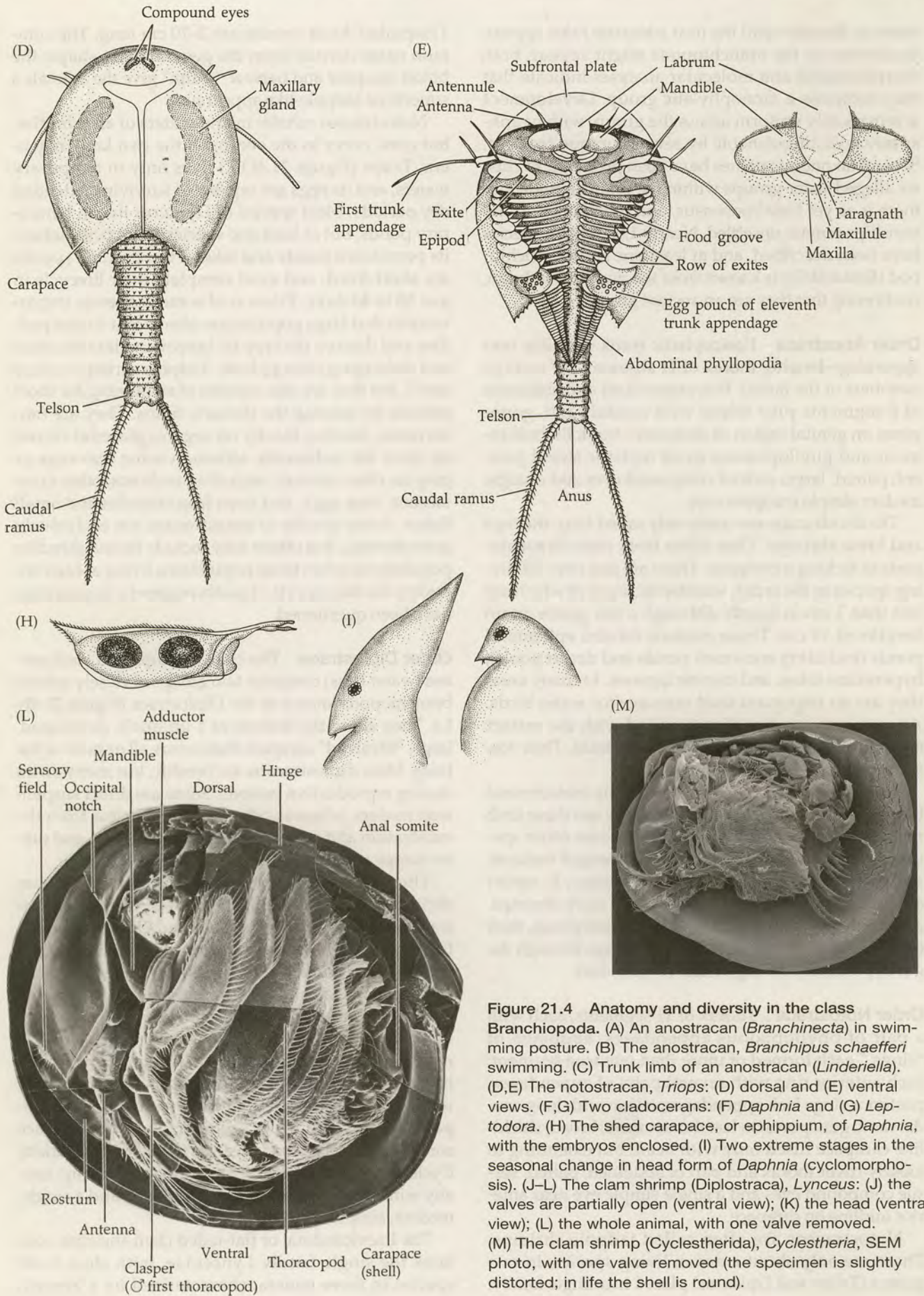
Cercopods (=caudal rami)

(K)

Figure 21.4   Anatomy and diversity in the class Branchiopoda. (A) An anostracan (*Branchinecta*) in swimming posture. (B) The anostracan, *Branchipus schaefferi* swimming. (C) Trunk limb of an anostracan (*Linderiella*). (D,E) The notostracan, *Triops*: (D) dorsal and (E) ventral views. (F,G) Two cladocerans: (F) *Daphnia* and (G) *Leptodora*. (H) The shed carapace, or ephippium, of *Daphnia*, with the embryos enclosed. (I) Two extreme stages in the seasonal change in head form of *Daphnia* (cyclomorphosis). (J–L) The clam shrimp (Diplostraca), *Lynceus*: (J) the valves are partially open (ventral view); (K) the head (ventral view); (L) the whole animal, with one valve removed. (M) The clam shrimp (Cyclestherida), *Cyclestheria*, SEM photo, with one valve removed (the specimen is slightly distorted; in life the shell is round).

years or decades until the next adequate rains appear. As diverse as the branchiopods might appear, both morphological and molecular analyses indicate that they comprise a monophyletic group. Development is remarkably uniform across the group, with naupliar larvae distinguishable by several unique features. Several taxonomic names have been proposed to cluster alleged sister-groups within the Branchiopoda, but there is as yet little consensus, and branchiopod relationships remain unsettled. Nearly 1,000 extant species have been described, and at least one fossil branchiopod (*Rehbachiella*) is known from the middle Cambrian, confirming that they are an ancient group.

Order Anostraca   Postcephalic trunk divisible into appendage-bearing thorax of 11 segments (17 or 19 in members of the family Polyartemiidae) and abdomen of 8 segments plus telson with caudal rami; gonopores on genital region of abdomen; trunk limbs biramous and phyllopodous; small cephalic shield present; paired, large, stalked compound eyes and a single median simple (naupliar) eye.

The anostracans are commonly called fairy shrimps and brine shrimps. They differ from other branchiopods in lacking a carapace. There are just over 300 living species in the order, worldwide, most of which are less than 1 cm in length, although a few giants attain lengths of 10 cm. These animals inhabit ephemeral ponds (including snowmelt ponds and desert pools), hypersaline lakes, and marine lagoons. In many areas they are an important food resource for water birds. Anostracans are sometimes united with the extinct order Lipostraca as the subclass Sarsostraca. Their fossil record dates back to the Devonian.

Anostracans swim ventral side up by metachronal beating of the trunk appendages. Many use these limb movements for suspension feeding. Some other species scrape organic material from submerged surfaces, and at least two species (*Branchinecta gigas*, *B. raptor*) are specialized as predators on other fairy shrimps. Although most anostracans live in isolated ponds, their eggs might be transported during passage through the gut of predatory diving beetles (Dytiscidae).

Order Notostraca   Thorax of 11 segments, each with a pair of phyllopodous appendages; abdomen of "rings," each formed of more than one true segment; each anterior ring with several pairs of appendages; posterior rings lack appendages; telson with long caudal rami; gonopores on last thoracomere; broad, shield-like carapace fused only with head, but extending to loosely cover thorax and part of abdomen; paired, sessile compound eyes and a single simple eye near anterior midline on carapace.

Notostracans are often called tadpole shrimps. There are only about a dozen living species, in two genera (*Triops* and *Lepidurus*) placed in a single family,

Triopsidae. Most species are 2–10 cm long. The common name derives from the general body shape: the broad carapace and narrow "trunk" give the animals a superficial tadpole-like appearance.

Notostracans inhabit inland waters of all salinities, but none occur in the ocean. Of the two known genera, *Triops* (Figure 21.4D,E) lives only in temporary waters, and its eggs are capable of surviving extended dry periods. Most species of *Lepidurus* live in temporary ponds, but at least one species (*L. arcticus*) inhabits permanent ponds and lakes. However, all species are short-lived, and most complete their lifecycle in just 30 to 40 days. *Triops* is of some economic importance in that large populations often occur in rice paddies and destroy the crop by burrowing into the mud and dislodging young plants. Tadpole shrimps mostly crawl, but they are also capable of swimming for short periods by beating the thoracic limbs. They are omnivorous, feeding mostly on organic material stirred up from the sediments, although some scavenge or prey on other animals, including molluscs, other crustaceans, frog eggs, and even frog tadpoles and small fishes. Some species of notostracans are exclusively gonochoristic, but others may include hermaphroditic populations (often those populations living at high latitudes). Earlier reports of parthenogenetic populations have been questioned.

Order Diplostraca   The clam shrimps and cladocerans (water fleas) comprise two groups of closely related branchiopods known as the Diplostraca (Figure 21.4J–L). They share the feature of a uniquely developed, large, "bivalved" carapace that covers all or most of the body. Most diplostracans are benthic, but many swim during reproductive periods. Some are direct suspension feeders, whereas others stir up detritus from the substratum and feed on suspended particles, and others scrape pieces of food from the sediment.

The species formerly lumped together as clam shrimps are now partitioned between the two diplostracan suborders, Laevicaudata and Onychocaudata. Diplostracans share several features: body divided into cephalon and trunk, the latter with 10–32 segments, all with appendages, and with no regionalization into thorax and abdomen; trunk limbs phyllopodous, decreasing in size posteriorly; males with trunk limbs 1, or 1–2, modified for grasping females during mating; trunk typically terminates in spinous anal somite or telson, usually with robust caudal rami (cercopods); gonopores on eleventh trunk segment; bivalved carapace completely encloses body; valves folded (Spinicaudata, Cyclestherida) or hinged (Laevicaudata) dorsally; usually with a pair of sessile compound eyes and a single, median, simple eye.

The Laevicaudata, or flat-tailed clam shrimps, contains the single family Lynceidae, with close to 40 species in three genera, characterized by a hinged,

globular carapace that encloses the entire animal. The Onychocaudata contains the spiny-tailed or "true" clam shrimp in the infraorder Spinicaudata, and the cladocerans (commonly called water fleas) in the infraorder Cladoceromorpha. Spinicaudatans include the commonly encountered freshwater genera *Limnadia, Eulimnadia, Leptestheria,* and *Cyzicus*. The Cladoceromorpha contains the well-known cladoceran water fleas *Daphnia, Moina, Diaphonosoma,* and *Leptodora,* as well as the unique genus *Cyclestheria* (in the Cyclestherida). Confusingly, *Cyclestheria* is also commonly called a clam shrimp, though it is more closely related to the water fleas).

The common name "clam shrimp" derives from the clamlike appearance of the valves, which usually bear concentric growth lines reminiscent of bivalved molluscs. The approximately 200 species of clam shrimps (including laevicaudatans, spinicaudatans, and *Cyclestheria*) live primarily in ephemeral freshwater habitats worldwide. *Cyclestheria hislopi,* the only member of the Cyclestherida, inhabits permanent freshwater habitats throughout the world's tropics, and is one of the most widespread animals on Earth. *Cyclestheria* is also the only clam shrimp with direct development, the larval and juvenile stages being passed within the brood chamber, one of the features allying it with the cladocerans.

In cladocerans, the carapace is never hinged (only folded dorsally, like a taco) and never covers the entire body, and appendages do not occur on all the trunk somites. The body segmentation is generally reduced. The thorax and abdomen are fused as a "trunk" bearing 4–6 pairs of appendages anteriorly and terminating in a flexed "postabdomen" with clawlike caudal rami. Trunk appendages are usually phyllopodous. The carapace usually encloses the entire trunk, but not the cephalon, serving as a brood chamber (and greatly reduced to this function) in some species; a single median compound eye is always present.

The cladocerans, or water fleas, include about 400 species of predominantly freshwater crustaceans, although several American marine genera and species are known (e.g., *Evadne, Podon*). Although there are relatively few species, the group exhibits great morphological and ecological diversity. Most cladocerans are 0.5–3 mm long, but *Leptodora kindtii* reaches 18 mm in length. Except for the cephalon and large natatory antennae, the body is enclosed by a folded carapace, which is fused with at least some of the trunk region. The carapace is greatly reduced in members of the families Polyphemidae and Leptodoridae, in which it forms a brood chamber.

Cladocerans are distributed worldwide in nearly all inland waters. Most are benthic crawlers or burrowers; others are planktonic and swim by means of their large antennae. One genus (*Scapholeberis*) is typically found in the surface film of ponds, and another (*Anchistropus*)

is ectoparasitic on *Hydra*. Most of the benthic forms feed by scraping organic material from sediment particles or other objects; the planktonic species are suspension feeders. Some (e.g., *Leptodora, Bythotrephes*) are predators on other cladocerans.

In sexual reproduction, fertilization generally occurs in a brood chamber between the dorsal surface of the trunk and the inside of the carapace. Most species have direct development. In the family Daphnidae the developing embryos are retained by a portion of the shed carapace, which functions as an egg case called an **ephippium** (Figure 21.4H), whereas in the Chydoridae the ephippium remains attached to the entire shed carapace. *Leptodora* exhibits a heterogenous life cycle, alternating between parthenogenesis and sexual reproduction, the latter of which results in free-living larvae (metanauplii hatch from the shed resting eggs).

Cladoceran life histories are often compared with those of animals such as rotifers and aphids. Dwarf males occur in many species in all three groups, and parthenogenesis is common. Members of two cladoceran families that undergo parthenogenesis (Moinidae and Polyphemidae) produce eggs with very little yolk. In these groups the floor of the brood chamber is lined with glandular tissue that secretes a fluid rich in nutrients, which is absorbed by the developing embryos. Periods of overcrowding, adverse temperatures, or food scarcity can induce parthenogenetic females to produce male offspring. Occasional periods of sexual reproduction have been shown to occur in most parthenogenetic species. Many planktonic cladocerans undergo seasonal changes in body form through succeeding generations of parthenogenetically produced individuals, a phenomenon known as cyclomorphism (Figure 21.4I).

Class Malacostraca

Body of 19–20 segments, including 6-segmented cephalon, 8-segmented thorax, and 6-segmented pleon (7-segmented in leptostracans), plus telson; with or without caudal rami; carapace covering part or all of thorax, or reduced, or absent; 0–3 pairs of maxillipeds; thoracopods primitively biramous, uniramous in some groups, phyllopodous only in members of the subclass Phyllocarida; antennules and antennae usually biramous; abdomen (pleon) usually with 5 pairs of biramous pleopods and 1 pair of biramous uropods; eyes usually present, compound, stalked or sessile; mainly gonochoristic; female gonopores on sixth, and male pores on eighth thoracomeres. When uropods are present, they are often broad and flat, lying alongside the broad telson to form a tail fan.

Most classification schemes divide the more than 40,200 species of malacostracans into three subclasses, Phyllocarida (leptostracans), Hoplocarida (stomatopods), and the megadiverse Eumalacostraca. The phyllocarids are typically viewed as representing the
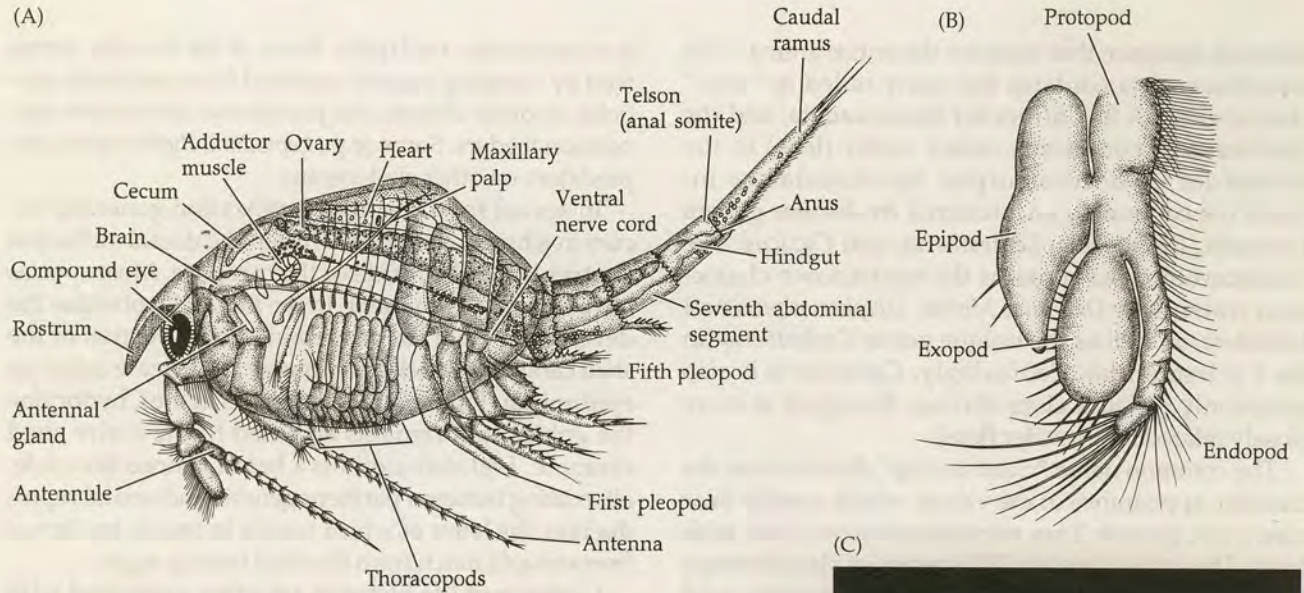
(A)

(B)

(C)

(D)

Figure 21.5 Anatomy in leptostracans (class Malacostraca, subclass Phyllocarida). (A) General anatomy of *Nebalia*. (B) Phyllopodous swimming limb of *Nebalia*. (C) SEM of *Nebalia*. (D) Anterior end of an oviger-ous *Nebalia*.

primitive malacostracan condition (6-8-7 body segments plus telson; Figure 21.5). The basic eumalacostracan body plan, characterized by the 6-8-6 (plus telson) arrangement of body segments, was recognized in the early 1900s by W. T. Calman, who termed the defining features of the Eumalacostraca "caridoid facies" (Figure 21.6). Much work has been done since Calman's day, but the basic elements of his caridoid facies are still present in all members of the subclass Eumalacostraca.

Subclass Phyllocarida

Order Leptostraca With the typical malacostracan characteristics, except notable for presence of seven free pleomeres (plus telson) rather than six, generally taken to represent the primitive condition for the class. Also, with phyllopodous thoracopods (all similar to one another); no maxillipeds; large carapace covering thorax and compressed laterally so as to from an unhinged bivalved "shell," with an adductor muscle; cephalon with a movable, articulated rostrum; pleopods 1–4 similar and biramous, 5–6 uniramous; no uropods; paired stalked compound eyes; antennules biramous; antennae uniramous; adults with both antennal and maxillary glands (Figures 21.5 and 21.21C).

The subclass Phyllocarida includes about 40 species in 10 genera. Most are 5–15 mm long, but *Nebaliopsis typica* is a giant at nearly 5 cm in length. The leptostracan body form is distinctive, with its loose bivalved
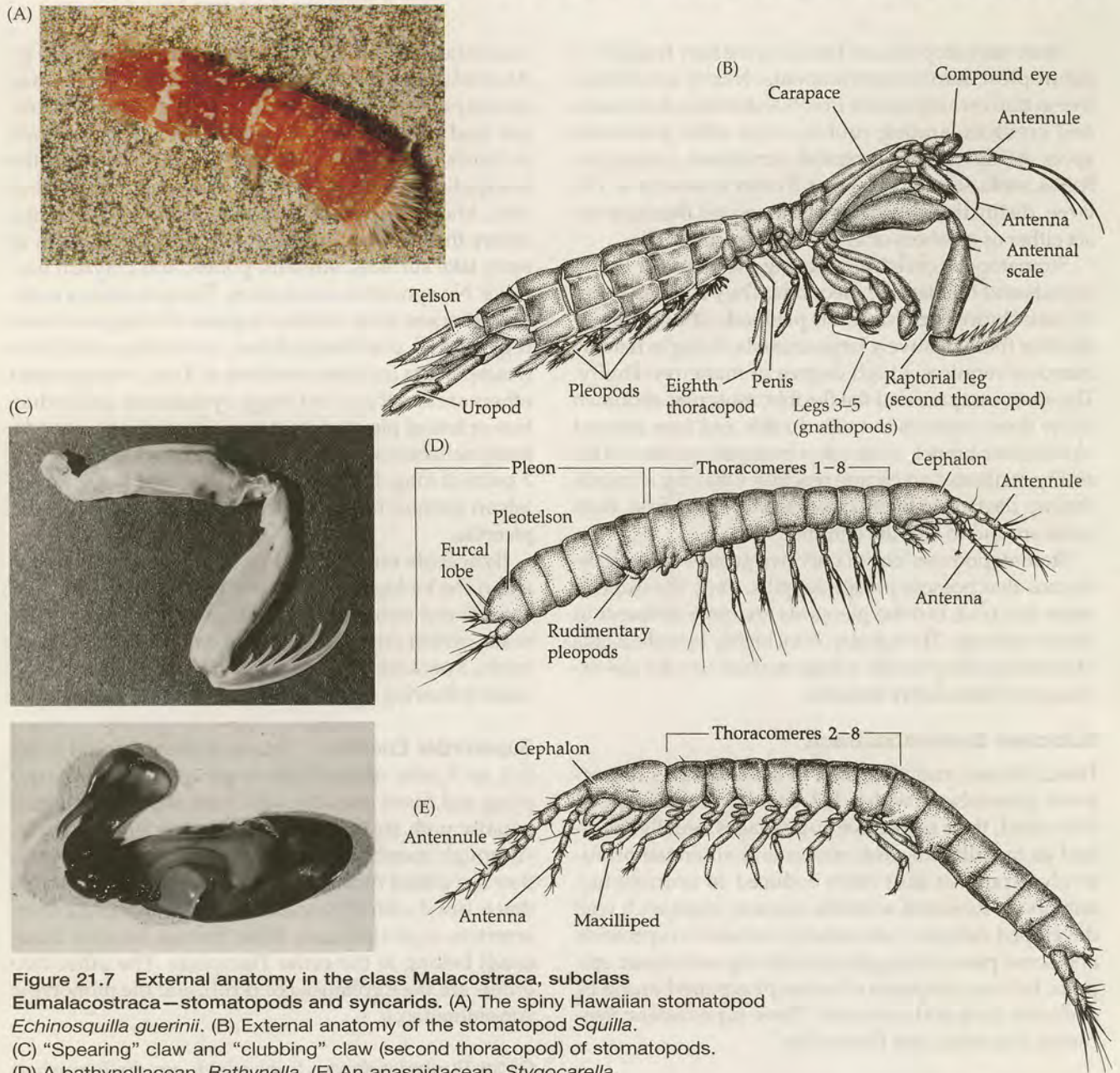
Figure 21.6 The basic eumalacostran body plan and the "caridoid facies." Note the thick (muscled) abdomen and the tail fan, which work in combination to produce a powerful tail flip escape reaction.
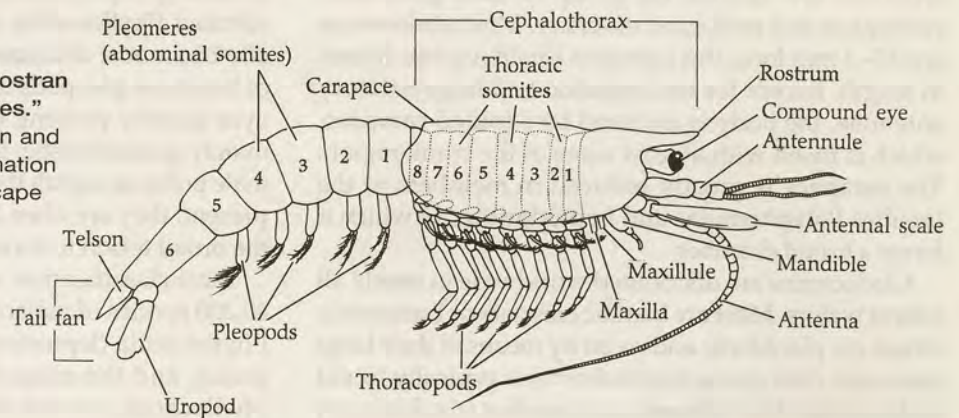
**Figure 21.7   External anatomy in the class Malacostraca, subclass
Eumalacostraca—stomatopods and syncarids.** (A) The spiny Hawaiian stomatopod
Echinosquilla guerinii. (B) External anatomy of the stomatopod *Squilla*.
(C) "Spearing" claw and "clubbing" claw (second thoracopod) of stomatopods.
(D) A bathynellacean, *Bathynella*. (E) An anaspidacean, *Stygocarella*.

carapace covering the thorax, a protruding rostrum, and an elongate abdomen. All leptostracans are marine, and most are epibenthic from the intertidal zone to a depth of 400 m; *Nebaliopsis typica* is bathypelagic. Most species seem to occur in low-oxygen environments. One species, *Dahlella caldariensis*, is associated with the hydrothermal vents of the Galapagos and the East Pacific Rise. *Speonebalia cannoni* is known only from marine caves.

Most leptostracans suspension feed by stirring up bottom sediments. They are also capable of grasping relatively large bits of food directly with the mandibles. Some are carnivorous scavengers, and some are known to aggregate in areas on the sea floor where large amounts of detritus accumulate. In many species the antennae or antennules of males are modified to hold females during copulation.

Subclass Hoplocarida

Order Stomatopoda   Carapace covering portion of head and fused with thoracomeres 1–4; head with movable, articulated rostrum; thoracopods 1–5 uniramous and subchelate, second pair massive and raptorial (all five are sometimes called "maxillipeds" or gnathopods because they are involved in feeding); thoracopods 6–8 biramous, ambulatory; pleopods biramous, with dendrobranchiate-like gills on exopods; antennules triramous; antennae biramous, with large, paired, stalked compound eyes that are unique in the animal kingdom (Figures 21.7A–C, 21.27D, and 21.33K).

All 500 or so living hoplocarids are placed in the order Stomatopoda, known as mantis shrimps. They are relatively large crustaceans, ranging in length from 2 to 30 cm. Compared with that of most malacostracans, the muscle-filled abdomen is notably robust.

Most stomatopods are found in shallow tropical or subtropical marine environments. Nearly all of them live in burrows excavated in soft sediments or in cracks and crevices, among rubble, or in other protected spots. All species are raptorial carnivores, preying on fishes, molluscs, cnidarians, and other crustaceans. The large, distinctive subchelae of the second thoracopods act either as crushers or as spears (Figure 21.7C).

Stomatopods crawl about using the posterior thoracopods and the flaplike pleopods. They also can swim by metachronal beating of the pleopods (the swimmerets). For these relatively large animals, living in narrow burrows requires a high degree of maneuverability. The short carapace and the flexible, muscular abdomen allow these animals to twist double and turn around within their tunnels or in other cramped quarters. This ability facilitates an escape reaction whereby a mantis shrimp darts into its burrow rapidly head first, then turns around to face the entrance.

Stomatopods are one of only two groups of malacostracans that possess pleopodal gills. Only the isopods share this trait, but the pleopods are quite different in the two groups. The tubular, thin, highly branched gills of stomatopods provide a large surface area for gas exchange in these active animals.

Subclass Eumalacostraca

Head, thorax, and abdomen of 6-8-6 somites respectively (plus telson); with 0, 1, 2, or 3 thoracomeres fused with head, their respective appendages usually modified as maxillipeds; antennules and antennae primitively biramous (but often reduced to uniramous); antennae often with scalelike exopod; most with well developed carapace, secondarily reduced in syncarids and some peracarids; gills primitively as thoracic epipods; tail fan composed of telson plus paired uropods; abdomen long and muscular. Three superorders: Syncarida, Eucarida, and Peracarida.

Superorder Syncarida Without maxillipeds (Bathynellacea) or with one pair of maxillipeds (Anaspidacea); no carapace; pleon bears telson with or without furcal lobes; at least some thoracopods biramous, eighth often reduced; pleopods variable; compound eyes present (stalked or sessile) or absent (Figure 21.7D,E). There are about 285 described species of syncarids in two orders, Anaspidacea and Bathynellacea.[4] To many workers, the syncarids represent a key group in eumalacostracan evolution, and they may represent an ancient relictual taxon that now inhabits refugial habitats. Through studies of the fossil record

and extant members of the order Anaspidacea (e.g., *Anaspides*), it has been suggested that syncarids may encompass the most primitive living eumalacostracan body plan. Bathynellaceans occur worldwide in interstitial or groundwater habitats, whereas the anaspididaceans are strictly Gondwanan in distribution. Many Anaspidacea are endemic to Tasmania, where they inhabit freshwater environments, such as open lake surfaces, streams, ponds, and crayfish burrows. No syncarids are marine. These reclusive eumalacostracans show various degrees of what some have regarded as paedomorphism, including small size (Anaspididae includes members to 5 cm, whereas most others are less than 1 cm long), eyelessness, and reduction or loss of pleopods and some posterior pereopods. Bathynellaceans are small (1–3 mm long), possess 6 or 7 pairs of long, thin swimming legs, and have a pleotelson formed by the fusion of the telson to the last pleonite.

Syncarids either crawl or swim. Little is known about the biology of most species, although some are considered omnivorous. Unlike most other crustaceans, which carry the eggs and developing early embryos, syncarids lay their eggs or shed them into the water following copulation.

Superorder Eucarida Telson without caudal rami; 0, 1, or 3 pairs of maxillipeds; carapace present, covering and fused dorsally with head and entire thorax; usually with stalked compound eyes; gills thoracic. Although members of this group are highly diverse, they are united by the presence of a complete carapace that is fused with all thoracic segments, forming a characteristic cephalothorax. Most species (several thousand) belong to the order Decapoda. The other two orders are the Euphausiacea (krill), and the monotypic Amphionidacea.

Order Euphausiacea Euphausids are distinguished among the eucarids by the absence of maxillipeds, the exposure of the thoracic gills external to the carapace, and the possession of biramous pereopods (the last 1 or 2 pairs sometimes being reduced). They are shrimplike in appearance. Adults have antennal glands. Most of them have photophores on the eyestalks, the bases of the second and seventh thoracopods, and between the first 4 pairs of abdominal limbs.

The 90 or so species of euphausids are all pelagic and range in length from 4 to 15 cm. The pleopods function as swimmerets. Euphausids are known from all oceanic environments to depths of 5,000 m. Most species are distinctly gregarious, and species that occur in huge schools (**krill**) provide a major source of food for larger nektonic animals (baleen whales, squids, fishes) and even some marine birds. Krill densities, particularly for *Euphausia superba*, often exceed 1,000 animals/m^3 (614

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[4]Until recently a third syncarid order was recognized, the Stygocaridacea, endemic to the Southern Hemisphere. Most workers now agree that the stygocarids should be reduced to the rank of family within the order Anaspidacea.
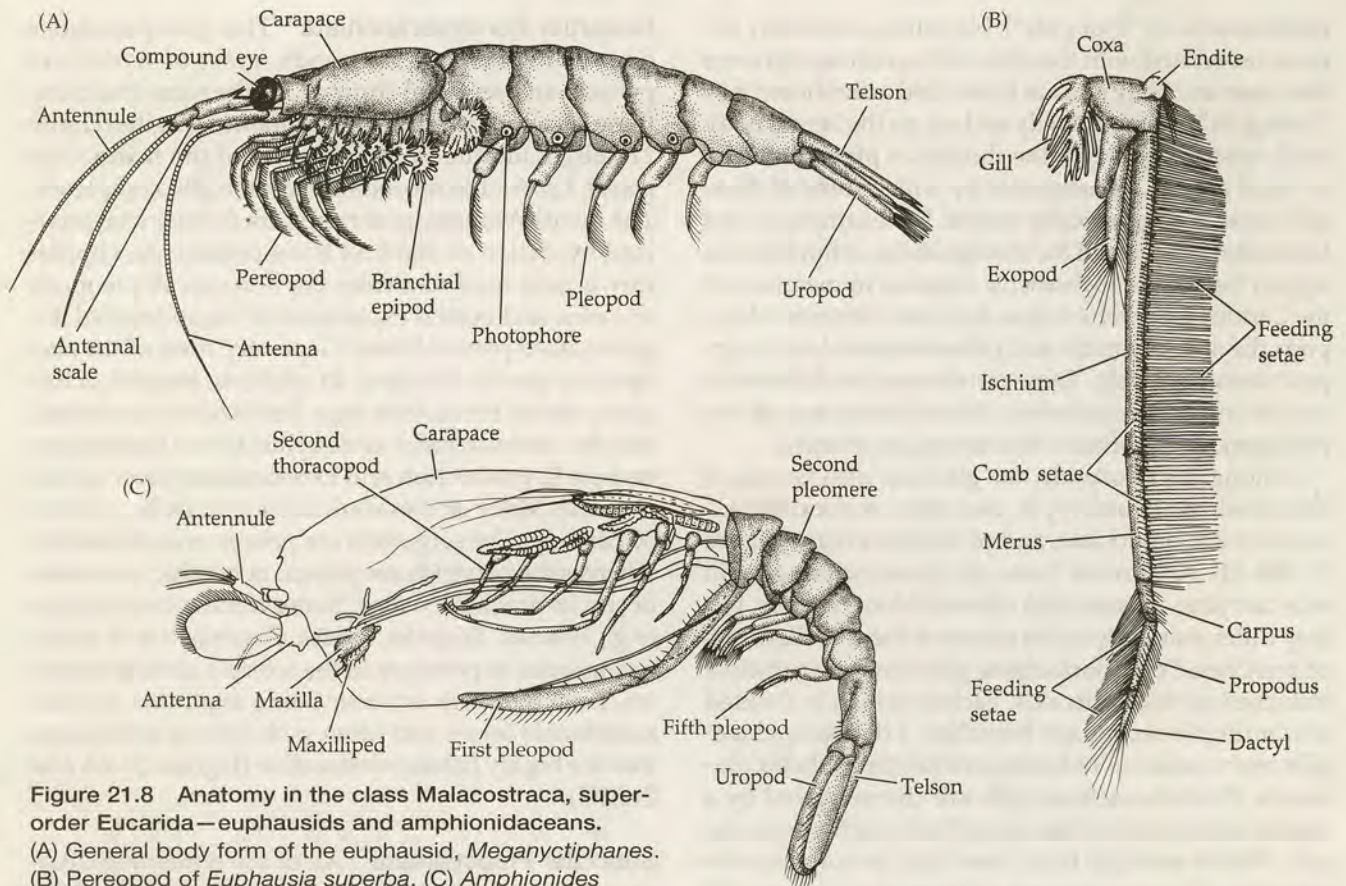
Figure 21.8 Anatomy in the class Malacostraca, super-order Eucarida—euphausids and amphionidaceans.
(A) General body form of the euphausid, *Meganyctiphanes*.
(B) Pereopod of *Euphausia superba*. (C) *Amphionides reynaudii* (female), the only living species of the Amphionidacea.

g wet weight/m³).[5] Generally, euphausids are suspension feeders, although predation and detritivory also occur (Figures 21.8A,B and 21.21E).

Order Amphionidacea   The single known species of the order Amphionidacea, *Amphionides reynaudii*, possesses an enlarged cephalothorax covered by a thin, almost membranous carapace that extends to enclose the thoracopods. The thoracopods are biramous with short exopods. The first pair is modified as maxillipeds, and the last pair is absent in females. Some of the mouthparts are highly reduced in females. The pleopods are biramous and natatory, except that the

first pair in females is uniramous and greatly enlarged, perhaps functioning to form a brood pouch extending under the thorax. Females have a reduced gut and apparently do not feed. *Amphionides* is a worldwide member of marine oceanic plankton and occurs to a depth of 1,700 m (Figure 21.8C).

Order Decapoda   The decapods are among the most familiar eumalacostracans. They possess a well developed carapace enclosing a branchial chamber, but they differ from other eucarid orders in always possessing 3 pairs of maxillipeds, leaving 5 pairs of functional uniramous or weakly biramous pereopods (hence the name, Decapoda); one (or more) pairs of anterior pereopods are usually clawed (chelate). Adults have antennal glands. Rearrangement of the subtaxa within this order is a popular carcinological pastime (see Martin and Davis 2001 for an entry into the vast literature on decapod classification). In vernacular terms, nearly every decapod may be recognized as some sort of shrimp, crab, lobster, or crayfish.

We do not want to belabor the issue of decapod gill nomenclature. However, the gills play a prominent role in the taxonomy of this group; thus, we provide brief descriptions of the basic types. All decapod gills arise as thoracic coxal exites (epipods), but their final placement varies. Those that remain attached to the coxae are

[5]Where krill densities exceed about 100 grams per cubic meter, they are often fished commercially. Krill schools can extend for tens of miles, contain millions of tons of krill, and stain the ocean red with their surface swarms in coastal waters. Large baleen whales can eat a ton of krill in one mouthful. Seals, fish, squid, and humans also eat krill. Krill fishing has been banned in most of North America, but it continues in Japan where tens of thousands of tons are landed annually and used mainly as feed for farmed fish. The largest krill fishery is in the ocean surrounding Antarctica, where they have been harvested commercially since the 1970s. In the 1980s, large fleets from the Soviet Union caught up to 400,000 tons of Antarctic krill annually, but the current catch is now down to about 120,000 tons (taken by Japan, Korea, Norway, Poland, the Ukraine, and the U.S.).

podobranchs (= "foot gills"), but others eventually become associated with the articular membrane between the coxae and body and are thus called arthrobranchs (= "joint gills"). Some actually end up on the lateral body wall, or side-surface of the thorax, as **pleurobranchs** (= "side gills"). The sequence by which some of these gills arise ontogenetically varies. For example, in the Dendrobranchiata and the Stenopodidea, arthrobranchs appear before pleurobranchs, whereas in members of the Caridea the reverse is true. In most of the other decapods the arthrobranchs and pleurobranchs tend to appear simultaneously. These developmental differences may be minor heterochronic dissimilarities and of less phylogenetic importance than actual gill anatomy.

Among the decapods, the gills can also be one of three basic structural types, described as dendrobranchiate, trichobranchiate, and phyllobranchiate (Figure 21.28B–D). All three of these gill types include a main axis carrying afferent and efferent blood vessels, but they differ markedly in the nature of the side filaments or branches. Dendrobranchiate gills bear two principal branches off the main axis, each of which is divided into multiple secondary branches. Trichobranchiate gills bear a series of radiating unbranched tubular filaments. Phyllobranchiate gills are characterized by a double series of platelike or leaflike branches from the axis. Within each gill type, there may be considerable variation. The occurrences of these three major gill types among various taxa are presented below.

Close inspection of the proximal parts of the pereopods usually reveals another decapod feature: in most forms, the basis and ischium are fused (as a basi-ischium), with the point of fusion often indicated by a suture line. Tegumental glands are also a ubiquitous feature among the Decapoda. These glands originate below the epidermal cells and produce a fluid that opens on the surface of the cuticle. They have been reported from gills, legs, pleopods, and uropods. The roles of tegmental glands are not well known, and they have been suspected to be involved in cuticular tanning, the production of mucus by the mouthparts, the production of cement substance involved with egg attachment, and possibly also grooming.

The 18,000 or so living species of decapods comprise a highly diverse group. They occur in all aquatic environments at all depths, and a few spend most of their lives on land. Many are pelagic, but others have adopted benthic sedentary, errant, or burrowing lifestyles. Decorating of the exoskeleton is frequently seen among the decapods, especially in spider crabs (Brachyura: Majoidea), which use Velcro-like hooked setae to attach dead or living plants and animals; decorating has been shown to reduce predation through camouflage and/or chemical deterrence. Decapod feeding strategies include suspension feeding, predation, herbivory, scavenging, and more. Most workers recognize two suborders: Dendrobranchiata and Pleocyemata.

Suborder Dendrobranchiata   This group includes over 500 species of decapods, most of which are penaeid and sergestid shrimps. As the name indicates, these decapods possess dendrobranchiate gills (Figure 21.28B), a unique synapomorphy of the taxon. One genus, *Lucifer*, has secondarily lost the gills completely. The dendrobranchiate shrimps are further characterized by chelae on the first three pereopods, copulatory organs modified from the first pair of pleopods in males, and ventral expansions of the abdominal tergites (called pleural lobes). Generally, none of the chelipeds is greatly enlarged. In addition, females of this group do not brood their eggs. Fertilization is external, and the embryos hatch as nauplius larvae (see the section on Reproduction and Development later in this chapter). Many of these animals are quite large, over 30 cm long. The sergestids are pelagic and all marine, whereas the penaeids are pelagic or benthic, and some occur in brackish water. Some dendrobranchiates (e.g., *Penaeus, Sergestes, Acetes, Sicyonia*) are of major commercial importance in the world's shrimp fisheries, most of which are now being exploited beyond sustainable levels and often with fishing techniques that are highly habitat-destructive (Figures 21.9A and 21.33G).

