Phylum Mollusca

M olluscs include some of the best-known invertebrates; almost everyone is familiar with snails, clams, slugs, squids, and octopuses. Molluscan shells have been popular since ancient times, and some cultures still use them as tools, containers, musical devices, money, fetishes, religious symbols, ornaments, and decorations and art objects. Evidence of historical use and knowledge of molluscs is seen in ancient texts and hieroglyphics, on coins, in tribal customs, and in archaeological sites and aboriginal kitchen middens or shell mounds. Royal or Tyrian purple of ancient Greece and Rome, and even Biblical blue (Num. 15:38), were molluscan pigments extracted from certain marine snails.[1] Many aboriginal groups have for millenia relied on molluscs for a substantial portion of their diet and for use as tools. Today, coastal nations annually harvest millions of tons of molluscs commercially for food.

There are approximately 80,000 described, living mollusc species and about the same number of described fossil species. However, many species still await names and descriptions, especially those from poorly studied regions and time periods, and it has been estimated that only about half of the living molluscs have so far been described. In addition to three familiar molluscan classes comprising the clams (Bivalvia), snails and slugs (Gastropoda), and squids and octopuses (Cephalopoda), five other extant classes exist: chitons (Polyplacophora), tusk shells (Scaphopoda), *Neopilina* and its kin (Monoplacophora), and the vermiform sclerite-bearing aplacophoran classes—Caudofoveata (or Chaetodermomorpha) and Solenogastres (or Neomeniomorpha). Although members of these eight classes differ enormously in superficial appearance, there is a suite of characters that diagnose their fundamental body plan (Box 13A).

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

[1]Archaeological sites in Israel reveal the probable use of two muricid snails (*Murex brandaris* and *Trunculariopsis trunculus*) as sources of the Royal purple dye.

Taxonomic History and Classification

Molluscs carry the burden of a very long and convoluted taxonomic history, in which hundreds of names for various taxa have come and gone. Aristotle recognized molluscs, dividing them into Malachia (the cephalopods) and Ostrachodermata (the shelled forms), the latter being divided into univalves and bivalves. Joannes Jonston (or Jonstonus) created the name Mollusca[2] in 1650 for the cephalopods and barnacles, but this name was not accepted until it was resurrected and redefined by Linnaeus nearly a hundred years later. Linnaeus's Mollusca included cephalopods, slugs, and pteropods, as well as tunicates, anemones, medusae, echinoderms, and polychaetes—but included chitons, bivalves, univalves, nautiloids, barnacles, and the serpulid polychaetes (which secrete calcareous tubes) in another group, Testacea. In 1795 Georges Cuvier published a revised classification of the Mollusca that was the first to approximate modern views. Henri de Blainville (1825) altered the name Mollusca to Malacozoa, which won little favor but survives in the terms malacology, malacologist, etc.

Much of the nineteenth century passed before the phylum was purged of all extraneous groups. In the 1830s, J. Thompson and C. Brumeister identified the larval stages of barnacles and revealed them to be crustaceans, and in 1866 Alexander Kowalevsky removed the tunicates from Mollusca. Separation of the brachiopods from the molluscs was long and controversial and not resolved until near the end of the nineteenth century.

The first sclerite-covered wormlike aplacophorans, members of what today we recognize as the class Caudofoveata, were discovered in 1841 by the Swedish naturalist Sven Lovén. He classified them with holothuroid echinoderms because of their vermiform bodies and the presence of calcareous sclerites in the body walls of both groups. In 1886, another Swede, Tycho Tullberg, described the first representative of the other aplacophoran group—the Solenogastres. Ludwig von Graff (1875) recognized both groups as molluscs and they were united in the Aplacophora in 1876 by Hermann von Ihering. The Aculifera hypothesis of Amélie Scheltema unites molluscs that

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[2]The name of the phylum derives from the Latin *molluscus*, meaning "soft," in allusion to the similarity of clams and snails to the mollusca, a kind of Old World soft nut with a thin but hard shell. The vernacular for Mollusca is often spelled mollusks in the United States, whereas in most of the rest of the world it is typically spelled molluscs. In biology, a vernacular or diminutive name is generally derived from the proper Latin name; thus the custom of altering the spelling of Mollusca by changing the c to k seems to be an aberration (although it may have its historic roots in the German language, which does not have the free-standing c; e.g., Molluskenkunde). We prefer the more widely used spelling "molluscs," which seems to be the proper vernacularization and is in line with other accepted terms, such as molluscan, molluscoid, molluscivore, etc.

BOX 13A   Characteristics of the Phylum Mollusca

1. Bilaterally symmetrical (or secondarily asymmetrical), unsegmented, coelomate protostomes
2. Coelom limited to small spaces in nephridia, heart and gonads
3. Principal body cavity is a hemocoel (open circulatory system)
4. Viscera concentrated dorsally as a "visceral mass"
5. Body covered by a cuticle-covered epidermal sheet of skin, the mantle
6. Mantle with shell glands that secrete calcareous epidermal sclerites, shell plates, or shells
7. Mantle overhangs and forms a cavity (the mantle cavity) in which are housed the ctenidia, osphradia, nephridiopores, gonopores, and anus
8. Heart situated in a pericardial chamber and composed of a single ventricle and one or more separate atria
9. Typically with large, well-defined muscular foot, often with a flattened creeping sole
10. Buccal region provided with a radula and muscular odontophore
11. Complete (through) gut, with marked regional specialization, including large digestive glands
12. With large, complex metanephridial "kidneys"
13. Cleavage spiral and embryogeny protostomous
14. With trochophore larva, and a veliger larva in two major groups

---

possess calcareous sclerites by placing Polyplacophora as the sister taxon of the aplacophorans (Caudofoveata + Solengastres). Aculifera was sometimes also called Amphineura, although this latter term has also been used by some workers to refer only to chitons. **Sclerites** are spicules, scales, and so on that cover or are embedded in the epidermis of molluscs and are often calcified.

The history of classification of species in the class Gastropoda has been volatile, undergoing constant change since Cuvier's time. Most modern malacologists adhere more or less to the basic schemes of Henri Milne-Edwards (1848) and J. W. Spengel (1881). The former, basing his classification on the respiratory organs, recognized the groups Pulmonata, Opisthobranchia, and Prosobranchia. Spengel based his scheme on the nervous system and divided the gastropods into the Streptoneura and Euthyneura. In subsequent classifications, Streptoneura was equivalent to Prosobranchia; Euthyneura included Opisthobranchia and Pulmonata. The bivalves have been called Bivalvia, Pelecypoda, and Lamellibranchiata. More recently, anatomical, ultrastructural, and molecular studies have brought about considerable changes to molluscan classification, as outlined below. Many taxa have multiple names and the more commonly encountered ones are noted below.

Molluscan classification at the generic and species levels is also troublesome. Many species of gastropods

and bivalves are also burdened with numerous names (synonyms) that have been proposed for the same species. This tangle is partly the result of a long history of amateur shell collecting beginning with the natural history cabinets of seventeenth century Europe, which required documentation and promoted multiple taxonomies and names based only on shell characters. Today, species are recognized based on a combination of shell, anatomical, and, most recently molecular characters. However, because of the tremendous diversity of gastropods and bivalves many species still remain known only from their shells.

Only taxa with extant members are included in the following classification and not all families are listed in the taxonomic synopses. The classification is mostly ranked, but in a few cases unranked group names are used.[3] Examples of the major molluscan taxa appear in Figure 13.1.

ABBREVIATED CLASSIFICATION OF THE PHYLUM MOLLUSCA

CLASS CAUDOFOVEATA   Caudofoveatan aplacophorans (spicule "worms")

CLASS SOLENOGASTRES   Solenogaster aplacophorans (spicule "worms")

CLASS MONOPLACOPHORA   Monoplacophorans. Deep sea, limpet-like

CLASS POLYPLACOPHORA   Chitons, with eight shell valves

CLASS GASTROPODA   Snails, slugs and limpet

    SUBCLASS PATELLOGASTROPODA   The true limpets

    SUBCLASS VETIGASTROPODA   "Primitive" marine top-shell snails, abalones and "limpets"

    SUBCLASS NERITIMORPHA   Marine, land and freshwater nerite snails and "limpets"

    SUBCLASS CAENOGASTROPODA   Marine, freshwater and land snails (creepers, periwinkles, conchs, whelks, cowries etc.) and some "limpets"

        "ARCHITAENIOGLOSSA"   Nonmarine basal caenogastropods (paraphyletic)

        INFRACLASS SORBEOCONCHA   All remaining caenogastropods

        SUPERORDER CERITHIOMORPHA   Creepers, turret shells, etc.

        COHORT HYPSOGASTROPODA   Higher caenogastropods

        SUPERORDER LITTORINIMORPHA   Periwinkles, cowries, triton shells, etc.

        SUPERORDER NEOGASTROPODA   Whelks, volutes, rock shells etc.

    SUBCLASS HETEROBRANCHIA   Marine, freshwater and land snails, most sea slugs, all land slugs, and some "false limpets"

    "LOWER HETEROBRANCHIA"   A few primitive heterobranch groups including sundial shells, valvatids, etc.

    INFRACLASS EUTHYNEURA   "Opisthobranchs" and "pulmonates"

        COHORT NUDIPLEURA   Side-gilled sea slugs and nudibranchs

        COHORT EUOPISTHOBRANCHIA   Bubble shells, sea hares, pteropods, etc.

        COHORT PANPULMONATA   "Pulmonates," pyramidellids, sacoglossan sea slugs, most land snails, all land slugs

CLASS BIVALVIA   Clams and their kin (bivalves)

    SUBCLASS PROTOBRANCHIA   "Primitive" deposit-feeding bivalves

    SUBCLASS AUTOBRANCHIA   "Lamellibranch" suspension-feeding bivalves

        COHORT PTERIOMORPHIA   Mussels, oysters, scallops, and their kin

        COHORT HETEROCONCHIA   Marine and freshwater clams

        MEGAORDER PALAEOHETERODONTA   Freshwater clams (mussels), broch shells

        MEGAORDER HETERODONTA   Most marine clams

        SUPERORDER ARCHIHETERODONTA   A few families of primitive marine clams

        SUPERORDER EUHETERODONTA   The majority of marine and some freshwater clams

CLASS SCAPHOPODA   Tusk shells

CLASS CEPHALOPODA   Nautilus, squids, octopuses

    SUBCLASS PALCEPHALOPODA

        COHORT NAUTILIDIA   Chambered nautilus

    SUBCLASS NEOCEPHALOPODA

        COHORT COLEOIDEA   Octopuses, squids, cuttlefish

        SUPERORDER OCTOPODIFORMES   Octopuses, vampire squid

        SUPERORDER DECAPODIFORMES   Cuttlefish, squid

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[3]Multitudes of extinct molluscs have been described. Perhaps the most well-known are some of the groups of cephalopods that had hard external shells, similar to those of living *Nautilus*. One of these groups was the ammonites. They differed from nautiloids in having shell septa that were highly fluted on the periphery, forming complex mazelike septal sutures. Ammonites also had the siphuncle lying against the outer wall of the shell, as opposed to the condition seen in many nautiloids where the siphuncle runs through the center of the shell.

Figure 13.1 Morphological diversity among the molluscs. (A) *Laevipilina hyalina* (Monoplacophora). (B) *Mopalia muscosa*, the mossy chiton (Polyplacophora). (C) *Epimenia australis* (Solenogastres). (D) *Haliotis rufescens*, the red abalone, (Gastropoda); note the exhalant holes in the shell. (E) *Conus*, a predatory neogastropod; note anterior siphon extending beyond shell. (F) The common garden snail, *Cornu aspersum* (Gastropoda). (G) *Aplysia*, the sea hare (Gastropoda: Euopisthobranchia). (H) The chambered *Nautilus* (Cephalopoda). (I) *Octopus bimaculoides* (Cephalopoda). (J) *Sepioteuthis lessoniana*, the bigfin reef squid (Cephalopoda). (K) *Histioteuthis*, a pelagic squid (Cephalopoda). (L) *Fustiaria*, a tusk shell (Scaphopoda). (M) Scallops (Bivalvia: Pteriomorphia: Pectinidae), with a hermit crab in the foreground. (N) The giant clam *Tridacna maxima* (note zooxanthellate mantle*)*, from the Marshall Islands, Northwest Pacific (Bivalvia: Heterodonta: Cardiida). (O) The European cockle *Acanthocardia tuberculata* (Bivalvia: Heterodonta: Cardiida). Note the partly extended foot. (P) *Lima*, a tropical clam that swims by clapping the valves together (Bivalvia). (Q) The highly modified bivalve *Brechites*. (Heterodonta: Poromyata). *Brechites* are known as watering pot shells. They begin their life as a typical small bivalve, but then secrete a large calcareous tube around themselves through which water is pumped for suspension feeding.

(J)

(K)

(L)

(M)

(O)

(N)

(P)

(Q)

(A)

(B)
Mouth
Constriction caused by retractor muscles

(D)

(C)

Salivary gland
Cerebral ganglion
Radula
Esophagus
Radular sac
Stomach
Dorsal aorta
Intestine
Gonad
Gonopericardial duct
Ventricle
Pericardium
Atrium
Suprarectal ganglion
Ctenidium
Mantle cavity
Anus
Cuticle
Mouth
Oral shield
Ventral (= pedal) nerve cord
Odontophore
Vertical septum
Ventral (= pedal) sinus
Digestive cecum
Lateral nerve cord
Vertical septum

(E)
Mouth
Pedal pit
Pedal groove
Gills

(F)
Pedal groove
Pedal pit
Anus

(G)
Warts

(H)
Vestibular opening
Mouth
Pedal pit
Pedal groove
Gill folds

SYNOPSES OF MOLLUSCAN GROUPS

CLASS CAUDOFOVEATA (= CHAETODERMOMORPHA) (Figure 13.2A–C). Spicule "worms." Marine, benthic, burrowing; body vermiform, cylindrical, lacking any trace of a shell; body wall with a chitinous cuticle and imbricating scale-like aragonitic calcareous sclerites; mouth shield anterior to or surrounding the mouth; small posterior mantle cavity with a pair of bipectinate ctenidia; radula present; gonochoristic. Without foot, eyes, tentacles, statocysts, crystalline style, osphradia, or nephridia. About 120 species; burrow in muddy sediments and consume microorganisms such as foraminiferans. (e.g., *Chaetoderma, Chevroderma, Falcidens, Limifossor, Prochaetoderma, Psilodens, Scutopus*)

CLASS SOLENOGASTRES (= NEOMENIOMORPHA) (Figure 13.2D–K). Spicule "worms." Marine, benthic; body vermiform and nearly cylindrical; vestibulum (= atrium) with sensory papillae anterior to the mouth; small posterior mantle cavity lacking ctenidia but often with respiratory folds; body wall with a chitinous cuticle and imbued with calcareous sclerites (as spines or scales); with or without radula; hermaphroditic; pedal glands opening into a pre-pedal ciliary pit, foot weakly muscular, narrow, and can be retracted into a ventral furrow or "pedal groove." Without eyes, tentacles, statocysts, crystalline style, osphradia or nephridia. About 260 described species, but many undescribed species are thought to exist; epibenthic carnivores, often found on (and consuming) cnidarians and a few other types of

(I)

(J)

50 µm

(K)

50 µm

(L)
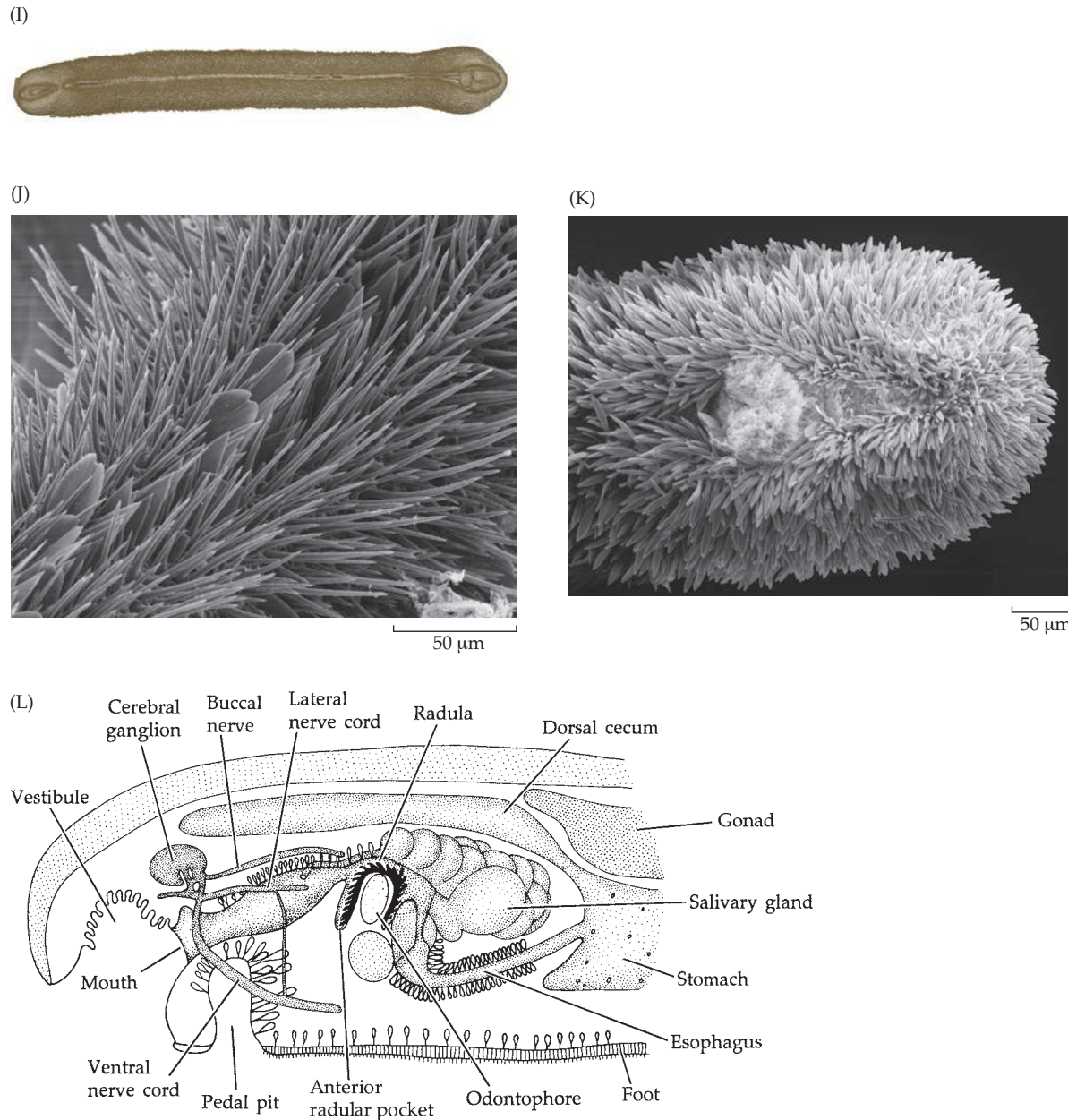
Figure 13.2   General anatomy of aplacophorans.
(A–C) Caudofoveata. (A) *Chaetoderma productum*.
(B) *Chaetoderma loveni*. (C) Internal anatomy of *Limifossor* (highly stylized sagittal section drawing). (D–L)
Solenogastres. (D) *Kruppomenia minima*. (E) *Pruvotina impexa*, ventral view. (F) *Proneomenia antarctica*.
(G) *Epimenia verrucosa*. The body is covered with warts.
(H) *Neomenia carinata*, ventral view. (I) *Entonomenia*
tricarinata, ventral view (X-ray micro-CT). (J) *Macellomenia morseae*. SEM of ventral surface showing two types of scale-like sclerites surrounding the foot and spiny sclerites covering the rest of the surface of the body.
(K) *Macellomenia schanderi*. SEM of ventral surface of anterior end showing densely ciliated pedal pit and mouth. (L) Anterior region of *Spengelomenia bathybia* (highly stylized sagittal section drawing).