Suborder Pleocyemata   All of the remaining decapods belong to the suborder Pleocyemata. Members of this taxon never possess dendrobranchiate gills. The embryos are brooded on the female's pleopods and hatch at some stage later than the nauplius larva. Included in this suborder are several kinds of shrimps, the crabs, crayfish, lobsters, and a host of less familiar forms. Most current workers now recognize 11 infraorders within the Pleocyemata, as we have done below, but a number of other schemes have been proposed and persist in the literature. One older approach divided decapods into two large groups, called the Natantia and Reptantia—the swimming and walking decapods, respectively. Although these terms have largely been abandoned as formal taxa, they still serve a useful descriptive purpose, and one continues to see references to natant decapods and reptant decapods.

Infraorder Procarididea   The procarids consist of a single family containing two genera of shrimp, *Procaris* and *Vetericaris*, that have been called "primitive shrimps." Like caridean shrimp (below) and most other pleocyemates, they bear flattened, platelike (nondendrobranch) gills, but they lack claws on any of their legs, have a very leglike (pediform) third maxilliped, and have epipods on all of the maxillipeds and pereopods, assumed to be an ancestral condition because most decapod groups no longer bear the full complement. They are known from anchialine habitats—inland pools with connections to the sea (Figure 21.9B).
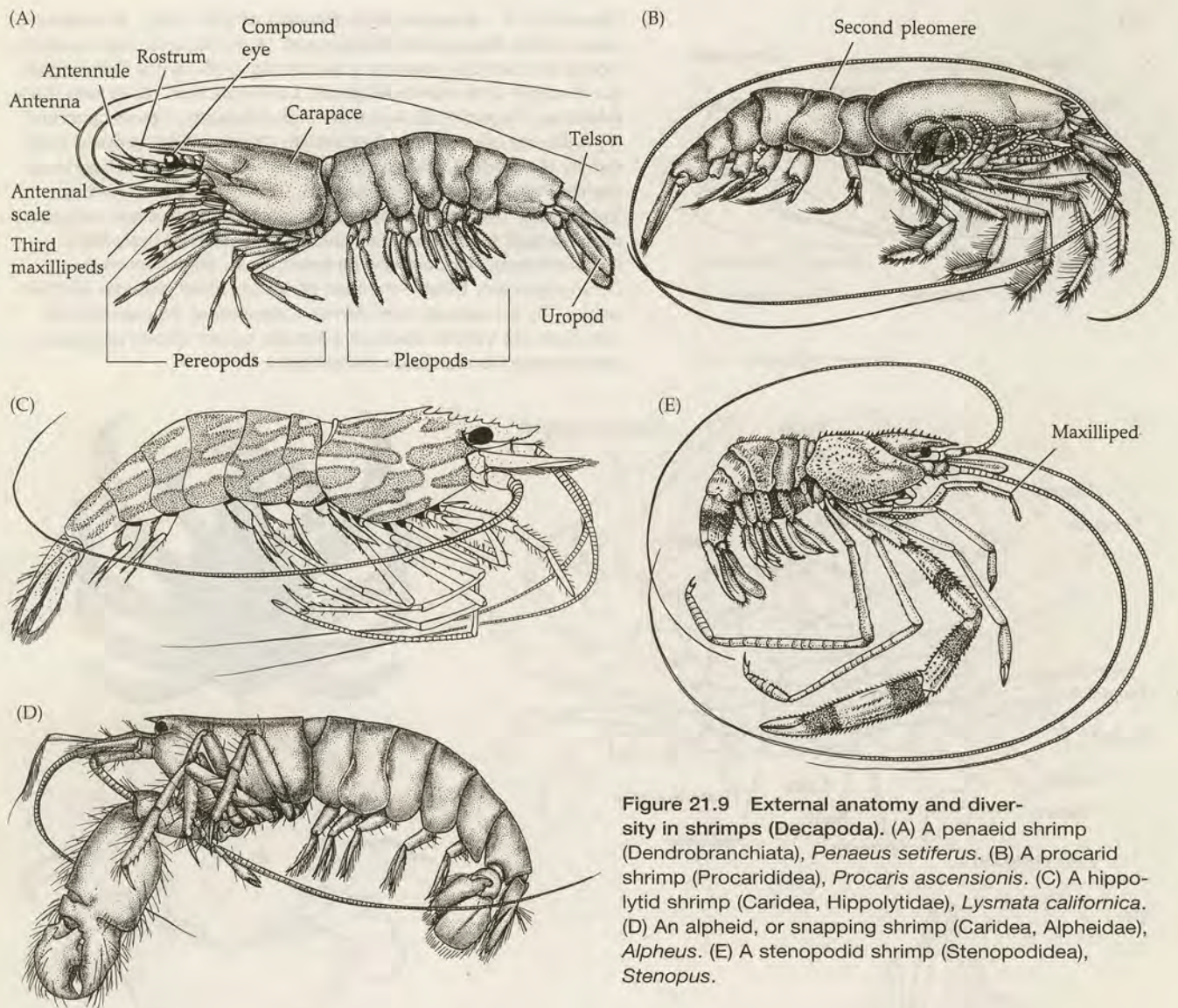
Figure 21.9 External anatomy and diversity in shrimps (Decapoda). (A) A penaeid shrimp (Dendrobranchiata), *Penaeus setiferus*. (B) A procarid shrimp (Procarididea), *Procaris ascensionis.* (C) A hippolytid shrimp (Caridea, Hippolytidae), *Lysmata californica*. (D) An alpheid, or snapping shrimp (Caridea, Alpheidae), *Alpheus*. (E) A stenopodid shrimp (Stenopodidea), *Stenopus*.

Infraorder Caridea The nearly 3,500 living species in this infraorder are generally referred to as the caridean shrimps. These swimming decapods have phyllobranchiate gills. The first 1 or 2 pairs of pereopods are chelate and variably enlarged. The second abdominal pleura (side walls) are distinctly enlarged to overlap both the first and third pleura. The first pleopods are generally somewhat reduced, but not much modified, in the males (Figures 21.1K, 21.9C,D, 21.24D, and 21.31D).

Infraorder Stenopodidea The 70 or so species in this infraorder belong to three families. The first 3 pairs of pereopods are chelate, and the third pair is significantly larger than the others. The gills are trichobranchiate. The first pleopods are uniramous in males and females, but are not strikingly modified. The second abdominal pleura are not expanded as they are in carideans (Figures 21.9E and 21.31B).

These colorful shrimps are usually only a few centimeters long (2–7 cm). Most species are tropical and associated with shallow benthic environments, especially with coral reefs; others are known from the deep sea. Many are commensal, and the group includes the cleaner shrimps (e.g., *Stenopus*) of tropical reefs, which are known to remove parasites from local fishes. Stenopodids often occur as male–female couples. Perhaps the most noted example of this bonding is associated with the glass sponge (*Euplectella*) shrimp, *Spongicola venusta*: A young male and female shrimp enter the atrium of a host sponge, eventually growing too large to escape and thus spending the rest of their days together.

Infraorder Brachyura These are the so-called "true crabs." The abdomen is symmetrical but highly reduced and flexed beneath the thorax, and uropods are usually absent. The body, hidden beneath a well-developed carapace, is distinctly flattened dorsoventrally and often expanded laterally. The gills are typically phyllobranchiate, but exceptions occur.
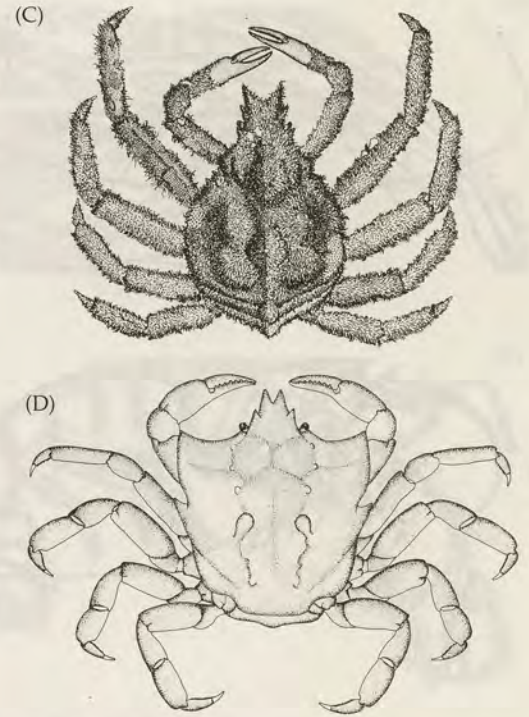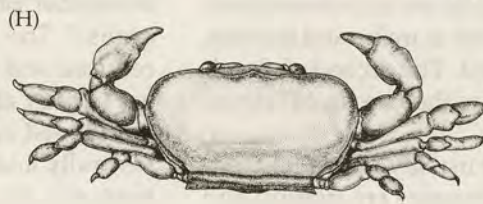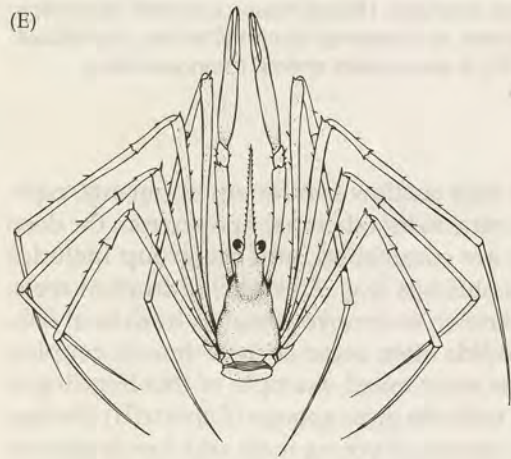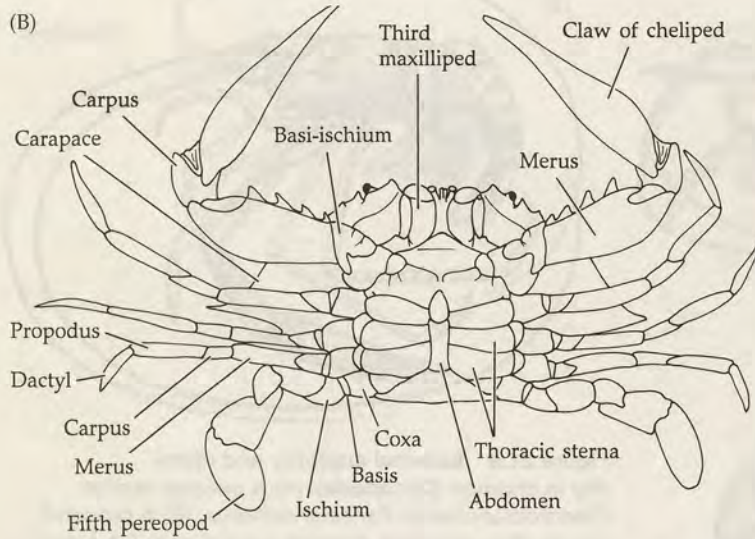
(A)

Palp of maxilliped   Antennule   Compound eye
Carapace   Antenna   Carpus
Orbit
Third maxilliped   Dactyl   Propodus
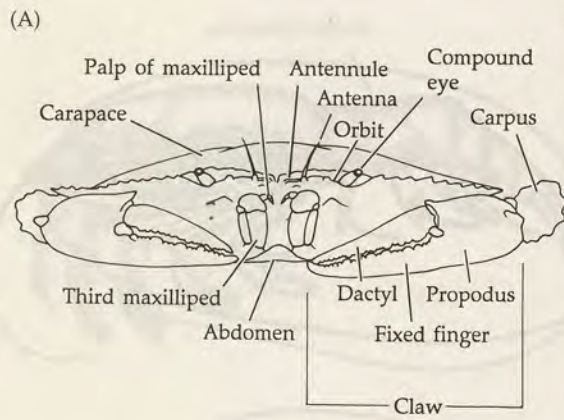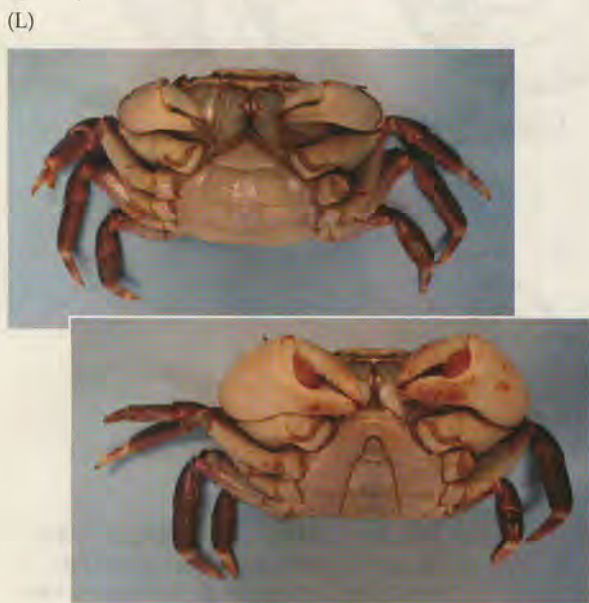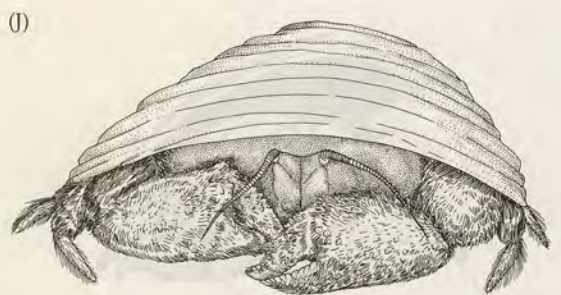Abdomen   Fixed finger
Claw

Figure 21.10 Anatomy and diversity of the "true," or brachyuran, crabs (Decapoda: Brachyura). (A,B) General crab anatomy: frontal and ventral views of a swimming crab (family Portunidae). (C) A spider crab (family Majidae), *Loxorhynchus*. (D) A kelp crab (Majidae), *Pugettia*. (E) An arrow crab (Majidae), *Stenorhynchus*. (F) A cancer crab (family Cancridae), *Cancer*. (G) A grapsid crab (family Grapsidae), *Pachygrapsus*. (H) A pinnotherid or pea crab (family Pinnotheridae), *Parapinnixa*. (I) A xanthid crab (family Xanthidae), *Trapezia*. Many members of this genus are obligate commensals in scleractinian corals. (J) A dromiid crab (family Dromiidae), *Hypoconcha* (anterior view). Members of the Dromiidae carry bivalve mollusc shells (or other objects) on their backs. (K) A calappid crab (family Calappidae), *Hepatus* (anterior view). (L) Ventral views of a female (upper photo) and (lower photo) male *Hemigrapsus sexdentatus*.

(B)

Third maxilliped   Claw of cheliped
Carpus
Carapace   Basi-ischium
Merus
Propodus
Dactyl
Carpus   Coxa
Merus   Thoracic sterna
Basis
Fifth pereopod   Ischium   Abdomen

(C)

(D)

(E)

(F)

(G)

(H)

(I)

(J)

(K)

(L)

The first pereopods are chelate and usually enlarged. Pereopods 2 to 5 are typically simple, stenopodous walking legs, although in some groups, the fifth pereopods are also chelate. The eyes are positioned lateral to the antennae. Males lack pleopods 3 to 5. The distinctive larval stage is called a zoea; its carapace is spherical and bears a ventrally directed rostral spine (or no spine) (Figures 21.1E, 21.10, 21.27H, 21.28F,G, 21.29C, 21.32, and 21.33H,I).

Brachyuran crabs are mostly marine, but freshwater, semi-terrestrial, and moist terrestrial species occur in the tropics. The land crabs (certain species in the families Gecarcinidae, Ocypodidae, Grapsidae, etc.) are still dependent on the ocean for breeding and larval development. The surprisingly large number of freshwater crabs (about 3,000 species, classified into about a dozen families) all have direct development, incubate their embryos, and are independent of sea water. Some freshwater crabs are intermediate hosts of *Paragonimus*, a cosmotropical parasitic human lung fluke, and others are obligate phoretic hosts of larval black flies (*Simulium*), the vector for *Onchocerca volvulus* (the causative agent of river blindness). A number of species carry other invertebrates on their carapace (e.g., sponges, tunicates) or on their claws (e.g., anemones); these associations are generally thought to be mutualistic, providing camouflage or predator deterrence for the crab while their partner is moved about in the environment and may feed off debris from their host's feeding activities. The opener photo for this chapter shows the tropical Pacific teddy-bear crab, *Polydectus cupulifer*, which is densely covered with setae and frequently carries a sea anemone on each cheliped. In the northeast Pacific, megalopae and juveniles of the crab *Cancer gracilis* ride (and feed) on the bell of certain jellyfish; individuals of *Phacellophora camtschatica* (Scyphozoa) have been found with hundreds of *C. graciils* megalopae. There are about 7,000 described species of Brachyura.

Infraorder Anomura   This group includes hermit crabs, galatheid crabs, king crabs, porcelain crabs, mole crabs, and sand crabs. The abdomen may be soft and asymmetrically twisted (as in hermit crabs) or symmetrical, short, and flexed beneath the thorax (as in porcelain crabs and others). Those with twisted abdomens typically inhabit gastropod shells or other empty "houses" not of their own making. King crabs (Lithodidae and Hapalogastridae) probably evolved out of hermit crab-like ancestors. Carapace shape and gill structure vary. The first pereopods are chelate; the third pereopods are never chelate. The second, fourth, and fifth pairs are usually simple, but occasionally they are chelate or subchelate. The fifth pereopods (and sometimes the fourth) are generally much reduced and do not function as walking limbs; the fifth pereopods function as gill cleaners and often are not visible externally. The pleopods are reduced or absent. The eyes are positioned medial to the antennae. The zoea larva is similar to that of the true crabs but is typically longer than broad, with the rostral spine directed anteriorly. Most anomurans are marine, but a few freshwater and semi-terrestrial species are known. The so-called "yeti crab" (*Kiwa hirsuta*) was discovered in 2005 from 2,200 m-deep hydrothermal vents south of Easter Island. It is remarkable for its "garden" of filamentous bacteria that grow on the long setae of the exoskeleton; the bacteria are heterotrophic, utilizing sulfides in the deep environment (the precise role of the bacteria, of several species, in the life history of the yeti crab is not yet well understood). A second species of *Kiwa* was described in 2011 (Figures 21.1F–J, 21.11C–G, 21.24A–C, 21.31A, and 21.33I).
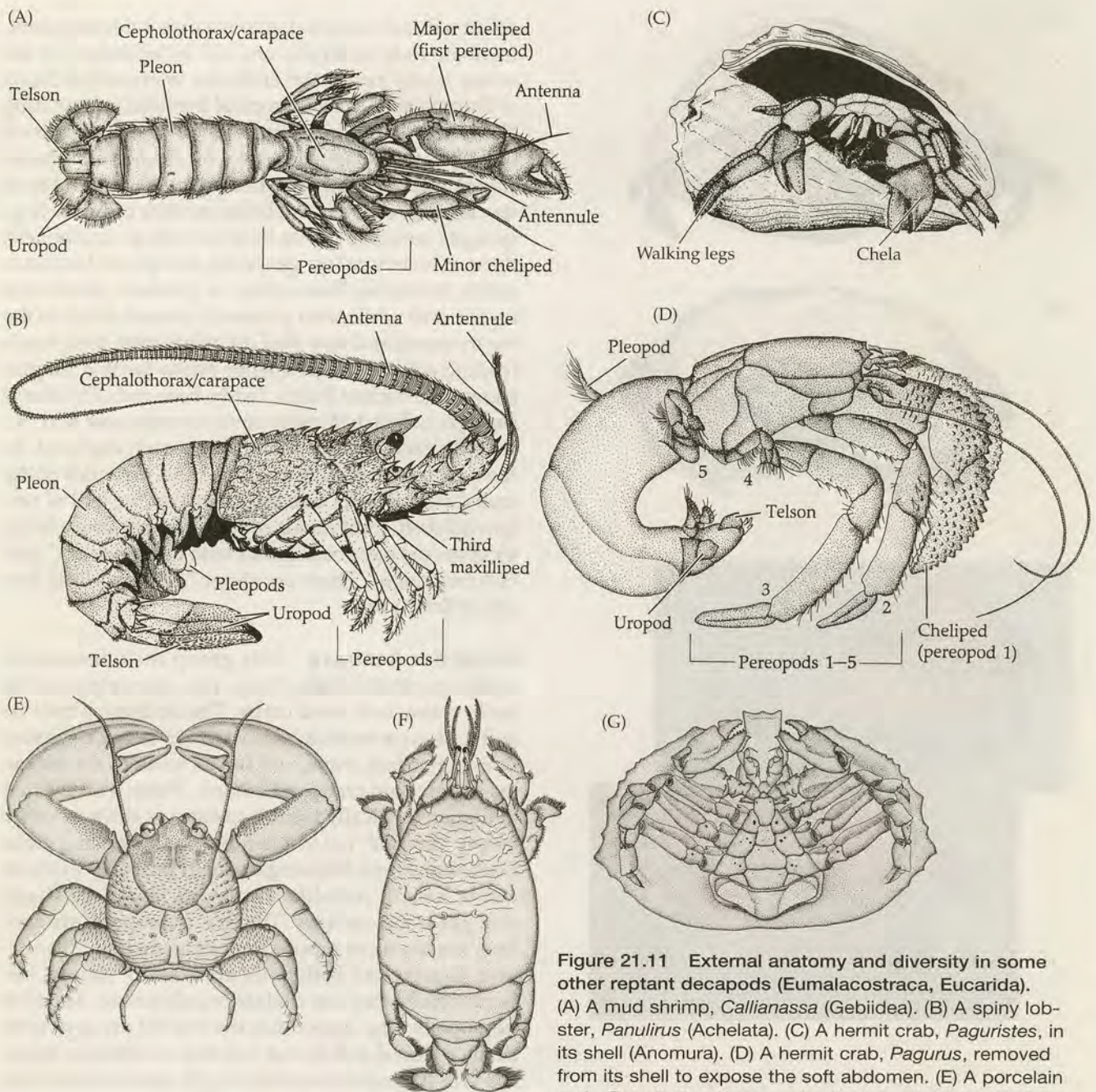
Figure 21.11 External anatomy and diversity in some other reptant decapods (Eumalacostraca, Eucarida). (A) A mud shrimp, *Callianassa* (Gebiidea). (B) A spiny lobster, *Panulirus* (Achelata). (C) A hermit crab, *Paguristes*, in its shell (Anomura). (D) A hermit crab, *Pagurus*, removed from its shell to expose the soft abdomen. (E) A porcelain crab, *Petrolisthes* (Anomura), with the reduced posterior pereopods extended. (F) A sand crab, *Emerita* (Anomura). (G) The umbrella crab *Cryptolithodes* (Anomura), in ventral view.

Infraorder Astacidea The 650+ species of crayfish and clawed lobsters comprise some of the most familiar decapods (Figure 21.2). As in most other decapods, the dorsoventrally flattened abdomen terminates in a strong tail fan. The gills are trichobranchiate. The first 3 pairs of pereopods are always chelate, and the first pair is greatly enlarged. *Homarus americanus*, the American or Maine lobster, is strictly marine and is the largest living crustacean by weight (the record weight being over 20 kilograms). Most crayfish live in fresh water, but a few species live in damp soil, where they may excavate extensive and complex burrow systems. The 600+ species of freshwater crayfish comprise a monophyletic group that is sister to clawed lobsters. Over 425 species

of crayfish occur in North America alone, where they show high levels of endemicity to particular regions or river drainages. (Figures 21.27E,G and 21.29B).

Infraorder Achelata This group includes the coral and spiny lobsters (family Palinuridae) and slipper lobsters (family Scyllaridae). The name Achelata comes from the fact that they lack chelae on all pereopods as adults (except for a small grooming claw on pereopod 5 in some females). The flattened abdomen bears a tail fan; the carapace may be cylindrical or flattened

dorsoventrally; the gills are trichobranchiate. The large, flattened larvae, called phyllosomas because of their leaf-like appearance, are unique and distinctive. All species are marine, and they are found in a variety of habitats throughout the tropics. Many species produce sounds by rubbing a process (the plectrum) at the base of the antennae against a "file" on the head (Figures 21.1M, 21.11B, 21.30A,C, and 21.33L).

Infraorders Gebiidea and Axiidea These two infraorders, traditionally referred to collectively as the Thalassinidea, have recently been recognized as distinct. The vernacular term "thalassinid" is still sometimes used to refer to them together. The mud and ghost shrimps are particularly difficult to place within the decapods. Sometimes they are depicted as related to the crayfish and chelate lobsters (Astacidea), and sometimes they are grouped with the hermit crabs and their relatives (Anomura). These decapods have a symmetrical abdomen that is flattened dorsoventrally and extends posteriorly as a well-developed tailfan. The carapace is somewhat compressed laterally, and the gills are trichobranchiate. The first 2 pairs of pereopods are chelate, and the first pair is generally much enlarged. Most of these animals are marine burrowers or live in coral rubble. They generally have a rather thin, lightly sclerotized cuticle, but some (e.g., members of the family Axiidae) have thicker skeletons and are more lobster-like in appearance. Gebiideans (particularly *Upogebia*, *Callianassa*, and related genera) often occur in huge colonies on tidal flats, where their burrow holes form characteristic patterns on the sediment surface (Figures 21.1L and 21.11A).

Infraorders Glypheidea and Polychelida The glypheids are something of a relict group, represented by two living genera (*Neoglyphea* and *Laurentaglyphea*), each with a single species, of a formerly diverse group known from the fossil record. Polychelids are a small group of blind deep-sea lobsters, notable for having chelae on all of their pereopods and unusual, large, globate larvae (called eryoneicus larvae) unique among the decapods.

Superorder Peracarida Telson without caudal rami; 1 (rarely 2–3) pair of maxillipeds; maxilliped basis typically produced into an anteriorly directed, bladelike endite; mandibles with articulated accessory processes in adults, between molar and incisor processes, called the **lacinia mobilis**; carapace, when present, not fused with posterior pereonites and usually reduced in size; gills thoracic or abdominal; with unique, thinly flattened thoracic coxal endites, called oostegites, that form a ventral brood pouch or marsupium in females all species except members of the order Thermosbaenacea (the latter using the carapace to brood embryos); young hatch as **mancas**, a

prejuvenile stage lacking the last pair of thoracopods (no free-living larvae occur in this group) (Figures 21.12–21.15).

The roughly 25,000 species of peracarids are divided among nine orders. The peracarids are an extremely successful group of malacostracan crustaceans and are known from many habitats. Although most are marine, many also occur on land and in fresh water, and several species live in hot springs at temperatures of 30–50°C. Aquatic forms include planktonic as well as benthic species at all depths. The group includes the most successful terrestrial crustaceans—the pillbugs and sowbugs of the order Isopoda—and a few amphipods that have invaded land and live in damp forest leaf litter or gardens. Peracarids range in size from tiny interstitial forms only a few millimeters long to planktonic amphipods over 12 cm long (*Cystisoma*), deepsea necrophagous amphipods exceeding 34 cm (*Alicella gigantea*), and benthic isopods growing to 50 cm in length (*Bathynomus giganteus*). These animals exhibit all sorts of feeding strategies; a number of them, especially isopods and amphipods, are commensals or parasites.

Order Mysida Carapace well developed, covering most of thorax, but never fused with more than four anterior thoracic segments; maxillipeds (1–2 pairs) not associated with cephalic appendages; thoracomere 1 separated from head by internal skeletal bar; abdomen with well developed tail fan; pereopods biramous, except last pair, which are sometimes reduced; pleopods reduced or, in males, modified; compound eyes stalked, sometimes reduced; gills absent; usually with a statocyst in each uropodal endopod; adults with antennal glands (Figures 21.12A,B, 21.30B, and 21.33C).

There are more than 1,050 species of mysids, ranging in length from about 2 mm to 8 cm. Most swim by action of the thoracic exopods. Mysids are shrimplike crustaceans that are often confused with the superficially similar euphausids (which lack oostegites and uropodal statocysts). Mysids are pelagic or demersal and are known from all ocean depths; a few species occur in freshwater. Some species are intertidal and burrow in the sand during low tides. Most are omnivorous suspension feeders, eating algae, zooplankton, and suspended detritus. In the past, mysids were combined with lophogastrids and the extinct Pygocephalomorpha as the "Mysidacea."

Order Lophogastrida Similar to mysids, except for the following: maxillipeds (1 pair) are associated with the cephalic appendages; thoracomere 1 not separated from head by internal skeletal bar; pleopods well developed; gills present; adults with both antennal and maxillary glands; without statocysts; all 7 pairs of pereopods well developed and similar (except among members of the family Eucopiidae, in which their structure varies) (Figures 21.12C,D and 21.21G).
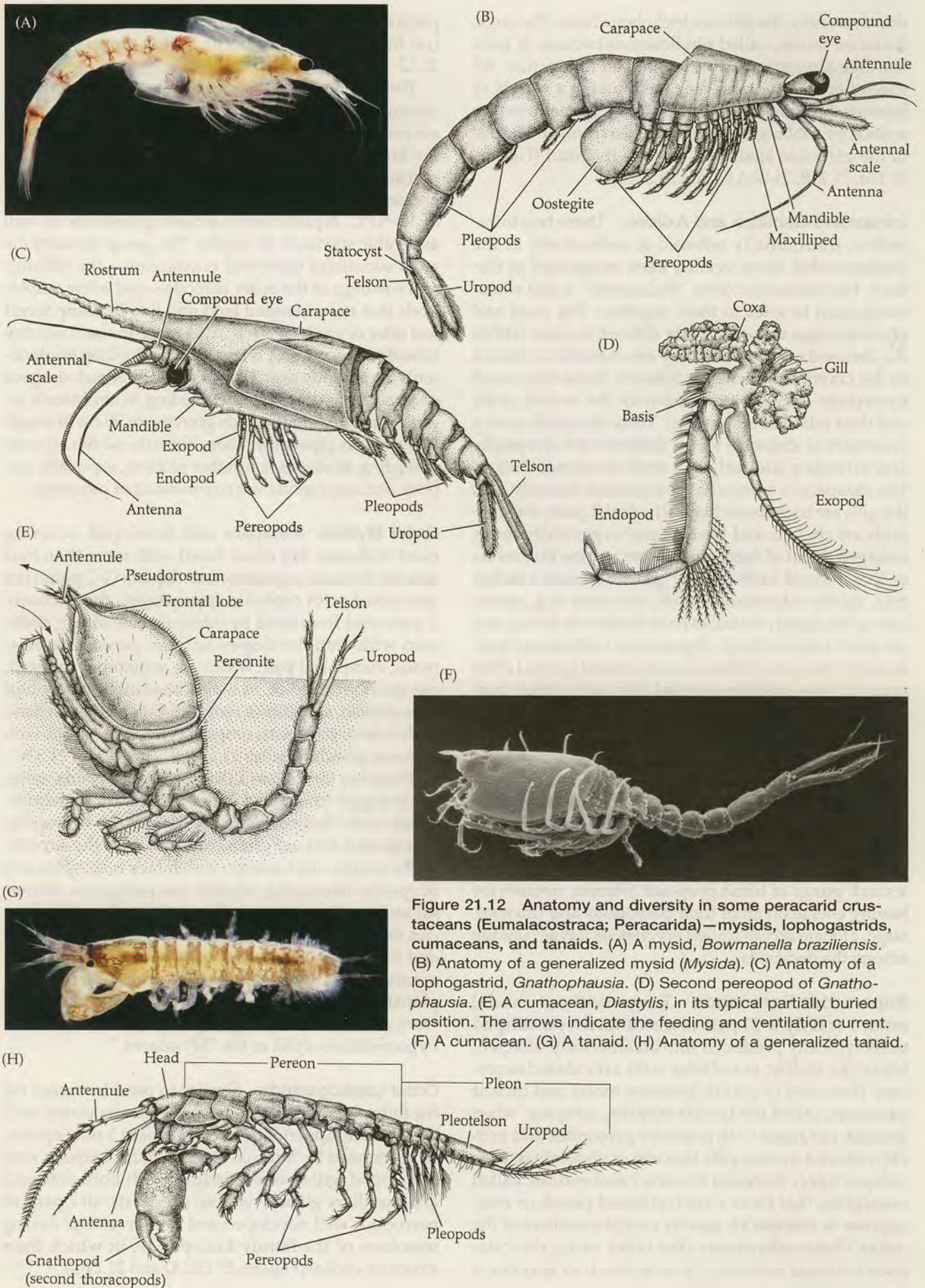
Figure 21.12 **Anatomy and diversity in some peracarid crustaceans (Eumalacostraca; Peracarida)—mysids, lophogastrids, cumaceans, and tanaids. (A)** A mysid, *Bowmanella braziliensis*. **(B)** Anatomy of a generalized mysid (*Mysida*). **(C)** Anatomy of a lophogastrid, *Gnathophausia*. **(D)** Second pereopod of *Gnathophausia*. **(E)** A cumacean, *Diastylis*, in its typical partially buried position. The arrows indicate the feeding and ventilation current. **(F)** A cumacean. **(G)** A tanaid. **(H)** Anatomy of a generalized tanaid.

There are about 60 known species of lophogastrids, most of which are 1–8 cm long, although the giant *Gnathophausia ingens* reaches 35 cm. All are pelagic swimmers, and the group has a cosmopolitan oceanic distribution. Lophogastrids are primarily predators on zooplankton.

Order Cumacea   Carapace present, covering and fused to first three thoracic segments, whose appendages are modified as maxillipeds, the first with modified branchial apparatus associated with branchial cavity formed by carapace; pereopods 1–5 ambulatory, simple, 1–4 may be biramous; pleopods usually absent in females and present in males; telson sometimes fused with sixth pleonite, forming pleotelson; uropods styliform; compound eyes absent, or sessile and usually fused (Figures 21.1P and 21.12E,F).

Cumaceans are small, odd-looking crustaceans with a large, bulbous anterior end and a long, slender posterior—resembling horizontal commas! The great carcinologist Waldo Schmitt referred to them as "little wonders and queer blunders." They occur worldwide and include about 1,500 species, most of which are between 0.1 and 2 cm long, though some species in cold water reach 3 cm in length. Most are marine, although a few brackish-water species are known. They live in association with bottom sediments, but are capable of swimming and probably leave the bottom to breed. Most are deposit feeders or predators on the meiofauna, others eat the organic film on sand grains.

Order Tanaidacea   Carapace present and fused with first two thoracic segments; thoracopods 1–2 are maxillipeds, the second being chelate; thoracopods 3–8 are simple, ambulatory pereopods; pleopods present or absent; uropods biramous or uniramous; telson and last one or two pleonites fused as pleotelson; adults with maxillary and (vestigial) antennal glands; compound eyes absent, or present and on cephalic lobes. Members of this order are known worldwide from benthic marine habitats; a few live in brackish or nearly fresh water. Most of the 1,500 or so species are small, ranging from 0.5 to 2 cm in length. They often live in burrows or tubes and are known from all ocean depths. Many are suspension feeders, others are detritivores, and still others are predators (Figure 21.12G,H).

Order Mictacea   Without a carapace, but with a well developed head shield fused with first thoracomere and produced laterally over bases of mouthparts; 1 pair of maxillipeds; pereopods simple, 1–5 or 2–6 biramous, exopods natatory; gills absent; pleopods reduced, uniramous or biramous; uropods biramous, with 2–5 segmented rami; telson not fused with pleonites; stalked eyes present (*Mictocaris*) but lacking any evidence of visual elements, or absent (*Hirsutia*) (Figure 21.13D–E).

Mictacea is the most recently (1985) established peracaridan order. The order was erected to accommodate two species of unusual crustaceans: *Mictocaris halope* (from marine caves in Bermuda) and *Hirsutia bathyalis* (from a benthic sample 1,000 m deep in the Guyana Basin off northeastern South America). A third species of Mictacea was described in 1988 from Australia, and a fourth from the Bahamas in 1992; there are now 6 species known. Mictaceans are small, 2–3.5 mm in length. *Mictocaris halope* is the best known of these species because many specimens have been recovered and some have been studied alive. It is pelagic in cave waters and swims by using its pereopodal exopods. The status of the Mictacea as a monophyletic grouping and its relationships to other peracarid orders is a subject of ongoing debate. Some workers recognize the family Hirsutiidae (containing *Hirsutia*, *Montucaris*, and *Thetispelecaris*) as a separate order, the Bochusacea (male pleopods biramous).

Order Spelaeogriphacea   Carapace short, fused with first thoracomere; 1 pair of maxillipeds; pereopods 1–7 simple, biramous, with shortened exopods; exopods on legs 1–3 modified for producing currents, on legs 4–7 as gills; pleopods 1–4 biramous, natatory; pleopod 5 reduced; tail fan well developed; compound eyes nonfunctional or absent, but eyestalks persist (Figures 21.13A and 21.21H). The order Spelaeogriphacea is currently known from only four living species. These rare, small (less than 1 cm) peracarids were long known only from a single species living in a freshwater stream in Bat Cave on Table Mountain, South Africa. A second species is known from a freshwater cave in Brazil, and a third and fourth species were described from an aquifer in Australia. Little is known about the biology of these animals, but they are suspected to be detritus feeders. Like thermosbaenaceans, spelaeogriphaceans are thought to be relicts of a more widespread shallow-water marine Tethyan fauna stranded in interstitial and ground-water environments during periods of marine regression.

Order Thermosbaenacea   Carapace present, fused with first thoracomere and extending back over 2–3 additional segments; 1 pair of maxillipeds; pereopods biramous, simple, lacking epipods and oostegites; carapace forms dorsal brood pouch (unlike all other peracarids, which form the brood pouch from ventral oostegites); 2 pairs of uniramous pleopods; uropods biramous; telson free or forming pleotelson with last pleonite; eyes absent (Figure 21.13B,C). About 34 species of thermosbaenaceans are recognized in seven genera. *Thermosbaena mirabilis* is known from freshwater hot springs in North Africa, where it lives at temperatures in excess of 40°C. Several species in other genera occur in much cooler fresh waters, typically in groundwater or in caves. Other species are marine or inhabit underground anchialine pools. Limited data suggest that thermosbaenaceans feed on plant detritus.
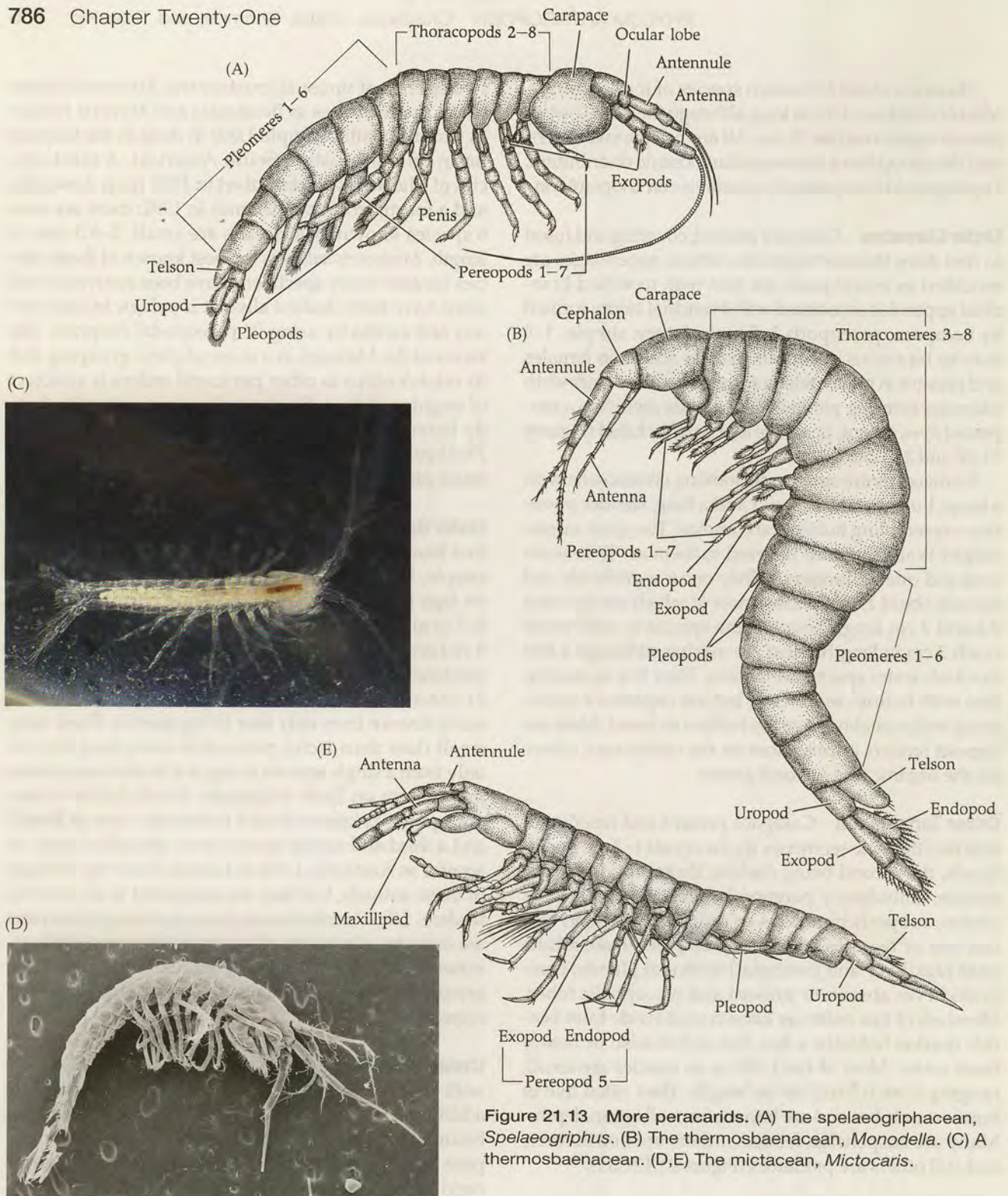
Figure 21.13 More peracarids. (A) The spelaeogriphacean, *Spelaeogriphus*. (B) The thermosbaenacean, *Monodella*. (C) A thermosbaenacean. (D,E) The mictacean, *Mictocaris*.

Order Isopoda Carapace absent; first thoracomere fused with head; 1 pair of maxillipeds; 7 pairs of uniramous pereopods, the first of which is sometimes subchelate, others usually simple (gnathiids have only five pairs of pereopods, as thoracopod 2 is a maxillipedal "pylopod" and thoracopod 8 is missing); pereopods variable, modified as ambulatory, prehensile, or swimming; in the more derived suborders pereopodal coxae are expanded as lateral side plates (coxal plates); pleopods biramous and well developed, natatory and for gas exchange (functioning as gills in aquatic taxa, and with air sacs called pseudotrachea in most terrestrial Oniscidea); adults with maxillary and (vestigial) antennal glands; telson fused with one to six pleonites, forming pleotelson; eyes usually sessile and compound, absent from some, pedunculate in most Gnathiidea; with biphasic molting (posterior region molts before anterior region) (Figures 21.1Q, 21.14, 21.21I, 21.28H,I, and 21.33M).

(A)
Rostrum
Antennule
Compound eye
Antenna
Cephalon
Pereon
Pereonite one (= thoracomere two)
Coxal plates
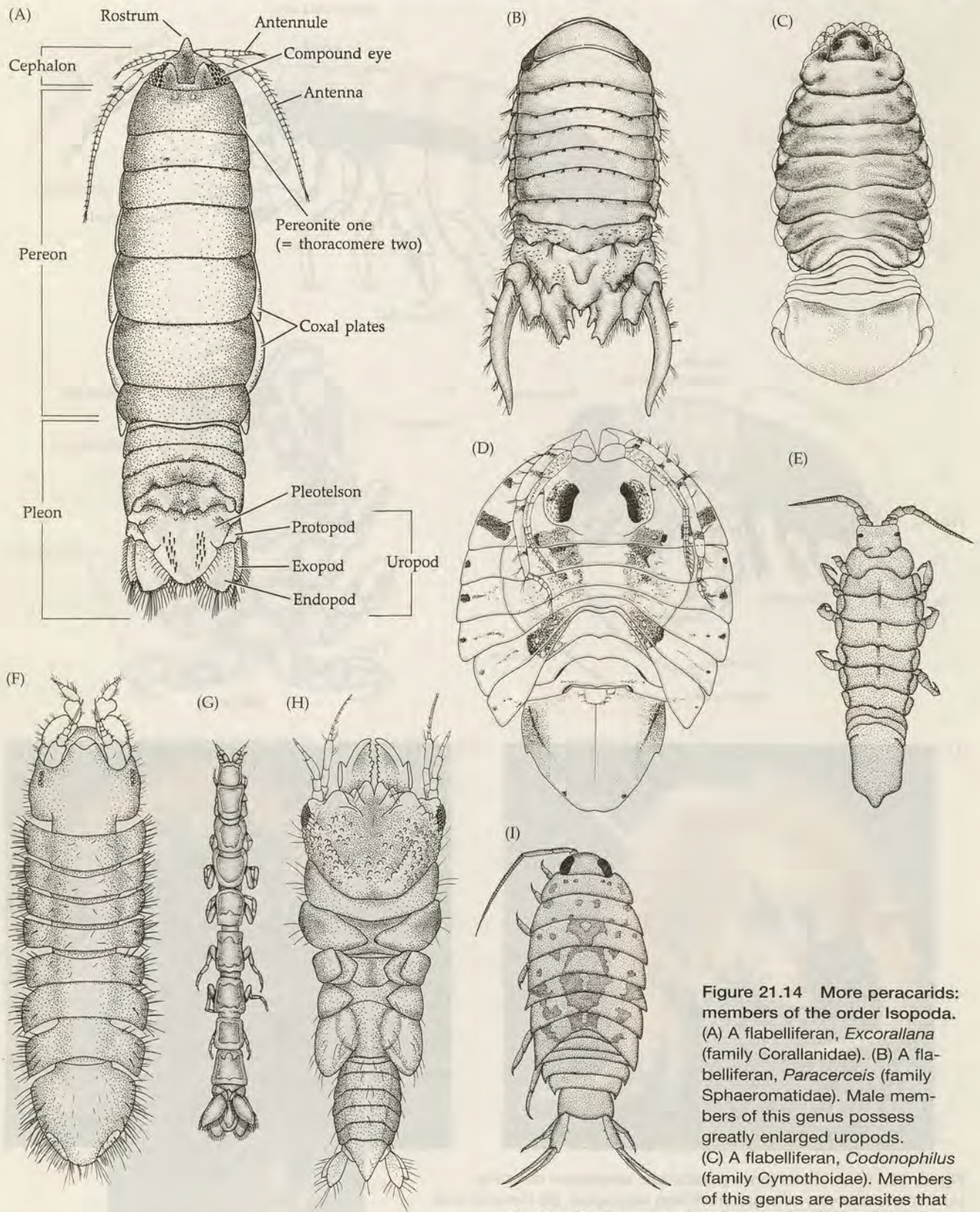Pleon
Pleotelson
Protopod
Exopod
Endopod
Uropod

Figure 21.14 More peracarids: members of the order Isopoda. (A) A flabelliferan, *Excorallana* (family Corallanidae). (B) A flabelliferan, *Paracerceis* (family Sphaeromatidae). Male members of this genus possess greatly enlarged uropods. (C) A flabelliferan, *Codonophilus* (family Cymothoidae). Members of this genus are parasites that attach to the tongues of various marine fishes. (D) A flabelliferan, *Heteroserolis* (family Serolidae). (E) A valviferan, *Idotea* (family Idoteidae). (F) An asellote, *Joeropsis* (family Joeropsididae). (G) An anthurid, *Mesanthura* (family Anthuridae). (H) A gnathiidean, *Gnathia* (family Gnathiidae). Note the grossly enlarged mandibles characteristic of male Gnathiidea. (I) An oniscidean, *Ligia* (the common seashore "rock louse").

The isopods comprise about 10,500 marine, freshwater, and terrestrial species, ranging in length from 0.5 to 500 mm, the largest being species of the benthic genus *Bathynomus* (Cirolanidae). They are common inhabitants of nearly all environments, and some groups are exclusively (e.g., Bopyridae, Cymothoidae) or partly
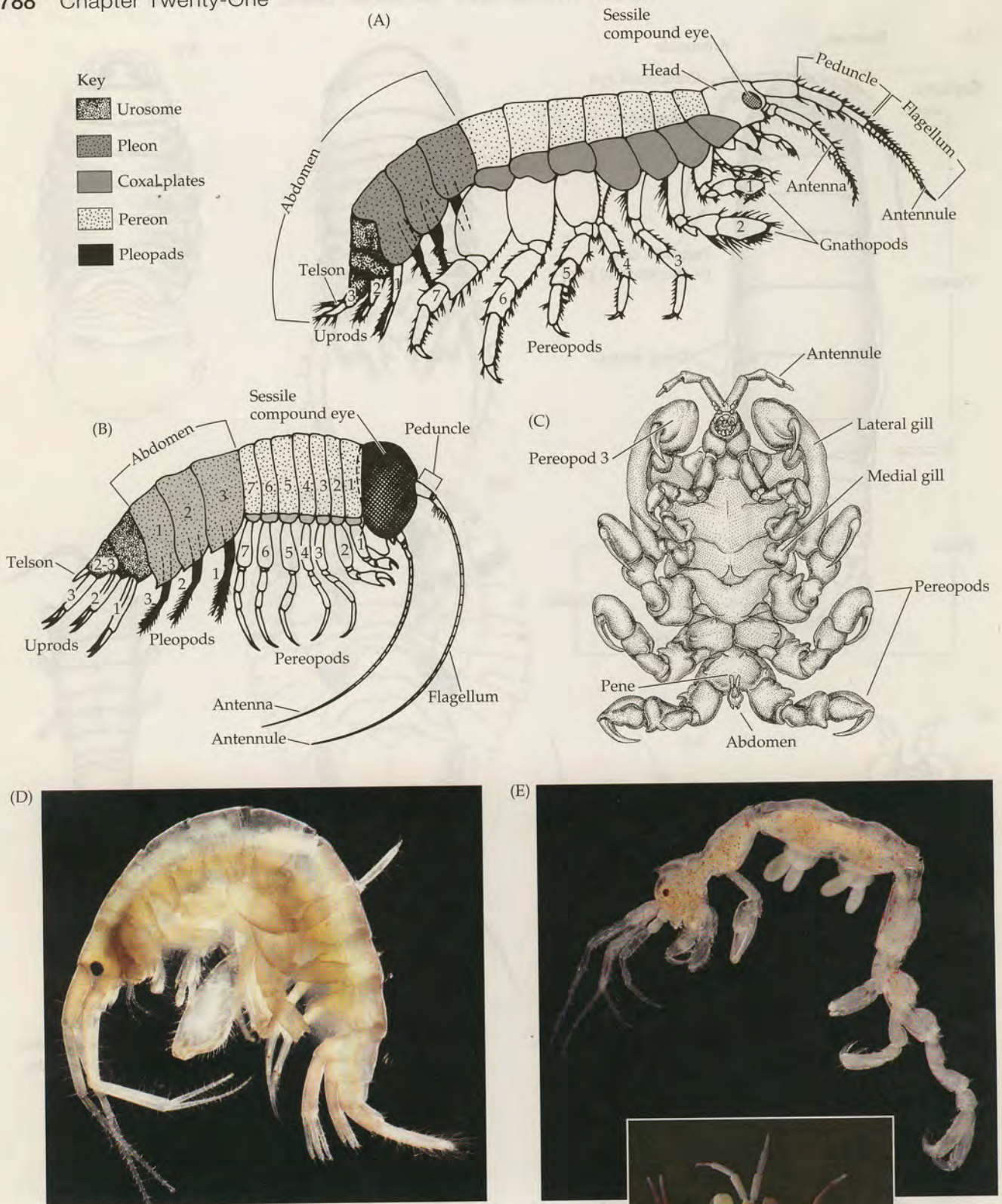
Figure 21.15 And still more peracarids: amphipod diversity.
(A) General anatomy of a gammaridean amphipod. (B) General anatomy of a hyperiidean amphipod. (C) General anatomy of a cyamid amphipod (*Cyamus monodontis*). (D) A gammaridean, *Melita*. (E) A caprellid amphipod. (F) A cyamid amphipod, *Cyamus erraticus*, parasitic on right whales. (G,H) Two gammaridean amphipods: (G) *Hyale*, a beach hopper, and (H) *Heterophlias*, an unusual, dorsoventrally flattened species. (I–K) Three hyperiidean amphipods: (I) *Primno*, (J) *Leptocottis*, and (K) a hyperiid on its host medusa. (L) A free-living caprellid, *Caprella*. (M) An ingolfiellid amphipod, *Ingolfiella*.
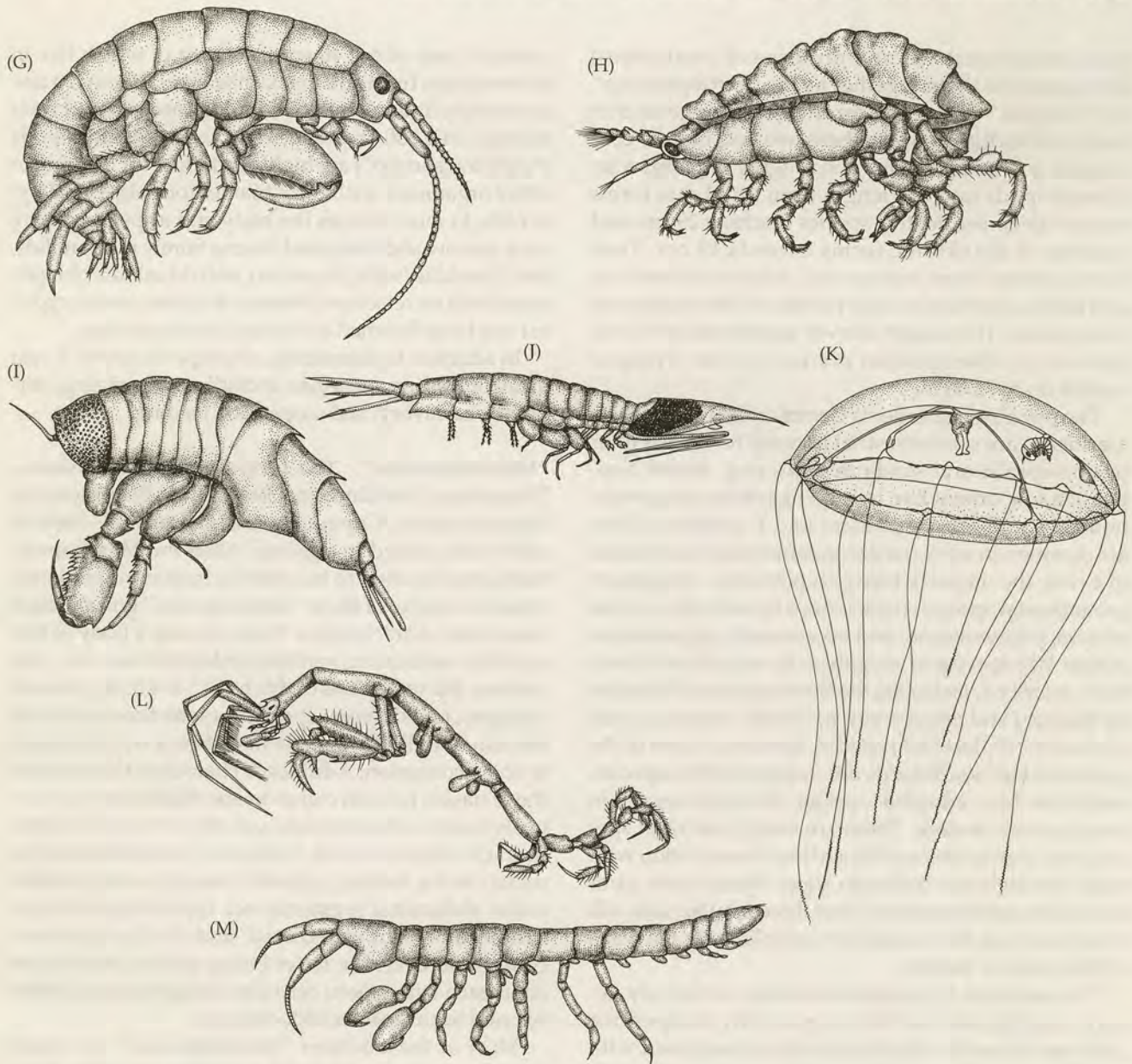
(e.g., Gnathiidae) parasitic. The suborder Oniscidea includes about 5,000 species that have invaded land (pillbugs and sowbugs); they are the most successful terrestrial crustaceans. Their direct development, flattened shape, osmoregulatory capabilities, thickened cuticle, and aerial gas exchange organs (pseudotrachea) allow most oniscideans to live completely divorced from aquatic environments. Fossils as old as 325 million years (Carboniferous) have been reported.

Isopod feeding habits are extremely diverse. Many are herbivorous or omnivorous scavengers, but direct plant feeders, detritivores, and predators are also common. Some are parasites (e.g., on fishes or on other crustaceans) that feed on the tissue fluids of their hosts. Overall, grinding mandibles and herbivory seem to represent the primitive state, with slicing or piercing mandibles and predation appearing later in the evolution of several isopod clades.

Order Amphipoda   Carapace absent; first thoracomere fused to head; 1 pair of maxillipeds; 7 pairs of uniramous pereopods, with first, second, and sometimes others frequently modified as chelae or subchelae; pereopodal coxae expanded as lateral side plates (coxal plates); gills thoracic (medial pereopodal epipods); adults with antennal glands; abdomen "divided" into two regions of three segments each, an anterior "pleon" and posterior urosome, with anterior appendages as typical pleopods and urosomal appendages modified as uropods; telson free or fused with last urosomite; other urosomites sometimes fused; compound eyes sessile, absent in some, huge in many (but not all) members of the suborder Hyperiidea (Figures 21.1N,O, 21.15, 21.23, 21.27F, and 21.29D).

Isopods and amphipods share many features and are often said to be closely related. Earlier workers recognized these similarities (e.g., sessile compound

eyes, loss of carapace, and presence of coxal plates) and classified them together as the "Edriopthalma" or "Acarida." However, recent work suggests that many similarities between these two taxa may be convergences or parallelisms. The roughly 11,000 species of amphipods range in length from tiny 1 mm forms to giant deep-sea benthic species reaching 29 cm, and a group of planktonic forms exceeds 10 cm. They have invaded most marine and freshwater habitats and often constitute a large portion of the biomass in many areas. The largest known amphipod is *Alicella gigantea*, a cosmopolitan marine species living at depths up to 7,000 m.

The principal suborder is Gammaridea. A few gammarideans are semiterrestrial in moist forest leaf litter or on supralittoral sandy beaches (e.g., beach hoppers); a few others live in moist gardens and greenhouses (e.g., *Talitrus sylvaticus* and *T. pacificus*). They are common in subterranean groundwater ecosystems of caves, the majority being stygobionts—obligatory groundwater species characterized by reduction or loss of eyes, pigmentation, and occasionally appendages. About 900 species of stygobiontic amphipods have been described, including the diverse genera *Niphargus* (in Europe) and *Stygobromus* (in North America), each with over 100 described species. However, most of the gammaridean amphipods are marine benthic species, and a few have adopted a pelagic lifestyle, usually in deep oceanic waters. There are many intertidal species, and a great many of these live in association with other invertebrates and with algae. Domicolous gammaridean amphipods in at least three families spin silk from their legs that is used for consolidating the walls of their tube or shelter.

The suborder Hyperiidea includes exclusively pelagic amphipods that have apparently escaped the confines of benthic life by becoming associated with other plankters, particularly gelatinous zooplankton such as medusae, ctenophores, and salps. The hyperiideans are usually characterized by huge eyes (and a few other inconsistent features), but several groups bear eyes no larger than those of most gammarideans. The Hyperiidea are almost certainly a polyphyletic group, and it is thought that several lineages are derived independently from various gammaridean ancestors, although a modern phylogenetic analysis has yet to be attempted. The precise nature of the relationships between hyperiideans and their zooplankton hosts remains controversial. Some appear to eat host tissue, others may kill the host to fashion a floating "home," and still others may utilize the host merely for transport or as a nursery for newly hatched young. Specimens of the scyphozoan *Phacellophora camtschtica* have been found with nearly 500 *Hyperia medusarum* riding (and feeding) on it.

There are two other small amphipod suborders: Ingolfiellidea and Caprellidea. The first suborder contains only about 40 species, most of which live in subterranean fresh and brackish waters, although a few are marine and interstitial. Little is known about their biology. The 300 or so species of caprellid amphipods ("skeleton shrimp") are highly modified for clinging to other organisms, including filamentous algae and hydroids. In most species the body and appendages are very narrow and elongated. In one family of caprellids, the Cyamidae (with 28 species), individuals are obligate symbionts on cetaceans (whales, dolphins, and porpoises) and have flattened bodies and prehensile legs.

In addition to parasitism, amphipods exhibit a vast array of feeding strategies, including scavenging, herbivory, carnivory, and suspension feeding.

"Maxillopodans"   The following seven classes—Thecostraca, Tantulocarida, Branchiura, Pentastomida, Mystacocarida, Copepoda, and Ostracoda—historically were united in a group called the Maxillopoda that is now known to be artificial (nonmonophyletic). However, many of these "maxillopodan" groups share some basic characteristics. These include a body of five cephalic, six thoracic, and four abdominal somites, plus a telson, but reductions of this basic 5-6-4 body plan are common, and different specialists sometimes interpret the nature of these tagmata in different ways, leading to some confusion. Additional characters that most of these classes have in common are: thoracomeres variously fused with cephalon; usually with caudal rami; thoracic segments with biramous (sometimes uniramous) limbs, lacking epipods (except in many ostracods); abdominal segments lack typical appendages; carapace present or reduced; with both simple and compound eyes, the latter being unique, with three cups, each with tapetal cells (an arrangement still often referred to as the maxillopodan eye).

Most of these former "maxillopodans" are small crustaceans, barnacles being a notable exception. They are generally recognizable by their shortened bodies, especially the reduced abdomen, and by the absence of a full complement of legs. The reductions in body size and leg number, emphasis on the naupliar eye, minimal appendage specialization, and certain other features have led biologists to hypothesize that paedomorphosis (progenesis) played a role in the origin of some of these classes. That is, in many ways, they resemble early postlarval forms that evolved sexual maturity before attaining all the adult features. Over 26,000 species have been described within the seven classes.

Class Thecostraca

This group includes the barnacles, parasitic ascothoracids, and mysterious "y-larvae." The thecostracan clade is defined by several rather subtle synapomorphies of cuticular fine structure, including cephalic chemosensory structures known as lattice organs. The group is

also supported by molecular phylogenetic analyses. All taxa have pelagic larvae, the terminal instar of which possesses prehensile antennules and is specialized for locating and attaching to the substratum of the sessile adult state.

Subclass Ascothoracida About 125 described species of parasites of anthozoans and echinoderms. Although greatly modified, they retain a bivalved carapace and the full complement of thoracic and abdominal segments (facts that suggest they might be the most primitive living thecostracans). Ascothoracids generally have mouthparts modified for piercing and sucking body fluids, but some live inside other animals and absorb the host's tissue fluids. In at least one species, *Synagoga mira*, males retain the ability to swim throughout their lives, attaching only temporarily while feeding on corals (Figure 21.16F).

Subclass Cirripedia Primitively with tagmata as in the class, but in most groups the adult body is modified for sessile or parasitic life; thorax of six segments with paired biramous appendages; abdomen without limbs; telson absent in most, although caudal rami persist on abdomen in some; nauplius larva with frontolateral horns; unique, "bivalved" cypris larva; adult carapace "bivalved" (folded) or forming fleshy mantle; first thoracomere often fused with cephalon and bearing maxilliped-like oral appendages; female gonopores near bases of first thoracic limbs, male gonopore on median penis on last thoracic or first abdominal segment; compound eyes lost in adults (Figures 21.1S,T, 21.16A–E, 21.25, 21.26, 21.27B,C, 21.32E, and 21.33F).

The 1,285 or so described cirripede species are mostly free-living barnacles, but this group also includes some strange parasitic "barnacles" rarely seen except by specialists. The common acorn and goose barnacles belong to the superorder Thoracica. The superorder Acrothoracica consists of minute animals that burrow into calcareous substrata, including corals and mollusc shells (Figure 21.16G). The superorder Rhizocephala are exceptionally modified parasites of other crustaceans, especially decapods (Figure 21.16H).

If the body plan of the cirripedes is derived from something similar to what is seen in other "maxillopodan" classes, then it has been so extensively modified that its basic features are nearly unrecognizable in adults of this subclass. The abdomen is greatly reduced in adults, and also in most cypris larvae. In cyprids (cypris larvae) the carapace is always present and "bivalved," the two sides being held by a transverse cypris adductor muscle; in adults the carapace may be lost (Rhizocephala) or modified as a membranous, saclike mantle (thoracicans and acrothoracicans). In the barnacles (Thoracica), it is this mantle that produces the familiar calcareous plates that enclose the body. Cyprids and adult acrothoracicans share a unique tripartite

crystalline cone structure in the compound eye, a feature not known from any other crustacean group and perhaps a vestige of the ancestral thecostracan body plan. Most species of barnacles are hermaphrodites, whereas separate sexes are the rule in acrothoracicans and rhizocephalans, and some androgonochoristic species (males + hermaphrodites; e.g., *Scalpellum*) have also been reported.
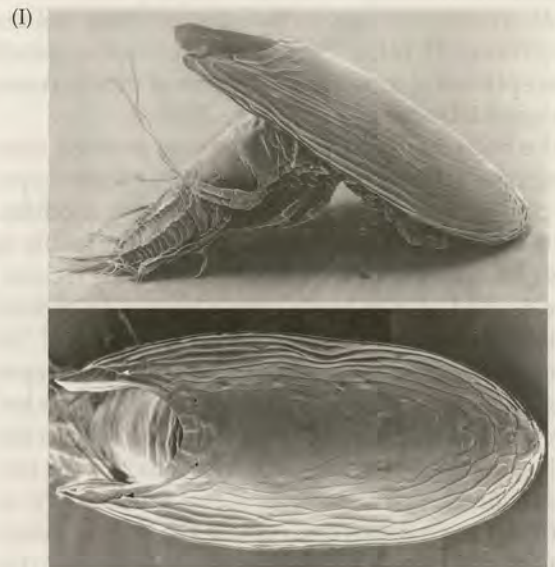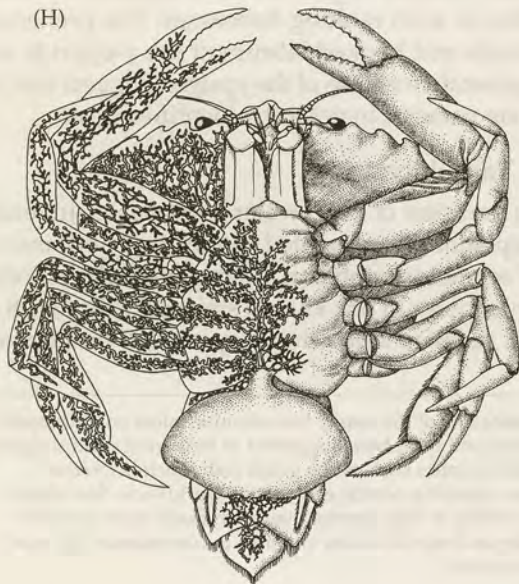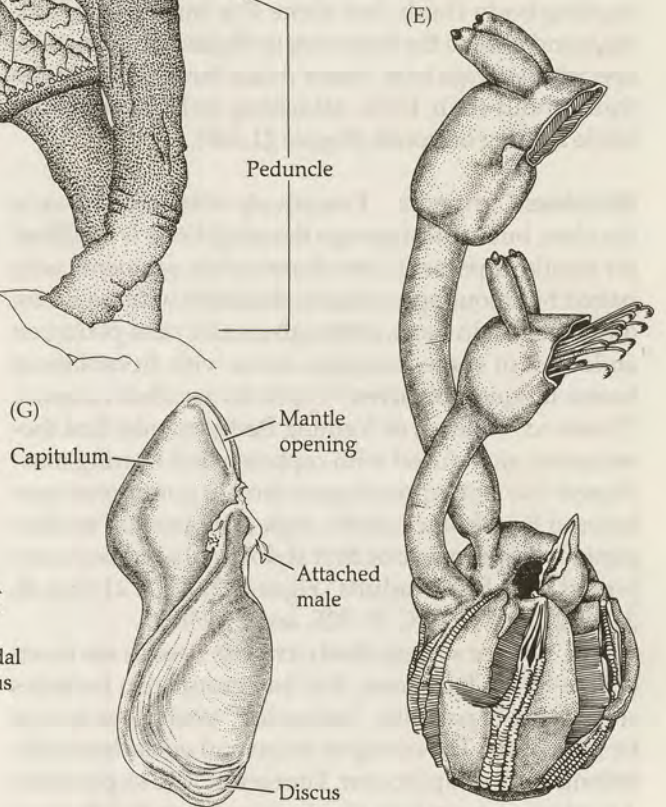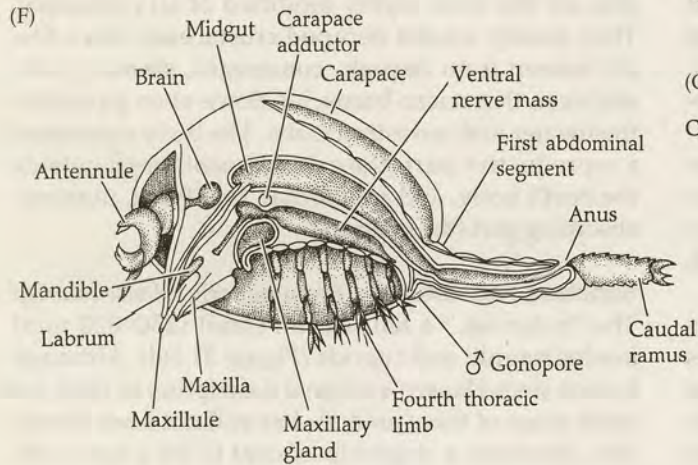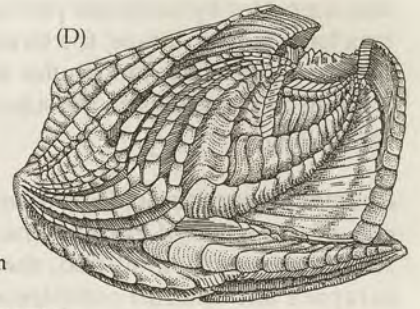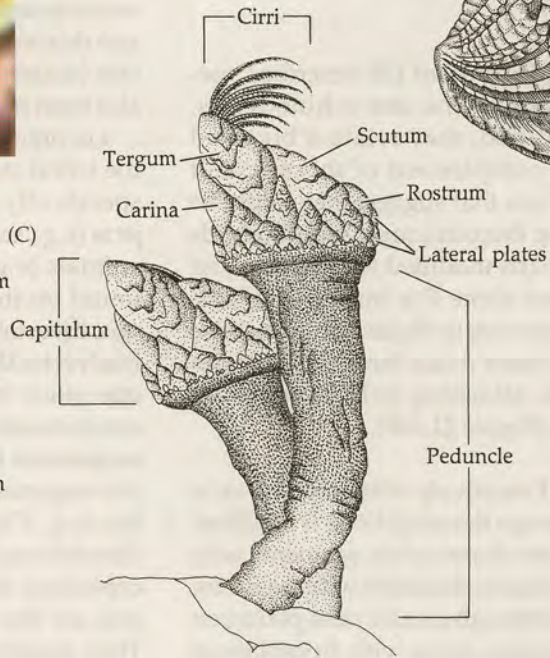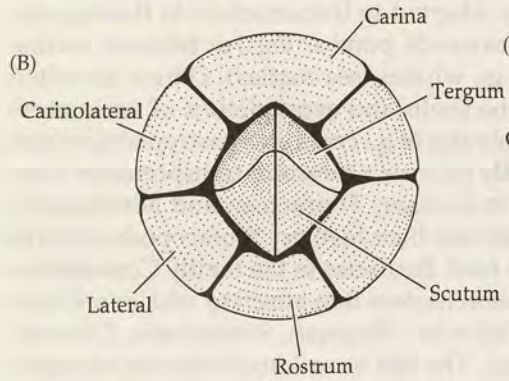
Locomotion in barnacles is generally confined to the larval stages, although adults of a few species are specifically adapted to live attached to floating objects (e.g., seaweeds, pumice, logs) or nektonic marine animals (e.g., whales, sea turtles). Others are often found on the shells and exoskeletons of various errant invertebrates (e.g., crabs and gastropods), which inadvertently provide a means of transportation from one place to another. Thoracican and acrothoracican barnacles use their feathery thoracopods (cirri) to suspension feed. Barnacles in the family Coronulidae are suspension feeders that attach to whales and turtles (e.g., *Chelonibia, Platylepas, Stomatolepas, Coronula, Xenobalanus*). The 265 or so known species of rhizocephalans are all endoparasitic in other Crustacea, and are the most highly modified of all cirripedes. They mainly inhabit decapod crustaceans, but a few are known from isopods, cumaceans, stomatopods, and even thoracican barnacles. Some even parasitize freshwater and terrestrial crabs. The body consists of a reproductive part (the externa) positioned outside the host's body, and an internal, ramifying, nutrient-absorbing part (the interna).[6]

Subclass Facetotecta Monogeneric (*Hansenocaris*): The "y-larvae," a half-dozen small (250–620 mm) marine nauplii and cyprids (Figure 21.16I). Although known since Hansen's original description in 1899, the adult stage of these animals has still not been identified. However, a stage subsequent to the y-larva, the slug-like ypsigon stage, has been induced by treating y-larvae with molting hormones. The prehensile antennules and hooked labrum of the y-cyprids and the degenerative nature of the ypsigon suggest that the adults are parasitic in yet-to-be-identified hosts.

Class Tantulocarida

Bizarre parasites of deep-water crustaceans. Juveniles with cephalon, 6-segmented thorax, and abdomen of up to 7 segments; cephalon lacking appendages (other than antennules in one known stage only) but with an internal median stylet; thoracopods 1–5 biramous, 6

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[6]Rhizocephalans of the family Sacculinidae infest only decapod crustaceans and have been suggested as biological control agents for invasive exotics such as the green crab (*Carcinus maenas*), which are upsetting coastal ecosystems worldwide. Sacculinds have the ability to take control over such major host functions as molting and reproduction, and also to compromise the host's immune system.

(A)

(B)

Carina

Carinolateral

Tergum

Lateral

Scutum

Rostrum

(C)

Cirri

Tergum

Carina

Capitulum

Scutum

Rostrum

Lateral plates

(D)

Peduncle

(E)

(F)

Brain

Midgut

Carapace adductor

Carapace

Ventral nerve mass

First abdominal segment

Antennule

Anus

Mandible

Labrum

Maxillule

Maxilla

Maxillary gland

Fourth thoracic limb

♂ Gonopore

Caudal ramus

(G)

Capitulum

Mantle opening

Attached male

Discus

(H)

(I)

Figure 21.16   Anatomy and diversity in the class Thecostraca—barnacles and their kin. (A–E) Thoracican barnacles. (A) A sessile (acorn) barnacle with its cirri extended for feeding. (B) Plate terminology in a balano-morph (acorn) barnacle. (C) The lepadomorph (stalked) barnacle *Pollicipes polymerus*. (D) *Verruca*, the "wart" bar-nacle. (E) Two thoracican barnacles that live in association with each other and with whales. The stalked barnacle *Conchoderma* attaches to the sessile barnacle *Coronula*, which in turn attaches to the skin of certain whales. (F) The ascothoracican *Ascothorax ophiocentenis*, a para-site that feeds periodically on echinoderms (longitudinal section). (G) An acrothoracican, *Alcippe*. Note the highly modified female and the tiny attached male. This species bores into calcareous substrata such as coral skeletons. (H) A crab (*Carcinus*) infected with the rhizocephalan *Sacculina carcini*. The crab's right side is shown as trans-parent, exposing the ramifying body of the parasite. (I) A cypris y-larva, in lateral and dorsal views.

uniramous; abdomen without appendages but with caudal rami; adults highly modified, with "unsegment-ed" sacciform thorax and a reduced abdomen bearing a uniramous penis on the first segment; female gono-pores on fifth thoracic segment.

The tiny tantulocarids are less than 0.5 mm long. They attach to their hosts by penetrating the body with a protruding cephalic stylet. The young bear natatory thoracopods. About three dozen species in 22 genera have been described (Figures 21.1V and 21.17). They are known from abyssal depths to the intertidal zone, from polar to tropical waters, and from anchialine pools and hydrothermal vents, always as parasites on other crustaceans. Until recently, members of this group had been assigned to various parasitic groups of Copepoda and Cirripedia. In 1983 Geoffrey Boxshall and Roger Lincoln proposed the new class Tantulocarida. Some early work on the group supported a view of these ani-mals as maxillopodans, although the presence of six or seven abdominal segments in juveniles of some species is inconsistent with this view; they are now believed to be allied to the Thecostraca. The life cycle is unique and includes a larva called the tantulus.

Class Branchiura

Body compact and oval, head and most of trunk cov-ered by broad carapace; antennules and antennae re-duced, the latter sometimes absent; mouthparts modi-fied for parasitism; no maxillipeds; thorax reduced

(A) Rostrum, Cuticular ornamentation, Ovary (?), Host antennule, Cephalic stylet
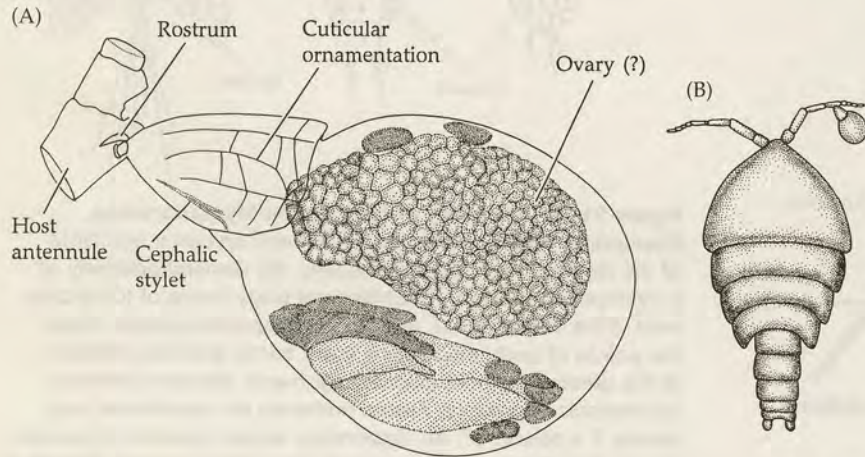
Figure 21.17   Anatomy in the class Tantulocarida. (A) An adult *Basipodella atlantica*. Note the absence of an abdomen and the modifications for parasitic life. (B) *Basipodella* attached to the antenna of a copepod host. (C,D) *Microdajus pectinatus* on a crustacean host, adult, and juvenile (SEM).
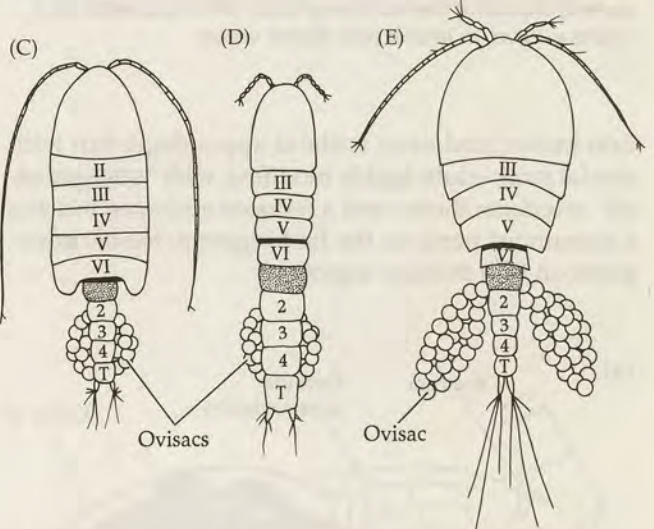
(A)

(B)

(C)

(D)

(E)
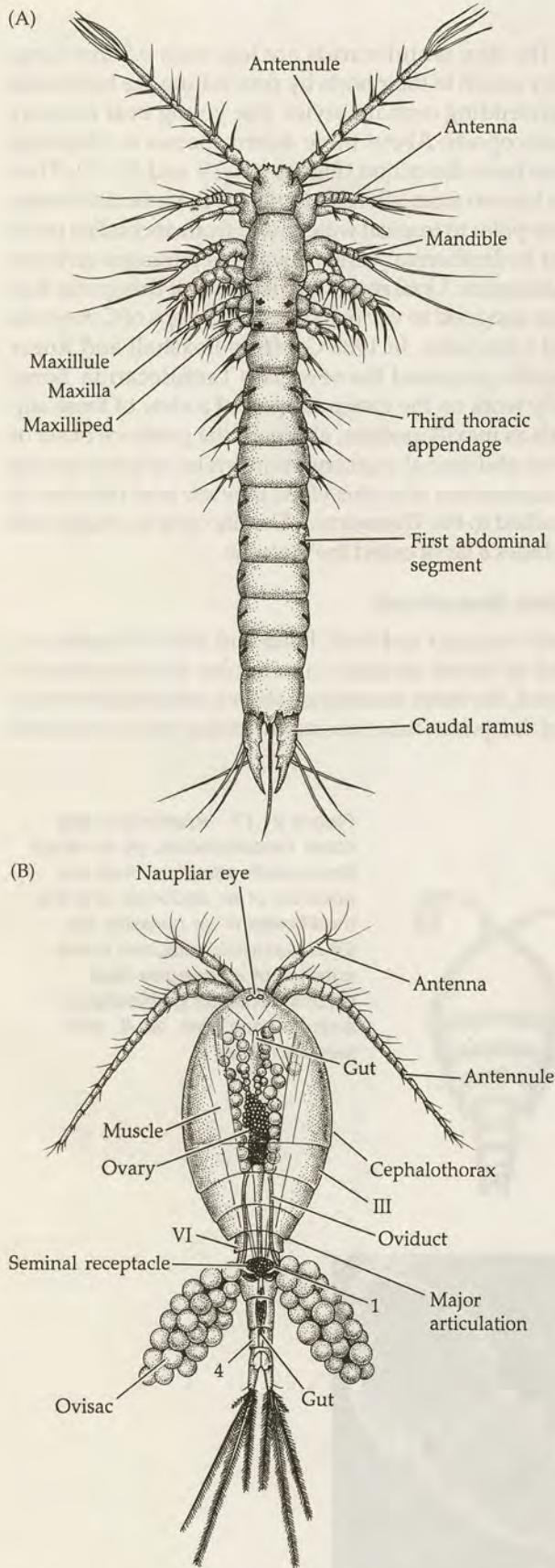
Figure 21.18 Anatomy of the classes Mystacocarida, Copepoda, and Branchiura. (A) General anatomy and SEM of the mystacocarid *Derocheilocaris*. (B) General anatomy of a cyclopoid copepod. (C–E) General body forms of (C) a calanoid, (D) a harpacticoid, and (E) a cyclopoid copepod. Note the points of body articulation (dark band) and the position of the genital segment (shaded segment). Roman numerals are thoracic segments; Arabic numerals are abdominal segments; T = telson. (F) An elaborately setose calanoid copepod adapted for flotation. (G) A poecilostomatid copepod, *Ergasilus pitalicus*, ectoparasitic on cichlid fishes. (H) A female siphonostomatid copepod (*Caligus* sp.) with egg sacs. (I) A female siphonostomatid copepod (*Trebius heterodont*, a parasite of horn sharks in California) with egg sacs. (J) A siphonostomatid copepod, *Clavella adunca*, showing extreme body reduction; this species attaches to the gills of fishes by its elongate maxillae. (K) *Notodelphys*, a wormlike cyclopoid copepod adapted for endoparasitism in tunicates. (L) *Argulus foliaceus*, a branchiuran that parasitizes fishes. Note the powerful hooked suckers (modified maxillules) on the ventral surface.

to four segments, with paired biramous appendages; abdomen unsegmented, bilobed, limbless, but with minute caudal rami; female gonopores at bases of fourth thoracic legs, male with single gonopore on midventral surface of last thoracic somite; paired, sessile compound eyes and one to three median simple eyes (Figure 21.18L).