invertebrates. Solenogastres and Caudofoveata are probably sister groups and are sometimes regarded as subclasses within the class Aplacophora. (e.g., *Alexandromenia*, *Dondersia*, *Epimenia*, *Kruppomenia*, *Neomenia*, *Proneomenia*, *Pruvotina*, *Rhopalomenia*, *Spengelomenia, Wirenia*)

CLASS MONOPLACOPHORA   Monoplacophorans. With a single, cap-like shell; foot forms weakly muscular ventral disc, with 8 pairs of retractor muscles; shallow mantle cavity around foot encloses 3–6 pairs ctenidia; 2 pairs gonads; 3–7 pairs nephridia; 2 pairs heart atria; a pair of statocysts; with radula and distinct but small head region; without eyes; short oral tentacles present around mouth; with posterior anus; without a crystalline style; gonochoristic or, rarely, hermaphroditic (Figures 13.1A and 13.3). Until the first living species (*Neopilina galatheae*) was discovered by the Danish Galathea Expedition in 1952, monoplacophorans were

(A)

(B)

(C)

(E)

(D)
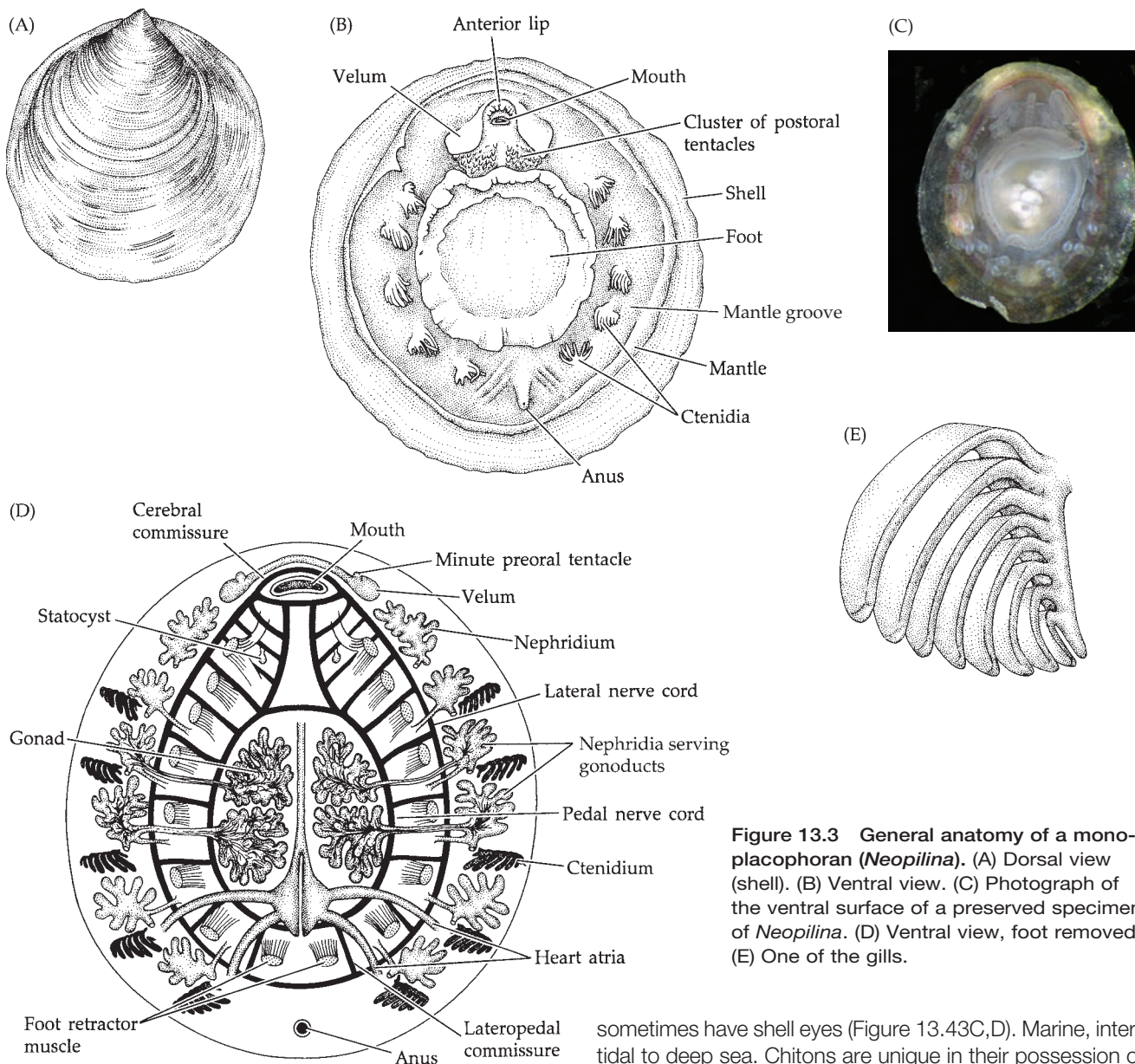
Figure 13.3 General anatomy of a mono-placophoran (*Neopilina*). (A) Dorsal view (shell). (B) Ventral view. (C) Photograph of the ventral surface of a preserved specimen of *Neopilina*. (D) Ventral view, foot removed. (E) One of the gills.

known only from lower Paleozoic fossils. Since then their unusual anatomy has been a source of much evolutionary speculation. Monoplacophorans are limpet-like in appearance, living species are less than 3 cm in length, and most live at considerable depths. About 30 described species, in 8 genera (*Adenopilina*, *Laevipilina*, *Monoplacophorus*, *Neopilina*, *Rokopella*, *Veleropilina*, *Vema*, *Micropilina*).

CLASS POLYPLACOPHORA Chitons (Figures 13.1B and 13.4). Flattened, elongated molluscs with a broad ventral foot and 8 dorsal shell plates (composed of aragonite); mantle forms thick girdle that borders and may partly or entirely cover shell plates; epidermis of girdle usually with calcareous spines, scales, or bristles; mantle cavity encircles foot and bears from 6 to more than 80 pairs of bipectinate ctenidia; 1 pair nephridia; head without eyes or tentacles; crystalline style, statocysts and osphradia absent; nervous system lacking discrete ganglia, except in buccal region; well-developed radula present. Shell canals (aesthetes)

sometimes have shell eyes (Figure 13.43C,D). Marine, intertidal to deep sea. Chitons are unique in their possession of 8 separate shell plates, called valves, and a thick marginal girdle; about 850 described species in one living order.[4]

ORDER NEOLORICATA Shells with unique articulamentum layer, which forms insertion plates that interlock the valves.

SUBORDER LEPIDOPLEURIDA Chitons with outer edge of shell plates lacking attachment teeth; girdle not extending over plates; ctenidia limited to a few posterior pairs. (e.g., *Choriplax*, *Lepidochiton*, *Lepidopleurus*, *Oldroydia*)

SUBORDER CHITONIDA Outer edges of shell plates with attachment teeth; girdle not extending over plates, or extending partly over plates; ctenidia occupying most of mantle groove, except near anus. (e.g., *Callistochiton*, *Chaetopleura*, *Ischnochiton*,

[4]Uncommon, aberrant individuals have been found with only 7 valves.

Figure 13.4 Generalized anatomy of chitons (Polyplacophora). (A,B) A typical chiton (dorsal and ventral views). (C) The Pacific lined chiton, *Tonicella lineata*. (D) Dorsal view of a chiton, shell plates (valves) removed. (E) Dorsal view of a chiton, dorsal musculature removed to reveal internal organs. (F) Dorsal view of a chiton, showing extensive nephridia. (G) The arrangement of internal organs in a chiton (lateral view).

(A)

Head (anterior) valve

Intermediate valve

Girdle

Tail (posterior) valve

(B)

Head
Mouth
Palps
Mantle groove
Girdle
Foot
Ctenidia
Exhalant chamber
Inhalant chamber
Gonopore
Nephridiopore
Anus

(C)

(D)

Anterior insertions of longitudinal and lateral muscles

Oblique muscles

Longitudinal muscle

Position of dorsal artery

Transverse muscle

Posterior insertion of longitudinal and lateral muscles

(E)

Salivary gland
Buccal mass
Buccal muscle
Esophagus
Stomach
Dorsal artery
Nephridium
Digestive gland
Intestine
Gonad
Oviduct
Ventricle
Pericardium
Atrium

(F)

Head
Mouth
Mantle
Groove between head and foot
Gills
Foot
Main nephridial canal
Gonad
Gonoduct
Nephrostome in pericardium
Gonopore
Nephridiopore
Nephridiopore
Anus
Pericardial chamber
Renopericardial canal

(G)

Right atrium
Intestine
Gonad
Dorsal artery
Ventricle
Valves
Mantle
Pericardium
Stomach
Hemocoel
Radula
Salivary gland
Girdle
Anus
Head
Right nephridiopore
Right gonopore
Right nephridium
Digestive gland
Foot
Pedal nerves
Nerve ring
Mouth
Esophagus

(A)

Mantle edge papillae protruding out of shell foramen

Shell

Mantle edge with papillae

Epipodial sense organ

Foot

Eye

Cephalic tentacles

(B)

Snout

Outer lip

Eye

Cephalic tentacle

Ctenidium (in mantle cavity)

Mouth

Foot

Shell muscle

(C)

Right nephridium

Pericardial cavity

Digestive gland

Anus

Stomach

Slit in mantle skirt

Style sac region of stomach

Ventricle

Gonad

Shell muscle

Ctenidium

Eye

Mantle skirt

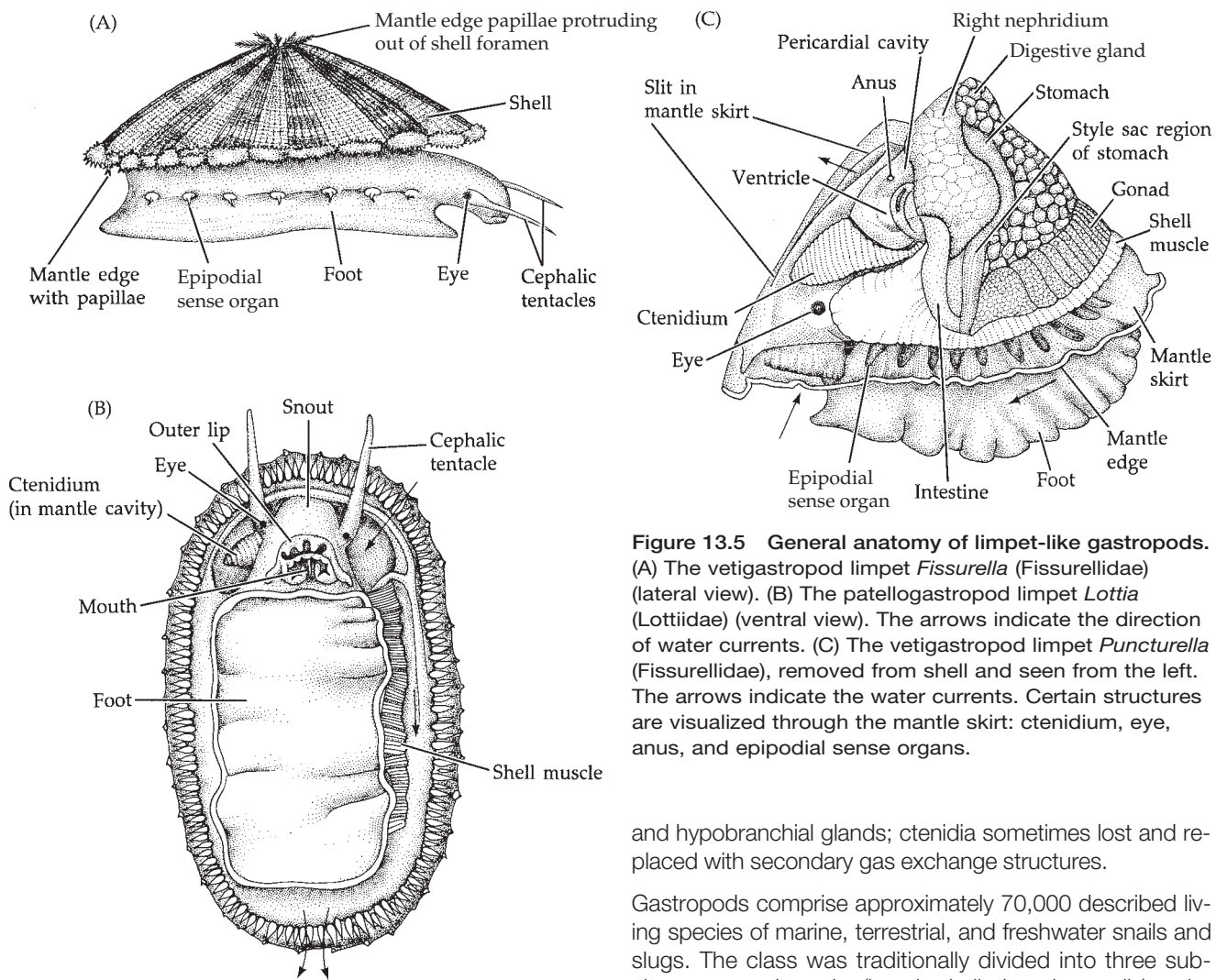Mantle edge

Epipodial sense organ

Intestine

Foot

Figure 13.5   General anatomy of limpet-like gastropods.
(A) The vetigastropod limpet *Fissurella* (Fissurellidae)
(lateral view). (B) The patellogastropod limpet *Lottia*
(Lottiidae) (ventral view). The arrows indicate the direction
of water currents. (C) The vetigastropod limpet *Puncturella*
(Fissurellidae), removed from shell and seen from the left.
The arrows indicate the water currents. Certain structures
are visualized through the mantle skirt: ctenidium, eye,
anus, and epipodial sense organs.

Katharina, *Lepidozona*, *Mopalia*, *Nuttallina*,
Placiphorella, *Schizoplax*, *Tonicella*)

SUBORDER ACANTHOCHITONIDA.   Outer edge of
shell plates with well-developed attachment teeth;
shell valves partially or completely covered by gir-
dle; ctenidia do not extend full length of foot. (e.g.,
Acanthochitona, *Cryptochiton*, *Cryptoplax*)

CLASS GASTROPODA   Snails, limpets and slugs (Figures
13.1D–G, 13.5, 13.6, and 13.7). Asymmetrical molluscs
with single, usually spirally coiled shell into which body can
be withdrawn; shell lost or reduced in many groups; dur-
ing development, visceral mass and mantle rotate 90–180°
on foot (a process known as torsion), so mantle cavity lies
anteriorly or on right side (rather than posteriorly as in other
molluscs), and gut and nervous system are twisted; some
taxa have partly or totally reversed the rotation (detorsion);
with muscular creeping foot (modified in swimming and
burrowing taxa); foot with operculum in larva and often in
adult; head with eyes (often reduced or lost), and 1–2 pairs
of tentacles, and a snout; most with radula and some with
crystalline style, the latter being absent in most primitive and
in many advanced groups; 1–2 nephridia; mantle (= pallium)
usually forms anterior cavity housing ctenidia, osphradia,

and hypobranchial glands; ctenidia sometimes lost and re-
placed with secondary gas exchange structures.

Gastropods comprise approximately 70,000 described liv-
ing species of marine, terrestrial, and freshwater snails and
slugs. The class was traditionally divided into three sub-
classes: prosobranchs (largely shelled marine snails), opis-
thobranchs (marine slugs), and pulmonates (terrestrial snails
and slugs). However, recent anatomical and molecular stud-
ies have shown that classification to be incorrect, as reflect-
ed in the classification below.

SUBCLASS PATELLOGASTROPODA   Cap-shaped
(limpets) with porcelaneous, nonnacreous shell; oper-
culum absent in adult; cephalic tentacles with eyes at
outer bases; radula docoglossate, with iron impregnat-
ed teeth, rest of gut with large esophageal glands and
simple stomach lacking a crystalline style; intestine long
and looped; gill configuration variable, single bipecti-
nate ctenidium sometimes present (Figure 13.5B), and/
or with mantle groove secondary gills, or gills lacking;
shell muscle divided into discrete bundles; mantle cavity
without siphon or hypobranchial glands; 2 rudimentary
osphradia; single atria; 2 nephridia; usually gonochoris-
tic; nervous system weakly concentrated, pleural ganglia
near pedal ganglia, pedal and lateral cords present. Pri-
marily marine with a few estuarine species; herbivorous.
The patellogastropods include 6 families: Patellidae (e.g.,
Patella, *Scutellastra*), Nacellidae (e.g., *Cellana*), Lottiidae
(e.g., *Lottia*), Acmaeidae (e.g., *Acmaea*), Lepetidae (e.g.,
Lepeta), and Neolepetopsidae (e.g., *Neolepetopsis*).
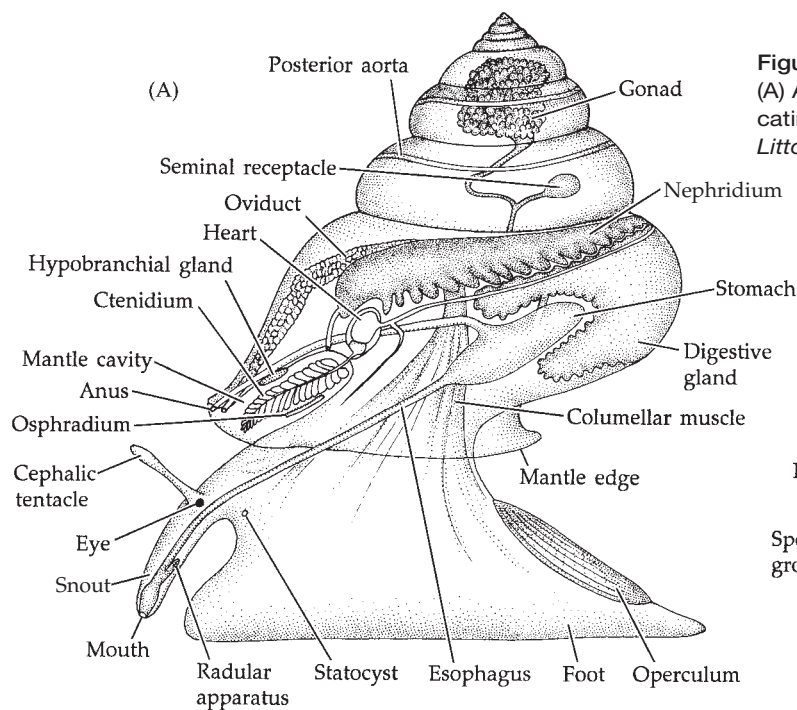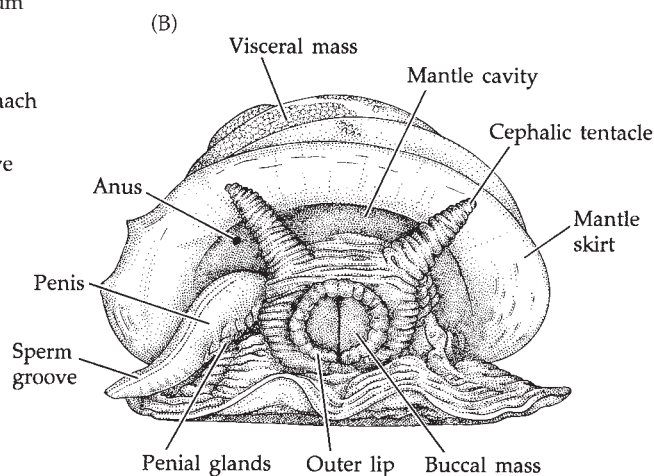These are often regarded as the "true" limpets.

Figure 13.6 General anatomy of coiled gastropods. (A) A generalized coiled-shell gastropod (female), indicating positions of internal organs. (B) The periwinkle, *Littorina*, removed from its shell (anterior view).

SUBCLASS VETIGASTROPODA Shells both porcelaneous and nacreous; cephalic tentacles usually with eyes on short processes on outer bases; operculum usually circular, with a central nucleus and often many spirals, horny or calcareous; radula usually rhipidoglossate (with numerous transverse rows of teeth), rest of gut with esophagus having large glands, complex stomach with style sac but no crystalline style, looped intestine; 1–2 bipectinate ctenidia; shell muscles paired or single; mantle cavity with 2 hypobranchial glands, 2 atria, and 2 nephridia; usually gonochoristic; male generally without penis; nervous system weakly concentrated, ganglia poorly formed, pedal cords present; 1–2 osphradia, small, inconspicuous. All marine and benthic. Many species are microdetritivores or feed on films of bacteria or other organisms, or are microherbivores; some are macroherbivores, some grazing carnivores, and a few suspension feeders. Most gastropods found at hydrothermal vents, cold seeps, and on deep sea hard substrates are vetigastropods. Vetigastropods comprise about 30 families and while the internal classification remains unsettled, three main groups are often recognized, which we treat here as orders.

ORDER TROCHIDA Most of the vetigastropods, including the slit-shelled snails Pleurotomaridae (e.g., *Perotrochus*, *Pleurotomaria*), Scissurellidae (e.g., *Scissurella*) and Anatomidae (e.g., *Anatoma*), the abalones Haliotidae (e.g., *Haliotis*), the keyhole and slit limpets Fissurellidae (e.g., *Diodora*, *Fissurella*, *Lucapinella*, *Puncturella*), deep sea limpets comprising the Lepetellidae and related families (e.g., *Lepetella*, *Pseudococculina*), trochids Trochidae (e.g., *Trochus, Monodonta*) and related families such as Calliostomatidae (e.g., *Calliostoma*), Margaritidae (e.g., *Margarites*), Tegulidae (e.g., *Tegula*), and turbans Turbinidae (e.g., *Turbo*, *Astrea*).

ORDER NEOMPHALIDA Comprises many of the hot vent snails and limpets Neomphalidae (e.g., *Neomphalus*), Peltospiridae (e.g., *Peltaspira*), Lepetodrilidae (e.g., *Lepetodrilus*).

ORDER COCCULINIDA (= COCCULINIFORMES IN PART) The small, deep-sea wood and bone limpets Cocculinidae (e.g., *Cocculina*).

SUBCLASS NERITIMORPHA Shell coiled, limpet-like, or lost (Titiscaniidae). Shell porcelaneous, with interior whorls reabsorbed in many coiled groups; operculum typically present, of few spirals and with non-central nucleus, horny or calcified, usually with internal peg; shell muscle divided into discrete bundles; only left ctenidium present; hypobranchial glands often lost on left side; stomach highly modified; right nephridium incorporated into complex reproductive system with multiple openings into mantle cavity; radula rhipidoglossate; most species gonochoristic, with copulatory structures; nervous system with ganglia concentrated, pleural ganglia near pedal ganglia, pedal cords present. Globally distributed in marine, estuarine, freshwater, and terrestrial habitats. There are 9 families of neritimorphans, four of which, Helicinidae (e.g., *Alcadia, Helicinia*), Hydrocenidae (*Hydrocena, Georissa*), Proserpinellidae (e.g., *Proserpinella*), and Proserpinidae (*Proserpina*) are exclusively terrestrial; also Neritopsidae (neritopsids, *Neritopsis*), Titiscaniidae (titiscaniid, *Titiscania*), Neritidae (nerites, e.g., *Nerita*, *Theodoxus*), Neritiliidae (cave nerites, e.g., *Pisulina, Neritilia*) and Phenacolepadidae (*Phenacolepas*).

SUBCLASS CAENOGASTROPODA Shell mainly porcelaneous; operculum usually present and corneous, rarely calcified, with few spirals and usually with a non-central nucleus, mostly non-nacreous, rarely with internal peg(s); head with pair of cephalic tentacles, with eyes at outer bases; mantle cavity asymmetrical, with incurrent

(A)

Figure 13.7 More gastropod anatomy; some caenogastropods (A–C) and heterobranchs (D–J). (A) The pelagic shelled heteropod *Carinaria* (Caenogastropoda). (B) Anatomy of *Carinaria*. (C) The shell-less heteropod *Pterotrachea* (Caenogastropoda). (D) The pelagic shelled pteropod *Clio* (Heterobranchia: Euopisthobranchia). The arrows indicate the direction of water flow; water enters all around the narrow neck and is forcibly expelled together with fecal, urinary, and genital products by contraction of the sheath. (E) A swimming pteropod, *Corolla* (Heterobranchia: Euopistho-branchia). (F–I) Various nudibranchs (Heterobranchia: Nudipleura). (F) A dorid nudibranch, *Diaulula*. (G) An aeolid nudibranch, *Phidiana*. (H) A dorid nudibranch, *Chromodoris geminus* (from the Red Sea). (I) The eastern Pacific "Spanish shawl" aeolid nudi-branch, *Flabellina*. (J) The lettuce sea slug, *Tridachia crispata* (Heterobranchia: Panpulmonata), from the Caribbean.

(B)

(C)

(D)

(E)

(F)

(G)

(H)

(I)

(J)

opening on anterior left, sometimes elaborated into an inhalant siphon; right ctenidium lost; left ctenidium monopectinate; left hypobranchial gland lost; right nephridium lost except for remnant incorporated into reproductive system; heart with only left atrium. Radula taenioglossate (7 rows of teeth), ptenoglossate (many rows of similar teeth), rachiglossate (1–3 rows of teeth), or toxoglossate (teeth modified as harpoons), or occasionally lost. Higher forms with concentrated ganglia, pleural ganglia usually near cerebral ganglia, pedal cords usually absent; osphradium conspicuous, often large, sometimes surface subdivided into lamellae. Most caenogastropods are gonochoristic. The caenogastropods, comprise the former "mesogastropods" and neogastropods, and they are often divided into two groups, as follows:

"ARCHITAENIOGLOSSA" Although this is not a monophyletic group, we retain it informally. Architaenioglossans differ from other caenogastropods in details of their nervous system and in the ultrastructure of their sperm and osphradia. They are divided among 10 families, including the freshwater Ampullariidae (apple snails, e.g., *Ampullaria, Pomacea, Pila*) and Viviparidae (river snails, e.g., *Viviparus*), and the terrestrial Cyclophoridae (e.g., *Cyclophorus*) and several related families such as Diplommatinidae (e.g., *Diplommatina* and *Opisthostoma*).

INFRACLASS SORBEOCONCHA This grouping contains all the rest of the caenogastropods. These are divided into two main groups, Cerithiomorpha and Hypsogastropoda.

SUPERORDER CERITHIOMORPHA Usually without a penis; eggs usually laid in jelly, often in strings, or are brooded. The anterior aperture may or may not have a notch, which houses a short siphon. Include marine, brackish, and freshwater species. About 19 families are recognized, including the marine Campanilidae (e.g., *Campanile*), Cerithiidae (horn shells, e.g., *Cerithidea, Cerithium*, *Liocerithium*), Siliquariidae (slit worm shells, e.g., *Siliquaria*), and Turritellidae (tower or turret shells, e.g., *Turritella*); and the freshwater Melanopsidae (e.g., *Melanopsis*), Thiaridae (e.g., *Thiara*), and Pleuroceridae (e.g., *Pleurocera*).

COHORT HYPSOGASTROPODA Comprises the remaining caenogastropods. The anterior mantle may be simple or can be enrolled forming an anterior siphon which emerges from an anterior notch in the aperture or, in some, is contained within an extension of the shell, the siphonal canal. Male with cephalic penis; eggs usually laid in capsules or sometimes brooded. Nervous system concentrated; operculum, if present, chitinous, rarely calcareous. This large group is divided into the Littorinimorpha and Neogastropoda.

SUPERORDER LITTORINIMORPHA Classification unsettled; includes the marine grazing snails Littorinidae (periwinkles, e.g., *Littorina*), a number of small-sized marine families including the Rissoidae (e.g., *Rissoa*, *Alvania*), and larger snails such as the Strombidae (conchs or strombids, e.g., *Strombus*), and the carrier shells Xenophoridae (e.g., *Xenophora*). Also includes the uncoiled suspension-feeding "worm" gastropods Vermetidae (e.g., *Serpulorbis*, *Dendropoma*) and the limpet-like Hipponicidae (e.g., *Hipponix*) which are deposit feeders, while Capulidae (e.g., *Capulus*) attach to other molluscs and mostly feed on their feces. The slipper shells Calyptraeidae (e.g., *Calyptraea*, *Crepidula*, *Crucibulum*) are suspension-feeders. The Carinariidae (one of several families of pelagic molluscs collectively called

heteropods, e.g., *Carinaria*) also have a cap-shaped shell.[5] Cypraeidae (cowries, e.g., *Cypraea*) are herbivores or grazing carnivores, while several other littorinimorph snail-like families are strictly carnivorous, including Naticidae (moon snails, e.g., *Natica*, *Polinices*) that feed mostly on bivalves, the ascidian-feeding Eratoidae (coffee bean shells, e.g., *Erato*, *Trivia*), and the soft coral feeding Ovulidae (ovulids or egg shells, e.g., *Jenneria*, *Ovula*, *Simnia*). Tonnidae (tun shells, e.g., *Malea*) and related families such as Cassididae (helmet shells, e.g., *Cassis*) mainly feed on echinoderms, whereas Ficidae (fig shells, e.g., *Ficus*) are primarily polychaete feeders. Epitoniidae (wentletraps or epitoniids, e.g., *Epitonium*) feed on cnidarians, while the floating violet snails Janthinidae (e.g., *Janthina*) feed on siphonophores that drift on the surface of the ocean. Eulimidae are ectoparasites on echinoderms, and the sponge-feeding Triphoridae (e.g., *Triphora*) and Cerithiopsidae (e.g., *Cerithiopsis*) are highly diverse. There are some diverse families of small-sized freshwater snails such as the Hydrobiidae (e.g., *Hydrobia*) and several related families including the Pomatiopsidae (e.g., *Pomatiopsis*, *Tricula*), and there are also a few terrestrial taxa in families such as Pomatiasidae (e.g., *Pomatias*) and the otherwise mainly supralittoral Assimineidae.

SUPERORDER NEOGASTROPODA   The most derived hypsogastropod clade. Radula rachiglossate or toxoglossate, with 1–5 teeth in each row; anterior siphon present; operculum, if present, chitinous; osphradium large and pectinate, lying near base of siphon. This highly diverse group comprises mostly carnivorous taxa.

The neogastropods comprise more than 30 living families of almost entirely marine snails, including: whelks such as Buccinidae (e.g., *Buccinum*, *Cantharus*, *Macron*, and the Asian freshwater genus *Clea*); Fasciolariidae (tulip shells and spindle shells, e.g., *Fasciolaria*, *Fusinus*, *Leucozonia*, *Troschelia*); Melongenidae (e.g., *Melongena*); Nassariidae (dog whelks and basket shells, e.g., *Nassarius*); dove shells Columbellidae (e.g., *Anachis*, *Columbella*, *Mitrella*, *Pyrene*, *Strombina*); harp shells Harpidae (e.g., *Harpa*); margin shells Marginellidae (e.g., *Marginella*, *Granula*); miter shells Mitridae (e.g., *Mitra*, *Subcancilla*) and Costellariidae (e.g., *Vexillum*, *Pusia*); rock shells and thaids Muricidae (e.g., *Hexaplex*, *Murex*, *Phyllonotus*, *Pterynotus*, *Acanthina*, *Morula*, *Neorapana*, *Nucella*, *Purpura*, *Thais*) and the related coral associated Coralliophilidae (e.g., *Coralliophila*, *Latiaxis*); Olividae (olive shells, e.g., *Agaronia*, *Oliva*); Olivellidae (e.g., *Olivella*); the volutes Volutidae (e.g., *Cymbium*, *Lyria*, *Voluta*) and nutmeg shells Cancellariidae (e.g., *Admete*, *Cancellaria*); cone shells Conidae (e.g., *Conus*) and the related Turridae

(e.g., *Turris*) and several other allied families including the auger shells Terebridae (e.g., *Terebra*).

SUBCLASS HETEROBRANCHIA   The heterobranchs were previously organized as two subclasses—Opisthobranchia (sea slugs and their kin) and Pulmonata (air breathing snails). Although this division was long accepted, recent morphological and molecular studies now divide the subclass into two main groups—an informal paraphyletic group often referred to as the "Lower Heterobranchia" (= Allogastropoda, Heterostropha) and the Euthyneura, which includes both pulmonates and the opisthobranchs.

The subclass Heterobranchia characterized by lacking a true ctenidium and, usually, a small to absent osphradium, a simple gut with the esophagus lacking glands, the stomach lacking a crystalline style in all but one group, and the intestine usually being short. The radula is highly variable ranging from rhipidoglossate to a single row of teeth or lost altogether. The shell may be well-developed, reduced, or absent; the operculum, if present, is horny; the larval shell is heterostrophic (i.e., coils in a different plane to the adult shell). The head bears one or two pairs of tentacles, with the eyes variously placed; all are hermaphroditic. The nervous system is streptoneurous or euthyneurous with various degrees of concentration of the ganglia; pleural ganglia near pedal or cerebral ganglia, pedal cords absent. Mostly benthic; with marine, freshwater and terrestrial species.

"LOWER HETEROBRANCHS"   This informal group includes some snails long thought to be "Mesogastropoda," such as staircase or sundial shells Architectonicidae (e.g., *Architectonica, Philippia*) and some groups of small-sized marine snails including Rissoellidae (e.g., *Rissoella*), Omalogyridae (e.g., *Omalogyra*), and the freshwater Valvatidae (e.g., *Valvata*) and marine relatives such as Cornirostridae. These snails are superficially similar to caenogastropods, but often possess secondary gills and long cephalic tentacles with cephalic eyes set in the middle of their bases or on their inner sides. Another group included here are tiny interstitial slugs of the family Rhodopidae.

INFRACLASS EUTHYNEURA   Include most of the former opisthobranchs and pulmonates. The euthyneuran body is characterized by: the shell being external or internal, or lost altogether; a heterostrophic larval shell; operculum horny, often absent in adult; body variously detorted; head usually with one or two pairs of tentacles, eyes on inner sides or on separate stalks; ctenidia and mantle cavity usually reduced or lost; hermaphroditic; euthyneurous with various degrees of nervous system concentration. Mostly benthic; with marine, freshwater, and terrestrial species.

The Euthyneura is divided into three major groups which we treat here as cohorts.

COHORT NUDIPLEURA   Includes both the internal-shelled Pleurobranchidae (e.g., *Berthella*, *Pleurobranchus*) and the Nudibranchia (shell-less or "true"

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[5]The term "heteropod" is an old taxonomic name now used informally for a group of planktonic, predatory caenogastropods that have a reduced shell or no shell at all.

nudibranchs) which includes many families, some examples being the doridoid nudibranchs such as Onchidorididae (e.g., *Acanthodoris, Corambe*), Polyceridae (e.g., *Polycera, Tambja*), Aegiretidae (e.g., *Aegires*), Chromodorididae (e.g., *Chromodoris*), Phyllidiidae (e.g., *Phyllidia*), Dendrodorididae (e.g., *Dendrodoris*), Discodorididae (e.g., *Discodoris*, *Diaulula, Rostanga*), Dorididae (e.g., *Doris*), Platydorididae (e.g., *Platydoris*), Hexibranchidae (e.g., *Hexabranchus*), Goniodorididae (e.g., *Okenia*), and the cladobranch nudibranchs including the Arminidae (*Armina*), Proctonotidae (e.g., *Janolus*), Embletoniidae (e.g., *Embletonia*), Scyllaeidae (e.g., *Scyllaea*), and Dendronotidae (e.g., *Dendronotus*). Also included are the cladobranch group collectively known as aeolididoids—including the Aeolidiidae (e.g., *Aeolidia*), Flabellinidae (e.g., *Coryphella*), Fionidae (e.g., *Fiona*), Facelinidae (e.g., *Hermissenda, Phidiana*), Tergipedidae (e.g., *Trinchesia*), Tethydidae (e.g., *Melibe*), and Glaucidae (e.g., *Glaucus*).

COHORT EUOPISTHOBRANCHIA Includes six main groups that could be treated at the ordinal level: (1) the basal acteonoideans including Acteonidae (barrel or bubble snails, e.g., *Acteon, Pupa, Rictaxis*); (2) several families grouped as Cephalaspidea, for example the slugs Aglajidae (e.g., *Aglaja, Chelidonura, Navanax*), Bullidae (bubble shells, e.g., *Bulla*), Haminoeidae (e.g., *Haminoea*), Retusidae (e.g., *Retusa*), and Scaphandridae (e.g., *Scaphander*); (3) the Runcinoidea, containing two families of tiny slugs, Ilbiidae (e.g., *Ilbia*) and Runcinidae (e.g., *Runcina*); (4) the Aplysiomorpha (= Anaspidea) or sea hares, including Aplysidae (e.g., *Aplysia*, *Dolabella*, *Stylocheilus*); (5) the pelagic pteropods, comprising two distant groups, the Thecosomata or shelled pteropods, which include the families Cavoliniidae (e.g., *Clio*, *Cavolinia*) and Limacinidae, (e.g., *Limacina*), and Gymnosomata or naked pteropods including Clionidae (e.g., *Clione*); and (6) the Umbrachulida, composed of the umbrella slugs, Umbraculidae (e.g., *Umbraculum*) and Tylodinidae (e.g., *Tylodina*).

COHORT PANPULMONATA This highly diverse group is characterized by: variable shell shape or loss of shell, minute or in moderate size; generally spirally coiled, planispiral, or limpet-shaped; usually without an operculum as adults; eyes at bases of sensory stalks; secondary gills present in some members (e.g., *Pyramidella, Siphonaria*); body detorted; nervous system highly concentrated (euthyneurous); mantle cavity-derived lung in the derived groups, with a contractile aperture in the Eupulmonata; marine (intertidal), brackish, freshwater and amphibious; includes freshwater limpets and the minute, meiofaunal Acochlidioidea (e.g., *Acochlidium*, *Unela*).