The Branchiura comprise about 230 species of ectoparasites on marine and freshwater fishes. The

(F)

(G)

(H)

(I)

(J)

Cephalon

Maxilla

Thorax

Egg sac

(K)

Cephalon   Appendages   Thorax   Abdomen

(L)

Antennule

Antenna

Spine

Eye

Maxillule (hooked sucker)

Maxilla

First
thoracic limb

Abdomen
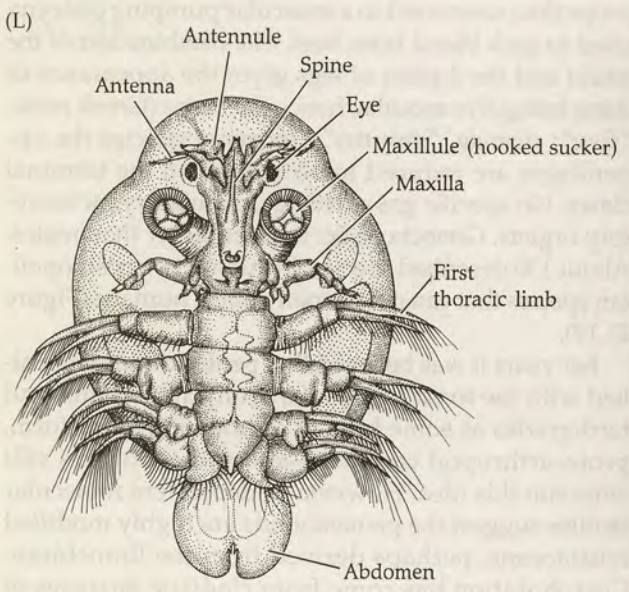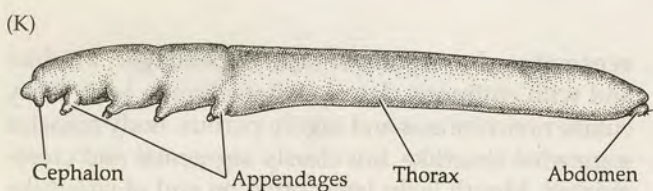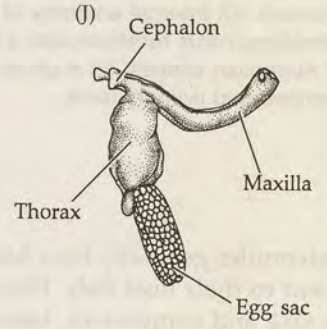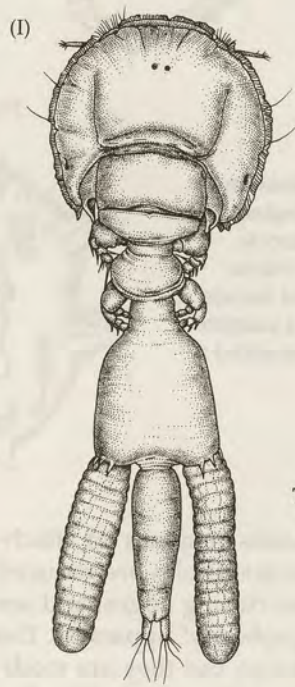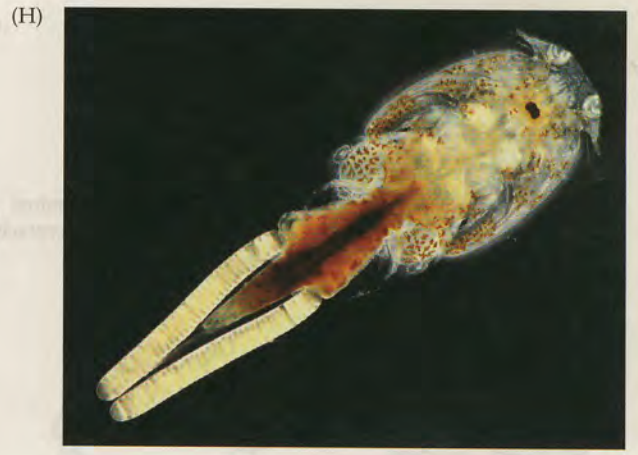
Figure 21.19 Anatomy and diversity in the class Pentastomida. (A) *Linguatula serrata*. (B) *Cephalobaena tetrapoda*. (C) Internal anatomy of female *Pentastomum*. (D) Internal anatomy of female *Waddycephalus teretiusculus*, a parasite of Australian snakes. (E) A generalized pentastomid primary larva.

antennules generally bear hooks or spines for attachment to their host fish. The mandibles are reduced in size and complexity, bear cutting edges, and are housed within a styliform "proboscis" apparatus. The maxillules are clawed in *Dolops*, but they are modified as stalked suckers in the other genera (*Argulus, Chonopeltis, Dipteropeltis*). The uniramous maxillae usually bear attachment hooks. The thoracopods are biramous and used for swimming when the animal is not attached to a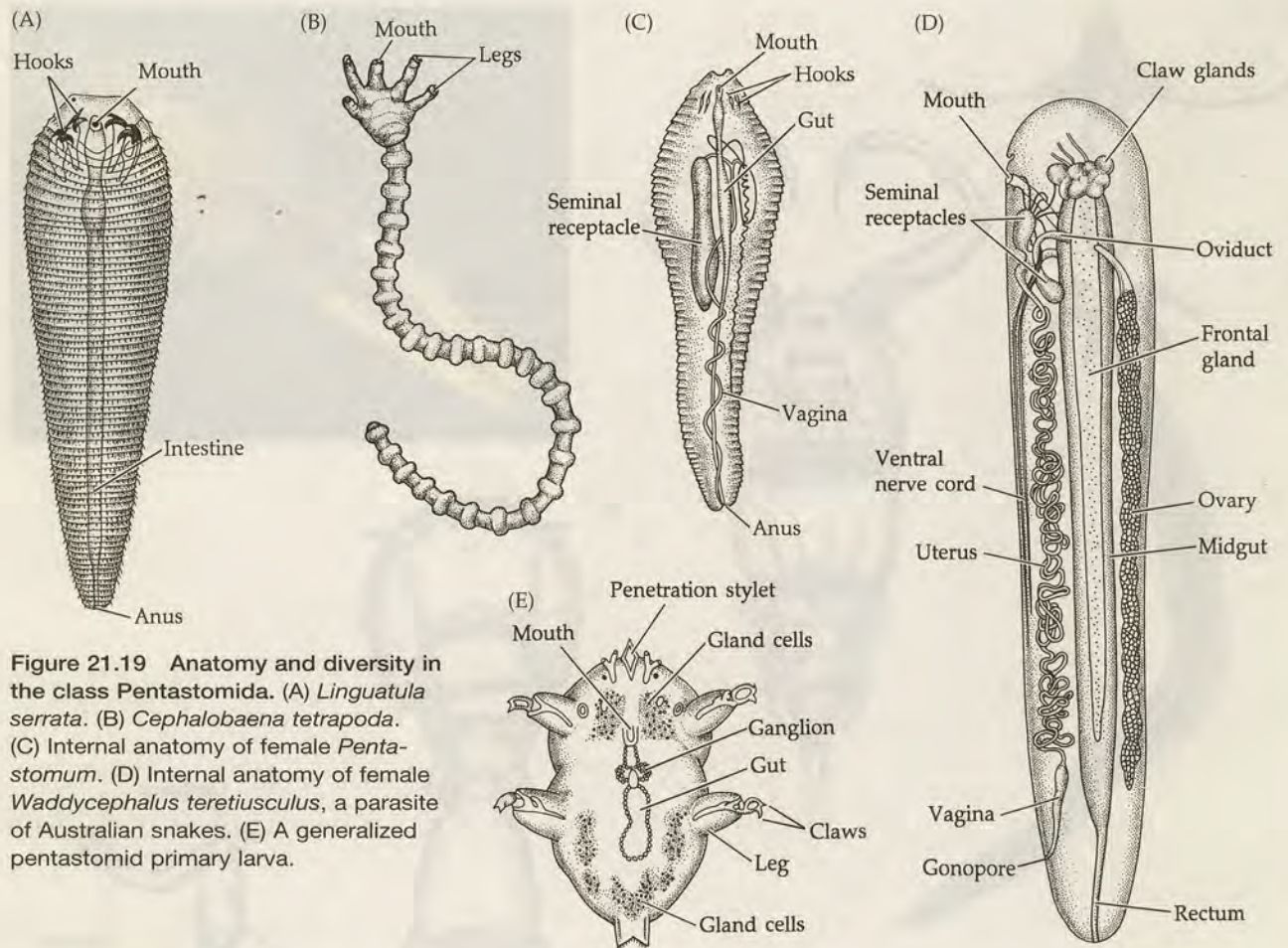 host. Branchiurans feed by piercing the skin of their hosts and sucking blood or tissue fluids. Once they locate a host, they crawl toward the fish's head and anchor in a spot where water flow turbulence is low (e.g., behind a fin or gill operculum).

Members of the genus *Argulus* occur worldwide, and can pose a serious problem to aquaculture, but members of the other genera have restricted distributions. *Chonopeltis* is found only in Africa, *Dipteropeltis* in South America, and *Dolops* in South America, Africa, and Tasmania.

Class Pentastomida

Obligatory parasites of various amphibians, reptiles, birds, and mammals. Adults inhabit respiratory tracts (lungs, nasal passages, etc.) of their hosts. Body highly modified, wormlike, 2–13 cm in length. Adult append-

ages reduced to 2 pairs of head appendages, lobelike and with chitinous claws used to cling to host. Body cuticle nonchitinous and highly porous. Body muscles somewhat sheetlike, but clearly segmental and cross-striated. Mouth lacks jaws; often on end of snoutlike projection; connected to a muscular pumping pharynx used to suck blood from host. The combination of the snout and the 2 pairs of legs gives the appearance of there being five mouths, hence the name (Greek *penta*, "five"; *stomida*, "mouths"). In many species the appendages are reduced to no more than the terminal claws. No specific gas exchange, circulatory, or excretory organs. Gonochoristic; females larger than males. About 130 described species, including two cosmopolitan species that can occasionally infest humans (Figure 21.19).

For years it was believed that pentastomids were allied with the fossil lobopodians, onychophorans, and tardigrades as some kind of segmented, vermiform, proto-arthropod creature—and some workers still entertain this idea. However, independent molecular studies suggest the pentastomids are highly modified crustaceans, perhaps derived from the Branchiura. Corroboration has come from cladistic analyses of sperm and larval morphology, nervous system anatomy, and cuticular fine structure.

Work on the Swedish Orsten fauna indicates that pentastomid-like animals had appeared as early as the late Cambrian (500 Ma), long before the land vertebrates had evolved. What might the original hosts of these parasites have been? Conodont fossils are common in all the Cambrian localities that have yielded pentastomids, raising the possibility that conodonts (also long a mystery, but now widely regarded as parts of early fishlike vertebrates) may have been at least one of the original hosts of these early Pentastomida.

Class Mystacocarida

Body divided into cephalon and 10-segmented trunk; telson with clawlike caudal rami; cephalon characteristically cleft; all cephalic appendages nearly identical, antennae and mandibles biramous; antennules, maxillules, and maxillae uniramous; first trunk segment bears maxillipeds but is not fused with cephalon; no carapace; gonopores on fourth trunk segment; trunk segments 2–5 with short, single-segment appendages (Figure 21.18A).

There are only 13 described species of mystacocarids, eight in the genus *Derocheilocaris* and five in *Ctenocheilocaris*. Most are less than 0.5 mm long, although *D. ingens* reaches 1 mm. The head is marked by a transverse "cephalic constriction" between the origins of the first and second antennae, perhaps a remnant of primitive head segmentation. In addition, the lack of fusion of the cephalon and maxillipedal trunk segment, the simplicity of the mouth appendages, and other features have led some workers to propose that the mystacocarids are among the most primitive living crustaceans. These attributes may, however, simply be related to a neotenic origin and specialization for interstitial habitats.

Mystacocarids are marine, interstitial crustaceans that live in littoral and sublittoral sands throughout the world's temperate and subtropical seas. Their rather vermiform body and small size are clearly adaptations to life among sand grains. Mystacocarids are thought to feed by scraping organic material from the surfaces of sand grains with their setose mouthparts.

Class Copepoda

Without a carapace, but with a well developed cephalic shield; single, median, simple maxillopodan eye (sometimes lacking); one or more thoracomeres fused to head; thorax of six segments, the first always fused to the head and with maxillipeds; abdomen of five segments, including anal somite (= telson); well developed caudal rami; abdomen without appendages, except an occasional reduced pair on the first segment, associated with the gonopores; point of main body flexure varies among major groups; antennules uniramous, antennae uniramous or biramous; 4–5 pairs of natatory thoracopods, most locked together for swimming; posterior thoracopods always biramous (Figures 21.1U, 21.18B–K, 21.27A, 21.30D, and 21.33D).

There are more than 12,500 described species of copepods. They can be incredibly abundant in the world's seas, and also in some lakes—by one estimate, they outnumber all other multicellular forms of life on Earth. Most are small, 0.5–10 mm long, but some free-living forms exceed 1.5 cm in length, and certain highly modified parasites may reach 25 cm. The bodies of most copepods are distinctly divided into three tagmata, the names of which vary among authors. The first region includes the five fused head segments and one or two additional fused thoracic somites; it is called a cephalosome (= cephalothorax) and bears the usual head appendages and maxillipeds. All of the other limbs arise on the remaining thoracic segments, which together constitute the metasome. The abdomen, or urosome, bears no limbs. The appendage-bearing regions of the body (cephalosome and metasome) are frequently collectively called the prosome. The majority of the free-living copepods, and those most frequently encountered, belong to the orders Calanoida, Harpacticoida, and Cyclopoida, although even some of these are parasitic. We focus here on these three groups and then briefly discuss some of the other, smaller orders and their modifications for parasitism. The calanoids are characterized by a point of major body flexure between the metasome and the urosome, marked by a distinct narrowing of the body. They possess greatly elongate antennules. Most of the calanoids are planktonic, and as a group they are extremely important as primary consumers in freshwater and marine food webs. The point of body flexure in the orders Harpacticoida and Cyclopoida is between the last two (fifth and sixth) metasomal segments. (Note: Some authors define the urosome in harpacticoids and cyclopoids as that region of the body posterior to this point of flexure.) Harpacticoids are generally rather vermiform, with the posterior segments not much narrower than the anterior; cyclopoids generally narrow abruptly at the major body flexure. Both the antennules and the antennae are quite short in harpacticoids, but the latter are moderately long in cyclopoids (although never as long as the antennules of calanoids). The antennae are uniramous in cyclopoids but biramous in the other two groups. Most harpacticoids are benthic, and those that have adapted to a planktonic lifestyle show modified body shapes. Harpacticoids occur in all aquatic environments; encystment is known to occur in at least a few freshwater and marine species. Cyclopoids are known from fresh and salt water, and most are planktonic.

The nonparasitic copepods move by crawling or swimming, using some or all of the thoracic limbs. Many of the planktonic forms have very setose appendages, offering a high resistance to sinking. Calanoids are predominantly planktonic feeders. Benthic harpacticoids are often reported as detritus feeders, but many

feed predominantly on microorganisms living on the surface of detritus or sediment particles (e.g., diatoms, bacteria, and protists).

Of the seven remaining orders, the Mormonilloida are planktonic; the Misophrioida are known from deep-sea epibenthic habitats as well as anchialine caves in both the Pacific and Atlantic; and the Monstrilloida are planktonic as adults, but the larval stages are endoparasites of certain gastropods, polychaetes, and occasionally echinoderms. Members of the orders Poecilostomatoida and Siphonostomatoida are exclusively parasitic and often have modified bodies. Siphonostomatoids are endo- or ectoparasites of various invertebrates as well as marine and freshwater fishes; they are often very tiny and show a reduction or loss of body segmentation. Poecilostomatoids parasitize invertebrates and marine fishes, and may also show a reduced number of body segments. The Platycopioida are benthic forms known primarily from marine caves; the Gelyelloida are known only from European groundwaters.

Class Ostracoda

Body segmentation reduced, trunk not clearly divided into thorax and abdomen, with 6 to 8 pairs of limbs (including the male copulatory limb); trunk with 1 to 3 pairs of limbs, variable in structure; caudal rami present; gonopores on lobe anterior to caudal rami; carapace bivalved, hinged dorsally and closed by a central adductor muscle, enclosing body and head; carapace highly variable in shape and ornamentation, smooth or with various pits, ridges, spines, etc.; most with one simple median naupliar eye (often called a "maxillopodan eye") and sometimes weakly stalked compound eyes (in Myodocopida); adults with maxillary and (in some) antennal glands; males with distinct copulatory limbs; caudal rami (furca) present (Figure 21.20).

Ostracods include about 30,000 described living species of small bivalved crustaceans, ranging in length from 0.1 to 2.0 mm, although some giants (e.g., *Gigantocypris*) reach 32 mm. They superficially resemble clam shrimps in having the entire body enclosed within the valves of the carapace. However, ostracod valves lack the concentric growth rings of clam shrimps, and there are major differences in the appendages. The shell is usually penetrated by pores, some bearing setae, and is shed with each molt. A good deal of confusion exists about the nature of ostracod limbs, and homologies with other crustacean taxa (and even within the Ostracoda) are unclear—this confusion is reflected in the variety of names applied by different authors. We have adopted terms here that allow the easiest comparison with other taxa.

Ostracods possess the fewest limbs of any crustacean class. The four or five head appendages are followed by 1–3 trunk appendages. Superficially, the (second) maxillae appear to be absent; however, the highly modified fifth limbs are in fact these appendages. The trunk seldom shows external evidence of segmentation, although all 11 postcephalic somites are discernable in some taxa. The trunk limbs vary in structure among taxa and on individuals. The third pair of trunk limbs bears the gonopores and constitutes the so-called copulatory organ.

Ostracods are one of the most successful groups of crustaceans. They also have the best fossil record of any arthropod group, dating from at least the Ordovician, and an estimated 65,000 fossil species have been described. Most are benthic crawlers or burrowers, but many have adopted a suspension-feeding planktonic lifestyle, and a few are terrestrial in moist habitats. One species is known to be parasitic on fish gills—*Sheina orri* (Myodocopida, Cypridinidae). Ostracods are abundant worldwide in all aquatic environments and are known to depths of 7,000 m in the sea. Some are commensal on echinoderms or other crustaceans. A few podocopans have invaded supralittoral sandy regions (members of the family Terrestricytheridae), and members of several families inhabit terrestrial mosses and humus. Two principal taxa (ranked as subclasses here) are recognized within the Ostracoda: Myodocopa and Podocopa.

Myodocopans are all marine. Most are benthic, but the group also includes all of the marine planktonic ostracods. The largest of all ostracods, the planktonic *Gigantocypris*, is a member of this group. Myodocopans include scavengers, detritus feeders, suspension feeders, and some predators. There are two orders: Myodocopida and Halocyprida.

Podocopans include predominantly benthic forms; although some are capable of temporary swimming, none are fully planktonic. Their feeding methods include suspension feeding, herbivory, and detritus feeding. The Podocopa are divided into three orders: the exclusively marine Platycopida, the ubiquitous Podocopida, and the Palaeocopida. The Palaeocopida were diverse and widespread in the Paleozoic, but are represented today only by the extremely rare Punciidae (known from a few living specimens, and from dead valves dredged in the South Pacific).

The Crustacean Body Plan

We realize that the above synopses are rather extensive, but the diversity of crustaceans demands emphasis before we attempt to generalize about their biology. The evolutionary success of crustaceans, like that of other arthropods, has been closely tied to modifications of the jointed exoskeleton and appendages, the latter having an extensive range of modifications for a great variety of functions.

The most basic crustacean body plan is a **head** (**cephalon**) followed by a long body (**trunk**) with many

Figure 21.20 Anatomy and diversity in the class Ostracoda. (A) Anatomy of *Sclerocypris* (Podocopa). (B) Anatomy of *Thaumatoconcha* (Myodocopa). (*Continued on next page*)

(C)   Antennula   Bellonci organ   Right valve

Antenna   Maxillula   Fifth limb   Furca
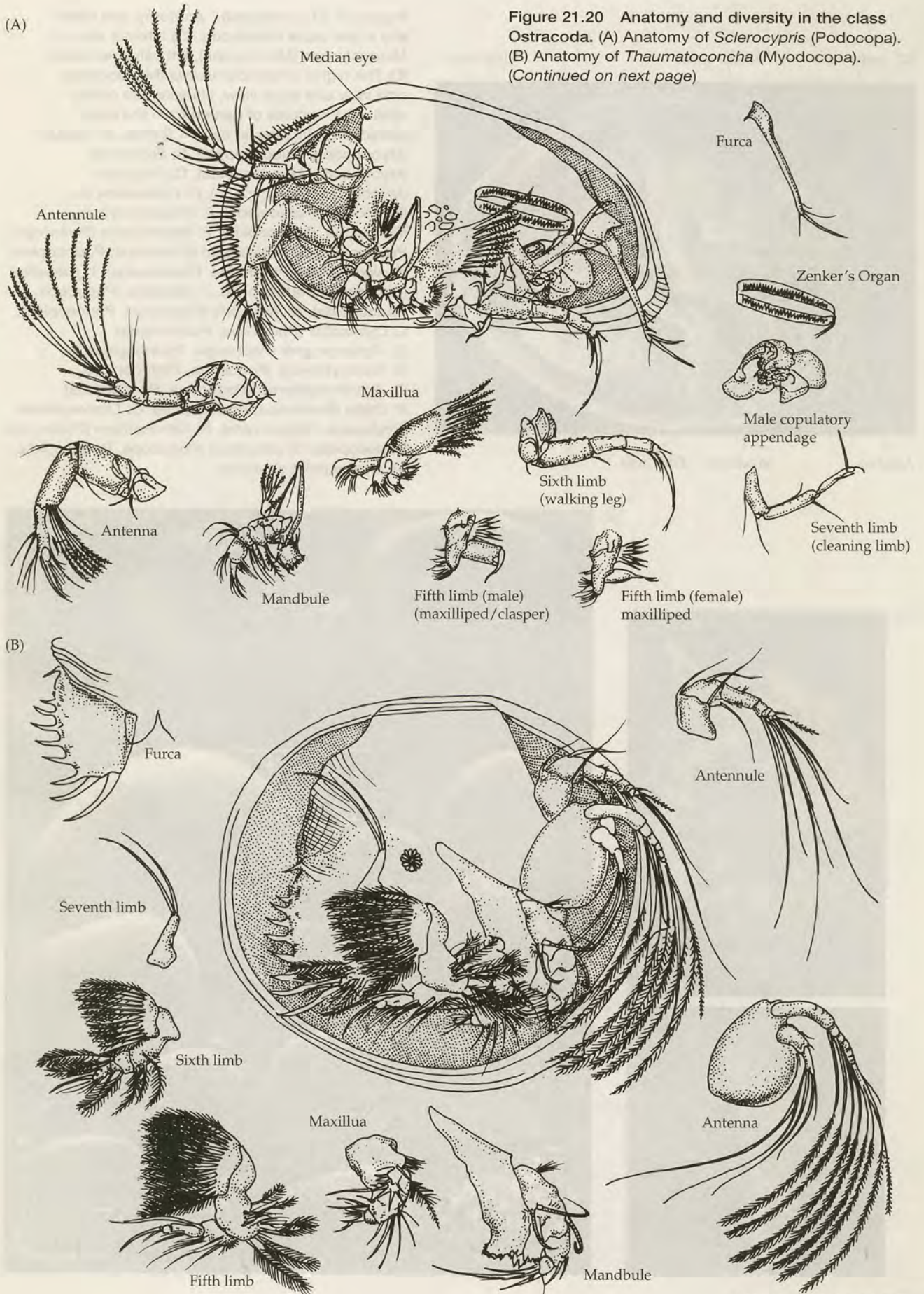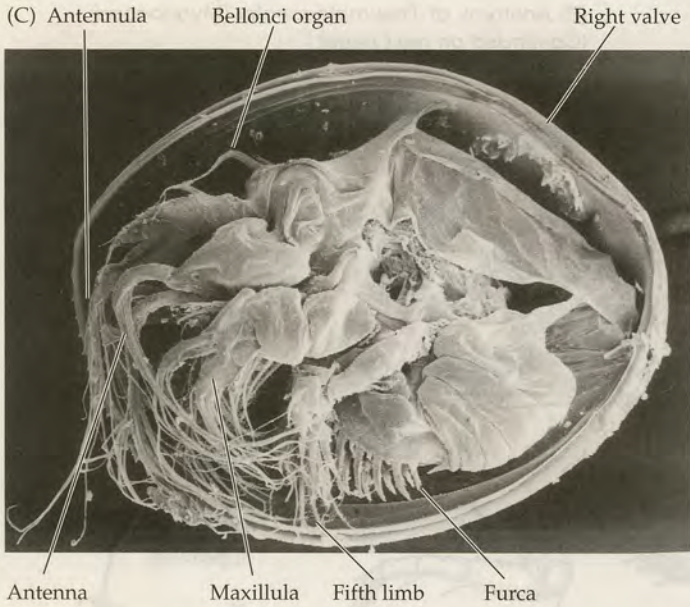
Figure 21.20 (continued)   Anatomy and diversity in the class Ostracoda. (C) Internal view of *Metapolycope* (Myodocopa), left valve removed. (D) The highly ornate *Eusarsiella* (Myodocopa); side view and edge view, showing the ornate shell. (E) Examples of genera from the major ostracod groups (scale bar = 1.0 mm). A: *Vargula* (Myodocopa, Myodocopida). B: *Eusarsiella* (Myodocopa, Myodocopida). C: *Polycope* (Myodocopa, Halocyprida). D: *Cytherelloidea* (Podocopa, Platycopida). E: *Propontocypris* (Podocopa, Podocopida). F: *Macrocypris* (Podocopa, Podocopida). G: *Saipanetta* (Podocopa, Podocopida). H: *Neonesidea* (Podocopa, Podocopida). I: *Triebelina* (Podocopa, Podocopida). J: *Candona* (Podocopa, Podocopida). K: *Ilyocypris* (Podocopa, Podocopida). L: *Cyprinotus* (Podocopa, Podocopida). M: *Potamocypris* (Podocopa, Podocopida). N: *Hemicytherura* (Podocopa, Podocopida). O: *Acanthocythereis* (Podocopa, Podocopida). P: *Celtia* (Podocopa, Podocopida). Q: *Limnocythere* (Podocopa, Podocopida). R: *Sahnicythere* (Podocopa, Podocopida). S: *Darwinula* (Podocopa, Podocopida). All arrows point anteriorly.

(E)

(D)
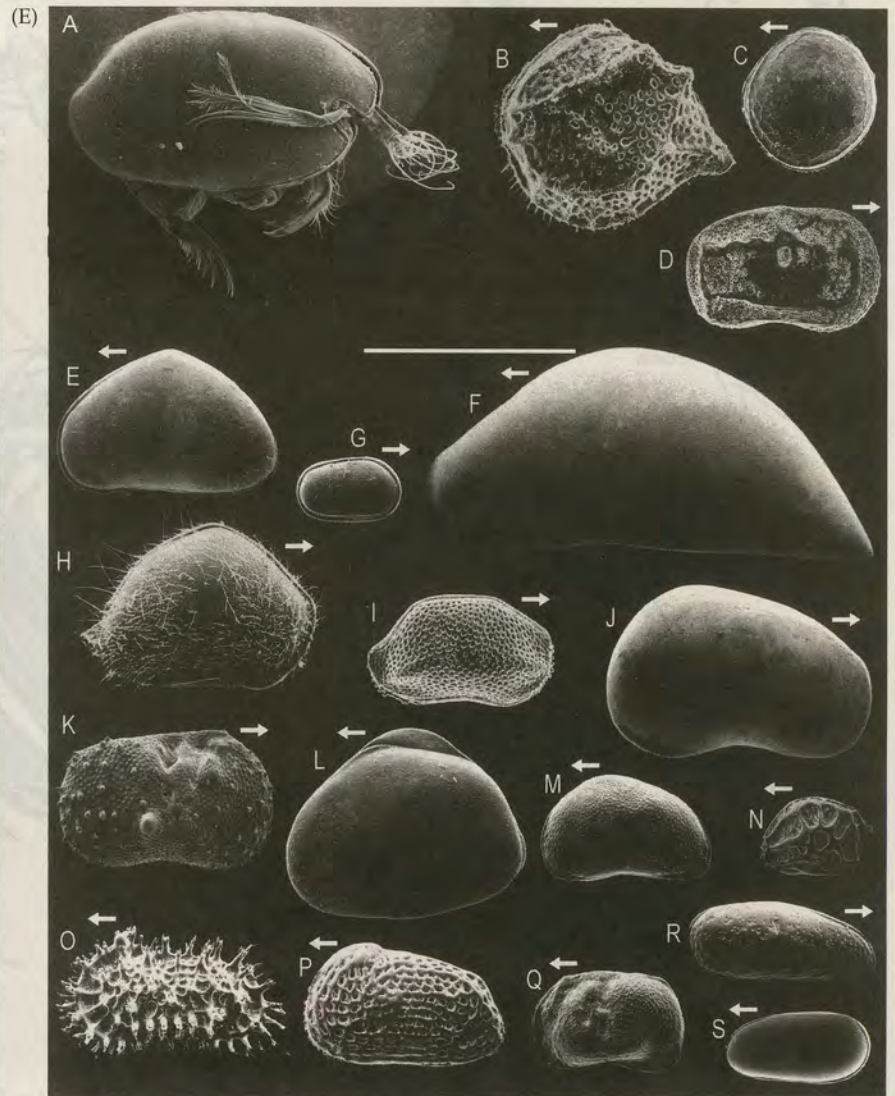
similar appendages, as seen in the class Remipedia (Figures 21.1A and 21.3D,E). In the other crustacean classes, however, various degrees of tagmosis occur, and the cephalon is typically followed by a trunk that is divided into two distinct regions, a **thorax** and an **abdomen**. All crustaceans possess, at least primitively, a **cephalic shield** (**head shield**) or a **carapace**. The cephalic shield results from the fusion of the dorsal head tergites to form a solid cuticular plate, often with ventrolateral folds (**pleural folds**) on the sides. Head shields are found in ancient Cambrian fossil crustaceans (e.g., from the Orsten fauna), and they are characteristic of the classes Remipedia and Cephalocarida; they also occur in some former maxillopodan groups and in malacostracans. The carapace is a more expansive structure, composed of the head shield and a large fold of the exoskeleton that probably arises (primitively) from the maxillary somite. The carapace may extend over the body dorsally and laterally as well as posteriorly, and it often fuses to one or more thoracic segments, thereby producing a **cephalothorax** (Figure 21.2A). Occasionally, the carapace may grow forward beyond the head as a narrow rostrum.

Most of the differences among the major groups of crustaceans, and the basis for much of their classification, arise from variations in the number of somites in the thorax and abdomen, the form of their appendages, and the size and shape of the carapace. A brief skimming of the synopses (above) and the corresponding figures will give you some idea of the range of variation in these characteristics.

Uniformity within the subphylum Crustacea is demonstrated particularly by the consistency of elements of the cephalon and the presence of a nauplius larva. Except for a few cases of secondary reduction, the head of all crustaceans has 5 pairs of appendages. From anterior to posterior, these are the **antennules** (first antennae), **antennae** (second antennae), **mandibles**, **maxillules** (first maxillae), and **maxillae** (second maxillae). The presence of 2 pairs of antennae is, among arthropods, unique to the Crustacea (as is the nauplius larva, although similar "head larvae" are known from other arthropod groups in the fossil record).[7] Although the eyes of some crustaceans are simple, most possess a pair of well developed compound eyes, either set directly on the head (sessile eyes) or borne on distinct movable stalks (stalked eyes).

In many crustaceans, from one to three anterior thoracic segments (**thoracomeres**) are fused with the cephalon. The appendages of these fused segments are typically incorporated into the head as additional mouthparts called **maxillipeds**. In the class Malacostraca, the remaining free thoracomeres are together termed the **pereon**. Each segment of the pereon is called a **pereonite** (= pereomere), and their appendages are called **pereopods**. The pereopods may be specialized for walking, swimming, gas exchange, feeding, and/or defense. Crustacean thoracic (and pleonal) appendages might be primitively biramous, although the uniramous condition is seen in a variety of taxa. The general crustacean limb is composed of a basal **protopod** (= sympod), from which may arise medial **endites** (e.g., gnathobases), lateral **exites** (e.g., **epipods**), and two rami, the endopod and exopod. Members of the classes Remipedia, Cephalocarida, Branchiopoda, and some ostracods possess appendages with uniarticulate (single-segment) protopods; the remaining classes usually have appendages with multiarticulate protopods (Table 21.1).[8]

The abdomen, called a **pleon** in malacostracans, is composed of several segments, or **pleonites** (= pleomeres), followed by a postsegmental plate or lobe, the **anal somite** or **telson**, bearing the anus (Figure 21.2B). In primitive crustaceans this anal somite bears a pair of appendage-like or spinelike processes conventionally called **caudal rami**. In the Eumalacostraca, the anal somite lacks caudal rami and is followed by a dorsal flattened cuticular flap; this flap is sometimes referred to as the telson.

In general, distinctive abdominal appendages (**pleopods**) occur only in the malacostracans. These appendages are almost always biramous, and often they are flaplike and used for swimming (e.g., Figures 21.9–21.15). The posteriorly directed last pair(s) of abdominal appendages is usually different from the other pleopods, and are called **uropods**. Together with the telson, the uropods form a distinct **tail fan** in many malacostracans (Figure 21.2B).

Crustaceans produce a characteristic, and unique, larval stage called the **nauplius** (Figures 21.25B,C and 21.33D), which bears a median simple (naupliar) eye and 3 pairs of setose, functional head appendages—destined to become the antennules, antennae, and mandibles. Behind the head segments is a growth-zone and the telson. In many groups (e.g., Peracarida, and most of Decapoda), however, the free-living nauplius larva is absent or suppressed. In such cases, development is either fully direct or mixed, with larval hatching taking place at some postnaupliar stage (Table 21.2). Often other larval stages follow the nauplius (or other hatching stage) as the individual passes through a series of molts, during which segments and appendages are gradually added. A recent compilation of all crustacean larval forms (Martin et al. 2014) includes

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[7]Cambrian crustacean-like larvae in the fossil record termed "head larvae" may be precursors to the distinctive nauplius stage seen in many modern crustaceans. See Martin et al. (2014)

[8]The term "peduncle" is a general name often applied to the basal portion of certain appendages; it is occasionally (but not always) used in a way that is synonymous with protopod. As noted in Chapter 20, the exopod might be no more than a highly modified exite that evolved from an ancestral uniramous condition.

TABLE 21.1   Comparison of Distinguishing Features among the 11 Crustacean Classes (and in Orders of the Class Branchiopoda and Subclasses of the Class Eumalacostraca)

Taxon	Carapace or cephalic shield	Body tagmata and number of segments in each (excluding telson)	Thoracopods	Maxillipeds
Class Remipedia	Cephalic shield	Cephalon (6) Trunk (up to 32)	Not phyllopodous	1 pair
Class Cephalocarida	Cephalic shield	Cephalon (6) Thorax (8) Abdomen (11)	Phyllopodous	None
Class Branchiopoda, Order Anostraca	Cephalic shield	Cephalon (6) Thorax (usually 11) Abdomen (usually 8)	Phyllopodous	None
Class Branchiopoda, Order Notostraca	Carapace	Cephalon (6), Thorax (11), Abdomen (many segments)	Phyllopodous	None
Class Branchiopoda, Order Diplostraca	Carapace (bivalved, hinged or folded)	Cephalon 6, Trunk 10–32, or obscured)	Phyllopodous	None
Class Malacostraca, Subclass Phyllocarida	Large, folded carapace covers thorax	Cephalon (6), Thorax (8), Abdomen (7)	Phyllopodous	None
Class Malacostraca, Subclass Hoplocarida	Well developed carapace covers thorax	Cephalon (6), Thorax (8), Abdomen (6)	Not phyllopodous	Five paris of thoracopods referred to as maxillipeds
Class Malacostraca, Subclass Eumalacostraca	Carapace well developed or secondarily reduced or lost	Cephalon (6), Thorax (8), Abdomen (6)	Not phyllopodous; uniramous in many	0 to 3 pairs
Class Thecostraca	Carapace bivalved (at some stage), often modified as a mantle	Cephalon (6), Thorax (6), Abdomen (4)	Not phyllopodous, often reduced	None
Class Tantulocarida	Cephalic shield	Cephalon (6), Thorax (6), Abdomen (up to 7)	Not phyllopodous, greatly reduced	None
Class Branchiura	Carapace broad, covering head and trunk	Cephalon (6), Thorax (6), Abdomen (4?)	Not phyllopodous (but all natatory)	None
Class Pentastomida	None	Not distinguishable; body vermiform	None	None
Class Mystacocarida	Cephalic shield	Cephalon (6), Trunk (10)	Not phyllopodous	1 pair
Class Copepoda	Cephalic shield	Cephalon (6), Thorax (6), Abdomen (5)	Not phyllopodous; natatory, often reduced	Usually 1 pair
Class Ostracoda	Carapace, bivalved	Subdivisions not clear; 6–8 pairs of limbs	Not phyllopodous, reduced	None

keys to the distinctive naupliar larvae in all groups that hatch as a nauplius as well as synopses of larval development in all crustaceans.

Locomotion

Crustaceans move about primarily by use of their limbs (Figure 21.21), and lateral body undulations are unknown. They crawl or swim, or more rarely burrow, "hitchhike," or jump. Many of the ectoparasitic forms (e.g., branchiurans, certain isopods, and copepods) are largely sedentary on their hosts, and most cirripedes are fully sessile.

Swimming is usually accomplished by a rowing action of the limbs. Archetypical swimming is exemplified by crustaceans with relatively undifferentiated trunks and high numbers of similar biramous appendages (e.g., remipedes, anostracans, notostracans). In general, these animals swim by posterior to anterior metachronal beating of the trunk limbs (Figure 21.22 and Chapter 20). The appendages of such crustaceans are often broad and flattened, and they usually bear fringes of setae that increase the effectiveness of the power stroke. On the recovery stroke the limbs are flexed, and the setae may collapse, reducing resistance.

Antennules	Antennae	Compound eyes	Abdominal appendages	Gonopore location
Biramous	Biramous	Absent	All trunk appendages similar	♂: protopods of trunk segment 15; ♀: trunk segment 8
Uniramous	Biramous	Absent	None	Common pores on protopods of thoracopods 6
Uniramous	Uniramous	Present	None	♀: on segment 12/13 or 20/21
Uniramous	Vestigial	Present	Present (posteriorly reduced)	Thoracomere 11 (both sexes)
Uniramous	Biramous	Present	All trunk appendages similar, or posterior segments limbless	Variable, on trunk segment 9 or 11, or on apodous posterior region (some Cladocera)
Biramous	Uniramous	Present	Pleopods (posteriorly reduced)	♂: coxae of thoracopods 8; ♀: coxae of thoracopods 6
Triramous	Biramous	Present, well developed	Well developed pleopods with gills; 1 pair of uropods	♂: coxae of thoracopods 8; ♀: coxae of thoracopods 6
Uniramous or biramous	Uniramous or biramous	Present, well developed	Usually 5 pairs of pleopods, 1 pair of uropods	♂: coxae of thoracopods 8 or sternum of thoracomere 8; ♀: coxae of thoracopods 6 or sternum of thoracomere 6
Uniramous	Biramous	Absent (in adults)	None	Variable; ♂ openings usually on trunk segment 4 or 7; ♀ on 1, 4, or 7
None (paired in one stage)	None	Absent	None	♀ openings on trunk segment 5
Uniramous, reduced	Biramous, reduced	Present	None	♂ single opening on thoracomere 6; ♀ gonopores at base of thoracopod 4
None	None	Absent	None	Common gonopore, location variable
Uniramous	Biramous	Absent	None	♂ and ♀ openings on trunk segment 4
Uniramous	Uniramous or biramous	Absent	None	Gonopores usually on urosomal segment 1
Uniramous	Biramous	Absent (typically)	None	Gonopores on lobe anterior to caudal rami

In members of some groups (e.g., Cephalocarida, Branchiopoda, Leptostraca), large exites or epipods arise from the base of the leg, producing broad, "leafy" limbs called **phyllopodia**. These flaplike structures aid in locomotion and may also serve as osmoregulatory (branchiopods) or gas exchange (cephalocardis and leptostracans) surfaces (Figure 21.21A–C). Although such epipods increase the surface area on the power stroke, they also are hinged so that they collapse on the recovery stroke, reducing resistance. Metachronal limb movements are retained in many of the "higher" swimming crustaceans, but they tend to be restricted to selected appendages (e.g., the pleopods of shrimps, stomatopods, amphipods, and isopods; the pereopods of euphausids and mysids). In swimming euphausids and mysids the thoracopods beat in a metachronal rowing fashion, with the exopod and setal fan extended on the power stroke and flexed on the recovery stroke. The movements and nervous–muscular coordination of crustacean limbs are deceivingly complex. In the common mysid *Gnathophausia ingens*, for example, twelve separate muscles power the thoracic exopod alone (three that are extrinsic to the exopod, five in the limb peduncle, and four in the exopodal flagellum).

(A)

Endites

Protopod

Epipod

Endopod

Exopod

(B)

Protopod

Epipod

Endites

Exopod

Endopod

(C)

Protopod

Epipod

Exopod

Endopod

(D)

Protopod

Exopod

Endopod

(E)

Basis

Coxa

Epipod

Ischium

Merus

Exopod

Endopod

Carpus

Propodus

Dactyl

(F)

Basis

Coxa

Ischium

Merus

Carpus

Propodus

Dactyl

(G)

Oostegite

Coxa

Basis

Preischium

Ischium

Merus

Endopod

Exopod

Carpo-propodus

Dactyl

(H)

Coxa

Basis

Ischium

Exopod

Endopod

Carpus

Merus

Propodus

Dactyl

(I)

Coxa

Basis

Ischium

Merus

Carpus

Propodus

Dactyl

◀ **Figure 21.21   Generalized thoracic appendages of various crustaceans.** (A–C) Biramous, phyllopodous thoracopods. (A) Cephalocarida. (B) Branchiopoda. Dashed lines indicate fold or "hinge" lines. (C) Leptostraca (Phyllocarida). (D) A biramous, flattened, but nonphyllopodous thoracopod: Remipedia. (E–I) Stenopodous thoracopods. (E) Euphausiacea. (F) Caridea (Decapoda). (G) Lophogastrida (Peracarida). (H) Spelaeogriphacea (Peracarida). (I) Isopoda (Peracarida). Because of the presence of large epipods on the legs of the cephalocarids, branchiopods, and phyllocarids, some authors refer to them as "triramous" appendages. However, smaller epipods also occur on many typical "biramous" legs, so this distinction seems unwarranted (and confusing). Note that in the four primitive groups of crustaceans (cephalocarids, branchiopods, phyllocarids, and remipedes) the protopod is composed of a single article. And in branchiopods and leptostracans, the articles of the endopod are not clearly separated from one another. In the higher crustaceans (Malacostraca and former "maxillopodans") the protopod comprises two or three separate articles, although in most former maxillopodans these may be reduced and not easily observed. In the lophogastrid (G), the large marsupial oostegite characteristic of female peracarids is shown arising from the coxa. In two groups (amphipods and isopods) all traces of the exopods have disappeared, and only the endopod remains as a long, powerful, uniramous walking leg.
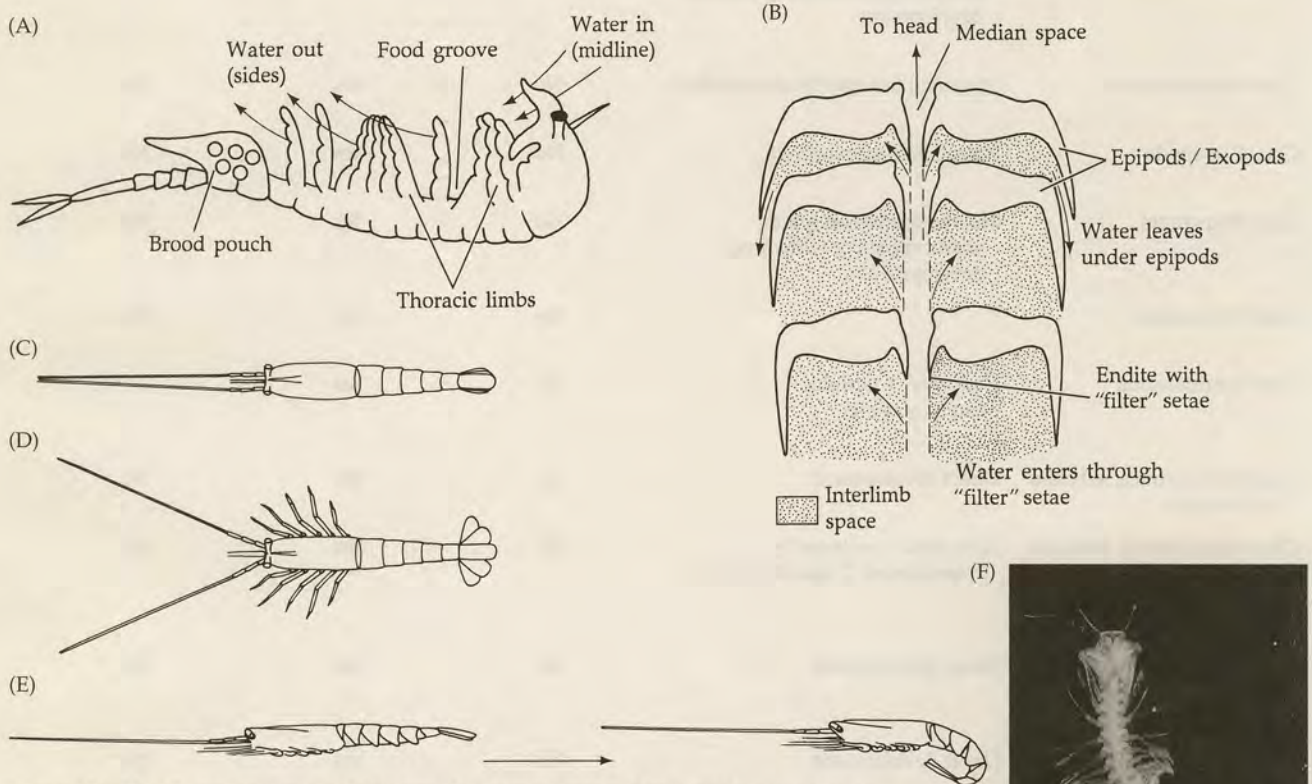
Figure 21.22   Some aspects of locomotion (and feeding) in three crustaceans (also see Chapter 20). (A,B) Generation of swimming and feeding currents in an anostracan. (A) An anostracan swimming on its back by metachronal beating of the trunk limbs. The limbs are hinged to fold on the recovery stroke, thereby reducing resistance. (B) Water is drawn from anterior to posterior along the midline and into the interlimb spaces, and food particles are trapped on the medial sides of the endites; excess water is pressed out laterally, and the trapped food is moved anteriorly to the mouth. (C–E) Locomotion in the postlarva of *Panulirus argus*. (C) Normal swimming posture when moving forward slowly. (D) Sinking posture with appendages flared to reduce sinking rate. (E) A quick retreat by rapid tail flexure (the "caridoid escape reaction"), a method commonly employed by crustaceans with well developed abdomens and tail fans. (F) A swimming remipede, *Lasionectes*. Note the metachronal waves of appendage movement.

TABLE 21.2   Summary of Crustacean Reproductive Features[a]

Taxon	Development type, or larval type at hatching	Hermaphroditic (at least some species)	Gonochoristic	Parthenogenesis (in at least some species)
Class Remipedia	Nauplius (anamorphic)	Yes	No	No
Class Cephalocarida	Metanauplius (anamorphic)	Yes	No	No
Class Branchiopoda, order Anostraca	Nauplius or metanauplius (anamorphic)	No	Yes	Yes
Class Branchiopoda, order Notostraca	Nauplius or metanauplius (anamorphic), or direct development	Yes	Yes	Yes
Class Branchiopoda, order Diplostraca	Nauplius (partly anamorphic)	No	Yes	Yes
Class Ostracoda	Direct, or with bivalved nauplius/ metanauplius with anamorphic development	No	Yes	Yes
Class Mystacocarida	Metanauplius (partly anamorphic)	No	Yes	No
Class Copepoda	Nauplius (metamorphic)	No	Yes	No
Class Branchiura	Metanauplius-like (partly anamorphic), or with direct development	No	Yes	No
Class Thecostraca	?	Yes	Yes	No
Class Tantulocarida	Nauplius? + tantulus (metamorphic)	No	Yes	?
Class Malacostraca, subclass Phyllocarida	Direct development	No	Yes	No
Class Malacostraca, subclass Hoplocarida	Zoea larva ("antizoea" or "pseudozoea") (metamorphic)	No	Yes	No
Class Malacostraca, subclass Eumalacostraca, superorder Syncarida	Direct development	No	Yes	No
Class Malacostraca, subclass Eumalacostraca, superorder Peracarida	Direct development	No	Yes	No
Class Malacostraca, subclass Eumalacostraca, superorder Eucarida, order Euphausiacea	Nauplius (metamorphic)	No	Yes	No
Class Malacostraca, subclass Eumalacostraca, superorder Eucarida, order Amphionidacea	Amphion (modified zoea) (weakly metamorphic)	No	Yes	No
Class Malacostraca, subclass Eumalacostraca, superorder Eucarida, order Decapoda	Pre-zoea or zoea, and with a nauplius in Dendrobranchiata (metamorphic), or direct development	Rare	Yes	No

[a] Also see Martin et al. 2014, Table 55.1.

Comments

Eight naupliar stages (2 orthonauplii and 6 metanauplii), followed by a"pre-juvenile"stage, have been reported.

One or two eggs at a time are fertilized and carried on genital processes of the first pleonites.

Embryos usually shed from ovisac early in development; resistant (cryptobiotic) fertilized eggs accommodate unfavorable conditions.

Eggs briefly brooded, then deposited on substrata; resistant (cryptobiotic) fertilized eggs accommodate unfavorable conditions.

Most cladocerans undergo direct development (*Leptodora* hatches as nauplii or metanauplii). Clam shrimps carry developing embryos on the thoracopods prior to releasing them as nauplii or metanauplii.

Embryos usually deposited directly on substrata; many myodocopans and some podocopans brood embryos between valves until hatching as a reduced adult; no metamorphosis; up to 8 preadult instars.

Little studied, but apparently the eggs are laid free and up to 7 preadult stages may occur.

Usually with 6 naupliar stages leading to a second series of 5"larval" stages called copepodites.

Embryos are deposited; only *Argulus* is known to hatch as metanauplii, others have direct development and hatch as juveniles.

Six naupliar stages followed by a unique larval form called a cypris larva.

A benthic non-feeding stage, possibly a nauplius, has been reported but not formally described. Development entails complex metamorphosis with infective"tantulus larva."

Undergo direct development in the female brood pouch, emerging as a postlarval/prejuvenile stage called a"manca."

Eggs brooded or deposited in burrow; hatch late as clawed pseudozoea larvae, or earlier as unclawed antizoea larvae. Both molt into distinct ericthus (and some into alima) larvae before settling on bottom as post-larvae or juveniles.

All free larval stages have been lost; eggs deposited on substratum.

Embryos brooded in marsupium of female typically formed from ventral coxal plates called oostegites; usually released as mancas (subjuveniles with incompletely developed 8th thoracopods). Brood pouch (marsupium) in Thermosbaenacea formed by dorsal carapace chamber.

Embryos shed or briefly brooded; typically undergo nauplius-metanauplius-calyptopis-furcilia-juvenile developmental series.

Eggs apparently brooded in female brood pouch; hatching likely occurs as eggs float upward after release; hatching probably as an amphion larva (a zoea with only one pair of thoracopods modified as maxillipeds), with perhaps 20 stages that metamorphose gradually to a subadult.

Dendrobranchiata shed embryos to hatch in water as nauplii or pre-zoea; all others brood embryos (on pleopods), which do not hatch until a pre-zoeal or zoeal stage (or later).

Recall from our discussions in Chapters 4 and 20 that at the low Reynolds numbers at which small crustaceans (such as copepods or larvae) swim about, the netlike setal appendages act not as a filtering net, but as a paddle, pushing water in front of them and dragging the surrounding water along with them due to the thick boundary layer adhering to the limb. Only in larger organisms, with Reynolds numbers approaching 1, do setose appendages (e.g., the feeding cirri of barnacles) begin to act as filters, or rakes, as the surrounding water acts less viscous and the boundary layer thinner. Of course, the closer together the setae and setules are placed, the more likely it is that their individual boundary layers will overlap; thus densely setose appendages are more likely to act as paddles.

Not all swimming crustaceans move by typical metachronal waves of limb action. Certain planktonic copepods, for example, move haltingly and depend on their long antennules and dense setation for flotation between movements (Figure 21.18F). Watch living calanoid copepods and you will notice that they may move slowly by use of the antennae and other appendages, or in short jerky increments, often sinking slightly between these movements. The latter type of motion results from an extremely rapid and condensed metachronal wave of power strokes along the trunk limbs. Although the long antennae may appear to be acting as paddles, they actually collapse against the body an instant prior to the beating of the limbs, thus reducing resistance to forward motion. Some other planktonic copepods create swimming currents by rapid vibrations of cephalic appendages, by which the body moves smoothly through the water. "Rowing" does occur in the swimming crabs (family Portunidae) and some deep-sea asellote isopods (e.g., family Eurycopidae), both of which use paddle-shaped posterior thoracopods to scull about.

Most eumalacostracans with well-developed abdomens exhibit a form of temporary, or "burst," swimming that serves as an escape reaction (e.g., mysids, syncarids, euphausids, shrimps, lobsters, and crayfish). By rapidly contracting the ventral abdominal (flexor) muscles, such animals shoot quickly backward, the spread tail fan providing a large propulsive surface (Figure 21.22C–E). This behavior is sometimes called a **tail-flip**, or "**caridoid escape reaction**."

Surface crawling by crustaceans is accomplished by the same general sorts of leg movements described in the preceding chapters for insects and other arthropods: by flexion and extension of the limbs to pull or push the animal forward. Walking limbs are typically composed of relatively stout, more or less cylindrical articles (i.e., stenopodous

limbs) as opposed to the broader, often phyllopodous limbs of swimmers (see Figure 21.21 for a comparison of crustacean limb types). Walking limbs are lifted from the substratum and moved forward during their recovery strokes; then they are placed against the substratum, which provides purchase as they move posteriorly through their power strokes, pulling and then pushing the animal forward. Like many other arthropods, crustaceans generally lack lateral flexibility at the body joints, so turning is accomplished by reducing the stride length or movement frequency on one side of the body, toward which the animal turns (like a tractor or tank slowing one tread). Many crustaceans migrate; perhaps the most famous is the Chinese mitten crab (*Eriocheir sinensis*), which spends most of its life in fresh water, but returns to the sea to breed. These crabs have been found over 1000 km upriver from the sea—testimony to their superb locomotory ability. Perhaps not unexpectedly, *E. sinensis* is also an important (and destructive) invasive species in North America and Europe. It has been accidently introduced into the Great Lakes several times, but has not yet been able to establish a permanent population.

Most walking crustaceans can also reverse the direction of leg action and move backward, and most brachyuran crabs can walk sideways. Brachyuran crabs are perhaps the most agile of all crustaceans. The extreme reduction of the abdomen in this group allows for very rapid movement because adjacent limbs can move in directions that avoid interference with one another (and much the same thing has happened, independently, in many anomurans with reduced abdomens). Brachyuran crab legs are hinged in such a way that most of their motion involves lateral extension (abduction) and medial flexion (adduction) rather than rotation frontward and backward. As a crab moves, its limbs move in various sequences, as in normal crawling, but those on the leading side exert their force by flexing and pulling the body toward the limb tips, while the opposite, trailing, legs exert propulsive force as they extend and push the body away from the tips. Still, this motion is simply a mechanical variation on the common arthropodan walking behavior. Many crustaceans move into mollusc shells or other objects, carrying these about as added protection. In most cases, the exoskeleton of the crustacean is reduced, especially the abdomen (e.g., hermit crabs). Of course, crustaceans grow in size as they go through their molts, so these mobile-home-carrying crustaceans must continually find larger shells to inhabit. Many hermit crabs assemble in congregations to exchange shells in a sort of group "passing of the shells" as they move into vacated larger abodes.

In addition to these two basic locomotor methods ("typical" walking and swimming by metachronal beating of limbs), many crustaceans move by other specialized means. Ostracods, cladocerans, and clam shrimp (Diplostraca), most of which are largely enclosed by their carapaces (Figures 21.4F,G,J,L,M and 21.20), swim by rowing with the antennae. Mystacocarids crawl in interstitial water using various head appendages. Most semi-terrestrial amphipods known as "beach hoppers" (e.g., *Orchestia* and *Orchestoidea*) execute dramatic jumps by rapidly extending the urosome and its appendages (uropods), reminiscent of the jumping of springtails described in Chapter 22. Most caprellid amphipods (Figure 21.15E) move about in inchworm fashion, using their subchelate appendages for clinging. There are also a number of crustacean burrowers, and even some that build their own tubes or "homes" from materials in their surroundings. Many benthic amphipods, for example, spin silk-lined mud burrows in which they reside. One species, *Pseudamphithoides incurvaria* (suborder Gammaridea), constructs and lives in an unusual "bivalved pod" cut from the thin blades of the same alga on which it feeds (Figure 21.23A). Another gammaridean amphipod, *Photis conchicola*, actually uses empty gastropod shells in a fashion similar to that of hermit crabs (Figure 21.23C). "Hitchhiking" (phoresis) occurs in various ectosymbiotic crustaceans, including isopods that parasitize fishes or shrimps and hyperiidean amphipods that ride on gelatinous drifting plankters.

In addition to simply getting from one place to another in their usual day-to-day activities, many crustaceans exhibit various migratory behaviors, employing their locomotor skills to avoid stressful situations or to remain where conditions are optimal. A number of planktonic crustaceans undertake daily vertical migrations, typically moving upward at night and to greater depths during the day. Such vertical migrators include various copepods, cladocerans, ostracods, and hyperiid amphipods (the latter may make their migrations by riding on their gelatinous hosts). Such movements place the animals in their near-surface feeding grounds during the dark hours, when there is probably less danger of being detected by visual predators. In the daytime, they move to deeper, perhaps safer, water. These crustaceans can form enormous shoals that contribute to the deep scattering layer seen on ship's sonar. Many intertidal crustaceans use their locomotor abilities to change their behaviors with the tides. Crab larvae in particular are known to migrate upward or downward according to daily rhythms, taking advantage of incoming or outgoing tides to move in and out of estuaries. Some anomuran and brachyuran crabs simply move in and out with the tide, or seek shelter beneath rocks when the tide is out, thus avoiding the problems of air exposure. One of the most interesting locomotor behaviors among crustaceans is the mass migration of the spiny lobster, *Panulirus argus*, in the Gulf of Mexico and northern Caribbean. Each autumn, lobsters queue up in single file and march in long lines across the seafloor for several days. They move from
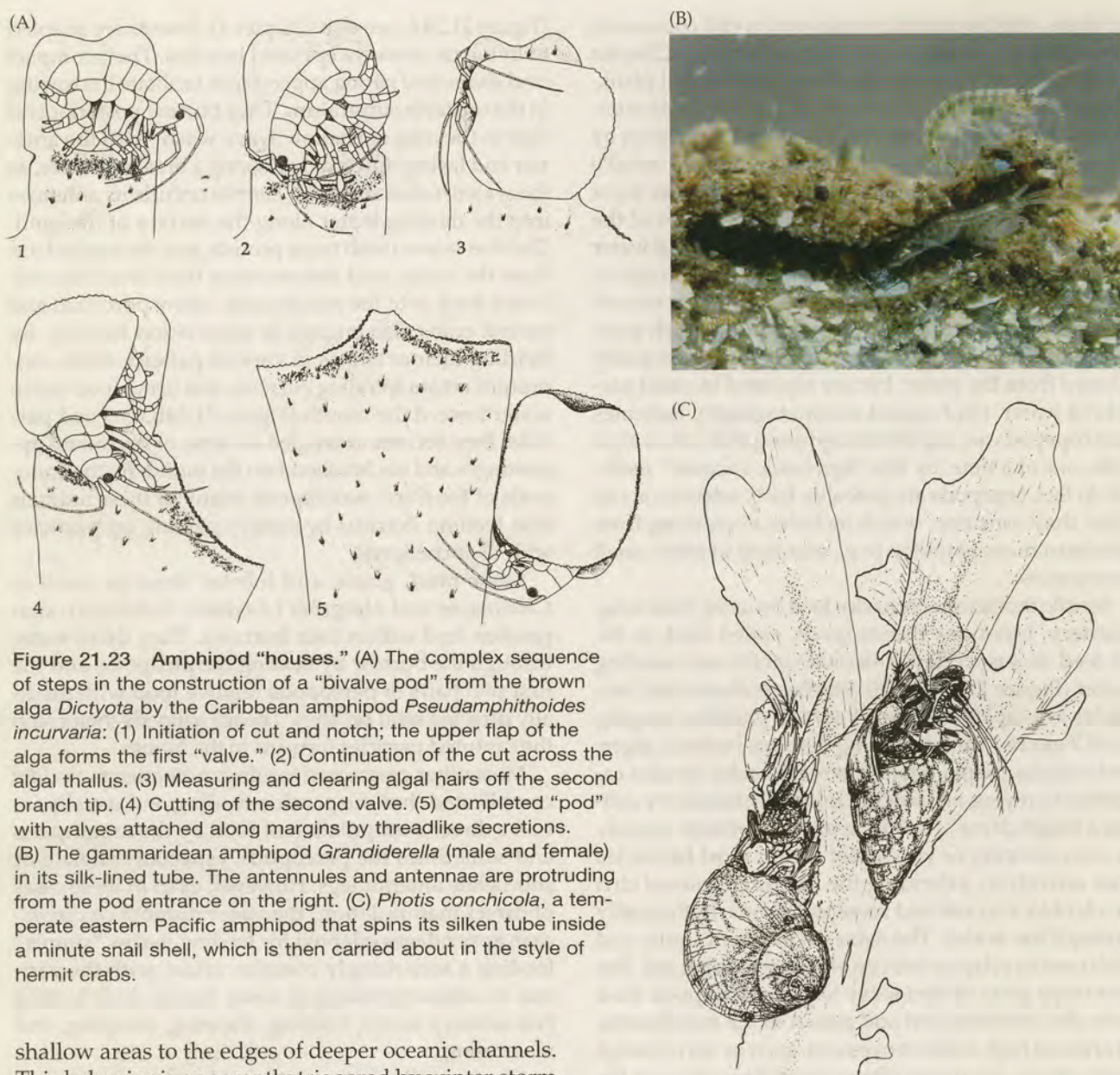
(A)

(B)

(C)

Figure 21.23   Amphipod "houses." (A) The complex sequence of steps in the construction of a "bivalve pod" from the brown alga *Dictyota* by the Caribbean amphipod *Pseudamphithoides incurvaria*: (1) Initiation of cut and notch; the upper flap of the alga forms the first "valve." (2) Continuation of the cut across the algal thallus. (3) Measuring and clearing algal hairs off the second branch tip. (4) Cutting of the second valve. (5) Completed "pod" with valves attached along margins by threadlike secretions. (B) The gammaridean amphipod *Grandiderella* (male and female) in its silk-lined tube. The antennules and antennae are protruding from the pod entrance on the right. (C) *Photis conchicola*, a temperate eastern Pacific amphipod that spins its silken tube inside a minute snail shell, which is then carried about in the style of hermit crabs.

shallow areas to the edges of deeper oceanic channels. This behavior is apparently triggered by winter storm fronts moving into the area, and it may be a means of avoiding rough water conditions in the shallows.

Feeding

With the exception of ciliary mechanisms, crustaceans have exploited virtually every feeding strategy imaginable (and some "unimaginable"). Even without cilia, many crustaceans generate water currents and engage in various types of suspension feeding. We have selected a few examples to demonstrate the range of feeding mechanisms that occur in this group.

In some crustaceans the action of the thoracic limbs simultaneously creates the swimming and suspension feeding currents. As the metachronal wave of appendage motion passes along the body, adjacent limb pairs are alternately moved apart and then pressed together, thus changing the size of each interlimb space (Figure 21.22A,B; see also Chapters 4 and 20). Surrounding

water is drawn into an interlimb space as the adjacent appendages move away from one another, and waterborne particles are trapped by setae on the endites as the appendages then close. From here, the trapped particles are moved to a midventral food groove and then anteriorly, toward the head. This mechanism of forming a boxlike "filter press" with setose phyllopodous limbs is the typical suspension feeding strategy of cephalocarids, most branchiopods, and many malacostracans.

Planktonic copepods were long thought to "filter" feed by generating lateral feeding gyres or currents by movements of the antennae and mouth appendages. It was believed that these gyres swept in small particles that were directly filtered by the maxillae. This classic idea of maxillary filtration, built on work by H. G. Cannon in the 1920s, has been questioned by recent

workers, but the model persists and is still commonly presented in general works. As mentioned in Chapter 4, we now know that copepods and other small planktonic crustaceans live in a world of low Reynolds numbers, a world dominated by viscosity rather than by inertia. Thus, the setose mouth appendages behave more like paddles than like sieves, with a water layer near the limb adhering to it and forming part of the "paddle." As the maxillae move apart, parcels of water containing food are drawn into the interlimb space. As the maxillae press together, the "parcel" is moved forward to the endites of the maxillules, which push it into the mouth. Thus, food particles are not actually filtered from the water, but are captured in small parcels of water. High-speed cinematography indicates that copepods are capable of capturing individual algal cells, one at a time, by this "hydraulic vacuum" method. In fact, copepods are probably fairly selective about what they consume, which includes everything from protistan microplankton (e.g., diatoms) to other small crustaceans.

Sessile thoracican barnacles feed by using their long, feathery, biramous thoracopods, called **cirri**, to filter feed on suspended material from the surrounding water (Figure 21.16A,C,E). Studies indicate that barnacles are capable of trapping food particles ranging from 2 μm to 1 mm, including detritus, bacteria, algae, and various zooplankters. Many barnacles are also capable of preying on larger planktonic animals by coiling a single cirrus around the prey, in tentacle fashion. In slow-moving or very quiet water, most barnacles feed actively by extending the last three pairs of cirri in a fanlike manner and sweeping them rhythmically through the water. The setae on adjacent limbs and limb rami overlap to form an effective filtering net. The first three pairs of cirri serve to remove trapped food from the posterior cirri and pass it to the mouthparts. In areas of high water movement, such as wave-swept rocky shores, barnacles often extend their cirri into the backwash of waves, allowing the moving water to simply run through the "filter," rather than moving the cirri through the water. In such areas you will often see clusters of barnacles in which all the individuals are oriented similarly, taking advantage of this labor-saving device.

Most krill (euphausids) feed in a fashion similar to barnacles, but while swimming. The thoracopods form a "feeding basket" that expands as the legs move outward, sucking food-laden water in from the front. Once inside the basket, particles are retained on the setae of the legs as the water is squeezed out laterally. Other setae comb the food particles out of the "trap" setae, while yet another set brushes them forward to the mouth region.

Sand crabs of the genus *Emerita* (Anomura) use their long, setose antennae in a fashion similar to that of barnacle cirri that "passively" strain wave backwash

(Figure 21.24A; see also Chapter 4). *Emerita* are adapted to living on wave-swept sand beaches. Their compact oval shape and strong appendages facilitate burrowing in the unstable substratum. They burrow posterior end first in the area of shallow wave wash, with the anterior end facing upward. Following a breaking wave, as the water rushes seaward, *Emerita* unfurls its antennae into the moving water along the surface of the sand. The fine setose mesh traps protists and phytoplankton from the water, and the antennae then brush the collected food onto the mouthparts. Many porcelain and hermit crabs also engage in suspension feeding. By twirling their antennae in various patterns these anomurans create spiraling currents that bring food-laden water toward the mouth (Figure 21.24B,C). Food particles then become entangled on setae of the mouth appendages and are brushed into the mouth by the endopods of the third maxillipeds. Many of these animals also feed on detritus by simply picking up particles with their chelipeds.

Some mud, ghost, and lobster shrimps, such as *Callianassa* and *Upogebia* (Axiidea, Gebiidea), suspension feed within their burrows. They drive water through the burrow by beating the pleopods, and the first two pairs of pereopods remove food with medially directed setal brushes. The maxillipeds then comb the captured particles forward to the mouth.

Most other crustacean feeding mechanisms are less complicated than suspension feeding and usually involve direct manipulation of food by the mouthparts and sometimes the pereopods, especially chelate or subchelate anterior legs. However, even in these cases of direct manipulation, the sheer number of crustacean appendages adapted for feeding makes "simple" feeding a surprisingly complex affair, with the various mouthparts taking on tasks that include tasting (via sensory setae), holding, chewing, scraping, and macerating.

Many small crustaceans may be classified as microphagous selective deposit feeders, employing various methods of removing food from the sediments in which they live. Mystacocarids, many harpacticoid copepods, and some cumaceans and gammaridean amphipods are referred to as "sand grazers" or "sand lickers." By various methods these animals remove detritus, diatoms, and other microorganisms from the surfaces of sediment particles. Interstitial mystacocarids, for example, simply brush sand grains with their setose mouthparts. On the other hand, some cumaceans pick up an individual sand grain with their first pereopods and pass it to the maxillipeds, which in turn rotate and tumble the particle against the margins of the maxillules and mandibles. The maxillules brush and the mandibles scrape, removing organic material. Some sand-dwelling isopods may employ a similar feeding behavior.

Predatory crustaceans include stomatopods, remipedes, and most lophogastrids, as well as many species
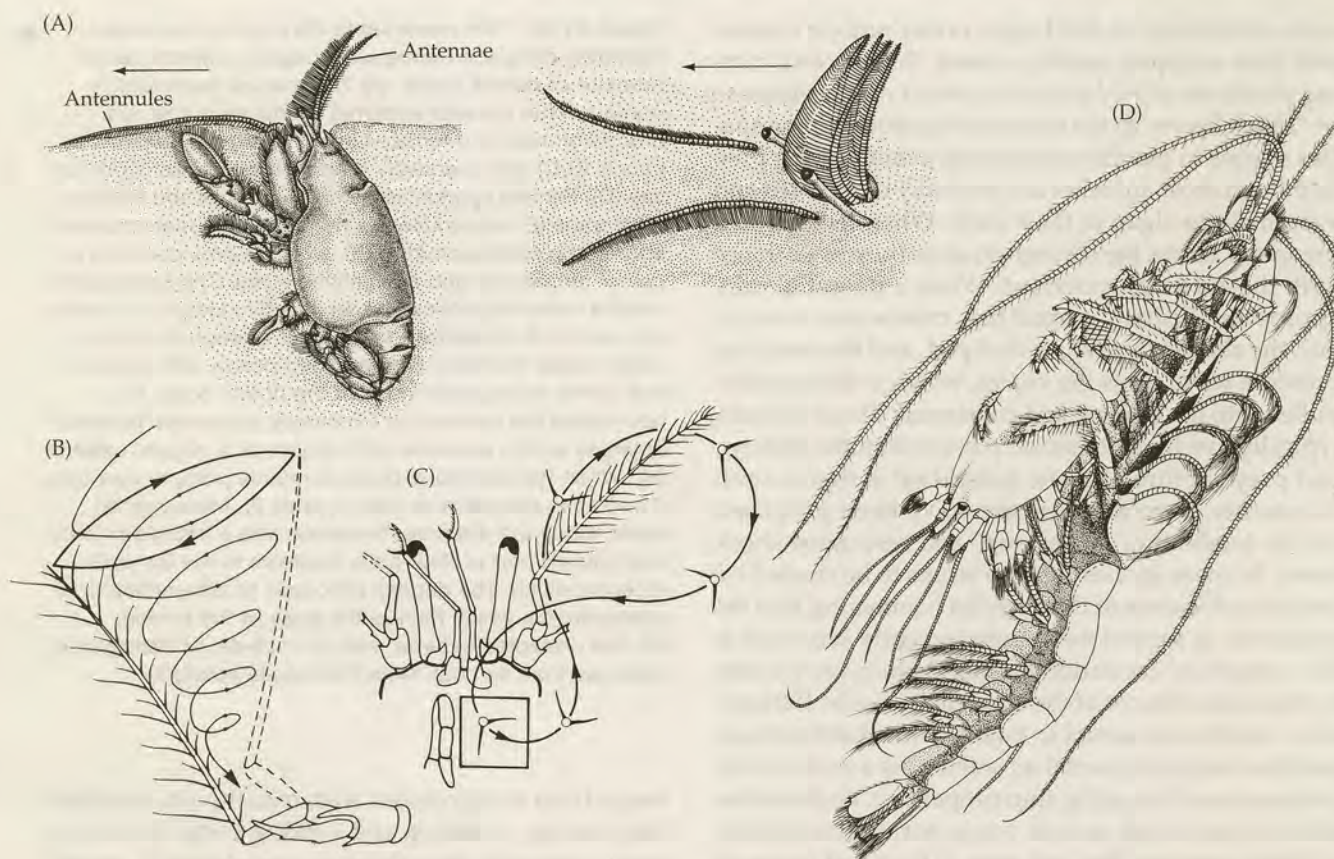
Figure 21.24   **Some crustacean feeding mechanisms** (see also Figure 21.22). (A) Suspension feeding in the sand crab *Emerita*. The arrows point seaward and indicate the direction of water movement as waves recede. The antennules direct water through branchial chambers. The antennae remove food particles from the water and then brush them onto the mouthparts. (B,C) The suspension feeding hermit crabs (B) *Australeremus cooki* and (C) *Paguristes pilosus* twirl their antennae, either in a circle or a figure eight, to create water currents that pull food particles to the mouth region. (D) The predatory shrimp *Procaris ascensionis* (Caridea) is shown here munching on another shrimp (*Typhlatya*) as it holds the prey in a "cage" formed by the pereopodal endopods.

of anostracans, cladocerans, copepods, ostracods, cirripedes, anaspidaceans, euphausids, decapods, tanaids, isopods, and amphipods. Predation typically involves grasping the prey with chelate or subchelate pereopods (or sometimes directly with the mouth appendages), or even with the antennae in the case of predatory anostracans, followed by tearing, grinding, or shearing with various mouthparts, particularly the mandibles. Perhaps the most highly adapted predatory specialists are the stomatopods (Figure 21.7), which possess greatly enlarged, raptorial subchelate limbs, which they use to stab or to club and smash prey. Some species search out prey, but many sit in ambush at their burrow entrance. The actual attack generally follows visual detection of a potential prey item, which may be another crustacean, a mollusc, or even a small fish. Once captured and stunned or killed by the raptorial claws, the prey is held against the mouthparts and shredded into ingestible pieces.

Although the cave-dwelling and often presumed "primitive" shrimp *Procaris* is omnivorous, its predatory behavior is particularly interesting. Its prey includes other crustaceans, particularly amphipods and shrimps. After *Procaris* locates a potential victim (probably by chemoreception), it moves quickly to the prey and grasps it within a "cage" formed by the pereopodal endopods (Figure 21.24D). Once captured, the prey is eaten while the shrimp swims about. Apparently the third maxillipeds press the prey against the mandibles, which bite off chunks and pass them to the mouth.

The remipedes capture prey with their raptorial mouth appendages (Figures 21.1A, 21.3D–F, and 21.22F), then immobilize the victim with an injection from the hypodermic maxillules. It is suspected that tissues are then sucked out of the prey by action of a mandibular mill and muscular foregut. They are probably also facultative suspension feeders and scavengers.

Another fascinating adaptation for predation can be seen in many species of Alpheidae (the snapping shrimps, e.g., *Alpheus, Synalpheus*) (Figure 21.9D). In such species, one of the chelipeds is much larger than the other, and the movable finger is hinged in such

a way that it can be held open under muscle tension and then snapped quickly closed; this forceful closing produces a loud popping sound and a pressure or "shock" wave in the surrounding water. Some species appear to use this mechanism in ambushing prey (although most alpheids are probably omnivores and even include algae in their diet). When feeding in a predatory mode, the shrimp sits at its burrow entrance with the antennae extended. When a potential prey approaches (usually a small fish, crustacean, or annelid), the shrimp "pops" its cheliped, and the resulting pressure wave stuns the victim, which is then quickly pulled into the burrow and consumed. These shrimps typically live in male-female pairs within the burrow, and prey captured by one individual is shared with its partner. Two mechanisms have been proposed for the production of the "pop" and associated shock wave. In some species the pop seems to be created by mechanical impact of the dactylus hammering into the propodus. A second mechanism recently proposed is the collapse of cavitation bubbles, which are created by the rapid closure of the claw (in excess of 100 km/sec). Captivation occurs in liquids when bubbles form and then implode around an object (it is a well-known phenomenon damaging ship propellers). Both mechanisms create shock waves. Some boring (endolithic) alpheids even use the claw snap to break off pieces of the rock into which they are digging. In some areas of the world, populations of snapping shrimp are so large that their noise disturbs underwater communication. In the Caribbean, colonies of alpheids have been likened to those of social insects (e.g., *Synalpheus regalis* colonies in Belize inhabit sponges and contain up to 350 sibling males and females, and a single dominant breeding female).