Other panpulmonate groups include: the sap-sucking sea slugs Sacoglossa (e.g., *Berthelinia*, *Elysia*, *Oxynoe*, *Tridachia,* and the "bivalve gastropods" Juliidae), which are shelled or shell-less; the small shell-less and sometimes spiculate acochlidioid slugs that are often interstitial and usually marine (although there are some freshwater species) and the ectoparasitic Pyramidellidae (e.g., *Odostomia, Pyramidella*, *Turbonilla*, *Amathina*), all of which were previously included in the Opisthobranchia. The remaining panpulmonates include all the members of the group previously known as Pulmonata, namely the mainly intertidal Siphonariidae (false limpets: e.g., *Siphonaria*, *Williamia*); two operculate families); the freshwater Glacidorbidae (e.g., *Glacidorbis*); the estuarine Amphibolidae (*Amphibola, Salinator*); the Hygrophila, including the mainly freshwater South American Chilinidae (e.g., *Chilina*), and freshwater Physidae (e.g., *Physa*), Planorbidae (e.g., *Bulinus*, *Planorbis, Ancylus*) and Lymnaeidae (e.g., *Lymnaea*, *Lanx*), these latter families being mostly snails, but some such as *Lanx* and *Ancylus* are limpets. The remaining "pulmonates" are contained within a superorder, Eupulmonata. The best known and largest group of eupulmonates is the order Stylommatophora, comprising the land snails and slugs. In some of the shelled forms, the shell is partly or completely enveloped by dorsal mantle. Their eyes are on the tips of long sensory stalks and there is an anterior pair of tentacles. Eupulmonates are all terrestrial and are an enormous group with over 26,000 described species in 104 families. Some of those included are the land snail families Helicidae (e.g., *Cornu* [= *Helix*], *Cepaea*), Achatinidae (e.g., *Achatina*), Bulimulidae (e.g., *Bulimulus*), Haplotrematidae (e.g., *Haplotrema*), Orthalicidae (e.g., *Liguus*), Cerionidae (e.g., *Cerion*), Oreohelicidae (e.g., *Oreohelix*), Pupillidae (e.g., *Pupilla*), Cerastidae (e.g., *Rhachis*), Succineidae (e.g., *Succinea*), and Vertiginidae (e.g., *Vertigo*), as well as terrestrial slug families such as Arionidae (e.g., *Arion*) and Limacidae (e.g., *Limax*).

The remaining Eupulmonata include the orders Systellommatophora and Ellobiacea. The former are slug-like, without internal or external shell; dorsal mantle integument forms a keeled or rounded notum; head usually with 2 pairs tentacles, upper ones forming contractile stalks bearing eyes. Included are the mainly marine family Onchidiidae (e.g., *Onchidella*, *Onchidium*) and the terrestrial Veronicellidae (e.g., *Veronicella*). The Ellobiacea includes the three superfamilies; the mainly supralittoral hollow-shelled ear snails Ellobioidea (, e.g., *Ellobium, Melampus, Carychium, Ovatella*), small intertidal snails or slugs of the Otinoidea (e.g., *Otina*), and the limpet-like intertidal Trimusculoidea (e.g., *Trimusculus*).

CLASS BIVALVIA (= PELECYPODA, = LAMELLIBRANCHIATA) Clams, oysters, mussels, scallops, etc. (Figures 13.1M–Q and 13.8). Laterally compressed; shell typically of two valves hinged together dorsally by elastic ligament and usually by shell-teeth; shells closed by adductor muscles derived from mantle muscles; head rudimentary, without eyes, tentacles or radula, but eyes may occur elsewhere on body; pair of large labial palps present composed of inner and outer parts that lie against one another; pair of statocysts present, associated with pedal ganglia, foot typically laterally compressed, often without a sole; 1 pair of large

(A)

Fused siphons

Right valve

Foot

(B) Hinge ligament

Intestine

Nephridium

Nerve

Efferent branchial vessel

Afferent branchial vessel

Intestine

Mantle

Valve

Pericardial chamber

Ventricle

Right atrium

Suprabranchial canal

Mantle vessel

Outer demibranch of ctenidium

Inner demibranch of ctenidium

Food groove

Gonad

Mantle cavity

Foot

(C) DORSAL

Hinge teeth   Hinge   Visceral mass

Ctenidium   Ventricle

Anterior foot retractor muscle   Posterior aorta

Rectum

Mouth   Posterior foot retractor muscle

Labial palp   Exhalant siphon

ANTERIOR   POSTERIOR

Anterior adductor muscle   Inhalant siphon

Foot   Posterior adductor muscle

VENTRAL   Mantle

(D) Digestive gland

Stomach

Cerebral ganglia   Intestine

Nephridium

Mouth   Pericardium

Labial palp   Atrium

Ventricle

Posterior foot retractor

Rectum

Anus

Posterior adductor

Exhalant siphon

Inhalant siphon

Visceral ganglion

Anterior adductor   Mantle

Pedal ganglion   Ctenidium (cut)

Foot   Gonad

(E)   Cut end of right labial palps

Cut edge of right ctenidium

Plicate membranes

Exhalant area

Anus

Inhalant area

Mouth

Cerebral ganglia

Cerebrovisceral connective

Labial palp

Foot

Byssal threads

Right urogenital pore

Cerebrovisceral connective

Right visceral ganglion

Left ctenidium

(F)

Digestive gland

Intestine

Anterior aorta

Ventricle

Right atrium

Intestine

Crystalline style sac

Posterior adductor muscle

Anus

Mouth

Esophagus

Cerebral ganglion

Stomach

Nephridium

Cerebropedal connective

Right pedal ganglion

Foot retractor muscle

Posterior end of kidney

Cerebrovisceral connective

Gonad

Right visceral ganglion

◀ **Figure 13.8   General anatomy of bivalves.** (A) *Tresus*, a deep-burrowing eulamellibranch (Mactridae), with a digging foot and long, fused siphons. (B) A typical eulamellibranch (cross section). (C) The eulamellibranch *Mercenaria* (Veneridae), with the left shell valve and mantle removed. (D) Internal anatomy of *Mercenaria*. The visceral mass is opened up, the foot is dissected, and most of the gills are cut away. (E) The common mussel, *Mytilus* (Mytilidae), seen from the right side after removal of the right shell valve and mantle. (F) *Mytilus*, with the visceral mass opened up, the foot dissected, and most of the gills cut away.

bipectinate ctenidia; large mantle cavity surrounds animal; mantle may be variously fused, sometimes forming extensions (siphons); 1 pair nephridia; nervous system simple, typically composed of cerebropleural, pedal and visceral ganglia

Bivalves are marine or freshwater molluscs, primarily microphagous or suspension feeders. The class includes about 9,200 living species represented at all depths and in all marine environments. Bivalve classification has been in a state of turmoil over the past 50 years and continues to be unsettled. Higher taxa have been delimited on the basis of shell characters (e.g., hinge anatomy, position of muscle scars), or, in other classifications, internal organ anatomy (e.g., ctenidia, stomach) have been used. However, beginning with the work of Giribet and Wheeler (2002), bivalve taxonomy has become more stable as both molecules and morphology have been combined with the fossil record to understand the relationships of the class.

SUBCLASS PROTOBRANCHIA   Includes the former Palaeotaxodonta in part. Ctenidia are 2 pairs of simple, unfolded, bipectinate, plate-like leaflets suspended in the mantle cavity. The ctenidia are mainly respiratory structures, while the labial palps are the primary food collecting organs. These are the most primitive living bivalves, comprising two superorders.

SUPERORDER NUCULIFORMII (= OPPONO-BRAN-CHIA)   Mantle open, with inhalant water entering anteriorly; shells with nacre and gill filaments along ctenidial axis arranged opposite one another; foot longitudinally grooved and with a plantar sole, without byssal gland; nervous system primitive, often with incomplete union of cerebral and pleural ganglia. Two orders.

ORDER NUCULIDA   Shell aragonitic, interior nacreous or porcelaneous; periostracum smooth; shell valves equal and taxodont (i.e., the valves have a row of similar interlocking short teeth along the hinge margins); adductor muscles equal in size; with large labial palps extended as proboscides used for food collection; ctenidia small, for respiration; marine (particularly in the deep sea), mainly infaunal detritivores. (e.g., Nuculidae, *Nucula*).

ORDER SOLEMYIDA (= CRYPTODONTA)   Shell valves thin, elongate, and equal in size; uncalcified along outer edges, without hinge teeth; anterior adductor muscle larger than posterior one; ctenidia large, used mainly for housing symbiotic bacteria. Gut reduced or absent. (e.g., Solemyidae, *Solemya*).

SUPERORDER NUCULANIFORMII   Mantle fused posteriorly, with siphons, inhalant water enters posteriorly; shells without nacre and gill filaments along ctenidial axis alternate. Several mainly deep-sea families including Nuculanidae (e.g., *Nuculana*), Malletiidae (e.g., *Malletia*) and Sareptidae (e.g., *Yoldia*).

SUBCLASS AUTOBRANCHIA (= AUTOLAMELLIBRAN-CHIATA)   Paired ctenidia, with very long filaments folded back on themselves so that each row of filaments forms two lamellae; adjacent filaments usually attached to one another by ciliary tufts (filibranch condition), or by tissue bridges (eulamellibranch condition). The greatly enlarged ctenidia are used in combination with the two pairs of labial palps in ciliary feeding; ctenidial surfaces capture water borne particles and transfer them to the labial palps where the capture debris is sorted and potential food particles routed to the mouth.

COHORT PTERIOMORPHIA (= FILIBRANCHIA)   Ctenidia with outer fold not connected dorsally to visceral mass, with free filaments or with adjacent filaments attached by ciliary tufts (filibranch condition); shell aragonitic or calcitic, sometimes nacreous; mantle margin unfused, with weakly differentiated incurrent and excurrent apertures or siphons; foot well developed or extremely reduced; usually attached by byssal threads or cemented to substratum (or secondarily free). These primitive lamellibranchs include several divergent ancient lineages separated as orders.

ORDER MYTILIDA   The true mussels, Mytilidae (e.g., *Adula, Brachidontes, Lithophaga, Modiolus, Mytilus*).

ORDER ARCIDA   The ark shells Arcidae (e.g., *Anadara, Arca, Barbatia*), and dog cockles Glycymerididae (e.g., *Glycymeris*).

ORDER OSTREIDA   The true oysters Ostreidae (true oysters, e.g., *Crassostrea, Ostrea*).

ORDER MALLDIDA (= PTERIOIDA, PTERIIDA)   Pearl oysters and their relatives Pteriidae (e.g., *Pinctada, Pteria*), hammer oysters Malleidae (e.g., *Malleus*), and pen shells Pinnidae (e.g., *Atrina, Pinna*).

ORDER LIMOIDA   File shells Limidae (e.g., *Lima*).

ORDER PECTINIDINA   Scallops. Pectinidae (e.g., *Chlamys, Lyropecten, Pecten*), thorny oysters Spondylidae (e.g., *Spondylus*), jingle shells Anomiidae (e.g., *Anomia, Pododesmus*).

COHORT HETEROCONCHIA   This clade encompasses the Paleoheterodonta and Heterodonta, previously treated as separate higher groups but shown to be sister groups in recent molecular phylogenies.

MEGAORDER PALAEOHETERODONTA   Shell aragonitic, pearly internally; periostracum usually well developed; valves usually equal, with few hinge teeth; elongate lateral teeth (when present) are not

separated from the large cardinal teeth; usually dimyarian; mantle opens broadly ventrally, mostly unfused posteriorly but with exhalant and inhalant apertures. About 1,200 species of marine and freshwater clams. Includes two very distinct groups classified as orders.

ORDER TRIGONIIDA The relictual marine broach shells (Trigoniidae), with only a few living species of *Neotrigonia* in Australia.

ORDER UNIONIDA Entirely freshwater, including the freshwater clams (or mussels), e.g., Unionidae (e.g., *Anodonta, Unio*), Margaritiferidae (e.g., *Margaritifera*), and Hyriidae (e.g., *Hyridella*).

MEGAORDER HETERODONTA Two main groups, ranked as superorders, are recognized—the Archiheterodonta (with a single living order) and the Euheterodonta (with four living orders).

SUPERORDER ARCHIHETERODONTA

ORDER CARDITIDA This group of primitive heterodonts is represented by the families Crassatellidae (e.g., *Crassatella*), Carditidae (e.g., *Cardita*) and Astartidae (e.g., *Astarte*).

SUPERORDER EUHETERODONTA

ORDER LUCINIDA Includes the families Luncinidae (e.g., *Lucina*, *Codakia*), a group with symbiotic bacteria in their gills and an anterior water current, and Thysiridae.

ORDER CARDIIDA (= VENERIDA) Usually thick-valved, equi-valved, and isomyarian, with posterior siphons. Includes: cockles and their kin, Cardiidae (e.g., *Cardium*, *Clinocardium*, *Laevicardium*, *Trachycardium,* and the giant clams e.g., *Tridacna*); surf clams, Mactridae (e.g., *Mactra*); solens, Solenidae (e.g., *Ensis*, *Solen*); tellins, Tellinidae (e.g., *Florimetis*, *Macoma*, *Tellina*); semelids, Semelidae (e.g., *Leptomya*, *Semele*); wedge shells, Donacidae (e.g., *Donax*); Venus clams, Veneridae (e.g., *Chione*, *Dosinia*, *Pitar*, *Protothaca*, *Tivela*); freshwater pea clams, Sphaeriidae (e.g., *Sphaerium, Pisidium*); the estuarine-to-freshwater Cyrenidae (e.g., *Corbicula, Batissa*); and zebra mussels, Dreissenidae (e.g., *Dreissena*). The latter two families contain important invasive species.

ORDER PHOLADIDA (= MYIDA) Thin-shelled burrowing forms with well-developed siphons. Includes: soft-shell clams, Myidae (e.g., *Mya*); rockborers or piddocks, Pholadidae (e.g., *Barnea*, *Martesia*, *Pholas*); shipworms, Teredinidae (e.g., *Bankia*, *Teredo*); and basket clams, Corbulidae (e.g., *Corbula*). The monophyly of this order is uncertain.

ORDER POROMYATA (= ANOMALODESMATA) Shells equivalved, aragonitic, of 2–3 layers, innermost consisting of sheet nacre; periostracum often incorporates granulations; with 0–1 hinge teeth; generally isomyarian, rarely amyarian; posterior siphons usually
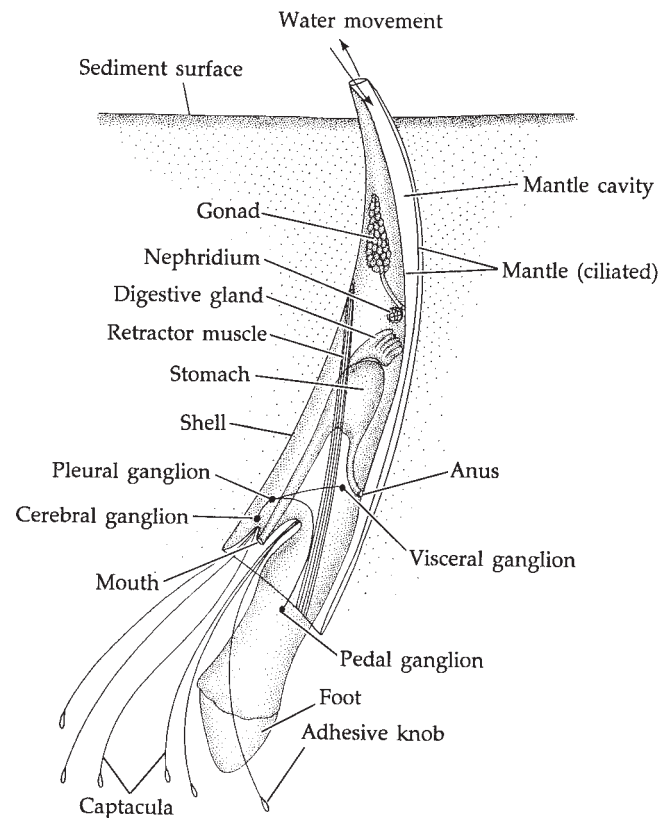

Figure 13.9   General anatomy of a scaphopod.

well developed; mantle usually fused ventrally, with anteroventral pedal gape, and posteriorly with ventral incurrent and dorsal excurrent apertures or siphons; ctenidia eulamellibranchiate or septibranchiate (modified as a muscular pumping horizontal septum). This ancient and very diverse group of marine bivalves includes about 20 living families, including the rare deep water Pholadomyidae (e.g., *Pholadomya*) and the aberrant watering pot shells Clavagellidae (e.g., *Brechites*), as well as Pandoridae, Poromyidae, Cuspidariidae, Laternulidae, Thraciidae, Cleidothaeridae, Myochamidae, and Periplomatidae.

CLASS SCAPHOPODA Tusk shells (Figures 13.1L and 13.9). Shell of one piece, tubular, usually tapering, open at both ends; head rudimentary, projecting from larger aperture; mantle cavity large, extending along entire ventral surface; without ctenidia or eyes; with radula, long, snout-like "proboscis," and paired clusters of long, thin contractile tentacles with clubbed ends (captacula) that serve to capture and manipulate minute prey; heart absent; foot somewhat cylindrical, with epipodium-like fringe. Over 500 species of marine, benthic molluscs in fourteen families and two orders.

ORDER DENTALIIDA Shell regularly tapering. Paired digestive gland with a muscular foot terminating in epipodial lobes and a cone-shaped process. Several families including Dentaliidae (e.g., *Dentalium*, *Fustiaria*) and Laevidentaliidae (e.g., *Laevidentalium*).

ORDER GADILIDA Shell regularly tapering or bulbous with maximum shell diameter approximately nearer
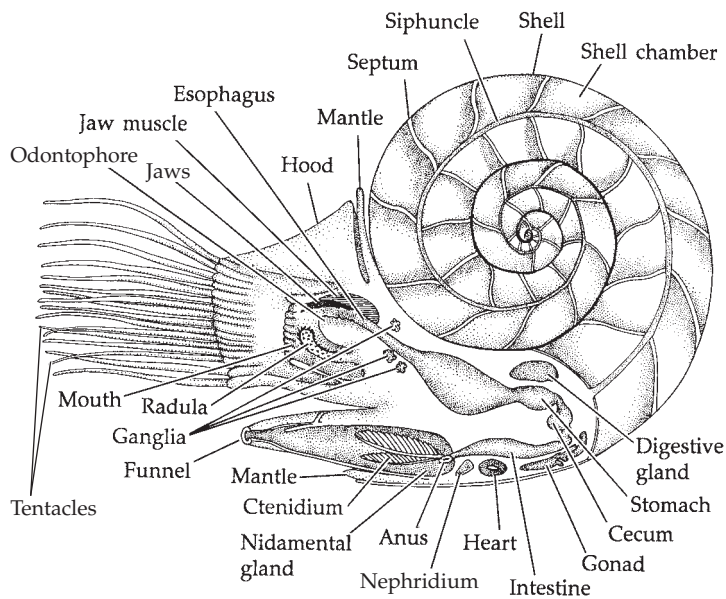
Figure 13.10   The anatomy of *Nautilus* (sagittal

center of shell. Single digestive gland and foot with a terminal disk surrounded by epipodial papilla. Families include Pulsellidae (e.g., *Pulsellum*, *Annulipulsellum*) and Gadilidae (e.g., *Cadulus*, *Gadila*).

CLASS CEPHALOPODA   Nautilus, squids, cuttlefish, and octopuses (Figures 13.1H–K, 13.10, 13.11, 13.12, 13.17, and 13.22). With linearly chambered shell, usually reduced or lost in living taxa; if external shell present (*Nautilus*), animal inhabits last (youngest) chamber, with a filament of living tissue (the siphuncle) extending through older chambers; circulatory system largely closed; head with large, complex eyes and circle of prehensile arms or tentacles around mouth; with radula and beak; 1–2 pairs ctenidia, and 1–2 pairs complex nephridia; mantle forms large ventral mantle cavity containing 1–2 pairs of ctenidia; with muscular funnel (the siphon) through which water is forced, providing jet propulsion; some tentacles of male modified for copulation; benthic or pelagic, marine; about 700 living species.

SUBCLASS PALCEPHALOPODA   Includes many fossil taxa, all with external shells, as well as the living pearly nautilus.

COHORT NAUTILIDIA (= TETRABRANCHIATA)   The pearly nautilus. Shell external, many-chambered, coiled in one plane, exterior porcelaneous, interior nacreous (pearly); head with many (80–90) suckerless tentacles (4 modified as spadix in male for copulation and protected by a fleshy hood); 13 tooth rows in radula; beak of chitin and calcium carbonate; funnel of 2 separate folds; 2 pairs ctenidia ("tetrabranchiate"); 2 pairs nephridia; eyes like a pinhole camera, without cornea or lens; nervous system with anterior elements concentrated into a brain, optic lobes large; statocyst simple; without chromatophores or ink sac. Fossil record rich, but represented today by a single order (Nautilida) and single genus, the chambered or pearly nautilus (*Nautilus*), with five or six Indo-Pacific species (although a second, controversial genus, *Allonautilus*, has also been proposed).

SUBCLASS NEOCEPHALOPODA   Includes one fossil group in addition to the coleoids. The shell is reduced and internal in most (and in all living taxa).

COHORT COLEOIDIA (= DIBRANCHIATA)   Octopuses, squids, and their kin. Shell reduced and internal or absent; head and foot united into a common anterior structure bearing 8 or 10 prehensile appendages (arms and tentacles) bearing suckers and, often, cirri, one arm usually modified in male for copulation; 7 tooth rows in radula; with chitinous beak; funnel a single closed tube; 1 pair ctenidia ("dibranchiate"); 1 pair nephridia; eyes complex, with lens and often with cornea; nervous system well developed and concentrated into a brain; with a complex statocyst; with chromatophores and ink sac.

SUPERORDER OCTOPODIFORMES   Members of this group, which includes the octopuses and vampire squid, do not have the head distinctly separated from the rest of the body; have 8 arms, with 2 additional retractile filaments in the vampire squids; lateral fins on the body are present or absent.

ORDER OCTOPODA   Octopuses. Body short, round, usually without fins; internal shell vestigial or absent; 8 similar arms joined by web of skin (interbrachial web); suckers with narrow stalks, most are benthic. About 200 species, in two groups: the Incirrata, including the benthic octopuses and some pelagic taxa that lack fins and cirri with examples being Octopodidae (e.g., *Octopus*) and Argonautidae (*Argonauta*), the paper nautilus; and Cirrata, which are mainly pelagic deep sea cephalopods with fins and cirri, such as Cirroteuthidae (e.g., *Cirroteuthis*), Opisthoteuthidae (e.g., *Opisthoteuthis*), and Stauroteuthidae (e.g., *Stauroteuthis*).

ORDER VAMPYROMORPHA   The vampire squid. Body plump, with 1 pair fins; shell reduced to thin, leaf-shaped, uncalcified, transparent vestige; 4 pairs equal-sized arms, each with one row of unstalked distal suckers and two rows of cirri; arms joined by extensive web of skin (interbrachial membrane); fifth pair of arms represented by 2 tendril-like, retractable filaments; hectocotylus lacking; radula well developed; ink sac degenerate; mostly deep water. One living species, *Vampyroteuthis infernalis*, that lives in the oxygen minimum zone of the deep sea.

SUPERORDER DECAPODIFORMES (= DECAPODA)   Members of this group, which includes the squid and cuttlefish, have the head distinctly separated from the rest of the body; with 8 arms and 2 retractile (into pits) tentacles with suckers only on expanded tips; suckers with wide bases, sometimes with spines or hooks; lateral fins on body. The internal shell is large (as in the cuttlefish or in *Spirula*), reduced to an uncalcified gladius, or lost.

ORDER SPIRULIDA   The only living species is the ram's horn, *Spirula spirula* (Spirulidae), a small deep sea squid with a coiled, internal, chambered shell.

ORDER SEPIIDA   Cuttlefish. Body short, dorsoventrally flattened, with lateral fins; shell internal, calcareous,

straight or slightly curved, chambered; or shell horny, or absent; 8 short arms, and 2 long tentacles; suckers lack hooks. Includes the shell-less Sepiolidae (e.g., *Rossia*, *Sepiola*), the Sepiidae (e.g., *Sepia*) with an internal calcareous shell, the cuttlebone, and Idiosepiidae (e.g., *Idiosepis*), being tiny squids that live in seagrass to which they attach with a special sucker. Their shell is reduced to a horny gladius.

ORDER MYOPSIDA Squids with the eye covered with a cornea and having a well developed gladius. Body elongate, tubular, with lateral fins. Loliginidae (e.g., *Loligo*, *Doryteuthis*).

ORDER OEGOPSIDA Includes the majority of squids (and the former Teuthoida in part); the eye lacks a cornea and the shell is a gladius. Body elongate, tubular, with lateral fins; suckers often with hooks. Some of the many families in this group include Architeuthidae (*Architeuthis*), Bathyteuthidae (e.g., *Bathyteuthis*; sometimes treated as a separate order), Chiroteuthidae (e.g., *Chiroteuthis*), Ommastrephidae (e.g., *Ommastrephes*, *Dosidiscus*, *Illex*), Gonatidae (e.g., *Gonatus*), Histoteuthidae (e.g., *Histioteuthis*), Lycoteuthidae (e.g., *Lycoteuthis*), and Octopoteuthidae (e.g., *Octopoteuthis*).

The Molluscan Body Plan

Mollusca is one of the most morphologically diverse phyla in the animal kingdom. Molluscs range in size from microscopic solenogasters, bivalves, snails, and slugs, to whelks attaining 70 cm in length, giant clams (Cardiidae) over a 1 m in length, and giant squids (*Architeuthis*) reaching at least 13 m in overall length (body plus tentacles). The giant Pacific octopus (*Octopus dofleini*) commonly attains an arm span of 3–5 m and a weight of over 40 kg. It is the largest living octopus, and one particularly large specimen was estimated to have an arm span of nearly 10 m and a weight of over 250 kg! Despite their differences, giant squids, cowries, garden slugs, eight-plated chitons, and wormlike aplacophorans are all closely related and share a common body plan (Box 13A). In fact, the myriad ways in which evolution has shaped the basic molluscan body plan provide some of the best lessons in homology and adaptive radiation in the animal kingdom.

Molluscs are bilaterally symmetrical, coelomate protostomes, but the coelom generally exists only as small vestiges around the heart (the **pericardial chamber**), the gonads, and parts of the nephridia (kidneys). The principal body cavity is a hemocoel composed of several large sinuses of the open circulatory system, except in some cephalopods that have a largely closed system. In general, the body comprises three distinguishable regions: a head, foot, and centrally concentrated visceral mass, but the configuration differs in different classes (Figure 13.13). The head may bear various sensory structures, most notably eyes and tentacles; statocysts may be located in the foot region and chemosensory structures can also be present.

The visceral mass is covered by a thick epidermal sheet of skin called the **mantle** (also known as the pallium), which is sometimes covered in cuticle and plays a critical role in the organization of the body. It secretes the hard calcareous skeleton, either as minute sclerites, or plates, that are embedded in the body wall or as a solid internal or external shell. Ventrally the body usually bears a large, muscular **foot**, which typically has a creeping **sole**.

Surrounding or posterior to the visceral mass is a cavity—a space between the visceral mass and folds of the mantle itself. This **mantle cavity** (also known as the pallial cavity) often houses the gills (the original molluscan gills are known as **ctenidia**), along with the openings of the gut, nephridial, and reproductive systems, and, in addition, special patches of chemosensory epithelium in many groups, notably the osphradia. In aquatic forms, water is circulated through this cavity, passing over the ctenidia, excretory pores, anus, and other structures.

Molluscs have a complete, or through-gut that is regionally specialized. The buccal region of the foregut typically bears a uniquely molluscan structure, the **radula**, which is a toothed, rasping, tongue-like strap used in feeding. It is located on a muscular **odontophore** that moves the radula through its feeding motions. The circulatory system usually includes a heart in a pericardial cavity and a few large vessels that empty into or drain hemocoelic spaces. The excretory system consists of one or more pairs of metanephridial kidneys (here simply referred to as nephridia), with openings (nephrostomes) to the pericardium via renopericardial canals and to the mantle cavity via the nephridiopore. The nervous system typically includes a dorsal cerebral ganglion, a nerve ring encircling the buccal area or esophagus, and two pairs of longitudinal nerve cords arise from paired pleural ganglia and connecting with the visceral ganglia more posteriorly in the body. Other anterior paired ganglia (buccal and labial) may be present. Pedal ganglia lie in the foot and may give off pedal nerve cords.

Gametes are produced by the gonad in the visceral mass and fertilization may be external or internal. Development is typically protostomous, with spiral cleavage and a trochophore larval stage. There is also a secondary larval form unique to gastropod and bivalve molluscs called the **veliger**.

Although this general summary describes the basic body plan of most molluscs, notable modifications occur and are discussed throughout this chapter. The eight classes are characterized above (see classification) and are briefly summarized below.

Some of the most bizarre molluscs are the "aplacophorans"—Solenogastres and Caudofoveata (Figure 13.1C and 13.2). Members of these groups are wormlike
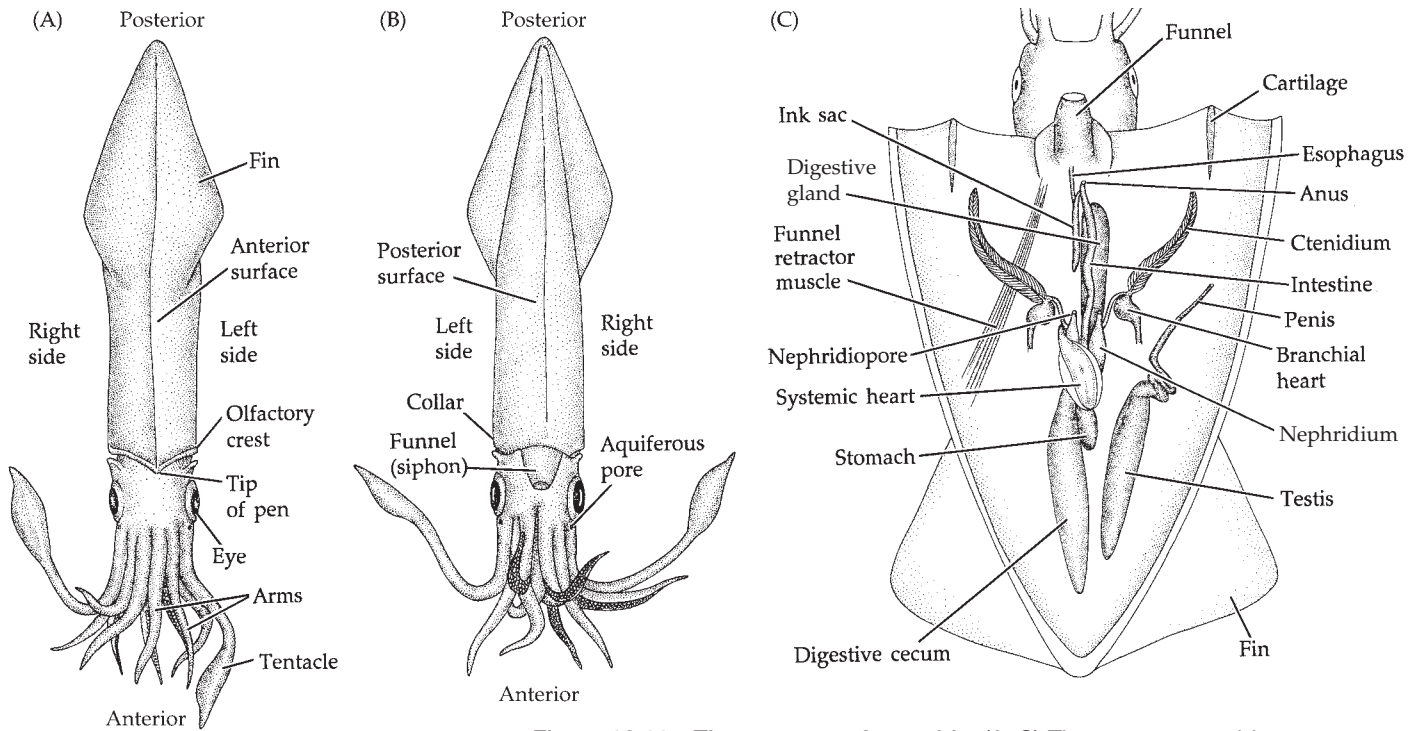
Figure 13.11 The anatomy of a squids. (A–C) The common squid, *Loligo*. (A) External morphology (anterior view). (B) External morphology (posterior view). (C) Internal anatomy of a male. The mantle is dissected open and pulled aside. (D) The giant squid (*Architeuthis dux*) netted off the coast of New Zealand in 1997.

and typically small, and either burrow in sediment (Caudofoveata) or may spend their entire lives on the branches of various cnidarians (Solenogastres) such as gorgonians upon which they feed. Caudofoveata lack a foot, but a reduced one is present in the Solenogastres, and neither group has a solid shell. Aplacophorans also have no distinct head, eyes, or tentacles. They were traditionally considered primitive molluscs that evolved before the appearance of solid shells, but some molecular and developmental data suggest they may actually be highly derived forms that have lost the shell and have secondarily acquired a simple body morphology.

Polyplacophorans, or chitons, are oval molluscs that bear eight (seven in Paleoloricata) separate articulating shell plates on their backs (Figures 13.1B and 13.4). They range in length from about 7 mm to over 35 cm. These marine animals are inhabitants of deep sea to intertidal regions around the world, at all latitudes.

Monoplacophorans are limpet-like molluscs with a single cap-shaped shell ranging from about 1 mm to about 4 cm in length (Figures 13.1A and 13.3). Most live in the deep sea, some at great depths (> 2,000 m). Their most notable feature is the repetitive arrangement of gills, gonads, and nephridia, a condition that has led some biologists to speculate that they must represent a link to some ancient segmented ancestor of the Mollusca (an idea no longer deemed reasonable).

Gastropods are by far the largest group of molluscs and include some of the best-studied species (Figures 13.1D–G, 13.5, 13.6, and 13.7). This class includes the common snails and slugs in all marine and many freshwater habitats, and they are the only molluscan class to have successfully invaded terrestrial environments. They are the only molluscs that undergo torsion during early development, a process involving a 90–180° rotation of the visceral mass relative to the foot (for details see section on torsion below).

Bivalves include the clams, oysters, mussels, and their kin (Figures 13.1M–Q and 13.8). They possess two separate shells, called **valves**. The smallest bivalves are members of the marine family Condylocardiidae some

of which are about 1 mm in length; the largest are giant tropical clams (*Tridacna*), one species of which (*T. gigas*) may weigh over 400 kg! Bivalves inhabit all marine environments and many freshwater habitats.

Scaphopods, the tusk shells, live in marine surface sediments at various depths. Their distinctive single, tubular uncoiled shells are open at both ends and range from a few millimeters to about 15 cm in length (Figures 13.1L and 13.9).

The cephalopods are among the most highly modified molluscs and include the pearly nautilus, squids, cuttlefish, octopuses, and a host of extinct forms, including the ammonites (Figures 13.1I–K, 13.10, 13.11, 13.12, 13.17, and 13.22). This group includes the largest of all living invertebrates, the giant squid, with body and tentacle lengths around 13 m. Among living cephalopods, only the nautilus has retained an external shell. The cephalopods differ markedly from other molluscs in several ways. For example, they have a spacious body cavity that includes the pericardium, gonadal cavity, nephriopericardial connections, and gonoducts, all of which form an interconnected system representing a highly modified but true coelom. In addition, unlike all other molluscs, many coleoid cephalopods have a functionally closed circulatory system. The nervous system of cephalopods is the most sophisticated of all invertebrates, with unparalleled learning and memory abilities. Most of these modifications are associated with the adoption of an active predatory lifestyle by these remarkable creatures.

The Body Wall

The body wall of molluscs typically comprises three main layers: the cuticle (when present), epidermis, and muscles (Figure 13.15A). The cuticle is composed largely of various amino acids and sclerotized proteins (called conchin), but it apparently does not contain chitin (except in the aplacophorans). The epidermis is usually a single layer of cuboidal to columnar cells, which are ciliated on much of the body. Many of the epidermal cells participate in secretion of the cuticle. Other kinds of secretory gland cells can also be present, some of which secrete mucus and these can be very abundant on external surfaces such as the sole of the foot. Other specialized epidermal cells occur on the dorsal body wall, or mantle. Many of these cells constitute the molluscan **shell glands**, which produce the calcareous sclerites or shells characteristic of this phylum. Still other epidermal cells are sensory receptors. The epidermis and outermost muscle layer are often separated by a basement membrane and occasionally a dermis-like layer.

The body wall usually includes three distinct layers of smooth muscle fibers: an outer circular layer, a middle diagonal layer, and an inner longitudinal layer. The diagonal muscles are often in two groups with fibers running at right angles to each other. The degree of development of each of these muscle layers differs among the classes (e.g., in solenogasters the diagonal layers are frequently absent).

The Mantle and Mantle Cavity

The significance of the mantle cavity and its importance in the evolutionary success of molluscs has already been alluded to. Here we offer a brief summary of the nature of the mantle cavity, and its disposition in each of the major groups of molluscs.

The mantle, as the name implies, is a sheet-like organ that forms the dorsal body wall, and in most molluscs it grows during development to envelop the molluscan body and at its edge there are one or two folds that contain muscle layers and hemocoelic channels (Figure 13.15C). The outward growth creates a space lying between the mantle fold(s) and the body proper. This space, the mantle cavity, may be in the form of a groove surrounding the foot or a primitively posterior chamber through which water is passed by ciliary or, in more derived taxa, by muscular action. Generally, the mantle cavity houses the respiratory surface (usually the ctenidia or other gill-like structures), and receives the fecal material discharged from the anus and excretory waste from the kidney. Gametes are also primitively discharged into the mantle cavity. Incoming water provides a source of oxygen for respiration, a means of flushing waste and, in some instances, also carries food for suspension feeding.

The mantle cavity of chitons is a groove surrounding the foot (Figures 13.4A and 13.13A,B). Water enters the groove from the front and sides, passing medially over the ctenidia and then posteriorly between the ctenidia and the foot. After passing over the gonopores and nephridiopores, water exits the back end of the groove and carries away fecal material from the posteriorly located anus.

The aplacophorans have a small mantle cavity, with either a pair of ctenidia (Caudofoveata) or lamella-like folds or papillae on the mantle cavity wall (Solenogastres). The paired coelomoducts and the anus also open into the mantle cavity

The single mantle cavity of gastropods originates during development as a posteriorly located chamber. As development proceeds, however, most gastropods undergo a 180° rotation of the visceral mass and shell to bring the mantle cavity forward, over the head (Figures 13.5, 13.6, and 13.13C) (see section on torsion that follows). The different orientation does not affect the water flow, which still passes through this chamber through the ctenidia, and then past the anus, gonopores, and nephridiopores. A great many secondary modifications on this plan have evolved in the Gastropoda, including rerouting of current patterns; loss or modification of associated structures such as the gills, hypobranchial glands and sensory organs; and even "detorsion," as discussed in later sections of this chapter.

Figure 13.12. The anatomy of *Octopus*.
(A) General external anatomy. (B) Right-side view of the internal anatomy.
(C) Arm and sucker (cross section).
(D) Tip of the hectocotylus arm. (E) The diminutive Eastern Pacific *Paroctopus digueti* well camouflaged on a sand bottom. (F) The tropical Pacific *Octopus chierchiae*. (G) The remarkable Indo-West Pacific *Abdopus horridus*.