Many crustaceans emerge from the benthos under cover of darkness to feed or mate in the water column. Many predatory isopods emerge at night to feed on invertebrates or fish, particularly weak or diseased fish (or fish caught in fishing nets).

Macrophagous herbivorous and scavenging crustaceans generally feed by simply hanging onto the food source and biting off bits with the mandibles (a feeding technique similar to that of grasshoppers and other insects). Notostracans, some ostracods, and many decapods, isopods, and amphipods are scavengers and herbivores. Certain isopods in the family Sphaeromatidae bore into the aerial roots of mangrove trees. Their activities often result in root breakage followed by new multiple root initiation, creating the stiltlike appearance characteristic of red mangroves (*Rhizophora*). A number of crustaceans are full-time or part-time detritivores; many scavenge directly on detritus, but others (e.g., cephalocarids) stir up the sediments in order to remove organic particles by suspension feeding.
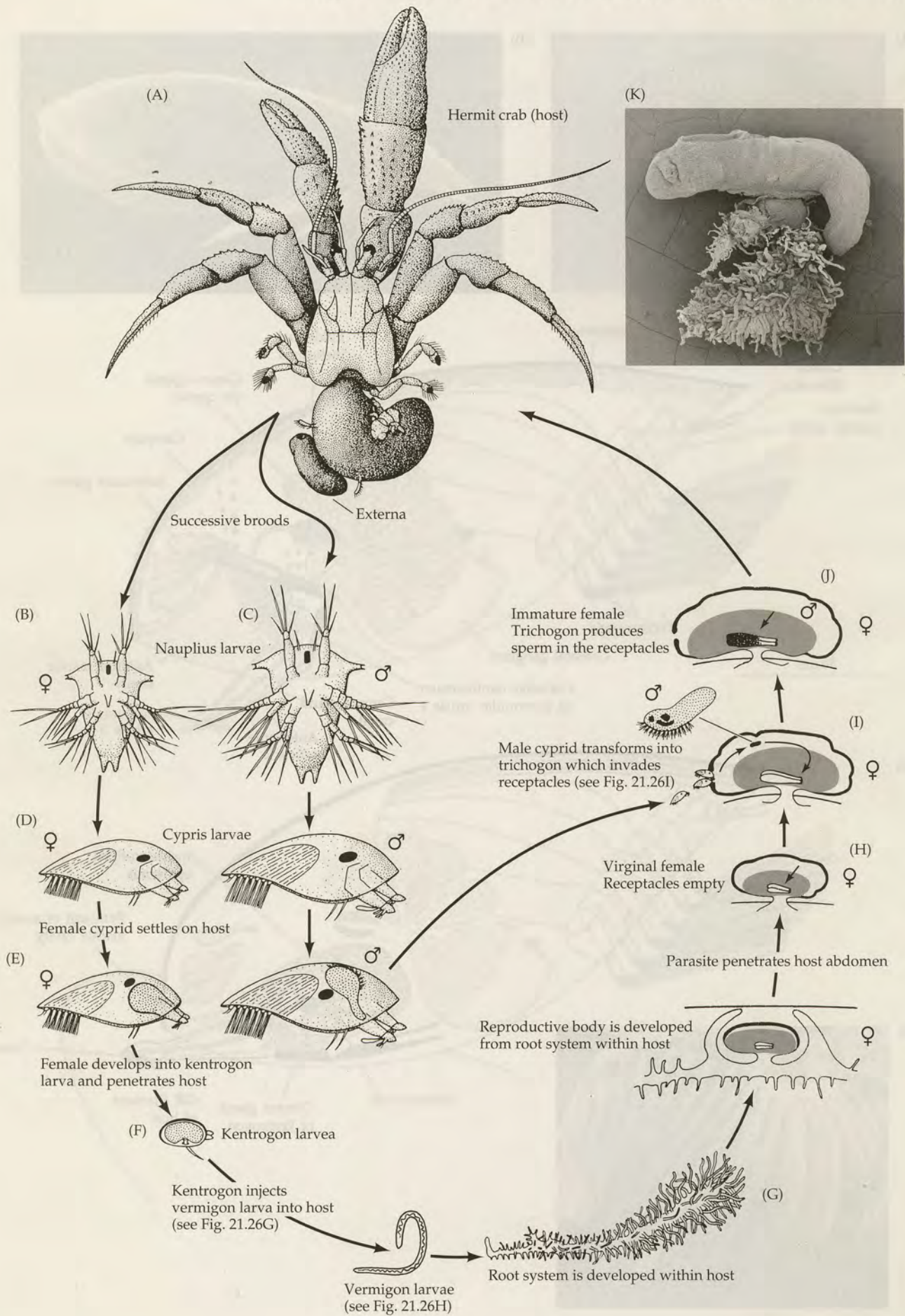
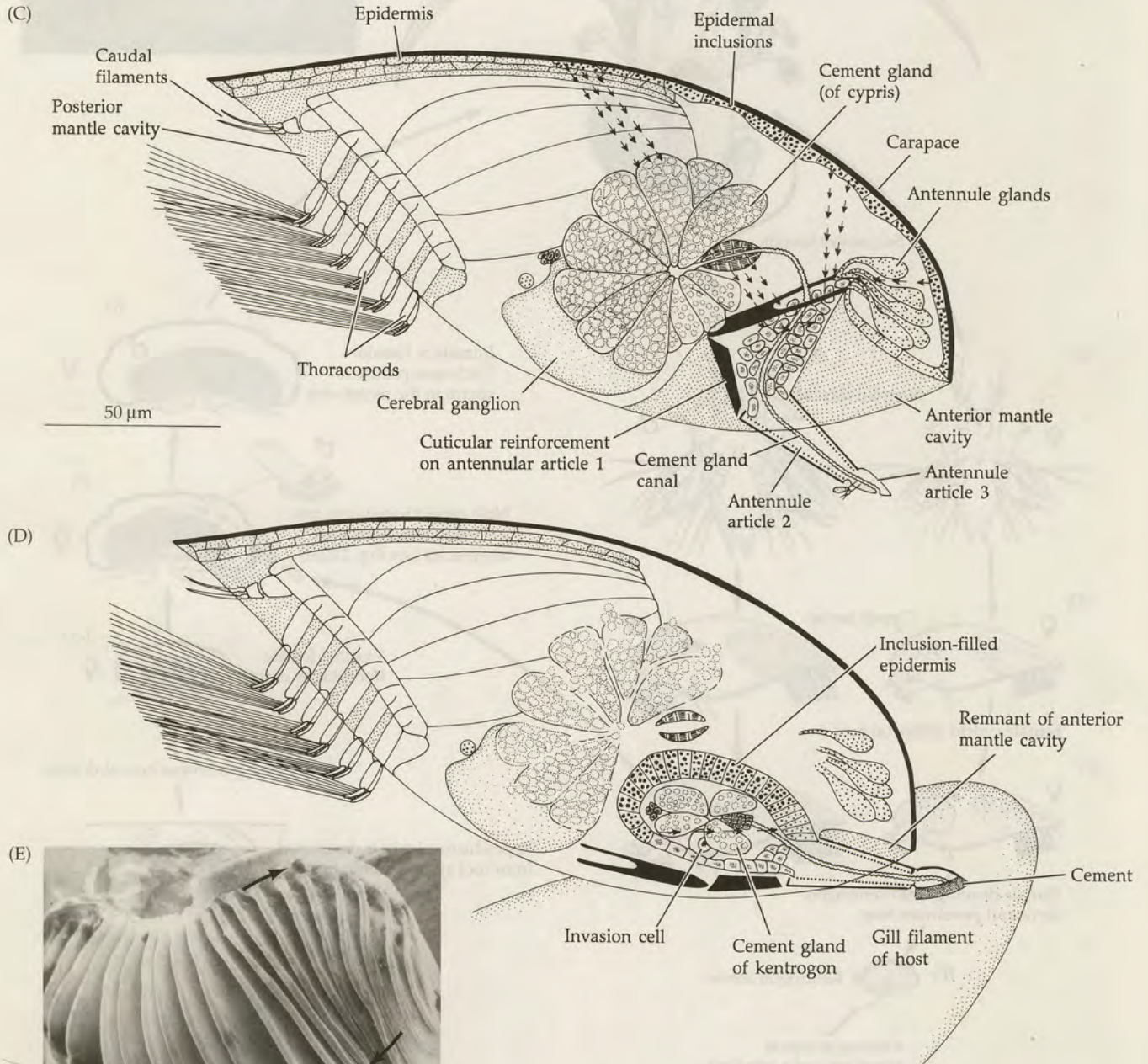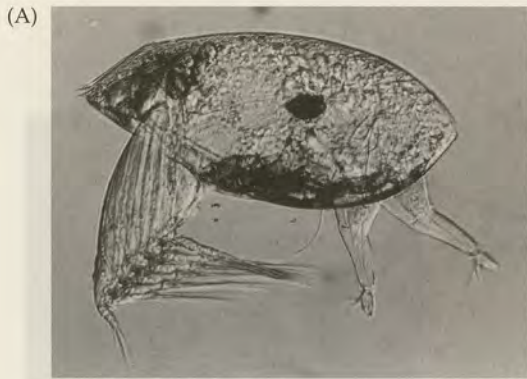Finally, several groups of crustaceans have adopted various degrees of parasitism. These animals

Figure 21.25 The remarkable life cycle of the rhizocephalan cirripede *Peltogaster paguri*, a kentrogonid parasite of hermit crabs. (A) The mature reproductive portion of the parasite (externa) produces numerous broods of male and female larvae, which are released as nauplii (B,C) and eventually metamorphose into cypris larvae (D). Female cyprids settle on the thorax and limbs of host crabs (E) and undergo a major internal metamorphosis into the kentrogon form (F), which is provided with a pair of antennules and an injection stylet. The kentrogon's viscera metamorphoses into an infective stage, the vermigon, which is transferred to the host through the hollow stylet. Inside the host, the vermigon grows with rootlets that ramify throughout much of the host's body; it is now called the interna (G). Eventually the female parasite emerges on the abdomen of the host as a virginal externa (H). When the externa acquires a mantle pore, or aperture, it becomes attractive to male cyprids (I). Male cyprids settle within the aperture, transform into a trichogon form, and implant part of their body contents in the female's receptacles (J). The deposit proceeds to differentiate into spermatozoa, which fertilize the eggs of the female. (K) The dissected externa, with its rootlets, of *Peltogaster*, removed from its host. Note the mantle aperture.

range from ectoparasites with mouthparts modified for piercing or tearing and sucking body fluids (e.g., many copepods, branchiurans, tantulocarids, several isopod families, and at least one species of ostracod) to the highly modified and fully parasitic rhizocephalans, whose bodies ramify throughout the host tissue and absorb nutrients directly (Figures 21.25 and 21.26).

Rhizocephalans, which are cirripeds that have been highly modified to become internal parasites of other crustaceans, are some of the most bizarre organisms in the animal kingdom. They may have typical cirripede nauplius and cypris larvae, but in this group the cyprid will settle only upon another crustacean, selected to be the unfortunate host.

The most complex rhizocephalan life cycle is that of the suborder Kentrogonida, which are obligate parasites of decapods. In this group, a settled female cypris larva undergoes an internal reorganization that rivals that of caterpillar pupae in scope, developing an infective stage, called the **kentrogon**, beneath the cyprid exoskeleton. Once fully developed, the kentrogon forms a hollow cuticular structure, the **stylet**, which injects a motile, multicellular, vermiform creature called the **vermigon** into the host. The vermigon is the active infection stage. It has a thin cuticle and epidermis, several types of cells, and the anlagen of an ovary. It invades the host's hemocoel by sending out long, branching, hollow rootlets that penetrate most of the host's body and draw nutrients directly from the hemocoel. So profound is the intrusion by the rootlets that the parasite takes over nearly complete control of the host's body, altering its morphology, physiology, and behavior. Once the parasite invades the host's gonads, parasitic castration may

(A)

Hermit crab (host)

(K)

Successive broods

Externa

(J)

Immature female
Trichogon produces
sperm in the receptacles

♂   ♀

(B)   (C)

Nauplius larvae

♀   ♂

Male cyprid transforms into
trichogon which invades
receptacles (see Fig. 21.26I)

♂

(I)

♀

(D)   Cypris larvae   ♂

♀

Virginal female
Receptacles empty

♀

(H)

Female cyprid settles on host

(E)

♀   ♂

Parasite penetrates host abdomen

Female develops into kentrogon
larva and penetrates host

Reproductive body is developed
from root system within host

♀

(F)   Kentrogon larvea

Kentrogon injects
vermigon larva into host
(see Fig. 21.26G)

(G)

Vermigon larvae
(see Fig. 21.26H)

Root system is developed within host

(A)

(B)

(C)

Epidermis

Caudal filaments

Posterior mantle cavity

Epidermal inclusions

Cement gland (of cypris)

Carapace

Antennule glands

Thoracopods

Cerebral ganglion

50 μm

Cuticular reinforcement on antennular article 1

Cement gland canal

Antennule article 2

Anterior mantle cavity

Antennule article 3

(D)

Inclusion-filled epidermis

Remnant of anterior mantle cavity

Cement

Invasion cell

Cement gland of kentrogon

Gill filament of host

(E)

(F)

Kentrogon
cement gland

Cuticle

Posterior
muscles

Inclusion-filled
epidermis

20 μm

Cement canal

Antennule
article 3

Invasion cell   Anterior muscles   Cement canal pore
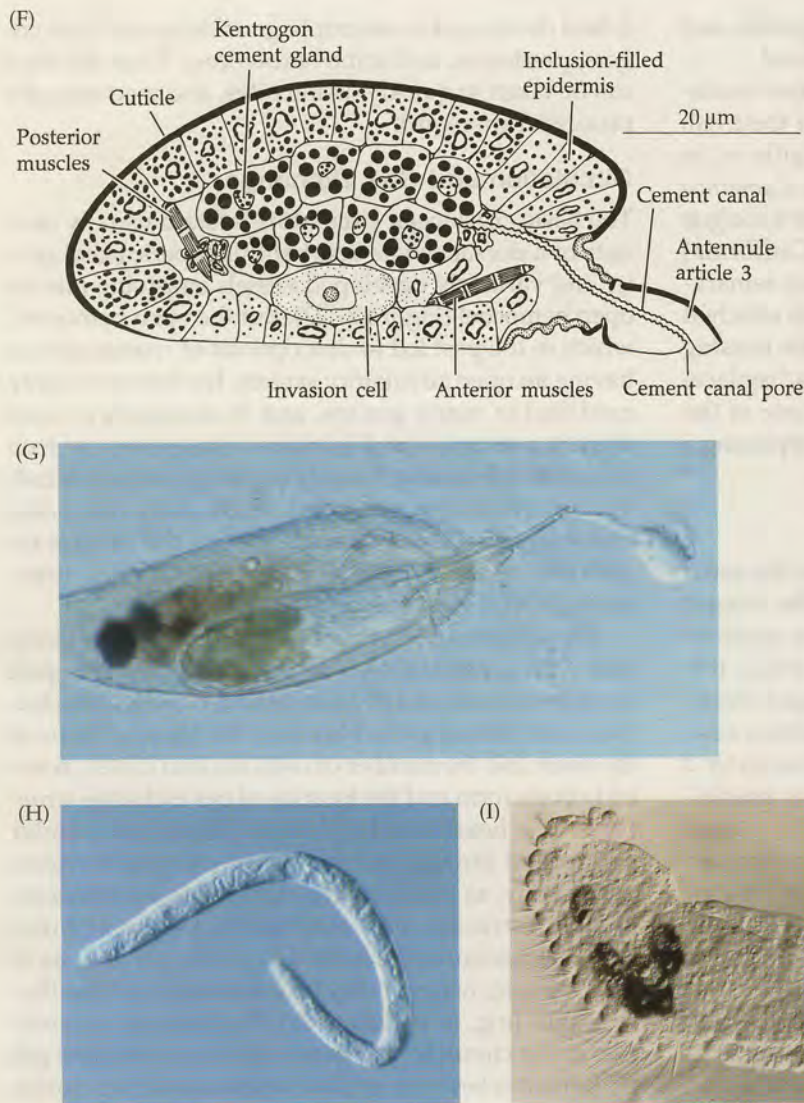
(G)

(H)

(I)

Figure 21.26   Various stages in the life cycle of parasitic rhizocephalans. (See Figure 21.25 for a full description of a rhizocephalan (kentrogonid) life cycle.) (A–D) Larvae of *Lernaeodiscus porcellanae*: (A) A live cyprid. (B) A cyprid (lateral view; SEM). (C,D) Diagrams of cyprid larvae before and after settlement (right side of carapace removed; naupliar eye omitted). The dotted line in the second antennular article indicates the primordial kentrogon cuticle, and the placement of muscle fibers in the cyprid are indicated by arrows; the muscles are hypothesized to effect formation of the kentrogon and separation of the old cyprid from the kentrogon. In D, kentrogon formation is complete. (E) A whole gill (SEM) of a host crab, *Petrolisthes cabrioli* (Anomura), with several attached kentrogons (arrows). (F) A 2-hour-old kentrogon (sagittal section). (G) A kentrogen injecting a vermigon via the stylet. (H) A vermigon. (I) A trichogon.

result (i.e., the gonads of parasitized crabs never produce mature gametes). Thus the host is transformed into a slave that serves the needs of its master. The internal root system, or **interna**, eventually develops an external reproductive body (the **externa**), where egg production occurs. A male cyprid settles on the externa, transforms into a minute sexually mature instar called a **trichogon**, and moves into the ovary-filled externa to take up residence, where its sole function is to produce sperm. It takes only one or two trichogons to stimulate the female ovaries to mature and begin releasing eggs into the chamber of the externa. Externa that fail to obtain male trichogons eventually die. The males are thus parasitic on the female (which is itself parasitic on the crustacean host), and kentrogonids are gonochoristic. A mature externa, usually arising from the host's abdomen, will produce a succession of larval broods, molting after each larval release (it is the only part of the rhizocephalan body that molts). The larvae are lecithotrophic and develop through several nauplius stages to the cyprid (Figures 21.25 and 21.26).

Members of the rhizocephalan order Akentrogonida parasitize a much wider range of crustacean hosts and do not have a kentrogon stage in their life cycle. Instead of injecting a vermigon, the female cyprid has long, slender antennules that it uses to attach to the abdomen of the host, one of which actually penetrates the host's cuticle, becomes hollow, and serves for the passage of embryonic cells from cyprid larva to host. Male cyprids somehow find infected hosts and penetrate them in the same fashion as the females, releasing their sperm in such a way that they actually enter the body of the female parasite.

The akentrogonid life cycle is similar to that of the Kentrogonida although, in some cases, more than one individual parasite might infect a single host, leading to multiple externas. And in at least one genus (*Thompsonia*), multiple externa can develop from a single infection. The anatomy of the externa is more variable than in kentrogonids, and the embryos develop directly into cypris larvae—there are no free-swimming nauplius stages. The extreme sexual size dimorphism

of kentrogonids does not occur in Akentrogonida, and no migrating trichogon stage has been observed.

Isopods of the family Cymothoidae use modified mouthparts to suck the body fluids of their fish hosts. They attach to their host's skin or gills or, in some genera, to the tongue. One species, *Cymothoa exigua*, sucks so much blood out of its host's tongue (the spotted rose snapper, in the Gulf of California) that the tongue completely degenerates. But, remarkably, the fish doesn't die; the isopod remains attached with its clawed legs to the basal muscles of the missing tongue, and the fish use the crustacean as a "replacement tongue" to continue to feed. This is one of the few known cases of a parasite functionally replacing a host organ it destroys.

Digestive System

The digestive system of crustaceans includes the usual arthropod foregut, midgut, and hindgut. The foregut and hindgut are lined with a cuticle that is continuous with the exoskeleton and molted with it (i.e., it is ectodermally derived). The stomodeal foregut is modified in different groups, but usually includes a relatively short pharynx–esophagus region followed by a stomach. The stomach often has chambers or specialized regions for storage, grinding, and sorting; these structures are best developed in the malacostracans (Figure 21.27G). The midgut forms a short or long intestine—the length depending mainly on overall body shape and size—and bears variably placed digestive ceca. The ceca are serially arranged only in the remipedes. In some malacostracans, such as crabs, the ceca fuse to form a solid glandular mass, best called a **digestive gland** but sometimes called a midgut gland or hepatopancreas, within which are many branched, blind tubules. The digestive gland in some crustaceans has been shown to store lipids. The hindgut is usually short, and the anus is generally borne on the anal somite or telson, or on the last segment of the abdomen (when the anal somite or telson is reduced or lost).

Examples of some crustacean digestive tracts are shown in Figure 21.27. After ingestion, the food material is usually handled mechanically by the foregut. This may involve simply transporting the food to the midgut or, more commonly, processing the food in various ways prior to chemical digestion. For example, the complex foregut of decapods (Figure 21.27G) is divided into an anterior cardiac stomach and a posterior pyloric stomach. Food is stored in the enlarged portion of the cardiac stomach and then moved a bit at a time to a region containing a gastric mill, which usually bears heavily sclerotized teeth. Special muscles associated with the stomach wall move the teeth, grinding the food into smaller particles. The macerated material then moves into the back part of the pyloric stomach, where sets of filtering setae prevent large particles from entering the midgut. This type of foregut arrangement is best developed in macrophagous decapods (scavengers, predators, and some herbivores). Thus the food can be taken in quickly, in big bites, and mechanically processed afterward.
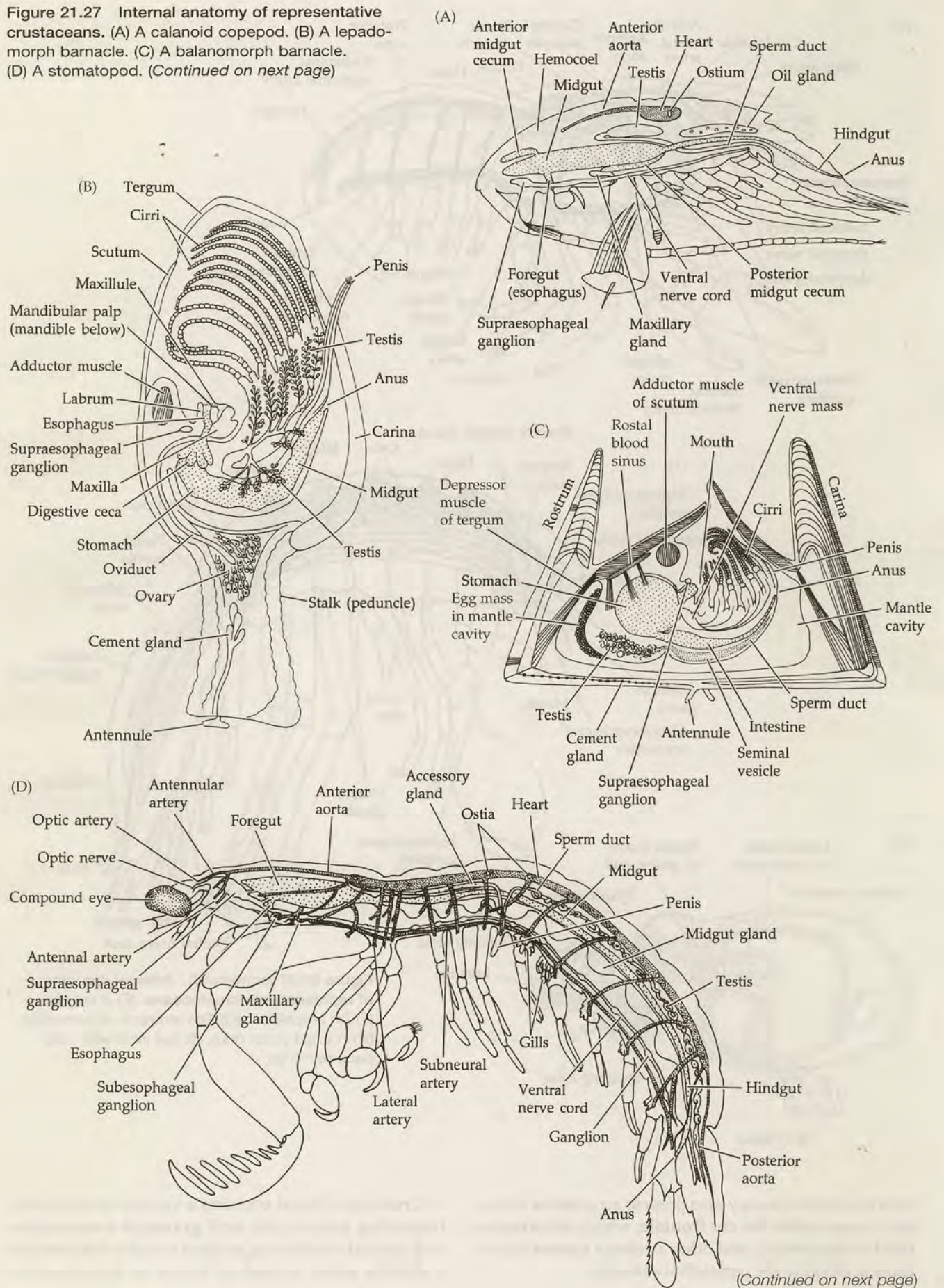
Circulation and Gas Exchange

The basic crustacean circulatory system usually consists of a dorsal ostiate heart within a pericardial cavity and variously developed vessels emptying into an open hemocoel (Figure 21.27). But the open hemocoel, which in the past led to descriptions of crustaceans as having an open circulatory system, has become highly modified in many groups, and in decapods at least there is a complex and intricate arrangement of true vessels that has only recently begun to be recognized. The heart is absent in most ostracods, many copepods, and many cirripedes. In some groups the heart is replaced or supplemented by accessory pumping structures derived from muscular vessels.

The primitive heart structure in crustaceans is a long tube with segmental ostia, a condition retained in part in cephalocarids and in some branchiopods, leptostracans, and stomatopods. However, the general shape of the heart and the number of ostia are also closely related to body form and the location of gas exchange structures. The heart may be relatively long and tubular and extend through much of the postcephalic region of the body, as it does in the remipedes, anostracans, and leptostracans, or it may tend toward a globular or box shape and be restricted to the thorax (e.g., as in cladocerans), where it may be associated with the thoracic gills (e.g., as in decapods). The intimate coevolution of the circulatory system with body form and gill placement is best exemplified when comparing closely related groups. Although isopods and amphipods, for instance, are both peracarids, their hearts are located largely in the pleon and in the pereon, respectively, corresponding to the pleopodal and pereopodal gill locations.

The number and length of blood vessels and the presence of accessory pumping organs are related to body size and to the extent of the heart itself. In most non-malacostracans, for example, there are no arterial vessels at all; the heart pumps blood directly into the hemocoel from both ends. These animals tend to have short bodies, long hearts, or both, an arrangement that facilitates circulation of the blood to all body parts. Sessile forms, such as most cirripedes, have lost the heart altogether, although it is replaced by a vessel pump in the thoracicans. Large malacostracans tend to have well developed vessel systems, thus ensuring that blood flows throughout the body and hemocoel and to the gas exchange structures (Figure 21.27D,E). Recent studies using corrosion casting techniques have shown just how complex these vessel systems can be and have even called into question the paradigm of "open" vs. "closed" circulatory systems in invertebrates. Large or

Figure 21.27   Internal anatomy of representative crustaceans. (A) A calanoid copepod. (B) A lepado-morph barnacle. (C) A balanomorph barnacle. (D) A stomatopod. (*Continued on next page*)
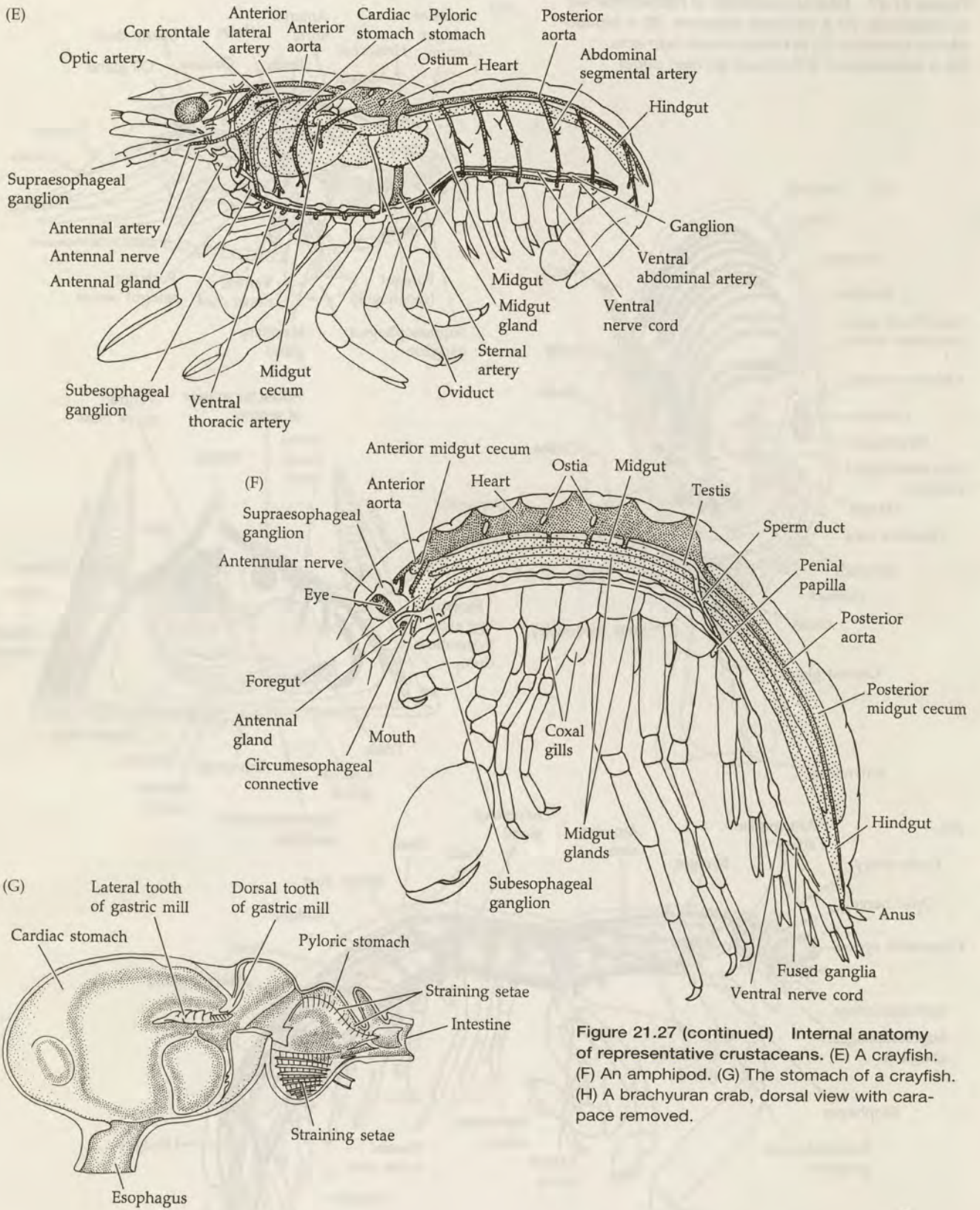

(A)
Anterior midgut cecum
Anterior aorta
Heart
Sperm duct
Hemocoel
Midgut
Testis
Ostium
Oil gland
Hindgut
Anus
Foregut (esophagus)
Ventral nerve cord
Posterior midgut cecum
Supraesophageal ganglion
Maxillary gland

(B)
Tergum
Cirri
Scutum
Maxillule
Mandibular palp (mandible below)
Adductor muscle
Labrum
Esophagus
Supraesophageal ganglion
Maxilla
Digestive ceca
Stomach
Oviduct
Ovary
Cement gland
Antennule
Penis
Testis
Anus
Carina
Midgut
Testis
Stalk (peduncle)

(C)
Adductor muscle of scutum
Ventral nerve mass
Rostal blood sinus
Mouth
Depressor muscle of tergum
Rostrum
Cirri
Carina
Penis
Anus
Stomach
Egg mass in mantle cavity
Mantle cavity
Testis
Cement gland
Antennule
Intestine
Sperm duct
Seminal vesicle
Supraesophageal ganglion

(D)
Antennular artery
Accessory gland
Anterior aorta
Ostia
Heart
Optic artery
Foregut
Sperm duct
Optic nerve
Midgut
Compound eye
Penis
Midgut gland
Antennal artery
Supraesophageal ganglion
Testis
Maxillary gland
Esophagus
Subneural artery
Gills
Hindgut
Subesophageal ganglion
Lateral artery
Ventral nerve cord
Ganglion
Posterior aorta
Anus

(*Continued on next page*)

(E)

Optic artery

Cor frontale

Anterior lateral artery

Anterior aorta

Cardiac stomach

Pyloric stomach

Ostium

Heart

Posterior aorta

Abdominal segmental artery

Hindgut

Supraesophageal ganglion

Antennal artery

Antennal nerve

Antennal gland

Subesophageal ganglion

Ventral thoracic artery

Midgut cecum

Oviduct

Sternal artery

Midgut gland

Midgut

Ventral nerve cord

Ventral abdominal artery

Ganglion

(F)

Anterior midgut cecum

Anterior aorta

Heart

Ostia

Midgut

Testis

Supraesophageal ganglion

Antennular nerve

Eye

Foregut

Antennal gland

Mouth

Circumesophageal connective

Subesophageal ganglion

Midgut glands

Coxal gills

Sperm duct

Penial papilla

Posterior aorta

Posterior midgut cecum

Hindgut

Anus

Fused ganglia

Ventral nerve cord

(G)

Cardiac stomach

Lateral tooth of gastric mill

Dorsal tooth of gastric mill

Pyloric stomach

Straining setae

Intestine

Straining setae

Esophagus

Figure 21.27 (continued) Internal anatomy of representative crustaceans. (E) A crayfish. (F) An amphipod. (G) The stomach of a crayfish. (H) A brachyuran crab, dorsal view with carapace removed.

active crustaceans may also possess an anterior accessory pump called the **cor frontale**, which helps maintain blood pressure, and often a venous system for returning blood to the pericardial chamber.

Crustacean blood contains a variety of cell types, including phagocytic and granular amebocytes and special wandering explosive cells that release a clotting agent at sites of injury or autotomy. In

(H)
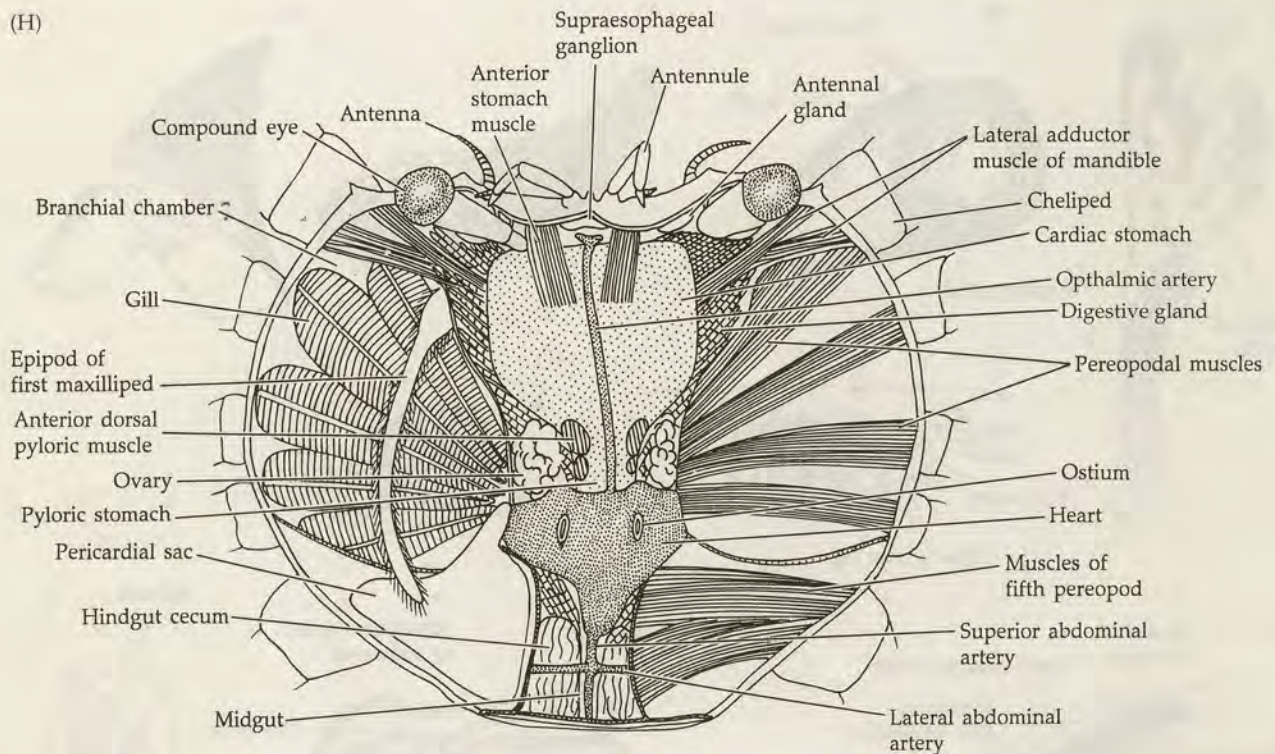
non-malacostracans, oxygen is either carried in solution or attached to dissolved hemoglobin. Most malacostracans possess hemocyanin in solution (although some contain hemoglobin within tissues). Hemoglobin uses iron as the oxygen-binding site, whereas hemocyanin uses copper. The latter can give a bluish color to the hemolymph; carotenoid pigments frequently give hemolymph a pale brown or orange color. Oxygen-binding pigments are never carried in corpuscles as they are in the vertebrates.

We have mentioned the form and position of gas exchange organs (gills) for some groups of crustaceans in the taxonomic synopses. Some small forms (e.g., copepods, some ostracods) lack distinct gills and rely on cutaneous exchange, which is facilitated by their relatively thin cuticles and high surface area-to-volume ratio. In the small forms of other groups a thin, membranous inner lining of the carapace serves this purpose (e.g., Cladocera, Cirripedia, Leptostraca, Cumacea, Mysida, clam shrimps, and even some members of the Decapoda).

Most crustaceans, however, possess distinct gills of some sort (Figure 21.28). These structures are commonly derived from epipods (exites) on the thoracic legs that have been modified in various ways to provide a large surface area. The inner hollow chambers of these gills are confluent with the hemocoel or their vessels. Although their structure varies considerably (recall the various decapod gills described earlier), they all operate on the basic principles of gas exchange organs addressed in Chapter 4 and throughout this text: the circulatory fluid is brought close to the oxygen source in

an organ with a relatively high surface area. The gills provide a thin, moist, permeable surface between the internal and external environments. The gills of stomatopods and isopods (Figure 21.28H,I) are formed from the abdominal pleopods. In the first case they are branched processes off the base of the pleopods, but in the isopods the flattened pleopods themselves are vascularized and provide the necessary surface area for exchange. Stomatopods also have epipodal gills on the thoracopods, but these are highly reduced.