(B)

Dorsal mantle cavity
Mantle muscles
Digestive gland
Poison gland
Crop
Cartilagenous cranium
Intestinal hemocoel
Brain
Ink sac
Cephalic vein
Stomach
Buccal mass
Shell rudiment
Brachial nerve
Ceca
Gonad
Systemic heart
Nephridium
Branchial heart
Ctenidium
Muscular septum of the ventral mantle cavity
Anus
Funnel
Beak

(A)

Visceral hump
Eye
Siphon
Arm with suckers

(C)

Brachial collector vein
Epidermis
Dermis
Vertical muscle
Horizontal muscle
Longitudinal muscle
Connective tissue
Brachial artery
Nerve cord
Central canal
Suction cup
Suction cup apparatus

(D)

Copulatory pad
Suckers
Spermatophore groove

(E)

(F)

(G)

Figure 13.13   Modifications of the shell, foot, gut, ctenidia, and mantle cavity in five classes of molluscs. (A,B) Lateral and cross sections of a chiton (Polyplacophora). (C) Side view of a snail (Gastropoda). (D,E) Cutaway side view and cross section of a clam (Bivalvia). (F) Lateral view of a tusk shell (Scaphopoda). (G) Lateral view of a squid (Cephalopoda). In cephalopods the foot is modified to form the funnel (= siphon) and at least parts of the arms.
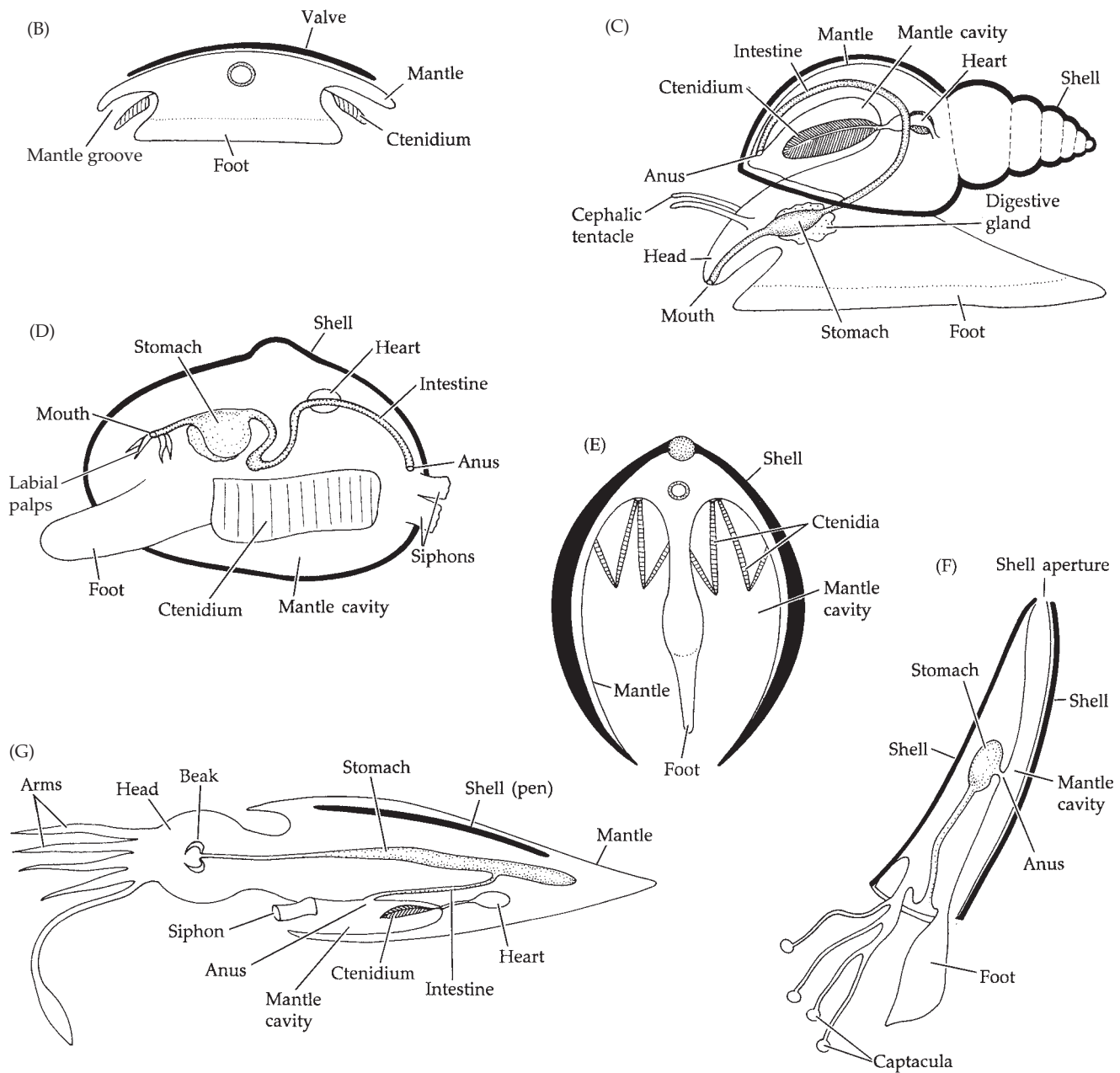
Bivalves possess a greatly enlarged mantle cavity that surrounds both sides of the foot and visceral mass (Figures 13.8 and 13.13D,E). The mantle lines the laterally placed shells, and the folds making up the mantle edges are often fused in various ways posteriorly to form inhalant and exhalant siphons, through which water enters and leaves the mantle cavity. The water passes over and through the ctenidia that, in autobranch bivalves, extract suspended food material as well as accomplishing gas exchange. The water flow then sweeps across the gonopores and nephridiopores, and lastly past the anus as it exits through the exhalant siphon.

Scaphopods have a tapered, tubular shell (Figures 13.9 and 13.13F). Water enters and leaves the elongate mantle cavity through the small opening in the top of the shell and flushes over the mantle surface, which, in

the absence of ctenidia, is the site of gas exchange. The anus, nephridiopores, and gonopores also empty into the mantle cavity.

While no detailed studies of the functioning of the monoplacophoran mantle cavity have been made, observations of the first living specimens in 1977 revealed that the gills vibrated, apparently circulating water through the mantle groove. It was also noted that shell movement was accompanied by an acceleration of gill beating. Vibrating gills are unknown in other molluscs where ciliary action, sometimes assisted by muscular contractions, moves water through the mantle cavity. The anus, nephridiopores, and gonopores also open into the mantle cavity.

With the exception of the monoplacophorans, in all of the above cases, water is moved through the mantle cavity by the action of long lateral cilia on the ctenidia. But in cephalopods the ctenidial gills are not ciliated. Instead, in *Nautilus* a ventilatory current is passed through the mantle cavity by the unduatory movements of two muscular flaps associated with the funnel lobes. In the coleoid cephalopods, however, well-developed, highly innervated mantle muscles perform this function through the regular pulsation of the mantle wall. The exposed, fleshy body surface of squids and octopuses is, in fact, the mantle itself (Figures 13.11, 13.12, and 13.13G). Unconstrained by an external shell, the mantle of these molluscs expands and contracts to draw water into the mantle cavity and then forces it out through the narrow muscular **funnel** (= **siphon**). The forceful expelling of this jet of exhalant water can also provide a means of rapid locomotion for most cephalopods. In the mantle cavity the water passes through the ctenidia, and then past the anus, reproductive pores, and excretory openings.

The remarkable adaptive qualities of the molluscan body plan are manifested in these variations in the position and function of the mantle cavity and its associated structures. In fact, the nature of many other structures is also influenced by mantle cavity arrangement, as shown schematically in Figure 13.14. That molluscs have been able to successfully exploit an extremely broad range of habitats and lifestyles can be explained in part by these variations, which are central to the story of molluscan evolution. We will have more to say about these matters throughout this chapter.

The Molluscan Shell

Except for the two aplacophoran classes, all molluscs have solid calcareous shells (either aragonite or calcite) produced by shell glands in the mantle. In the Caudofoveata and Solenogastres, aragonite sclerites or scales are formed extracellularly in the mantle epidermis and are embedded in the cuticle. In the other classes molluscan shells vary greatly in shape and size, but they all adhere to the basic construction plan of calcium carbonate produced extracellularly, laid down

on a protein matrix in layers, and often covered by a thin organic surface coating called a **periostracum** (called the **hypostracum** in chitons) (Figure 13.15). The periostracum is composed of a type of conchin (largely quinone-tanned proteins) similar to that found in the epidermal cuticle. The calcium layers have four crystal types: prismatic, spherulitic, laminar, and crossed structures. All incorporate conchin onto which the calcareous crystals precipitate. The majority of living molluscs have an outer prismatic layer and an inner porcelaneous, crossed layer. In monoplacophorans, cephalopods and in some gastropods and bivalves, an iridescent, nacre (laminar) layer replaces the layer of crossed crystals. Shells are often made up of multiple layers of different crystal types.

Molluscs are noted for their wonderfully intricate and often flamboyant shell color patterns and sculpturing (Figure 13.16), but very little is known about the evolutionary origins and functions of these features. Some molluscan pigments are metabolic by-products, and thus shell colors might largely represent strategically deposited food residues, while others appear to have no relationship to diet. Molluscan shell pigments include such compounds as pyrroles and porphyrins. Melanins are common in the integument (cuticle and epidermis), the eyes, and internal organs, but they are rare in shells.

Some shell sculpture patterns are correlated with specific behaviors or habitats. For example, shells with low spires are more stable in areas of heavy wave shock or on vertical rock surfaces. Similarly, the low, cap-shaped shells of limpets (Figures 13.5A and 13.16H,I) are presumably adapted for withstanding exposure to strong waves. Heavy ribbing, thick or inflated shells, and a narrow gape in bivalves are all possible adaptations to provide protection from predators. In some gastropods, fluted shell ribs help them land upright when they are dislodged from rocks. Several groups of soft-bottom benthic gastropods and bivalves have long spines on the shell that may help stabilize the animals in loose sediments as well as provide some protection from predators. Many molluscs, particularly clams, have shells covered with living epizootic organisms such as sponges, annelid tube worms, ectoprocts, and hydroids. Some studies suggest that predators have a difficult time recognizing such camouflaged molluscs as potential prey.

Molluscs may have one shell, two shells, eight shells, or no shell. In the latter case the outer body wall may contain calcareous sclerites of various sorts. In the aplacophorans, for example, the cuticular sclerites vary in shape and range in length from microscopic to about 4 mm. These sclerites are essentially crystals composed almost entirely of calcium carbonate as aragonite. Caudofoveates produce platelike cuticular sclerites that give their body surface a scaly texture and appearance. The sclerites in both taxa appear to be secreted by a

(A) (B) (C) (D)

Pharyngeal pouches

(E) (F) CT (G)

CT

(H) Accessory "heart"

CT

Key

A   Atrium
AN   Anus
CT   Ctenidium
G   Gonad
N   Nephridium
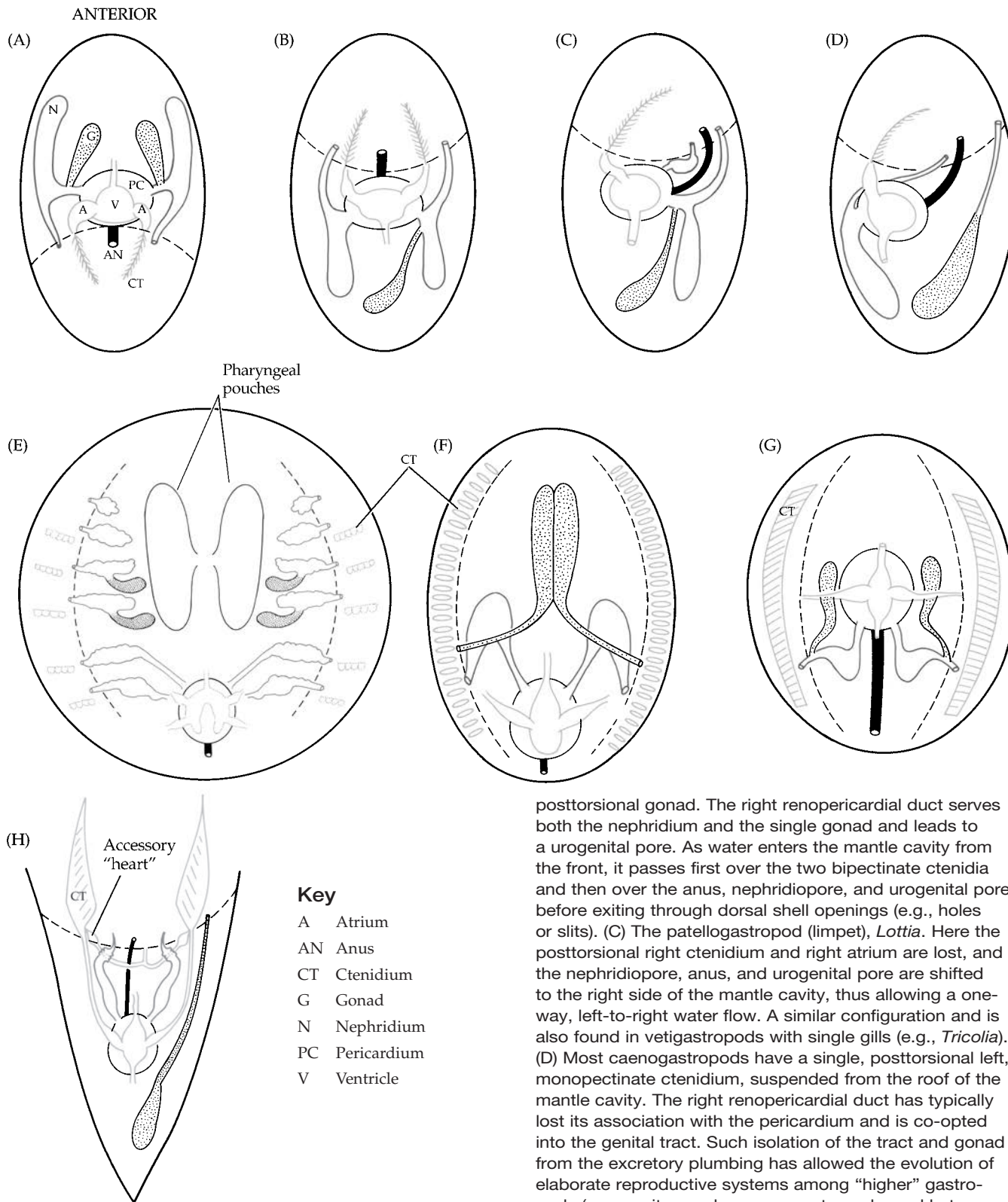PC   Pericardium
V   Ventricle

Figure 13.14 Variations in the mantle cavity, circulatory system, ctenidia, nephridia, reproductive system, and position of the anus in molluscs (dorsal views). Although schematic, these drawings give some idea of the evolutionary changes in arrangement of these structures and systems in the phylum Mollusca. (A) A hypothetical, untorted, gastropod-like mollusc with a posterior mantle cavity and symmetrically paired atria, ctenidia, nephridia, and gonads. (B) A posttorsional vetigastropod (e.g., *Fissurella*) wherein all paired organs are retained except the left posttorsional gonad. The right renopericardial duct serves both the nephridium and the single gonad and leads to a urogenital pore. As water enters the mantle cavity from the front, it passes first over the two bipectinate ctenidia and then over the anus, nephridiopore, and urogenital pore before exiting through dorsal shell openings (e.g., holes or slits). (C) The patellogastropod (limpet), *Lottia*. Here the posttorsional right ctenidium and right atrium are lost, and the nephridiopore, anus, and urogenital pore are shifted to the right side of the mantle cavity, thus allowing a one-way, left-to-right water flow. A similar configuration and is also found in vetigastropods with single gills (e.g., *Tricolia*). (D) Most caenogastropods have a single, posttorsional left, monopectinate ctenidium, suspended from the roof of the mantle cavity. The right renopericardial duct has typically lost its association with the pericardium and is co-opted into the genital tract. Such isolation of the tract and gonad from the excretory plumbing has allowed the evolution of elaborate reproductive systems among "higher" gastropods (e.g., neritomorphs, caenogastropods, and heterobranchs) and probably important in the story of gastropod success. (E) The condition in monoplacophorans includes the serial repetition of several organs. (F) In polyplacophorans, the gonoducts and nephridioducts open separately into the exhalant regions of the lateral pallial grooves. (G) A generalized bivalve condition. The gonads and nephridia may share common pores, as shown here, or else open separately into the lateral mantle chambers. (H) The condition in a generalized cephalopod with a single, isolated reproductive system and an effectively closed circulatory system.
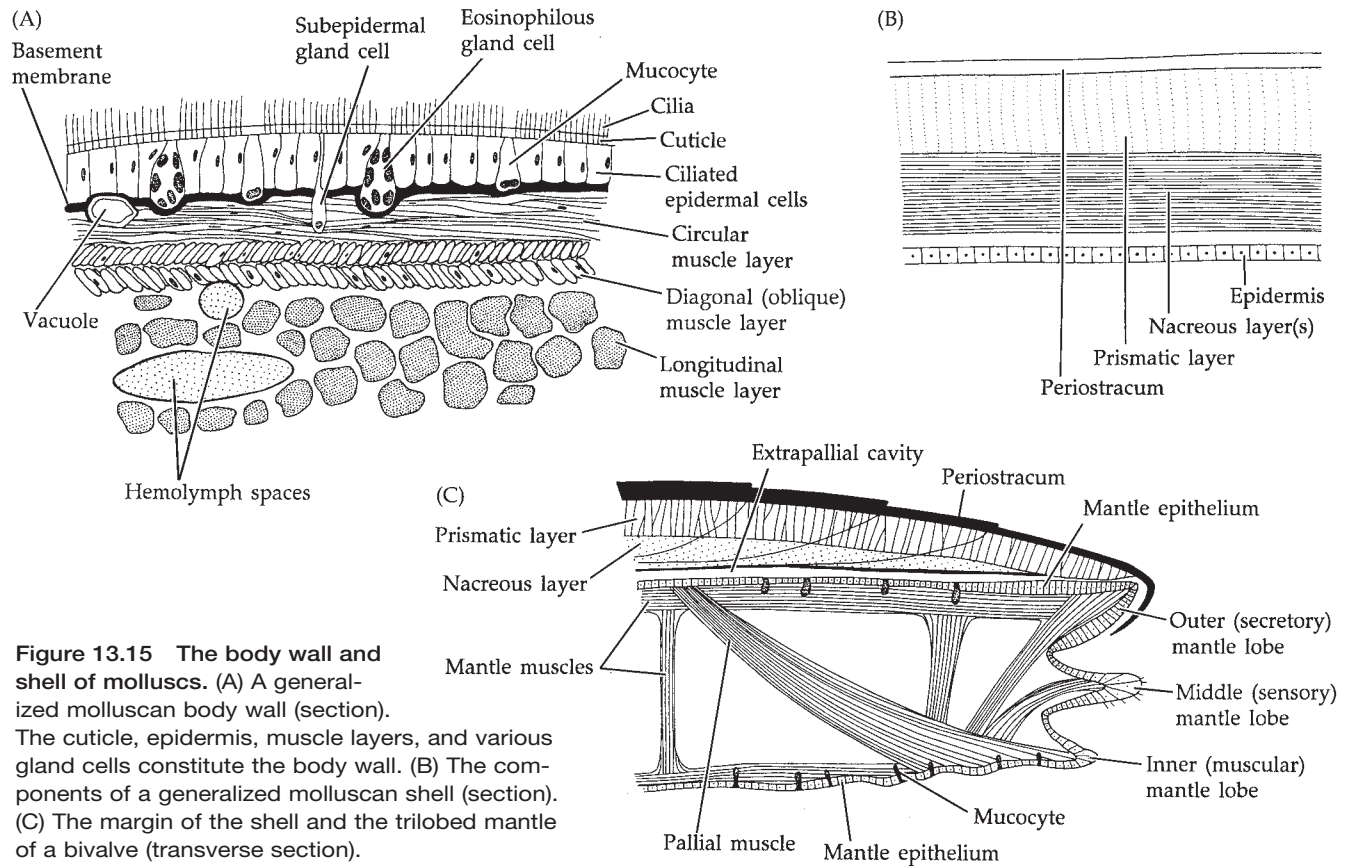
Figure 13.15   The body wall and shell of molluscs. (A) A generalized molluscan body wall (section). The cuticle, epidermis, muscle layers, and various gland cells constitute the body wall. (B) The components of a generalized molluscan shell (section). (C) The margin of the shell and the trilobed mantle of a bivalve (transverse section).

diffuse network of specialized groups of cells and different shapes are found in different regions of the body.

The eight transverse plates, or valves (Figures 13.4 and 13.16A–F), of polyplacophorans are encircled by and embedded in a thickened region of the mantle called the **girdle**. The size of the girdle varies from narrow to broad and may cover much of the valves. In the giant Pacific "gumboot" chiton, *Cryptochiton stelleri*, the girdle completely covers the valves. The girdle is thick, heavily cuticularized, and usually beset with calcareous sclerites, spines, scales, or noncalcareous bristles secreted by specialized epidermal cells. These sclerites are probably homologous with those in the body wall of aplacophorans.

The anterior and posterior valves of chitons are referred to as the end valves, or cephalic (= anterior) and anal (= posterior) plates; the six other valves are called the intermediate valves. Some details of chiton valves are shown in Figure 13.16A–F. The shells of chitons are three-layered, with an outer periostracum, a colored **tegmentum**, and an inner calcareous layer, or **articulamentum**. The periostracum is a very thin, delicate organic membrane and is not easily seen. The tegmentum is composed of organic material (probably a form of conchin) and calcium carbonate suffused with various pigments. It is penetrated by vertical canals that lead to minute pores in the surface of the valves. The pores are of two sizes: the larger ones (megapores) housing the **megaesthetes** and the smaller ones (micropores)

the **microaesthetes**. In some species, megaesthetes may be modified as **shell eyes**, with compound lenses made of large crystals of araganite. The vertical aesthete canals arise from a layer of horizontal canals in the lower part of the tegmentum and the articulamentum (Figure 13.43C) and some pass through the articulamentum to join with nerves in the mantle at the lower edge of the shell valve. The articulamentum is a thick, calcareous, porcelaneous layer that differs in certain ways from the shell layers of other molluscs.

Monoplacophorans have a single, limpet-like shell with the apex situated far forward (Figures 13.1A and 13.3). The shell has a distinctive outer prismatic layer and an inner nacreous layer. As in chitons, the mantle encircles the body and foot as a circular fold, forming lateral mantle grooves.

The bivalves possess two shells, or **valves,** that are connected dorsally by an elastic, proteinaceous **ligament**, and enclose the body and spacious mantle cavity (Figures 13.1M–P, 13.8, and 13.16J,K). Shells of bivalves typically have a thin periostracum, covering two to four calcareous layers that vary in composition and structure. The calcareous layers are often aragonite or an aragonite/calcite mixture, and they usually have a substantial organic framework. The periostracum and organic matrix may account for over 70% of the shell's dry weight in some thin-shelled taxa. Each valve has a dorsal protuberance called the umbo, which is the oldest part of the shell. Concentric growth lines radiate
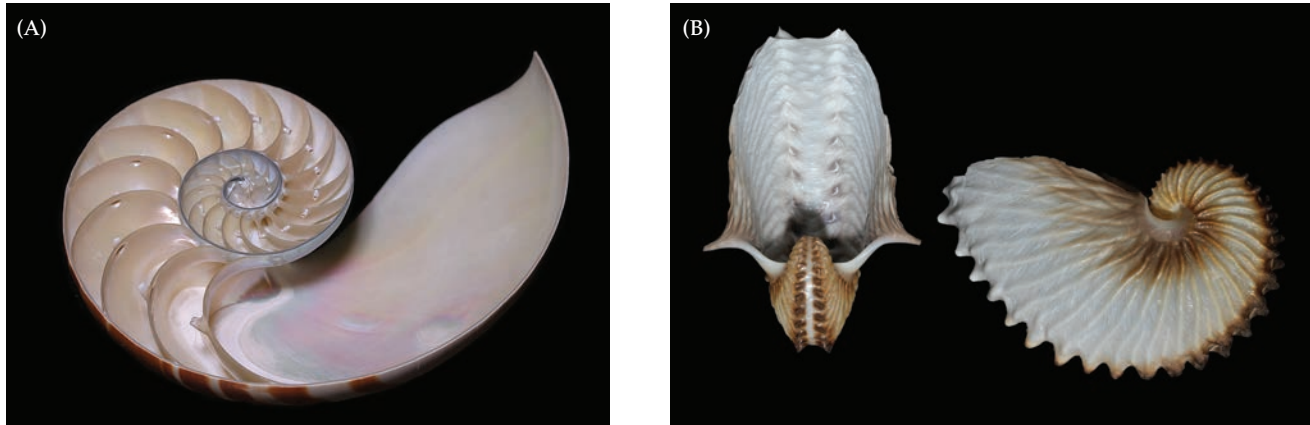
Figure 13.16 Shell morphology and terminology. (A–F) Chiton shells (Polyplacophora): (A) A chiton showing the eight valves (dorsal view). (B) Isolated valves of *Cryptochiton stelleri*, the giant "gumboot" chiton. (C) An anterior valve (ventral view). (D,E) An intermediate valve (dorsal and ventral views). (F) A posterior valve (ventral view). (G) Internal and external features of a spiral gastropod shell. (H) A lottiid limpet (Patellogastropoda) (side view). (I) The shell of a veti-gastropod keyhole limpet (top view). (J) Inside view of the left valve of a heterodont clam shell (Bivalvia). (K) Dorsal view of a heterodont clam shell.

Figure 13.17   Two very different kinds of cephalopod shells. (A) The chambered shell of *Nautilus*, cut in longitudinal section. (B) The egg case "shell" of the paper nautilus, *Argonauta.*

outward from the umbo. When the valves are closed by contraction of the adductor muscles, the outer part of the ligament is stretched and the inner part is compressed. Thus, when the adductor muscles relax, the resilient ligament causes the valves to open. The hinge apparatus comprises various sockets and tooth-like pegs or flanges (hinge teeth) that align the valves and prevent lateral movement. In most bivalves, the adductor muscles contain both striated and smooth fibers, facilitating both rapid and sustained closure of the valves. This division of labor is apparent in some bivalves as for example in oysters where the large single adductor muscle is clearly composed of two parts, a dark striated region that functions as a rapid closure muscle, and a white smoother region that functions to hold the shell tightly closed for long periods of time.

The thin mantle lines the inner valve surfaces in bivalves and separates the visceral mass from the shell. The edge of a bivalve mantle bears three longitudinal ridges or folds—the inner, middle, and outer folds (Figure 13.15C). The innermost fold is the largest and contains radial and circular muscles, some of which attach the mantle to the shell. The line of mantle attachment appears on the inner surface of each valve as a scar called the **pallial line** (Figure 13.16J), and this scar is often a useful diagnostic character. The middle mantle fold is sensory in function, and the outer fold is responsible for secreting the shell. The cells of the outer lobe are specialized: the medial cells lay down the periostracum, and the lateral cells secrete the first calcareous layer. The entire mantle surface is then responsible for secreting the remaining innermost calcareous portion of the shell. A thin extrapallial space lies between the mantle and the shell, and it is into this space that materials for shell formation are secreted and mixed. Should a foreign object, such as a sand grain, lodge between the mantle and the shell, it may become the nucleus around which are deposited concentric layers

of smooth nacreous or porcelaneous shell. The result is a pearl, either free in the extrapallial space or partly embedded in the growing shell.[6]

Scaphopod shells resemble miniature, hollow elephant tusks, hence the vernacular names "tusk shell" and "tooth shell" (Figures 13.1L and 13.9). The scaphopod shell is open at both ends, with the smaller opening at the dorsal end of the body. Most tusk shells are slightly curved, the concave side being the equivalent to the anterior of other molluscs. The mantle is large and lines the entire posterior surface of the shell. The dorsal aperture serves for both inhalant and exhalant water currents.

Most extant cephalopods have a reduced shell or are shell-less. A completely developed external shell is found only in fossil forms and the living species of *Nautilus*. In squids and cuttlefish the shell is reduced and internal, and in octopuses it is entirely lacking or present only as a small rudiment.

The shell of *Nautilus* is coiled in a planispiral fashion (whorls lie in a single plane) and has a thin periostracum (Figures 13.10, 13.17A, and 13.22B). *Nautilus* shells (and all cephalopod shells) are divided into internal chambers by transverse septa, and only the last chamber is occupied by the body of the living animal. As the animal grows, it periodically moves forward, and the posterior part of the mantle secretes a new septum behind it. Each septum is interconnected by a tube through which extends a cord of tissue called the **siphuncle**. The siphuncle helps to regulate buoyancy of the animal by varying the amounts of gas and fluid in the shell chambers. The shell is composed of an inner nacreous layer and an outer porcelaneous layer containing prisms of calcium carbonate and an organic matrix. The outer surface may be pigmented or pearly white. The junctions between septa and the shell wall are called **sutures**, and are simple and straight, or slightly waved (as in *Nautilus*), or were highly convoluted (as in the extinct

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[6]Pearls are also found in some gastropods with nacreous inner shell layers, such as abalone.

ammonoids). In cuttlefish (order Sepiida), the shell is reduced and internal, with chambers that are very narrow spaces separated by thin septa. Like *Nautilus*, a cuttlefish can regulate the relative amounts of fluid and gas in its shell chambers. The small, coiled, septate, gas-filled shells of the deep-water squid *Spirula* are occasionally found washed up on beaches.

Fossil data suggest that the first cephalopod shells were probably small curved cones. From these ancestors both straight and coiled shells evolved, although secondary uncoiling probably occurred in several groups. Some straight-shelled cephalopods from the Ordovician period exceeded 5 m in length, and some Cretaceous coiled species had shell diameters of 3 m.

Gastropod shells are extremely diverse in size and shape (Figure 13.1D,G). The smallest are microscopic (less than 1 mm) and the largest may reach 70 cm in length. The "typical" shape is the familiar conical spiral wound around a central axis or columella (Figure 13.16G). The turns of the spire form whorls, demarcated by lines called sutures. The largest whorl is the last (or body) whorl, which bears the aperture through which the foot and head protrude. The traditional view of a coiled gastropod shell with the spire uppermost, is actually "upside down," since the lower edge of the aperture is anterior and the apex of the shell spire is posterior. The first few, very small, whorls at the apex are the larval shell, or **protoconch** (or its remnant), which usually differs in sculpturing and color from the rest of the shell. The last whorl and aperture may be notched and drawn out into an anterior **siphonal canal**, to house a siphon when present. A smaller posterior canal may also be present on the rear edge of the aperture that houses a siphon-like fold of the mantle where waste and water are expelled.

Every imaginable variation on the basic spiraled shell occurs among the gastropods (and some unimaginable): the shell may be long and slender (e.g., auger shells) or short and plump (e.g., trochids), or the shell may be flattened, with all whorls more-or-less in one plane (e.g., sundials). In some the spire may be more or less incorporated into the last whorl and eventually disappear from view (as in cowries). In some with a much larger last whorl, the aperture may be reduced to an elongated slit (Figure 13.1E (e.g., cowries, olives, and cones). In a few groups the shell may coil so loosely as to form a meandering wormlike tube (e.g., the so-called "tube snails," vermetids and siliquariids; Figure 13.19E). In a number of gastropod groups the shell may be reduced and overgrown by the mantle, or it may disappear entirely resulting in a slug (see below). Most gastropods spiral clockwise; that is, they show right-handed, or dextral, coiling. Some are sinistral (left-handed), and some normally dextral species may occasionally produce sinistral individuals. In limpets the shell is cap-shaped, with a low conical shape with no or little visible coiling (Figure 13.16H,I). The limpet

shell form has been derived from coiled ancestors on numerous occasions during gastropod evolution.

Gastropod shells consist of an outer thin organic periostracum and two or three calcareous layers: an outer prismatic (or palisade) layer, and middle and inner lamellar or crossed layers. In many vetigastropods the inner layer is nacreous. In some patellogastropods up to six calcareous layers are distinguishable but in the great majority of living gastropods the shell structure is primarily one layer composed of crossed crystals (crossed lamellar shell structure). Gastropods in which the shell is habitually covered by mantle lobes lack a periostracum (e.g., olives and cowries), but in some other groups the periostracum is very thick and sometimes it is produced into lamellae or hairs. The prismatic and lamellate layers consist largely of calcium carbonate, either as calcite or aragonite. These two forms of calcium are chemically identical, but they crystallize differently and can be identified by microscopic examination of sections of the shell. Small amounts of other inorganic constituents are incorporated into the calcium carbonate framework, including chemicals such as phosphate, calcium sulfate, magnesium carbonate, and salts of aluminum, iron, copper, strontium, barium, silicon, manganese, iodine, and fluorine.

An intriguing aspect of gastropod evolution is shell loss and the achievement of the "slug" form. Despite the fact that evolution of the coiled shell led to great success for the gastropods—75% of all living molluscs are snails—secondary loss of the shell occurred many times in this class but mostly in various groups of euthyneurans such as the sea slugs and land slugs. In forms such as the land and sea slugs, the shell may persist as a small vestige covered by the dorsal mantle (e.g., in the euthyneuran sea slugs Aplysiinae and Pleurobranchidae, and the caenogastropod family Velutinidae), or as a small external rudiment as in the carnivorous land slug *Testacella*, or it may be lost altogether (e.g., the nudibranchs, the systellommatophorans and some terrestrial stylommatophoran slugs, and in the neritimorph slug *Titiscania*). In the nudibranchs (Nudibranchia) the larval shell is first covered, then resorbed, by the mantle during ontogeny. Shell loss occurred numerous times in gastropods, particularly among the sea slugs ("opisthobranchs") and stylommatophoran pulmonates. Shells are energetically expensive to produce and require a reliable source of calcium in the environment, so it might be advantageous to eliminate them if compensatory mechanisms exist. For example, most, if not all, sea slugs secrete chemicals that make them distasteful to predators. In addition, the bright coloration of many nudibranchs may serve a defensive function. In some species, the color matches the animal's background such as the small red nudibranch, *Rostanga pulchra*, which matches almost perfectly the red sponge on which it feeds. Many nudibranchs, are however,
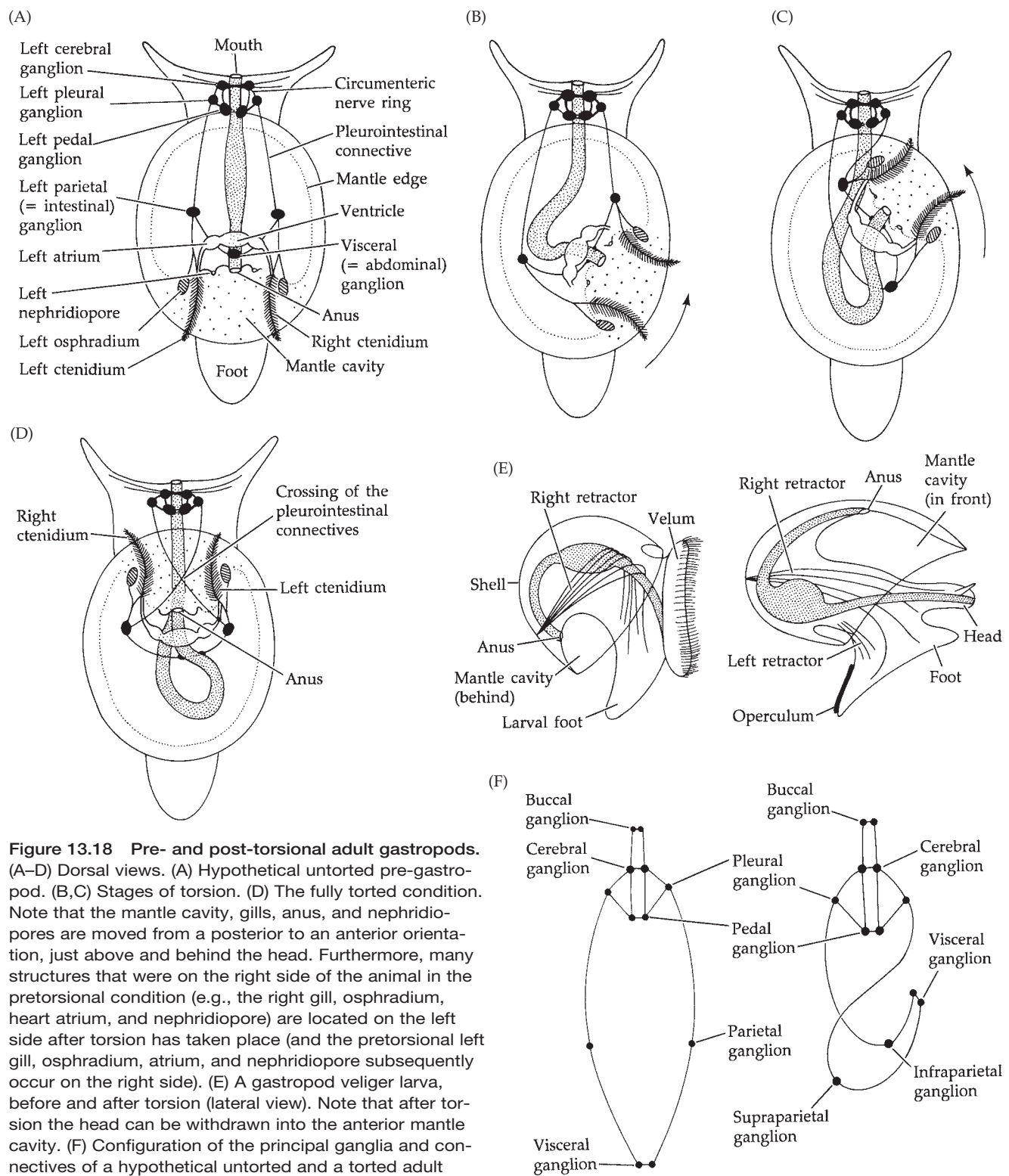
Figure 13.18 Pre- and post-torsional adult gastropods.
(A–D) Dorsal views. (A) Hypothetical untorted pre-gastropod. (B,C) Stages of torsion. (D) The fully torted condition. Note that the mantle cavity, gills, anus, and nephridiopores are moved from a posterior to an anterior orientation, just above and behind the head. Furthermore, many structures that were on the right side of the animal in the pretorsional condition (e.g., the right gill, osphradium, heart atrium, and nephridiopore) are located on the left side after torsion has taken place (and the pretorsional left gill, osphradium, atrium, and nephridiopore subsequently occur on the right side). (E) A gastropod veliger larva, before and after torsion (lateral view). Note that after torsion the head can be withdrawn into the anterior mantle cavity. (F) Configuration of the principal ganglia and connectives of a hypothetical untorted and a torted adult gastropod.

conspicuous in nature. In these cases, the color may serve to warn predators of the noxious taste of the slug or, as suggested by Rudman (1991), predators may simply ignore such bright "novelties" in their environment.

Torsion, or "How the Gastropod Got Its Twist"

One of the most remarkable and dramatic steps taken during the course of molluscan evolution was the ad-

vent of torsion, a unique synapomorphy of gastropods, and it is quite unlike anything else in the animal kingdom. Torsion takes place during development in all gastropods, usually during the late veliger larval stage. It is a rotation of the visceral mass and its overlying mantle and shell as much as 180° with respect to the head and foot (Figures 13.18, and 13.53). The twisting is always in a counterclockwise direction (viewing the animal from above), and it is completely different from the phenomenon of coiling (= spiraling). During

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torsion, the mantle cavity and anus are moved from a posterior to an anterior position, somewhat above and behind the head. Visceral structures and incipient organs that were on the right side of the larval animal end up on the left side of the adult. The gut is twisted into a U-shape, and when the longitudinal nerve cords connecting the pleural to the visceral ganglia develop, they are crossed rather like a figure eight. Most veligers have nephridia, which reverse sides, but the adult gills and gonads are not fully developed when torsion occurs.