For gills to be efficient, a flow of water must be maintained across them. In stomatopods and aquatic isopods a current is generated by the beating of the pleopods. Similarly, the pereopodal gills of euphausids are constantly flushed by water as the animal swims. In many crustaceans, however, the gills are concealed to various degrees and require special mechanisms in order to produce the ventilating currents. In most decapods, for example, the gills are contained in branchial chambers formed between the carapace and the body wall (Figure 21.28). Thus the delicate gills, while still technically outside the body, appear to be (and are protected as though they were) internal organs. While such an arrangement provides protection from damage to the fragile gill filaments, the openings to the chambers are generally small, restricting the passive flow of water. Not surprisingly, the solution to this dilemma comes once again from the evolutionary plasticity of crustacean appendages. Most decapods have elongate exopods on the maxillae, called gill bailers or scaphognathites, that vibrate to create ventilating currents through the branchial
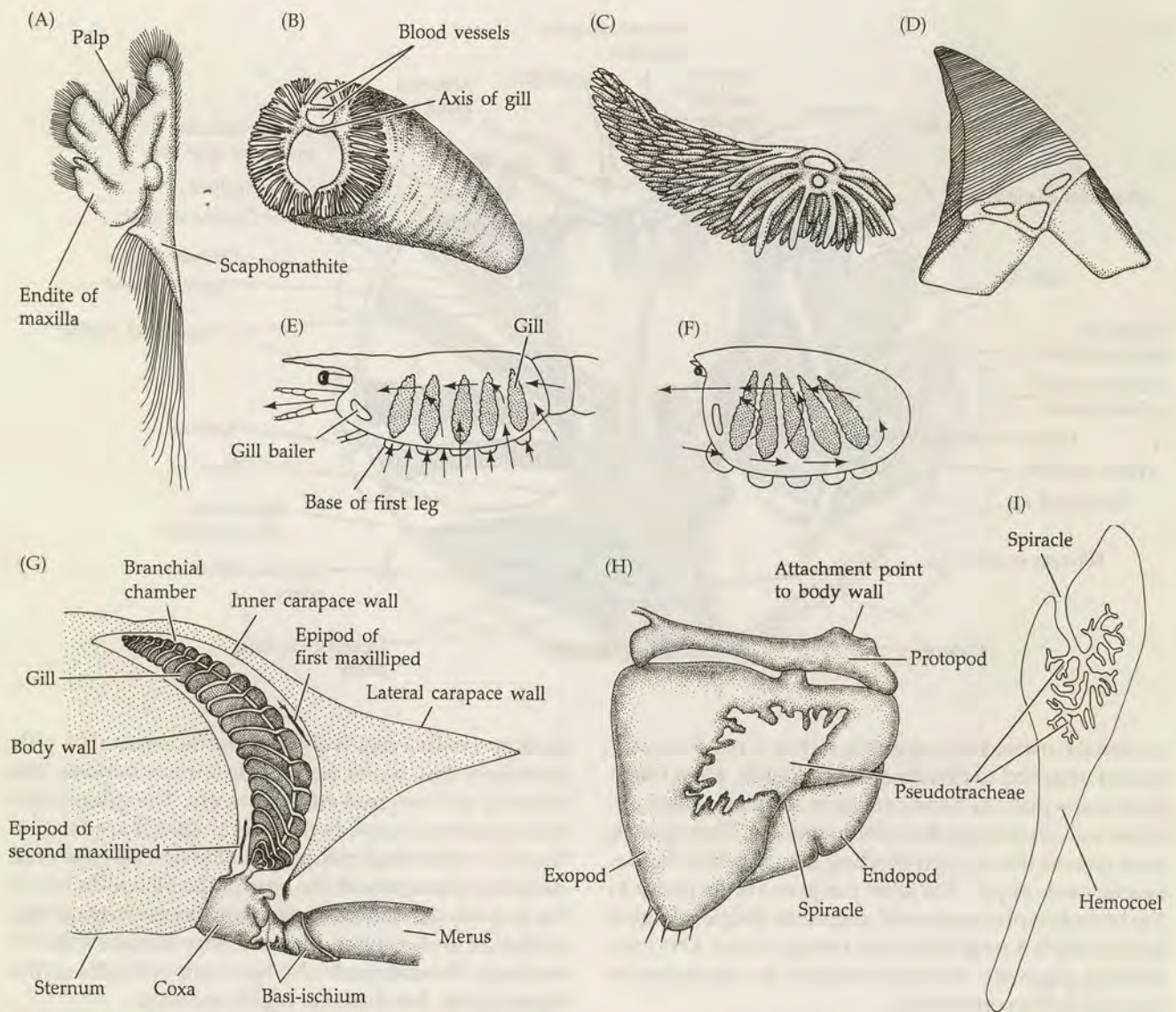
Figure 21.28 Gas exchange structures. (A) Maxilla of the shrimp *Pandalus*. Note the setose scaphagnathite used to generate the ventilating current. (B–D) Cross sections of types of decapod gills: (B) Dendrobranchiate. (C) Trichobranchiate. (D) Phyllobranchiate. (E,F) Paths of ventilating currents through the left branchial chambers of (E) a shrimp and (F) a brachyuran crab. (G) The branchial chamber (cross section) of a brachyuran crab, showing the position of a single phyllobranchiate podobranch. (H,I) A pleopod of the terrestrial isopod *Porcellio* (surface view and section). Note the pseudotracheae.

chambers (Figure 21.28A). These currents typically enter from the sides and rear through small openings around the coxae of the pereopods (called in crabs **Milne-Edwards openings**, after their discoverer), and exit anteriorly from under the carapace in the vicinity of the mouth field (and antennal glands). They can be easily seen by observing a crab or lobster in quiet water. The flow rate of the currents can be altered, depending on environmental factors, and can also be reversed, thus allowing certain decapods to burrow in

sand or mud with only their front ends exposed to the water.

The positioning of the gills in branchial chambers protects them from desiccation during low tides and thus enables many crustaceans to live in littoral habitats; diffusion of respiratory gases commonly continues even during low tides. Some decapods have even invaded land, especially certain crayfish and the anomuran and brachyuran crabs known as land crabs (e.g., the hermit crab *Coenobita* and the coconut crab *Birgus*; Figure 21.1H). In these semi-terrestrial species the gills are typically reduced in size. In *Birgus* the original gills are very small, and the vascularized cuticular surface of the gill chamber is used for gas exchange. Although young *Birgus* may carry shells (or coconuts) to protect their soft abdomen, adults do not and the abdomen is hardened. Another striking decapod adaptation to life in air is displayed by the sand-bubbler crabs of the Indo-Pacific region (family Dotillidae: *Scopimera*, *Dotilla*). These crabs possess membranous discs on

their legs or sternites that were once thought to be auditory organs (tympana), but are now thought to function as gas exchange surfaces.

The most successful crustaceans on land are not the decapods, however, but the familiar sowbugs and pillbugs. The success of these oniscidean isopods (e.g., *Porcellio*) is due in part to the presence of aerial gas exchange organs called **pseudotrachea** (Figure 21.28H,I). These organs are inwardly directed, moderately branched, thin-walled, blind sacs located in some of the pleopodal exopods, connected to the outside via small pores (similar to insect tracheae and spiracles). Air circulates through these sacs, and gases are exchanged with the blood in the pleopods. Thus, in these animals the original aquatic pleopodal gills have been refashioned for air breathing by moving the exchange surfaces inside, where they remain moist. The superficially similar tracheal systems of isopods, insects, and arachnids evolved independently, by convergence, in association with other adaptations to life on land.

Excretion and Osmoregulation

Like other fundamentally aquatic invertebrates, crustaceans are ammonotelic, whether in fresh water or seawater or on land. They release ammonia both through nephridia and by way of the gills. As discussed in Chapter 20, most crustaceans possess nephridial excretory organs in the form of either antennal glands or maxillary glands (Figures 21.5A and 21.27). These are serially homologous structures, constructed similarly but differing in the position of their associated pores (at the base of the second antennae or the second maxillae, respectively). The inner blind end is a coelomic remnant of the nephridium called the sacculus, which leads through a variably coiled duct to the pore. The duct may bear an enlarged bladder near the opening. Antennal glands are sometimes called "green glands."

Most crustaceans have only one pair of these nephridial organs, but lophogastrids and mysids have both antennal and maxillary glands, and a few others (cephalocarids and a few tanaids and isopods) have well developed maxillary and rudimentary antennal glands. Most non-malacostracans have maxillary glands, as do stomatopods, cumaceans, and most tanaids and isopods. Adult ostracods have maxillary glands, but antennal glands also occur in freshwater species. All of the other malacostracans have antennal glands.

Blood-filled channels of the hemocoel intermingle with branched extensions of the sacculus epithelium, creating a large surface area across which filtration occurs. The cells of the sacculus wall also actively take up and secrete material from the blood into the lumen of the excretory organ. These processes of filtration and secretion are to some degree selective, but most of the regulation of urine composition is accomplished by active exchange between the blood and the excretory tubule. These activities not only regulate the loss of metabolic wastes but are also extremely important in water and ion balance, particularly in freshwater and terrestrial crustaceans.

The excretion and osmoregulation carried out by antennal and maxillary gland activity are supplemented by other mechanisms. The cuticle itself acts as a barrier to exchange between the internal and external environments and, as we have mentioned, is especially important in preventing water loss on land or excessive uptake of water in fresh water. Moreover, thin areas of the cuticle, especially the gill surfaces, serve as sites of waste loss and ionic exchange. The epipods on the legs of Branchiopoda were long assumed to function in gas exchange (as "gills") but they are now known to serve primarily as sites of osmoregulation (hence, the taxonomic name Branchiopoda, meaning gill-footed, is a misnomer!). Phagocytic blood cells and certain regions of the midgut are also thought to accumulate wastes. In some terrestrial isopods, ammonia actually diffuses from the body in gaseous form.

Nervous System and Sense Organs

The central nervous system of crustaceans is constructed in concert with the segmented body structure, along the same lines as seen in other arthropods (Figure 21.29). In the more primitive condition it is ladderlike, the segmental ganglia being largely separate and linked by transverse commissures and longitudinal connectives (Figure 21.29A). The crustacean brain is composed of three fused ganglia, the two anterior being the dorsal (supraesophageal) protocerebrum and deutocerebrum, which are thought to be preoral in origin. From the protocerebrum, optic nerves innervate the eyes. From the deutocerebrum, antennulary nerves run to the antennules, while smaller nerves innervate the eyestalk musculature. The third ganglion of the brain is the posterior tritocerebrum, which presumably represents the first postoral somite ganglion. The tritocerebrum forms a pair of circumenteric connectives that extend around the esophagus to a subesophageal or subenteric ganglion and link the brain with the ventral nerve cord bearing the segmental body ganglia. From the tritocerebrum also arise the antennary nerves as well as certain sensory nerves from the anterior region of the head.

The nature of the ventral nerve cord often clearly reflects the influence of body tagmosis. In crustaceans with relatively homonomous bodies (e.g., remipedes, cephalocarids, and anostracan and notostracan branchiopods), the ganglia associated with each postantennary segment remain separate along the ventral nerve cord. In more heteronomous forms, however, a single large subenteric ganglionic mass is formed by the fusion of ganglia associated with the postoral cephalic segments (e.g., those of the mandibles, maxillules, maxillae, and, when present, maxillipeds). The ganglia
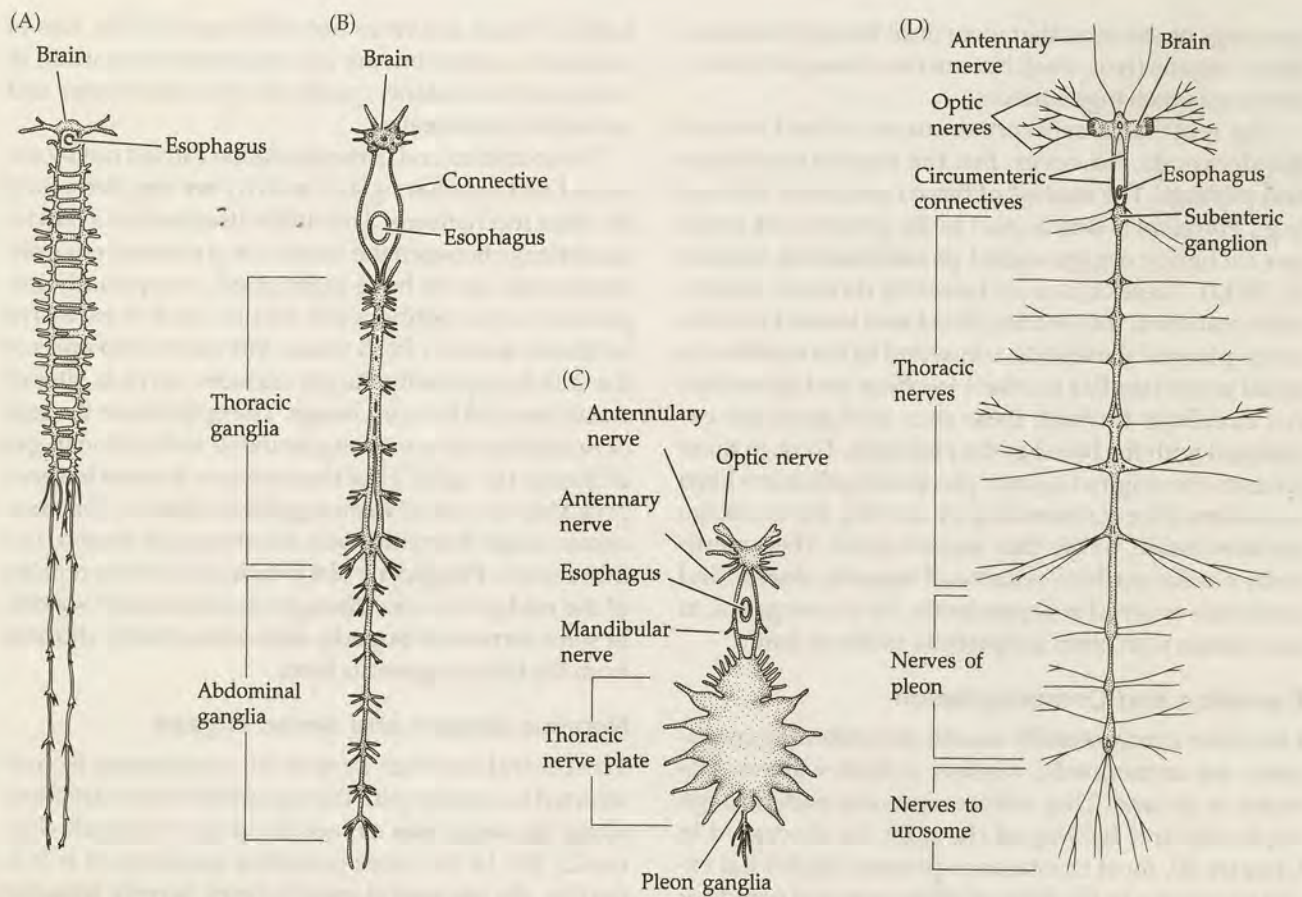
Figure 21.29 Central nervous systems of four crustaceans. (A) The ladderlike system of an anostracan. Note the absence of well developed ganglia in the posterior, apodous, portion of the trunk. (B) Elongate metameric system of a crayfish. (C) Highly compacted system of a brachyuran crab, wherein all thoracic ganglia have fused and the abdominal ganglia are reduced. (D) Nervous system of a hyperiid amphipod. Note the loss of the urosomal ganglia typical of all amphipods.

of the thorax and abdomen may also be variably fused, depending on segment fusion and body compaction. For example, in most long-bodied decapods (lobsters and crayfish), the thoracic and abdominal ganglia are largely fused across the body midline, but remain separate from one another longitudinally (Figure 21.29B). However, in short-bodied decapods (e.g., crabs), all of the thoracic segmental ganglia are fused to form a large ventral nerve plate, and the abdominal ganglia are much reduced (Figure 21.29C).

Most crustaceans have a variety of sensory receptors that transmit information to the central nervous system in spite of the imposition of the exoskeleton (as previously explained for arthropods in general) (Figure 21.30). Among the most obvious of these sensory structures are the many innervated setae or **sensilla** that cover various regions of the body and appendages (Figure 21.31). Studies of these structures suggest most function as both mechanoreceptors (sensing touch and currents) and chemoreceptors. Most crustaceans also possess special chemoreceptors in the form of clumps or rows of soft, tubular, cuticular processes called **aesthetascs** (Figure 21.30A) located on the first antennae.

In decapods, hundreds of neurons can innervate each aesthetasc. Thermoreceptors probably occur in many crustaceans (those living near hydrothermal vents in the deep sea would seem likely candidates) but are not yet documented. However, behaviors related to thermal avoidance and temperature preferences have been shown, with thermosensitivities reported from 0.2 to 2.0° C. A pair of unique sensory structures whose function is unknown, called **frontal processes**, occurs on the head of remipedes. Many crustaceans have dorsal organs, poorly understood glandular–sensory structures on the head, which actually constitute several different types of sensory structures that may or may not be homologous.

Like all arthropods, crustaceans contain well-developed proprioceptors that provide information about body and appendage position and movement during locomotion. A few taxa within the class Malacostraca possess statocysts, which either are fully closed and contain a secreted statolith (e.g., mysids, some anthurid isopods) or open to the outside through a small pore and contain a statolith formed of sand grains (e.g., many decapods) (Figure 21.30B,C). In the latter

case the statocyst not only serves as a georeceptor, but also detects the angular and linear acceleration of the body relative to the surrounding water as well as the movement of water past the animal (i.e., the statolith is rheotactic). And, in some shrimp, the statocyst is apparently also engaged in hearing.

There are two types of rhabdomeric photoreceptors among crustaceans, median simple eyes and lateral compound eyes; both are innervated by the protocerebrum. Many species possess both kinds of eyes, either simultaneously or at different stages of development. The compound eyes may be sessile or stalked. Stalked compound eyes occur in the Anostraca, many Malacostraca, and perhaps some Cumacea (and perhaps also some trilobites). These are the only examples of moveable stalked compound eyes in the animal kingdom.

The median eye generally first appears during the nauplius larval stage, and for that reason it is often called a **naupliar eye**. Like the nauplius larva itself, the median eye is thought to be an ancestral (defining) feature of the Crustacea; it is secondarily reduced or lost in many taxa in which the corresponding larval stage is suppressed. Median eyes are in a sense "compound" in that they are composed of more than one photoreceptor unit (Figure 21.30D). There are typically three such units in the median eyes of nauplii and up to seven in the eyes of adults in which they persist. Except for their basic rhabdomeric nature, however, the structure of median eye units is unlike that of the ommatidia of true compound eyes. The former are inverse pigment cups, each with relatively few retinular (photoreceptor) cells. Cuticular lenses are present over the median eyes of most ostracods and some copepods. Simple crustacean eyes probably function only to detect light direction and intensity. Such information is of particular value as a means of orientation in planktonic forms without compound eyes, such as nauplius larvae, many copepods, etc. In some branchiopods, a space above the median eye is connected to the external environment by a small pore, perhaps indicating an invagination of the eye at some point in the distant past, although the nature and function of the pore is not known.

The structure and function of compound eyes (ommatidia) were reviewed in Chapter 20. In terms of
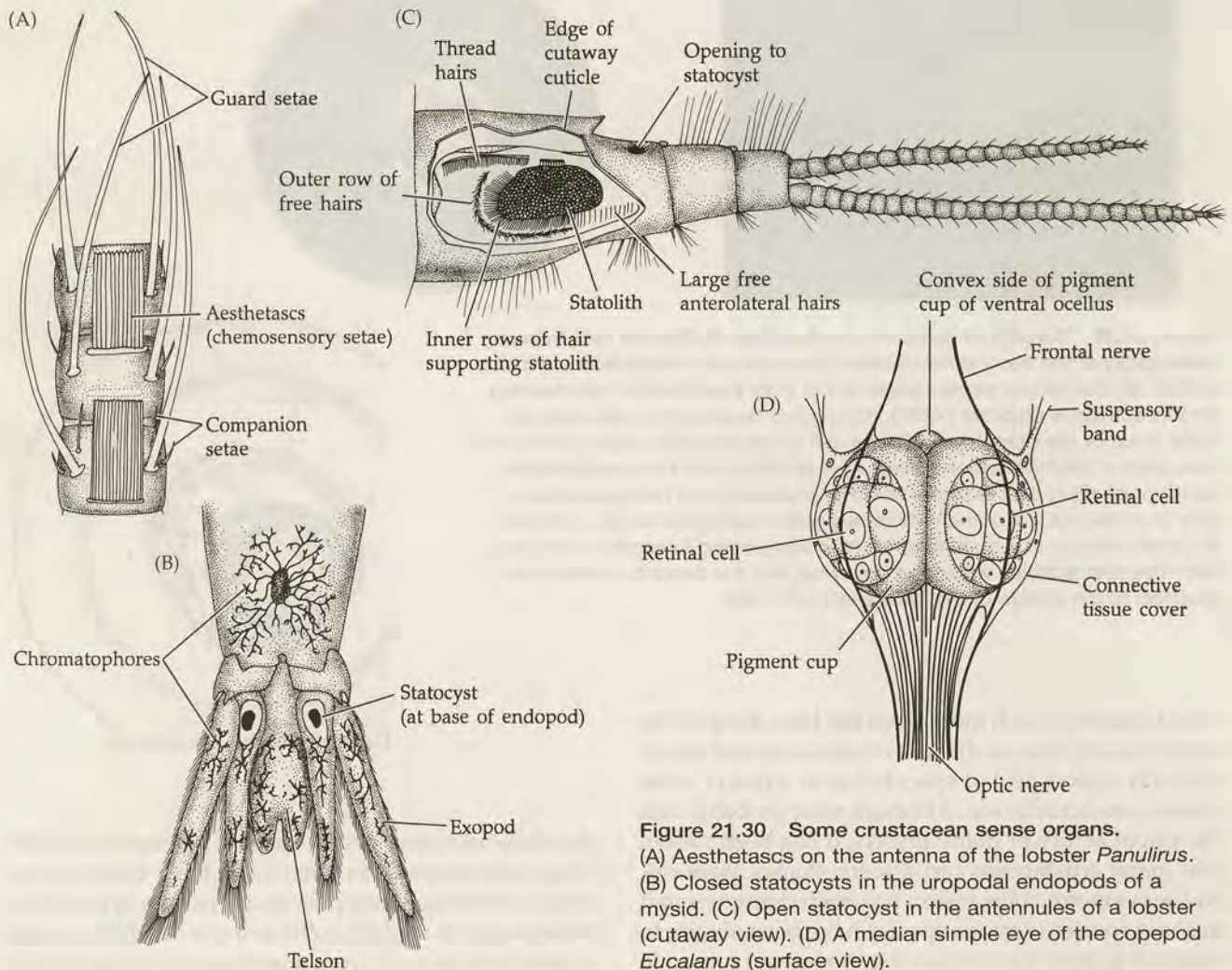

Figure 21.30   Some crustacean sense organs.
(A) Aesthetascs on the antenna of the lobster *Panulirus*.
(B) Closed statocysts in the uropodal endopods of a mysid. (C) Open statocyst in the antennules of a lobster (cutaway view). (D) A median simple eye of the copepod *Eucalanus* (surface view).
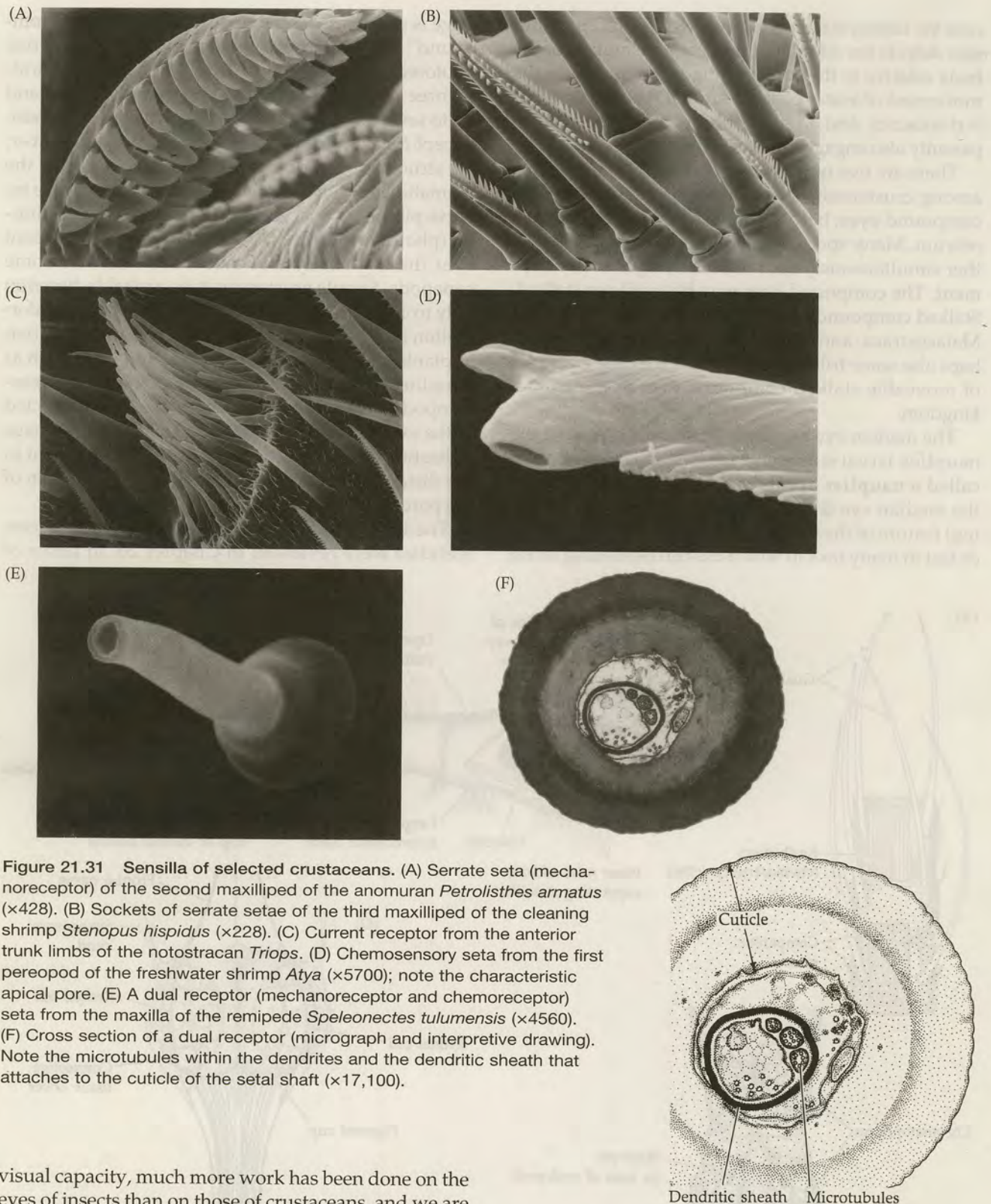
Figure 21.31 **Sensilla of selected crustaceans.** (A) Serrate seta (mechanoreceptor) of the second maxilliped of the anomuran *Petrolisthes armatus* (×428). (B) Sockets of serrate setae of the third maxilliped of the cleaning shrimp *Stenopus hispidus* (×228). (C) Current receptor from the anterior trunk limbs of the notostracan *Triops*. (D) Chemosensory seta from the first pereopod of the freshwater shrimp *Atya* (×5700); note the characteristic apical pore. (E) A dual receptor (mechanoreceptor and chemoreceptor) seta from the maxilla of the remipede *Speleonectes tulumensis* (×4560). (F) Cross section of a dual receptor (micrograph and interpretive drawing). Note the microtubules within the dendrites and the dendritic sheath that attaches to the cuticle of the setal shaft (×17,100).

visual capacity, much more work has been done on the eyes of insects than on those of crustaceans, and we are left with a good deal of speculation in terms of what crustaceans actually see. Although most probably lack the visual acuity of many insects, it has been shown that many crustaceans can discern shapes, patterns, and movement; color vision has been demonstrated in some species (various species have been shown to respond to light waves from the blue-green region to the ultraviolet and far-red spectra, at least to 470–570 nm). Stomatopods, in particular, have been shown to have extremely complex and sensitive eyes with a wide range of capabilities. Running through the center of each stomatopod eye is a midband of 6 ommatidial

rows—which in most species contain 4 rows that make up a color vision system with 12 visual pigments—as well as 2 rows that analyze both linearly and circularly polarized light. The ommatidia that deal with color have a three-tier structure: the top tier contains an ultraviolet-sensitive pigment, and below this are 2 tiers with different pigments sensitive to wavelengths in the human visible spectrum. The upper and lower halves of each eye also have overlapping visual fields, so that each eye can act as a stereoscopic rangefinder. The 12 different photoreceptor types each sample a narrow set of wavelengths ranging from deep UV to far red (300 to 720 nm).

Although both insects and crustaceans have tetrapartite ommatidia, there are certain structural differences between the compound eyes of insects and those of crustaceans, probably as a result of adaptation to the requirements of aerial and aquatic vision. In water, light has a more restricted angular distribution, a lower intensity, and a narrower range of wavelengths than it does in air. Contrast is also somewhat reduced in water. All of these factors place a premium on enhancing the sensitivity and contrast perception of the eyes of aquatic creatures. Mounting the eyes on stalks is one dramatic way in which many crustaceans increase the amount of information available to the eyes, by increasing the field of view and binocular range. Eyestalks are complex structural features with a dozen or so muscles controlling their movement.

Typical tetrapartite compound eyes are lacking in the small crustaceans formerly combined as "maxillopodans" (copepods, barnacles, etc.), but various forms of "compound eyes" do occur among the Branchiura, Ostracoda (Cypridinacea), and Cirripedia. Eyes in the first two taxa most closely resemble those of other crustaceans in general structure and may be homologous with them. In the Cirripedia, the median eye and two lateral eyes are all derived from a single tripartite ocellar eye of the nauplius larva, which splits into its three components, each forming an adult photoreceptor following metamorphosis of the nauplius into a cypris larva. All three of these eyes thus appear to be composed of simple ocelli, although the lateral eyes have three photoreceptor cells and for this reason are often called "compound eyes." Rhizocephalan nauplii also have a tripartite nauplius eye, which persist into the cyprid larval stage.

Compound eyes are lacking altogether in many crustacean taxa (e.g., Copepoda, Mystacocarida, Cephalocarida, Tantulocarida, Pentastomida, Remipedia, and some Ostracoda). Members of some other groups possess compound eyes only in late larval stages and lose them at metamorphosis (e.g., some cirripedes). Reduction or loss of eyes is also common in many deep-sea species, burrowers, cave dwellers, and parasites.

Crustaceans have complex endocrine and neurosecretory systems, although our understanding of these systems is far from complete. In general, the phenomena of molting (see Chapter 20), chromatophore activity, and various aspects of reproduction are under hormonal and neurosecretory control. Interesting recent work indicates that juvenile hormone-like compounds, long thought to occur only in insects, may also occur in at least some crustaceans. (Juvenile hormones are a family of compounds that regulate adult metamorphosis and gametogenesis in insects.) Bioluminescence also occurs in several crustacean groups. It is common among pelagic decapods, and it has also been reported in certain myodocopan ostracods, hyperiid amphipods, and copepod larvae.

Reproduction and Development

Reproduction We have often mentioned the relationships between an animal's reproductive and developmental pattern and its lifestyle and overall survival strategy. With the exception of purely vegetative processes such as asexual budding, the crustaceans have managed to exploit virtually every life history scheme imaginable. The sexes are usually separate, although hermaphroditism is the rule in remipedes, cephalocarids, most cirripedes, and a few decapods. Sequential hermaphroditism is not uncommon and usually is expressed as protandry (individuals first mature as males, then later become females), although protogyny occurs in a few species (e.g., the marine isopod *Gnorimosphaeroma orgonense*). In addition, parthenogenesis is known in some branchiopods and certain ostracods. In one species of clam shrimp (*Eulimnadia texana*) a rare type of mixed mating system exists, called **androgonochorism** (i.e., androdioecy in plants), in which males coexist with hermaphrodites, but there are no true females. Androgonochorism is rare, but is also known in the nematode *Caenorhabditis elegans*, some thoracican barnacles (e.g., *Balanus galeatus*, *Scalpellum scalpellum*), and from several other branchiopod crustaceans.

The reproductive systems of crustaceans are generally quite simple (Figure 21.27). The gonads are derived from coelomic remnants and lie as paired elongate structures in various regions of the trunk. In many cirripedes, however, the gonads lie in the cephalic region. In some cases the paired gonads are partially or wholly fused into a single mass. A pair of gonoducts extends from the gonads to genital pores located on one of the trunk segments, either on a sternite, on the arthrodial membrane between the sternite and leg protopods, or on the protopods themselves. In many crustaceans the paired penes are fused into a single median penis (e.g., in tantulocarids, cirripedes, and some isopods). The female system sometimes includes seminal receptacles. The position of the gonopores varies among the classes (Table 21.1).

The curious phenomenon of **intersex**—having both male and female secondary sexual characteristics—is

widespread among crustaceans. Intersexual development is associated directly with the presence of endoparasites such as bacteria and microsporidia, and it has also been correlated with the presence of endocrine-disrupting pollutants that seem to induce opposing secondary sexual characterisitcs.

Most crustaceans copulate, and many have evolved courtship behaviors, the most elaborate and well known of which occur among the decapods. Although many crustaceans are gregarious (e.g., certain planktonic species, barnacles, many isopods and amphipods), most decapods live singly except during the mating season. More or less permanent, or at least seasonal, pairing is known among many crustaceans (e.g., stenopodid shrimps; certain parasitic and commensal isopods; pinnotherid "pea" crabs, which often live as pairs in the mantle cavities of bivalve molluscs or in burrows of thalassinid shrimps).

Even the parasitic pentastomids copulate (within the host's respiratory system) and have internal fertilization, relying on a transfer of sperm to the female's vagina by way of the male's cirri (penes). Pentastomid early embryos metamorphose into a so-called primary larva with two pairs of double-clawed legs and one or more piercing stylets (Figure 21.19E). The larvae may be autoinfective in the primary host, or they may migrate to the host's gut and pass out with the feces. In the latter case, an intermediate host is required, which may be almost any kind of vertebrate. The larvae bore through the gut wall of the intermediate host, where they undergo further development to the infective stage. Once the intermediate host is consumed by a definitive host (usually a predator), the parasite makes its way from the new host's stomach up the esophagus, or bores through the intestinal wall, eventually settling in the respiratory system.

Mating in nonpaired crustaceans requires mechanisms that facilitate location and recognition of partners. Among decapods, and perhaps many other crustaceans, scattered individuals apparently find one another either by distance chemoreception (pheromones) or through synchronized migrations associated with lunar periodicity, tidal movements, or some other environmental cue. Contact sex pheromones are also utilized. Males of some marine myodocopan ostracods (some Halocyprididae, some Cyprididae) produce complex bioluminescent displays, similar to those of fireflies, to attract females. Once prospective mates are near each other, recognition of conspecifics of the opposite sex may involve several mechanisms. Over 60 speceis of cypridinid ostracods engage in luminescent courtship behavior in the Caribbean alone. Apparently, most decapods employ chemotactic cues requiring actual contact. Vision is known to be important in the stenopodid shrimps (most of which live in pairs), in certain anomurans (e.g., the family Porcellanidae), and in brachyurans (many grapsids and ocypodids).

Figure 21.32 Reproduction in Crustacea. (A–D) Mating behaviors of the fiddler crab Uca. (A) Two males in ritualized combat for the favor of a female, while she watches (B). (C) A single male waving his enlarged cheliped to attract a female. (D) A male fiddler crab engaged in claw-waving behavior to attract a female. (E) A balanomorph barnacle, with cirri and groping penis extended, impregnating a neighbor. The advantage of a long penis in sessile animals is made obvious by this illustration. (F) Ventral views of a male and female brachyuran crab, Cancer magister, showing the modified pleopods (setose appendages to retain eggs in female; modified as gonopod in male). (G) A copulating pair of Hemigrapsus sexdentatus. (H) The planktonic copepod Sapphirina, with egg sacs.

A good deal of work has been done on fiddler crabs of the genus Uca (family Ocypodidae). In these species, males engage in dramatic cheliped waving (of their greatly enlarged chela, or **major claw**, which can account for more than 50% of the male's total mass—more than the largest rack of a male elk!) to attract females and repel competing males (Figure 21.32A–D). In addition, males produce sounds by stridulation and substratum thumping, which are thought to attract potential mates. Mating generally takes place once the male has enticed the female into his burrow. Males of some fiddler crab species build sand structures at the entrance of their burrow, which have been shown to attract females.

Among many crustaceans, the external sexual characteristics are associated with the actual mating process. In some males, particular appendages, such as the antennae of anostracans and some cladocerans, ostracods, and copepods, are modified for grasping the female. Additionally, many males bear special sperm transfer structures, in the form of either modified appendages or special penes such as those of the thoracican barnacles (Figure 21.32E), anostracans, and ostracods. Examples of modified appendages include the last trunk limbs of copepods and the anterior pleopods of most male malacostracans (called gonopods in most malacostracans, or **petasma** in Dendrobranchiata) (Figure 21.32F). Sperm are transferred either loose in seminal fluid or (in many malacostracans and in copepods) packaged in spermatophores. Motile flagellated sperm occur only in some of the former maxillopodan groups; in other crustaceans the sperm are nonmotile. Crustacean sperm are highly variable in shape, even bizarre in many instances, often being large round or stellate cells that move by pseudopods or are, seemingly, nonmotile.[9] Sperm are deposited directly into the oviduct or into a seminal receptacle in or near the female reproductive system. In some crustaceans

[9]The sperm of freshwater ostracods are the longest in the animal kingdom, relative to body size (up to 10× body length). Even though their sperm are aflagellate, they are filiform and range from several hundred microns to millimeters in length.
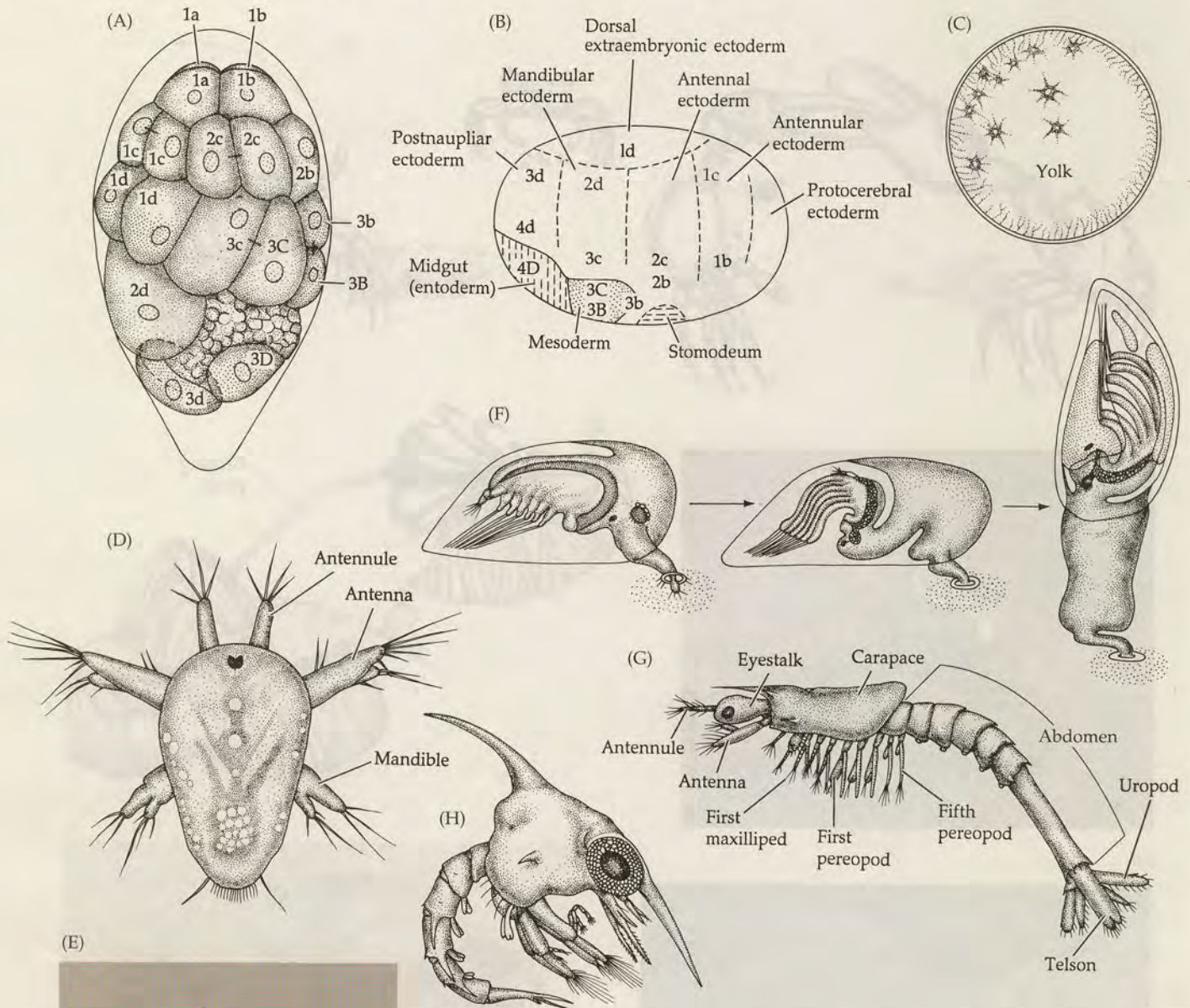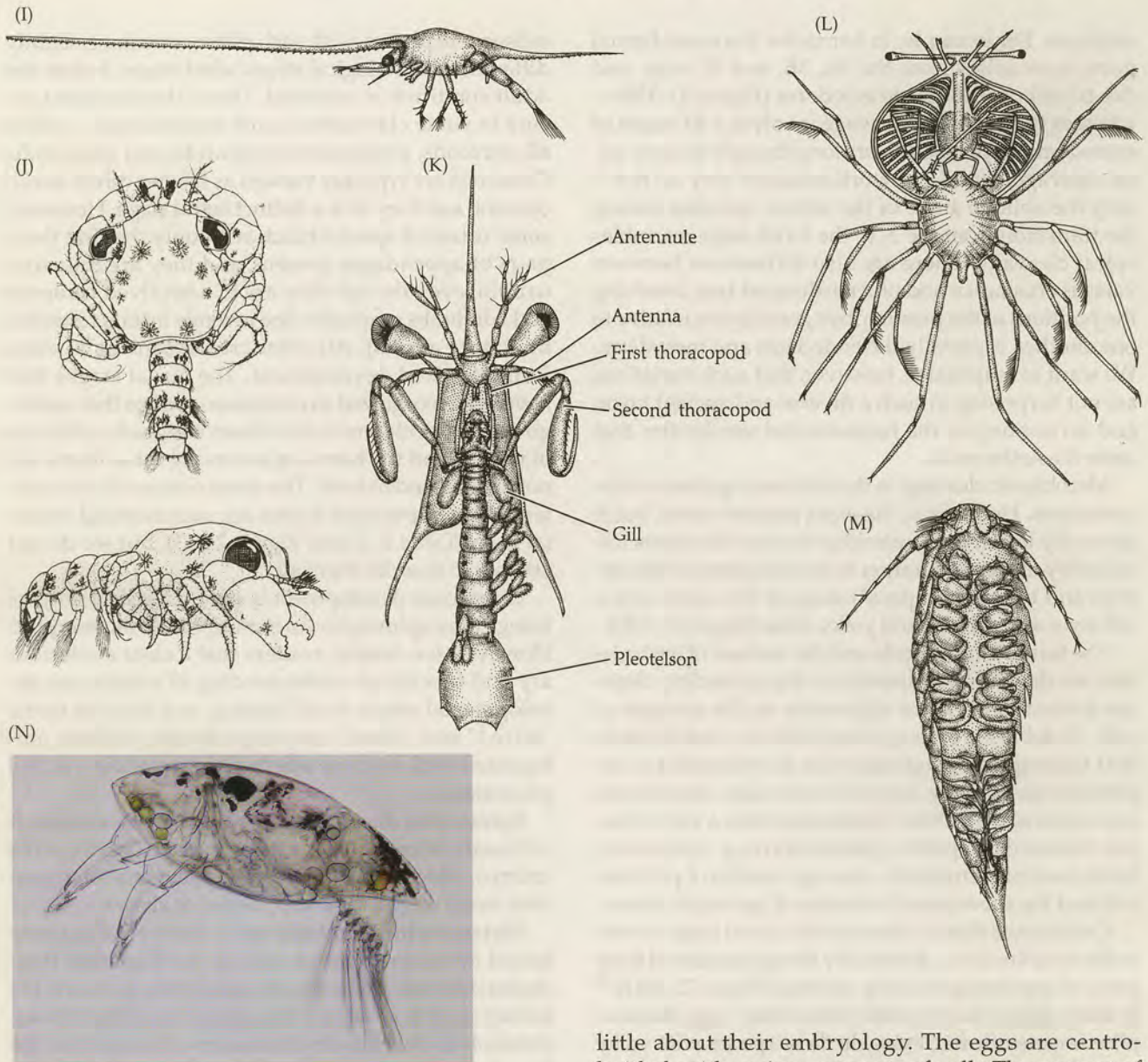
(A)

(B)

(C)

(D)

(E)

Groping
penis

(F)

(G)

(H)
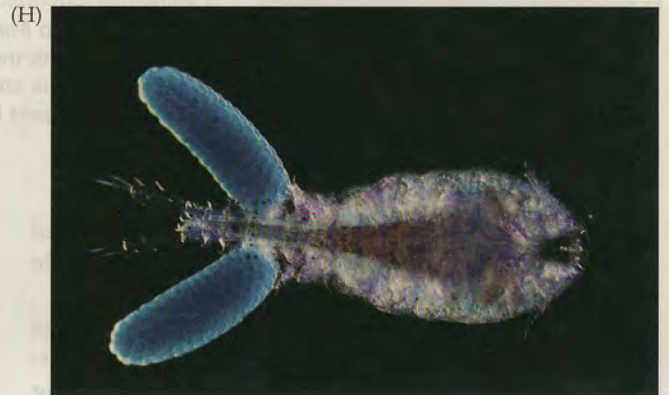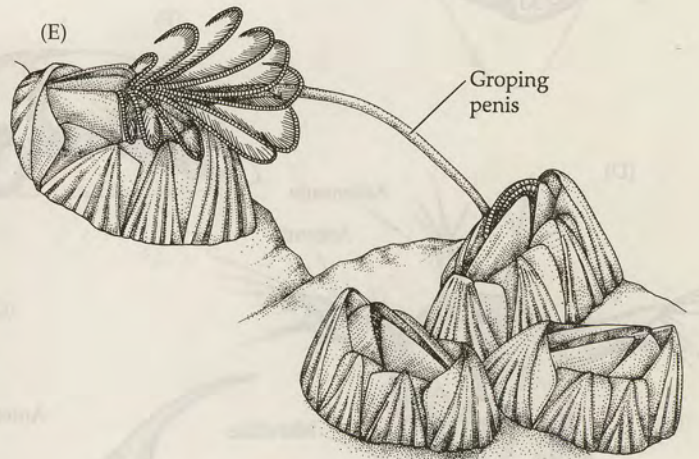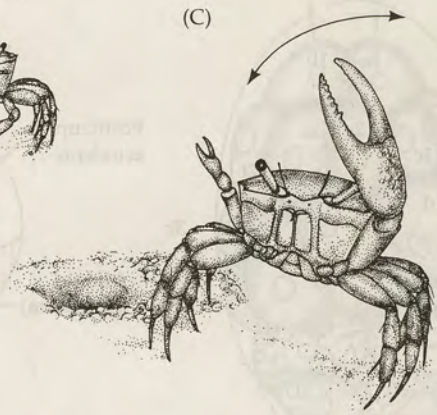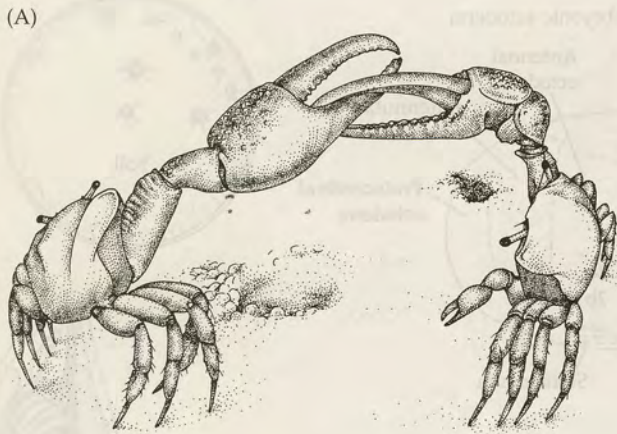
Figure 21.33 Cleavage and posthatching stages among crustaceans.
(A) Modified holoblastic spiral cleavage has produced a 28-cell embryo of the cirripede *Tetraclita*. The cells are labeled as in Wilson's coding system. (B) A fate map of a cirripede blastula (right-side view). (C) Intralecithal nuclear divisions in the early cleavage of a mysid. (D) Newly hatched copepod nauplius larva. (E) Nauplius of a copepod. (F) Settling and metamorphosis of a cypris larva of a lepadomorph barnacle. (G) The zoea ("mysis") stage larva of the dendrobranchiate shrimp *Penaeus*. (H) Zoea larva of the brachyuran crab *Callinectes sapidus*. (I) Zoea larva of a porcelain crab. (J) Megalopa larvae of the xanthid crab *Menippe adina*. (K) The characteristic antizoea larva of a stomatopod. (L) The translucent, paper-thin phyllosoma larva of the lobster *Jassa*. (M) Cryptoniscus stage (not a true larva) of the epicaridean isopod *Probopyrus bithynis*. (N) Cyprid larva of a barnacle.

females can store sperm for long periods (e.g., several years in the lobster *Homarus*), thus facilitating multiple broods from single inseminations.

The great majority of crustaceans brood their eggs until hatching occurs, and a variety of brooding strategies has evolved. Peracarids brood the developing embryos in a marsupium, a ventral brood pouch formed from inwardly directed plates of the leg coxae called **oostegites** (thermosbaenaceans are an exception among the Peracarida and use the carapace as a brood chamber). Other crustaceans attach the embryos to endites on the bases of the legs or to the pleopods

(I)

(J)

(K)

- Antennule
- Antenna
- First thoracopod
- Second thoracopod

- Gill

- Pleotelson

(L)

(M)

(N)

(Figure 21.32F), usually using mucus secreted by specialized glands. In some cladocerans, brooding takes place in a dorsal brood chamber formed by the carapace. However, the syncarids, almost all dendrobranchiate shrimps, and most euphausids shed the zygotes directly into the water. A few others deposit their fertilized eggs in the environment, usually attaching them to some object (e.g., branchiurans, some ostracods, many stomatopods). These deposited embryos may be abandoned or, as is the case in stomatopods, carefully tended by the female. Nonetheless, parental protection of the embryos until they hatch as larvae or juveniles is typical in crustaceans. Thus, crustaceans usually engage in mixed or direct life histories (Table 21.2).

Development   Although crustaceans are the most widespread animals on Earth, we know surprisingly

little about their embryology. The eggs are centrolecithal, with various amounts of yolk. The amount of yolk greatly influences the type of early cleavage and is often related to the time of hatching (Chapter 4). As far as is known, the zygotes of most non-malacostracans undergo some form of holoblastic cleavage, as do those of syncarids, euphausids, penaeids, amphipods, and parasitic isopods. However, cleavage patterns are extremely variable, ranging from equal to unequal and from radial-like to spiral-like. The occurrence of modified spiral cleavage (Figure 21.33A) reported from some crustaceans had generally viewed as evidence of close ties between the crustaceans and other spiralian groups such as the annelids. However, the generality of spiral-like cleavage among crustaceans has been called into question with evidence from molecular phylogenetics that indicates arthropods belong to the Ecdysozoa clade of Protostomia, not the Spriralia (where annelids are nested). And in some crustacean groups, the cell lineages and germ layer origins are quite different from those of typical spirally cleaving

embryos. For example, in barnacles the mesodermal germ layer arises from the 3A, 3B, and 3C cells, and the 4d cell contributes to ectoderm (Figure 21.33B)—whereas typical spiral cleavage involves a 4d origin of mesoderm. Euphausids were long thought to have spiral cleavage, but recent work indicates they do not—only the oblique angle of the mitotic spindles during the transition from the 2- to the 4-cell stage resembles spiral cleavage. There are also differences between various crustacean and other arthropod taxa involving the positions of the presumptive germ layers relative to one another, especially the endoderm and mesoderm. We want to emphasize, however, that such variations are not surprising in such a diverse and ancient taxon and do not negate the fundamental similarities that unite the Arthropoda.

Meroblastic cleavage is the rule among many malacostracans. Here again, the exact pattern varies, but it generally involves intralecithal nuclear divisions followed by nuclear migration to the periphery of the embryo and subsequent partitioning of the nuclei into a cell layer around a central yolky mass (Figure 21.33C).

The form of the blastula and the method of gastrulation are dependent primarily on the preceding cleavage pattern and hence ultimately on the amount of yolk. Holoblastic cleavage may lead to a coeloblastula that undergoes invagination (as in syncarids) or ingression (as in many copepods and some cladocerans and anostracans). Other crustaceans form a stereoblastula followed by epibolic gastrulation (e.g., cirripedes). Most cases of meroblastic cleavage result in a periblastula and the subsequent formation of germinal centers.

Crustaceans share a characteristic larval stage known as the nauplius larva, denoted by the appearance of three pairs of appendage-bearing somites (Figure 21.33D).[10] In those groups having little yolk in their eggs, the nauplius is generally free living. In those species with yolky eggs, the nauplius stage is generally passed through as part of a longer period of embryonic development (or a long brood period), and it is sometimes referred to as an **egg nauplius**. Free-living nauplii are usually planktotrophic, and their release corresponds to the depletion of stored yolk. However, in a few groups of crustaceans (e.g., euphausids and dendrobranchiate shrimps), the nauplius exhibits lecithotrophy.

Crustacean development is either direct, with the embryos hatching as juveniles that resemble miniature adults, or mixed, with embryos brooded for a brief or prolonged period and then hatching as a distinct larval form. These larval forms may pass through several

subsequent phases, with each phase containing slightly different morphological steps called stages, before the adult condition is achieved. Direct development occurs in some cladocerans and branchiurans, and in all ostracods, phyllocarids, syncarids, and peracarids. Ostracods are typically viewed as having direct development, and they lack a distinct larval stage. However, some ostracod species hatch with only the first three pairs of appendages present, and they are thus true nauplii, even though they are in a bivalved carapace and add limbs gradually (the juvenile instars resemble miniature adults). All other crustaceans have some form of mixed development. The larval stages that have been recognized in crustacean groups that undergo mixed development have been assigned a plethora of names, and the homologies among these forms are not always understood. The more commonly encountered developmental forms are summarized below (also see Table 21.2 and Figure 21.33), but we do not attempt to describe them all.

Crustacean development is sometimes described as being either epimorphic, metamorphic, or anamorphic. However, we caution readers that a clear evolutionary and functional understanding of crustacean developmental stages is still lacking, and thus the terms "mixed" and "direct" may be preferable, and less ambiguous, until we have a better understanding of this phenomenon.

Epimorphic development is direct; in crustaceans it is thought to result from a delay in the hatching of the embryo, which causes the nauplius (and any other possible larval stages) to be suppressed or absent.

Metamorphic development is the type of extreme mixed development seen among the Eucarida; it includes dramatic transitions in body form from one life history stage to another. (This pattern is similar to holometabolous development in insects—for example, the transformation of a caterpillar into a butterfly.) In general, up to five distinct preadult, or larval, phases may be recognized among crustaceans: **nauplius**, **metanauplius**, **protozoea**, **zoea**, and "**postlarva**." The zoeal phase shows the greatest diversity in form among the various taxa, and especially in decapods it has been given different names in different groups (e.g., acanthosoma, antizoea, mysis, phyllosoma, pseudozoea). It is common for the zoeal phase to contain a large number of stages, each differing only slightly from the one preceding it.[11] Regardless of name, zoea are characterized by the presence of natatory exopods on some or all of the thoracic appendages and by the pleopods being absent (or rudimentary). Use of the term "postlarva" is unfortunate, as these stages differ dramatically from the preceding larvae as well as from the adults; they

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[10]It was not until J. V. Thompson discovered the nauplius larvae of barnacles in the nineteenth century that this group was finally classified as Crustacea, a discovery that also marked the first use of larval features in understanding the phylogeny of marine invertebrates. A recent atlas of crustacean larvae (Martin et al. 2014) includes historical notes on larval development in all major crustacean groups.

[11]The zoea larvae of panulirid lobsters (phyllosoma larvae) are large, bizarre-appearing creatures (Figure 21.33L), which can occur in such large numbers as to be a favorite food of tuna.

represent unique transitional stages (both morphologically and ecologically). Examples in the Decapoda include the **megalopa** of true crabs and the **puerulus** larvae of spiny lobsters. In this phase of development, the role of swimming has switched from the thoracopodal limbs to the appendages of the abdomen.

Anamorphic development is a less extreme type of indirect development in which the embryo hatches as a nauplius larva, but the adult form is achieved through a series of gradual changes in body morphology as new segments and appendages are added (it is similar in many ways to hemimetabolous development in insects). In other words, the postnaupliar stages gradually take on the adult form with succeeding molts; the classic example of anamorphic development is often said to be the Anostraca. Cephalocarida, Remipedia, many Branchiopoda, and Mystacocarida are anamorphic—the nauplius larva grows by a series of molts that add new segments and appendages gradually as the adult morphology appears. In many groups hatching is somewhat delayed, and the emergent nauplius larva is termed a metanauplius. The basic nauplius possesses only three body somites, while the metanauplius has a few more; however, both possess only three pairs of similar-appearing appendages (which become the adult antennules, antennae, and mandibles). The end of the naupliar/metanaupliar stage is defined by the appearance of the fourth pair of functional limbs, the maxillules. In copepods a postnaupliar stage called a **copepodite** (simply a small juvenile) is often recognized.

The most extreme forms of metamorphic, or mixed, development occur in the malacostracan superorder Eucarida. The most complex developmental sequences are seen among the dendrobranchiate shrimps, which hatch as a typical nauplius larva that eventually undergoes a metamorphic molt to become a protozoea larva, with sessile compound eyes and a full complement of head appendages. The protozoea, after several molts, becomes a zoea larva, with stalked eyes and three pairs of thoracopods (as maxillipeds). The zoea eventually yields a juvenile stage (the "postlarva," a better term for which is "decapodid") that resembles a miniature adult, but is not sexually mature. In some other eucarid groups (Caridea and Brachyura) the postlarva is called a **megalopa**, and in the Anomura it is often called a **glaucothoe**; in both cases there are setose natatory pleopods on some or all of the abdominal somites. In other eucarids, some (or all) of these stages are absent.

Various other terms have been coined for different (or similar) developmental stages. For example, the modified zoeal stages of some stomatopods are called **antizoea** and **pseudozoea** larvae, and the advanced zoeal stage of many other malacostracans is often called a **mysis larva**. In euphausids, the nauplius is followed by two stages, the **calyptopis** and the **furcilia**, which roughly correspond to protozoea and zoea stages, before the juvenile morphology is attained.

From this wealth of terms and diversity of developmental sequences, we can draw two important generalizations concerning the biology and evolution of the crustaceans. First, different developmental strategies reflect adaptations to different lifestyles. In spite of many exceptions, we can cite the early release of dispersal larvae by groups with limited adult mobility, such as thoracican barnacles, and by those whose resources may not permit production of huge quantities of yolk, such as the copepods. At the other end of this adaptive spectrum is the direct development of peracarids—a major factor allowing the invasion of land by certain isopod lineages. Between these extremes we see all degrees of mixed life histories, with larvae being released at various stages following brooding and care. Second, because developmental stages also evolve, an analysis of developmental sequences can sometimes provide information about the radiation of the principal crustacean lineages. For example, the evolution of oostegites and of direct development combine as a unique synapomorphy of the Peracarida. Similarly, the addition of a unique larval form, such as the **cypris larva** that follows the nauplius in the cirripedes, can be viewed as a unique specialization that demarcates that group (Cirripedia). The cyprid either hatches as the only free-living larva, or it is the final larval stage after a series of lecithotrophic or planktotrophic nauplius larval stages.

It should also be noted that the branchiopods and some freshwater ostracods have evolved specialized ways of coping with the harsh conditions of many freshwater environments. Parthenogenesis, for example, is common in freshwater ostracods. Other adaptations include production of special overwintering forms, usually eggs or zygotes that can survive extreme cold, lack of water, or anoxic conditions. Perhaps most remarkable in this respect are the large-bodied branchiopods (fairy shrimp, tadpole shrimp, and clam shrimp) whose encysted embryos are capable of an extreme state of anaerobic quiescence, or diapause. During these resistant stages, the metabolic rate of the embryos may drop to less than 10% of their normal rate.

Many crustaceans have **indeterminate growth**, that is, they continue to molt throughout their life. In contrast, other species have **determinate growth** and cease molting following puberty (this life history stage is sometimes referred to as the terminal molt, or terminal anecdysis). In some species, the terminal molt is sex specific; for example, in American blue crabs (*Callinectes sapidus*) only females have a terminal molt.

Crustacean Phylogeny

Countless phylogenetic studies have been published on the topic of crustacean evolution. General agreement has been reached in some areas, but despite a great deal of effort, many fundamental mysteries re-

main unsolved, including the broad structure of the Pancrustaca tree. The use of molecular gene sequence data in crustacean phylogenetics is only just beginning. While in some cases it has resolved longstanding issues or confirmed previous hypotheses, in other cases it has led to still more questions. There are several particularly problematic issues. What are the basalmost living crustaceans, what sort of body did they have, and what are the relationships among them? What are the relationships of, and among, the taxa that were once united as "maxillopodans" (the copepods, branchiurans, thecostracans, tantulocarids, mystacocarids, and pentastomids)? Where do the Ostracoda, Cephalocarida, and Remipedia fit into crustacean phylogeny? What are the relationships among the Peracarida, especially of the many orders and families of Isopoda and Amphipoda? What are the major decapod lineages and how are they related to one another? What group of crustaceans is represented by the mysterious "y-larvae" (the Facetotecta), beyond the subsequent sluglike ypsigon stage that is clearly still not an adult? And, of course, what is the crustacean sister group to the Hexapoda?

Debates on crustacean phylogeny often center on whether paddle-legged Crustacea are ancestral or derived. The paddle-legged ancestry hypothesis holds that the first crustaceans had leaflike (phyllopodous) thoracic legs that were used both for swimming and for suspension feeding, as seen in the living cephalocarids, leptostracans, and many branchiopods. Or that the first crustaceans had simple, paddle-like legs that were used for swimming, but not for feeding; instead, the tasks of feeding were undertaken by the cephalic appendages—a plan perhaps best represented among living crustaceans by the remipedes. However, the opposing view, that paddle-legged crustaceans are more derived, is supported by the recent multigene studies.

A large molecular study suggested a highly-derived sister group relationship between the two most many-segmented and "wormlike" groups, the cephalocarids and remipedes, both being paddle-legged groups, uniting them in a proposed clade (called Xenocarida) that would be the sister to the hexapods (Regier et al. 2010; Figure 21.34B). Another recent phylogenomic study concluded that Remipedia are the closest extant relatives of insects (Misof et al. 2014), and some comparative neurological work also supports this view. In contrast, a traditional, morphology-based phylogeny of the Crustacea hypothesizes a paddle-legged ancestry, but places the Remipedia at the base of the crustacean tree (Figure 21.34A). Comparative spermatological studies, on the other hand, seem to ally the remipedes with certain former maxillipodans. Clearly, we have a good way to go before we will deeply understand the phylogeny of Crustacea.

The Regier et al. (2010) study, summarized here in Figure 21.34B, strongly supported some traditionally recognized groupings, such as Branchiopoda,

Thecostraca (barnacles and their kin), and Malacostraca, but challenged others, and proposed several new names and clades (e.g., Oligostraca and Vericrustacea) that have yet to withstand the test of time.

In the 1950s, Russian biologist W. N. Beklemischev and Swedish carcinologist E. Dahl independently proposed that the copepods and several related classes constitute a monophyletic clade. Dahl proposed the class Maxillopoda for these taxa, and that term has been employed often since then. Characters shared by these small taxa include the shortening of the thorax to six or fewer segments and of the abdomen to four or fewer segments, reduction of the carapace (or, in the case of ostracods and cirripedes, extreme modification of the carapace), loss of abdominal appendages, and other associated changes, all thought to be tied to early paedomorphic events during the larval (or post-larval) stage of this lineage as it began to radiate (an idea first proposed in 1942 by R. Gurney). However, molecular phylogenetic studies since then have shown Maxillopda to be a nonmonophyletic grouping, and the taxon has been abandoned by most modern workers. Yet two of those groups, the copepods and thecostracans, have since been reunited in one study (Oakley et al. 2013) that posits a clade (the Hexanauplia) based on the same number (6) of naupliar larval stages in these groups.

The monophyletic nature of the class Malacostraca has rarely been questioned. Within the Malacostraca are two clades: Leptostraca, which have phyllopodous limbs and seven abdominal somites, and Eumalacostraca, which lack phyllopodous limbs and have six abdominal segments. Whether the Hoplocarida are members of the Eumalacostraca or deserving of their own subclass of the Malacostraca is still a subject of debate, but we consider them a separate subclass here. Hoplocarids and eumalacostracans also have the sixth abdominal appendages modified as uropods (which work in conjunction with the telson as a tail fan). Relationships among the three main eumalacostracan lines (syncarids, peracarids, and eucarids), and even within the Eucarida, are far from settled and have provided zoologists with many generations of lively debate.

The class Branchiopoda is usually monophyletic in molecular analyses, but it is difficult to define on the basis of unique synapomorphies because it shows such great morphological variation. But larval (naupliar) characters, such as the reduced and tubular first antenna and uniramous mandibles, strongly support their monophyly, as do almost all studies employing molecular data. As is true with so many crustacean groups, our early classifications greatly underappreciated their diversity, and relationships among the constituent groups are far more complex than was first thought. Apparently some branchiopods have secondarily lost
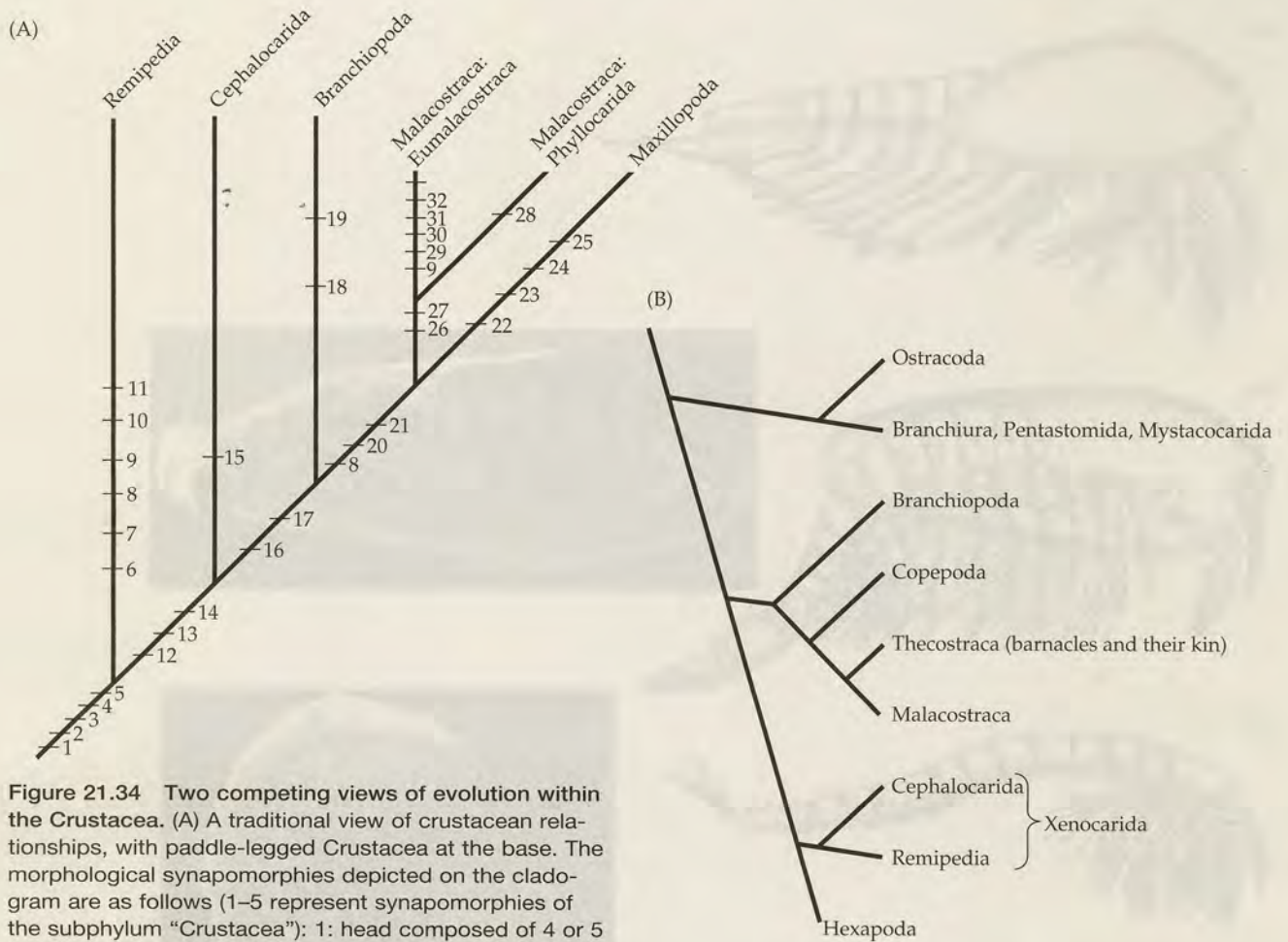
(A)

(B)

Figure 21.34 **Two competing views of evolution within the Crustacea.** (A) A traditional view of crustacean relationships, with paddle-legged Crustacea at the base. The morphological synapomorphies depicted on the cladogram are as follows (1–5 represent synapomorphies of the subphylum "Crustacea"): 1: head composed of 4 or 5 fused segments (plus acron) with 2 pairs of antennae and 2 or 3 pairs of mouth appendages; 2: biramous second antennae; 3: nauplius larva; 4: phyllopodous body limbs (with large epipods); 5: with head shield or small carapace; 6: raptorial mouth appendages; 7: mouth appendages situated in posteriorly directed atrium; 8: anterior thoracopods (one or more pairs) modified as maxillipeds (a highly variable trait that occurs in remipedes, malacostracans, and some former "maxillopodans"); 9: loss of phyllopodous condition on trunk appendages; 10: trunk appendages oriented laterally; 11: maxillules function as hypodermic fangs; 12: postcephalic trunk regionalized as thorax and abdomen; 13: loss of internal organ homonomy (e.g., segmental gut ceca); 14: reduction in number of body segments; 15: reduction of abdomen (to 11 segments); 16: fully developed carapace (reduced in several subsequent lineages); 17: reduction of abdomen to fewer than 9 segments; 18: reduction (or loss) of abdominal appendages; 19: first and second maxillae reduced or lost; 20: thorax shortened to fewer than 11 segments; 21: abdomen shortened to fewer than 8 segments; 22:

with maxillopodan naupliar eye; 23: thorax of 6 or fewer segments; 24: abdomen of 4 or fewer segments; 25: genital appendages on the first abdominal somite (associated with male gonopores); 26: 8-segmented thorax and 7-segmented abdomen (plus telson); 27: male gonopores fixed on thoracomere 8/females on thoracomere 6; 28: carapace forms large "folded" structure enclosing most of body; 29: abdomen reduced to 6 segments (plus telson); 30: last abdominal appendages modified as uropods and forming tail fan with telson; 31: caridoid tail flip locomotion (escape reaction); 32: thoracopods with stenopodous endopods; 33: replacement of thoracic suspension feeding and phyllopodous thoracic limbs with cephalic feeding and nonphyllopodous thoracic limbs. Note that loss of the phyllopodous trunk limbs (character 9) has occurred several times, in the Remipedia, Eumalacostraca, some lineages of Branchiopoda, and most of the former "maxillopodan" groups. (B) Phylogeny of the Pancrustacea clade as derived by Regier et al. 2010.

the carapace, and others have secondarily lost most or all of the abdominal appendages.

That a group of crustaceans gave rise to the megadiverse group of arthropods called the Hexapoda (insects and their kin) is now almost universally agreed upon, based on a wide array of evidence that includes molecular sequence data and neuroanatomy. This

realization renders the group called Crustacea paraphyletic. The monophyletic clade containing both crustaceans and insects is most often referred to as the Pancrustacea (see Chapter 20), but it is also sometimes called the Tetraconata, a name that recognizes the square shape of the ommatidia of many species. Earlier work suggested that Branchiopoda was the likely sister

(A)

(B)

(C)

100 µm

(D)
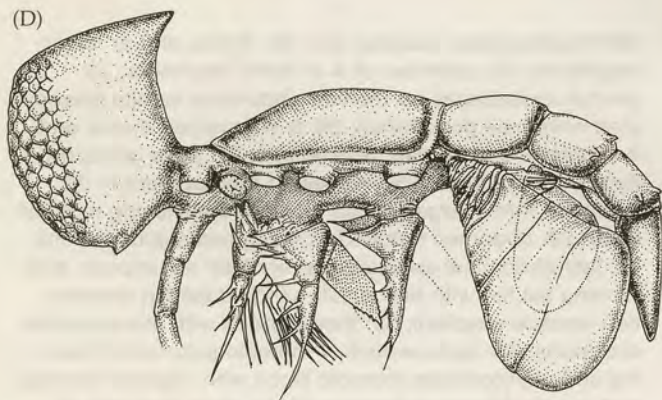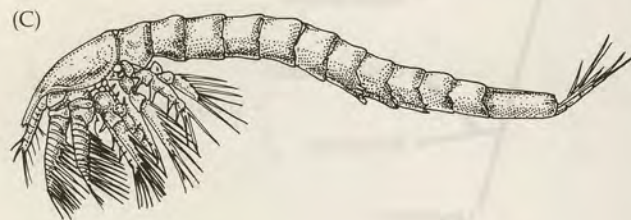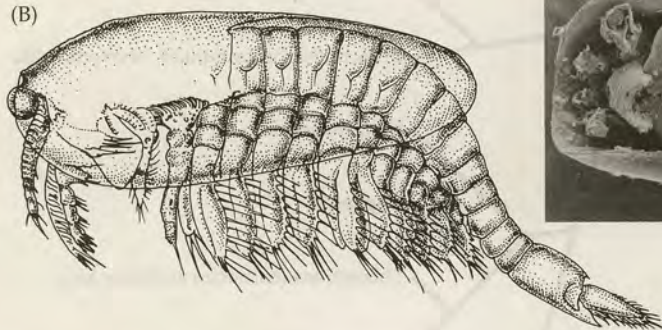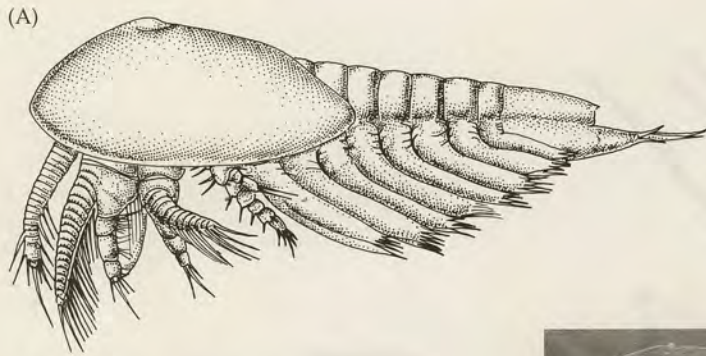
group to Hexapoda, but recent research supports the origin of the Hexapoda from either the Remipedia or a remipede-cephalocarid clade—the later grouping (Remipedia-Cephalocarida-Hexapoda) has been named Miracrustacea, meaning "surprising crustaceans." Like the arthropods in general, crustaceans exhibit high levels of evolutionary parallelism and convergence and many apparent reversals of character states. This genetic flexibility is no doubt due in part to the nature of the segmented body, the serially homologous appendages, and the flexibility of developmental genes, which, as we have stressed, provide enormous

opportunity for evolutionary experimentation. Any conceivable cladogram of crustacean phylogeny will require the acceptance of considerable homoplasy.

Fossil data (including that of the Orsten fauna, Figure 21.35) seems to favor phyllopodous limbs as the primitive condition. However, developmental studies following the expression of *Distal-less* and other developmental genes suggest that the early embryogeny of limbs is very similar among crustaceans. For example, trunk limbs always emerge as ventral, subdivided limb buds. In phyllopodous limbs, the subdivisions of these limb buds grow to become the endites and
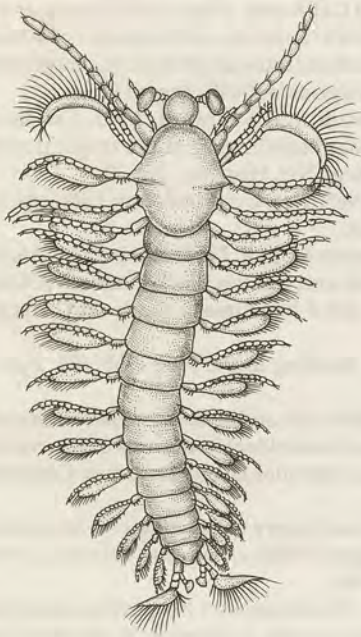
(E)
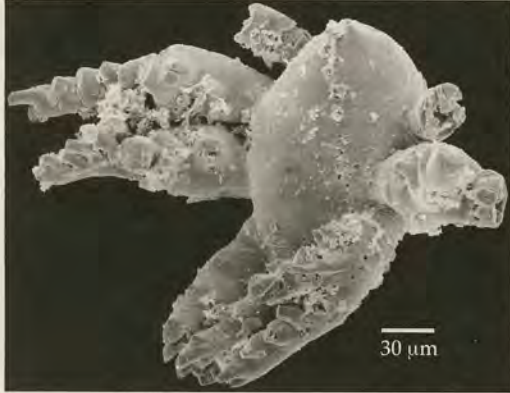
(F)

Figure 21.35 (A–E) Examples of Upper Cambrian (~510 Ma), probably meiofaunal crustacean fossils from the spectacular Swedish Orsten deposits. This ancient crustacean fauna possessed the key attributes of modern Crustacea, including compound eyes, head shields/carapaces, naupliar larvae (with locomotory first antennae), and biramous appendages on the second and third head segments (the second antennae and mandibles). (A) *Bredocaris*. (B) *Rehbachiella*, an early branchiopod, lateral (drawing) and ventral (SEM) views. (C) *Skara*, drawing and SEM. (D) *Cambropachycope clarksoni*, a bizarre species with an expanded head and two pairs of enlarged thoracopods, drawing and SEM. (E) *Martinssonia elongata*, SEMs of first larva and postlarval stage. (F) *Ercaia minuscula*, an early Cambrian (520 Ma) crustacean from South China.

the endopod of the natatory/filtratory adult limbs. In stenopodous limbs, the same limb bud subdivisions end up developing into the actual segments of the adult limb. Hence, the endites of phyllopodous limbs appear to be homologous to the segments of the stenopodous limbs. This discovery supports an emerging view of developmental plasticity in arthropod limbs, and it suggests that relatively simple genetic "switches" can account for major differences in adult morphologies. Thus, it is quite plausible that stenopodous limbs have evolved multiple times from phyllopodous ancestors, and this is the scenario depicted in the cladogram in Figure 21.34A.

Work by Klaus Müller and Dieter Waloszek on three-dimensionally preserved microscopic arthropods from the middle Cambrian Orsten (around 510 Ma) deposits of Sweden has documented a diverse fauna of minute crustaceans and their larvae. Among them, for example, is *Skara* (Figure 21.35C), a cephalocarid- or mystacocarid-like crustacean for which both naupliar larvae and adults have been recovered (the nauplius

larvae are only a couple hundred microns long; adults are about 1 mm in length). *Skara* and many other Orsten Crustacea were probably meiofaunal animals not unlike modern marine meiofaunal crustaceans (e.g., the mystacocarids). Dozens of Orsten microcrustacea have so far been described (Figure 21.35). Recently, a beautifully preserved fossil crustacean, *Ercaia minuscula*, was described from the middle Cambrian (520 Ma) of South China. It has an untagmatized, 13-segmented trunk with serially repeated biramous appendages and a head with stalked eyes and five pairs of head appendages, including two pairs of antennae. *Ercaia minuscula* is only 2–4 mm long (hence the species name), and bears resemblances to both cephalocarids and maxillopodans (Figure 21.35F).

Studies on the Swedish Orsten fauna (510 Ma), the Middle Cambrian (520 Ma) Burgess Shale-like deposits from around the world, and the Lower Cambrian (530 Ma) Chengjiang fossils from China have shown that Cambrian Crustacea had all the attributes of modern crustaceans, such as compound eyes, an acron, distinct head and trunk tagmata, at least four head appendages, a carapace (or head shield), naupliar (or "head") larvae (with locomotory first antennae), and biramous appendages on the second and third head somites (the second antennae and mandibles). We now know that the crustaceans are an ancient group. Their fossil record dates back to the early Cambrian, or likely the Ediacaran period if some arthropod fossils from those strata are viewed as Crustacea. The earliest known crustacean larval stage is a fossil of a slightly advanced nauplius (called a metanauplius) from the early

Cambrian (525 Ma) of China that in many ways resembles the naupliar larvae of modern cirripedes. This is remarkable, as it confirms not only of the great age of the Crustacea as a whole but also the age of groups within the Crustacea, such as the cirripedes, that were already becoming distinct. Depending on one's definition of "Crustacea," it may even be that the first arthropods were themselves crustaceans.

Selected References

The amount of published literature on crustaceans is vast. Much of the key work on classification and phylogenetics was reviewed by Martin and Davis (2001), and on larval development by Martin et al. (2014). We refer readers to those works for an entrée into those fields.

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