Torsion is usually a two-step process. During larval development, an asymmetrical velar or foot retractor muscle develops. It extends from the shell on the right, dorsally over the gut, and attaches on the left side of the head and foot. At a certain stage in the veliger's development, contraction of this muscle causes the shell and enclosed viscera to twist about 90° in a counterclockwise direction. This first 90° twist is usually rapid, taking place in a few minutes to a few hours. The second 90° twist is typically much slower and results from differential tissue growth. By the end of the process, the viscera have been pulled from above toward the left, ultimately leading to the figure-eight arrangement of the adult visceral nerves. But the figure-eight arrangement is not perfect as the left esophageal ganglion usually comes to lie dorsal to the gut and is thus called the supraesophageal (= supraintestinal) ganglion; however, the right esophageal ganglion lies ventral to the gut, as a subesophageal (= subintestinal) ganglion (Figures 13.18 and 13.40).

Gastropods that retain torsion into adulthood are said to be **torted**; those that have secondarily reverted back to a partially or fully untorted state in adulthood are **detorted**. The torted, figure-eight configuration of the nervous system is referred to as **streptoneury**. The detorted condition, in which the visceral nerves are secondarily untwisted, is referred to as **euthyneury**.

Detorted gastropods, such as many heterobranchs, undergo a postveliger series of changes through which the original torsion is reversed to various degrees. The process shifts the mantle cavity and at least some of the associated organs about 90° back to the right (as in many "pulmonates" and some sea slugs), or in some cases all the way back to the rear of the animal (the detorsion seen in some nudibranchs).

After torsion the anus lies in front; this means that the first gastropods could no longer grow in length easily. Subsequent increase in body size thus occurred by the development of loops or bulges in the middle portion of the gut region, thereby producing the characteristic coiled visceral hump. The first signs of torsion and coiling occur at about the same time during gastropod development. The earliest coiled gastropod shells in the fossil record include both planispiral and conispiral forms, and it is possible that coiling predated the appearance of torsion in gastropods. Once both features were established, they coevolved in various ways to produce what we see today in living gastropods.

The evolution of asymmetrically coiled shells had the effect of restricting the right side of the mantle cavity, a restriction that led to reduction or loss of the structures it contained on the adult right side (the original left ctenidium, atrium, and osphradium). At the same time, these structures on the adult left side (the original right ctenidium, atrium, and osphradium) tended to enlarge. Possibly correlated with torsion and coiling was the loss of the left post-torsional gonad. The single remaining gonad opens on the right side via the post-torsional right nephridial duct and nephridiopore. Patellogastropods and most vetigastropods retain two functional nephridia, although the post-torsional left one is often reduced. In other gastropods the post-torsional right nephridium is lost, but its duct and pore remain associated with the reproductive tract in neritimorphs and caenogastropods.

Such profound changes in spatial relations between major body regions as those brought about by torsion and spiral coiling in gastropods are rare among other animals. Several theories on the adaptive significance of torsion have been proposed and are still being argued. The great zoologist Walter Garstang suggested that torsion was an adaptation of the veliger larva that served to protect the soft head and larval ciliated velum from predators (see the section on development later in this chapter). When disturbed, the immediate reaction of a veliger is to withdraw the head and foot into the larval shell, whereupon the larva begins to sink rapidly. This theory may seem reasonable for evasion of very small planktonic predators, but it seems illogical as a means of escape from larger predators in the sea, which no doubt consume veligers whole—and any adaptive value to adults is not explained. Two zoologists finally tested Garstang's theory by offering torted and untorted abalone veligers to various planktonic predators; they found that, in general, torted veligers were not consumed any less frequently than untorted ones (Pennington and Chia 1985). Garstang first presented his theory in verse, in 1928, as he was often taken to do with his zoological ideas.

The Ballad of the Veliger, or How the Gastropod Got Its Twist

The Veliger's a lively tar, the liveliest afloat,
A whirling wheel on either side propels his little boat;
But when the danger signal warns his bustling submarine,
He stops the engine, shuts the port, and drops below unseen.
He's witnessed several changes in pelagic motorcraft;
The first he sailed was just a tub, with a tiny cabin aft.
An Archi-mollusk fashioned it, according to his kind,
He'd always stowed his gills and things in a mantle-sac behind.
Young Archi-mollusks went to sea with nothing but a velum—
A sort of autocycling hoop, instead of pram—to wheel 'em;

And, spinning round, they one by one acquired parental features,

A shell above, a foot below—the queerest little creatures.

But when by chance they brushed against their neighbors in the briny,

Coelenterates with stinging threads and Arthropods so spiny,

By one weak spot betrayed, alas, they fell an easy prey—

Their soft preoral lobes in front could not be tucked away!

Their feet, you see, amidships, next the cuddly-hole abaft,

Drew in at once, and left their heads exposed to every shaft.

So Archi-mollusks dwindled, and the race was sinking fast,

When by the merest accident salvation came at last.

A fleet of fry turned out one day, eventful in the sequel,

Whose left and right retractors on the two sides were unequal:

Their starboard halliards fixed astern alone supplied the head,

While those set aport were spread abeam and served the back instead.

Predaceous foes, still drifting by in numbers unabated,

Were baffled now by tactics which their dining plans frustrated.

Their prey upon alarm collapsed, but promptly turned about,

With the tender morsel safe within and the horny foot without!

This manoeuvre (vide Lamarck) speeded up with repetition,

Until the parts affected gained a rhythmical condition,

And torsion, needing now no more a stimulating stab,

Will take its predetermined course in a watchglass in the lab.

In this way, then, the Veliger, triumphantly askew,

Acquired his cabin for'ard, holding all his sailing crew—

A Trochosphere in armour cased, with a foot to work the hatch,

And double screws to drive ahead with smartness and dispatch.

But when the first new Veligers came home again to shore,

And settled down as Gastropods with mantle-sac afore,

The Archi-mollusk sought a cleft, his shame and grief to hide,

Crunched horribly his horny teeth, gave up the ghost, and died.

Other workers have hypothesized that torsion was an adult adaptation that might have created more space for retraction of the head into the shell (perhaps also for protection from predators), or for directing the mantle cavity with its gills and water-sensing osphradia anteriorly. Still another theory asserts that torsion evolved in concert with the evolution of a coiled shell—as a mechanism to align the tall spiraling shells from a position in which they stuck out to one side (and were presumably poorly balanced and growth limiting), to a position more in alignment with the longitudinal (head–foot) axis of the body. The latter position would theoretically allow for greater growth and elongation of the shell while reducing the tendency of the animal to topple over sideways.

No matter what the evolutionary forces were that led to torsion in the earliest gastropods, the results were to move the adult anus, nephridiopores, and gonopores to a more anterior position, corresponding to the new position of the mantle cavity. It should be noted however, that the actual position and arrangement of the mantle cavity and its associated structures show great variation; in many gastropods these structures, while pointing forward, may actually be positioned further towards the posterior region of the animal's body. Torsion is not a perfectly symmetrical process.

Most of the stories of gastropod evolution focus on changes in the mantle cavity and its associated structures, and many of these changes seem to have been driven by some negative impacts of torsion. Many anatomical modifications of gastropods appear to be adaptations to avoid fouling, for without changing the original flow of water through the mantle cavity in a primitive gastropod with two ctenidia, waste from the centrally positioned anus (and perhaps the nephridia) would be dumped on top of the head and potentially pollute the mouth and ctenidia. Hence, it has long been hypothesized that the first step, subsequent to the evolution of torsion, was the development of slits or holes in the shell, thus altering water flow so that a one-way current passed first over the ctenidia, then over the anus and nephridiopore, and finally out the slit or shell holes. This arrangement is seen in some vetigastropods, such as the slit shells (Pleurotomarioidea) and abalone and keyhole limpets (Figures 13.1D, 13.16I, and 13.36). As reasonable as it sounds, there has been surprisingly little empirical evidence in support of this hypothesis. In addition, the adaptive significance of shell holes was examined by Voltzow and Collin (1995), who found that blocking the holes in keyhole limpets did not result in damage to the organs of the mantle cavity. Thus, the adaptive significance of torsion in gastropod evolution remains an open question.

Once evolutionary reduction or loss of the gill and osphradium on the right side had taken place, water flow through the mantle cavity was from left to right, passing through the left gill and osphradium first, then across the nephridiopore and anus, and on out the right side. This strategy also had the effect of allowing structures on the left side to enlarge and eventually to develop more control over water flow into and out of the mantle cavity, including the evolution of long siphons. While most gastropods have retained full or partial torsion, many of the heterobranch gastropods, all of which lost the original ctenidium, have undergone various degrees of detorsion, and a host of other modifications, perhaps in response to the absence of constraints originally brought on by torsion.
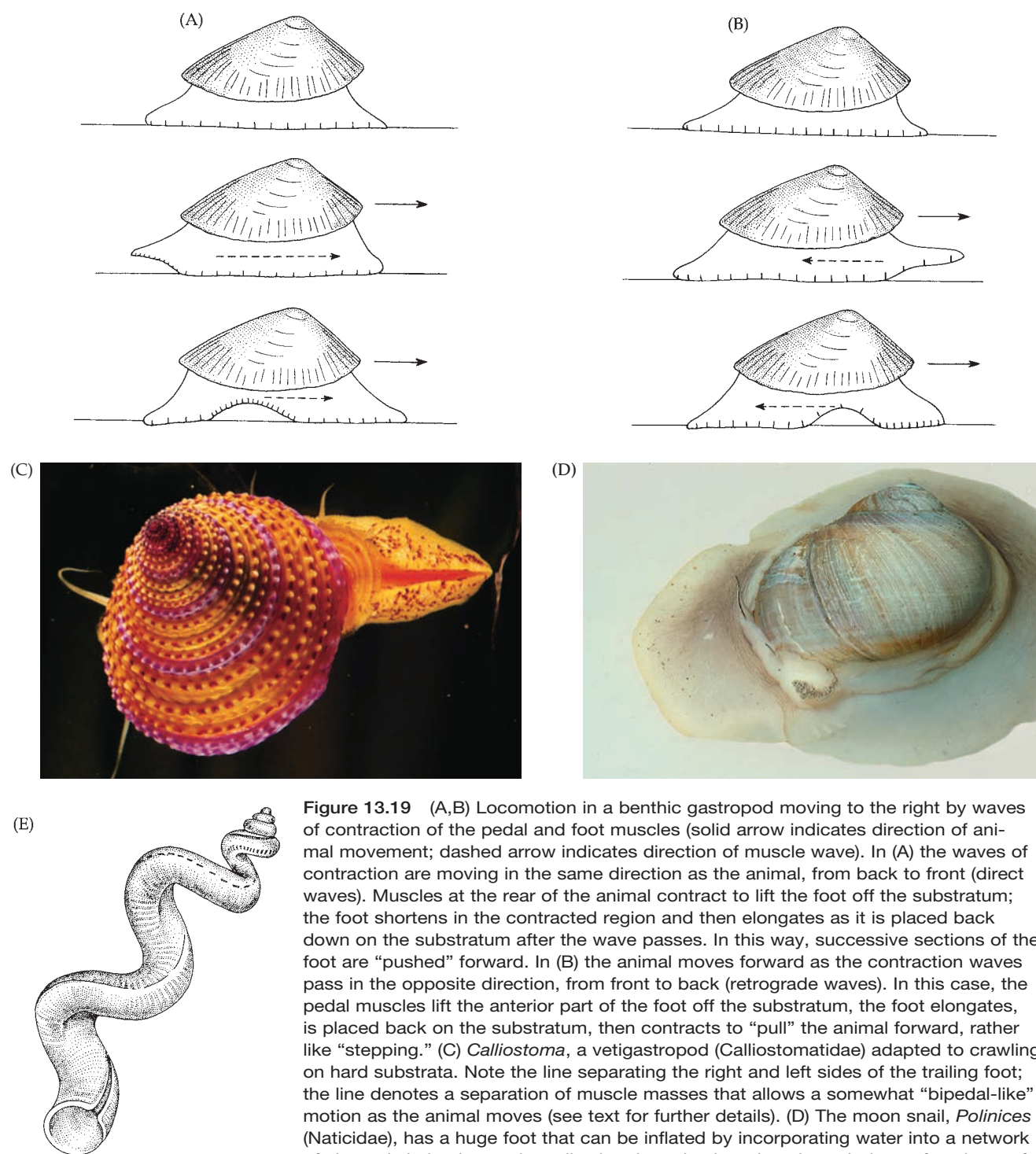
Figure 13.19 (A,B) Locomotion in a benthic gastropod moving to the right by waves of contraction of the pedal and foot muscles (solid arrow indicates direction of animal movement; dashed arrow indicates direction of muscle wave). In (A) the waves of contraction are moving in the same direction as the animal, from back to front (direct waves). Muscles at the rear of the animal contract to lift the foot off the substratum; the foot shortens in the contracted region and then elongates as it is placed back down on the substratum after the wave passes. In this way, successive sections of the foot are "pushed" forward. In (B) the animal moves forward as the contraction waves pass in the opposite direction, from front to back (retrograde waves). In this case, the pedal muscles lift the anterior part of the foot off the substratum, the foot elongates, is placed back on the substratum, then contracts to "pull" the animal forward, rather like "stepping." (C) *Calliostoma*, a vetigastropod (Calliostomatidae) adapted to crawling on hard substrata. Note the line separating the right and left sides of the trailing foot; the line denotes a separation of muscle masses that allows a somewhat "bipedal-like" motion as the animal moves (see text for further details). (D) The moon snail, *Polinices* (Naticidae), has a huge foot that can be inflated by incorporating water into a network of channels in its tissue, thus allowing the animal to plow through the surface layer of soft sediments. (E) *Tenagodus* (Siliquariidae), a sessile siliquariid worm snail.

Locomotion

The foot in aplacophorans is either rudimentary or lost (Figure 13.2). Caudofoveata are mostly infaunal burrowers and move by peristaltic movements of the body wall, using the anterior mouth shield as a burrowing device and anchor. The foot of solenogasters is only weakly muscular, and locomotion is primarily by slow ciliary gliding movements through or upon the substratum. Caudofoveata are mostly infaunal burrowers,

and Solenogastres are largely symbiotic on various cnidarians. With the exception of these two groups, most other molluscs possess a distinct and obvious foot, with the exception of the cephalopods where it is very highly modified. In chitons, monoplacophorans and most gastropods the foot often forms a flat, ventral, creeping sole (Figures 13.3B, 13.4B, 13.5B, and 13.19). The sole is ciliated and imbued with numerous gland

cells that produce a mucous trail over which the animal glides. In gastropods, enlarged pedal glands supply substantial amounts of mucus (slime), this being especially important in terrestrial species that must glide on relatively dry surfaces. In most gastropods, there is an anterior mucus gland, which opens in a slit on or just behind the anterior edge of the foot. This anterior lobe is called the **propodium**, the rest of the foot the **metapodium**. In some caenogastropods, an enlarged metapodial mucus gland opens into the middle of the sole. Small molluscs may move largely by ciliary propulsion but most move primarily by waves of muscular contractions that move along the foot.

The gastropod foot possesses sets of pedal retractor muscles, which attach to the shell and dorsal mantle at various angles. These and smaller muscles in the foot act in concert to raise and lower the sole or to shorten it in either a longitudinal or a transverse direction. Contraction waves may move from back to front (direct waves), or from front to back (retrograde waves) (Figure 13.19A,B). Direct waves depend on contraction of longitudinal and dorsoventral muscles beginning at the posterior end of the foot; successive sections of the foot are thus "pushed" forward. Retrograde waves involve contraction of transverse muscles interacting with hemocoelic pressure to extend the anterior part of the foot forward, followed by contraction of longitudinal muscles. The result is that successive areas of the foot are "pulled" forward (Figure 13.19A,B). In some gastropods the muscles of the foot are separated by a midventral line, so the two sides of the sole operate somewhat independently of each other. The right and left sides of the foot alternate in their forward motion, almost in a stepping fashion, resulting in a sort of "bipedal" locomotion.

Modifications of this general benthic locomotory scheme occur in many groups. Some gastropods, such as moon snails (Figure 13.19D), plow through the sediment, and some even burrow beneath the sediment surface. Such gastropods often possess an enlarged, shield-like propodium that acts like a plough and some naticids and cephalaspideans possess a dorsal flaplike fold of the foot that covers the head as a protective shield. Other burrowers, such as augers, dig by thrusting the foot into the substratum, anchoring it by engorgement with hemolymph, and then pulling the body forward by contraction of longitudinal muscles. In the conch *Strombus*, the operculum forms a large "claw" that digs into the substratum and is used as a pivot point as the animal thrusts itself forward like a pole-vaulter using its muscular, highly modified foot. In some heterobranchs, notably the sea hares (Aplysidae), lateral flaps of the foot expand dorsally as parapodia and these fuse dorsally in some species.

Some molluscs that inhabit high-energy littoral habitats, such as chitons and limpets, have a very broad foot that can adhere tightly to hard substrata. Chitons also use their broad girdle for additional adhesion to the substratum by clamping down tightly and raising the inner margin to create a slight vacuum. Some snails, such as the Vermetidae and Siliquariidae are entirely sessile, the former attached to hard substrata, the latter (Figure 13.19E) living in sponges. These gastropods have typical larval and juvenile shells; but after they settle and start to grow, the shell whorls become increasingly separated from one another, resulting in a corkscrew or twisted shape. Other gastropods, such as slipper shells, are sedentary. They tend to remain in one location and feed on organic particles in the surrounding water. The sole of the hipponicid limpets secretes a calcareous plate and the adults are thus oyster-like and deposit feed using their long snout.

Some limpets and a few chitons exhibit homing behaviors. These activities are usually associated with feeding excursions stimulated by changing tide levels or darkness, after which the animals return to their homesites which is seen as a scar or even a depression on the rock surface. Homing behaviors are also seen in some land snails and slugs.

Most bivalves live in soft benthic habitats, where they burrow to various depths in the substratum (Figure 13.20E–I). In these infaunal species the foot is usually blade-like and laterally compressed (the word pelecypod means "hatchet foot"), as is the body in general. The pedal retractor muscles in bivalves are somewhat different from those of gastropods, but they still run from the foot to the shell (Figure 13.8D). The foot is directed anteriorly and used primarily in burrowing and anchoring. It operates through a combination of muscle action and hydraulic pressure (Figure 13.20A–D). Extension of the foot is accomplished by engorgement with hemolymph, coupled with the action of a pair of pedal protractor muscles. With the foot extended, the valves are pulled together by the shell adductor muscles. More hemolymph is forced from the visceral mass hemocoel into the foot hemocoel, causing the foot to expand and anchor in the substratum. Once the foot is anchored, the anterior and posterior pairs of pedal retractor muscles contract and pull the shell downward. Withdrawal of the foot into the shell is accomplished by contraction of the pedal retractors coupled with relaxation of the shell adductor muscles. Many infaunal bivalves burrow upward in this same manner, but others back out by using hydraulic pressure to push against the anchored end of the foot. Most motile bivalves possess well-developed anterior and posterior adductor muscles (the dimyarian condition).

There are several groups of bivalves that have epifaunal lifestyles and are permanently attach to the substratum either by cementing one valve to a hard surface as in the true oysters such as the rock oysters (Ostreidae) and rock scallops (Spondylidae). Others use special anchoring threads (**byssal threads**), as
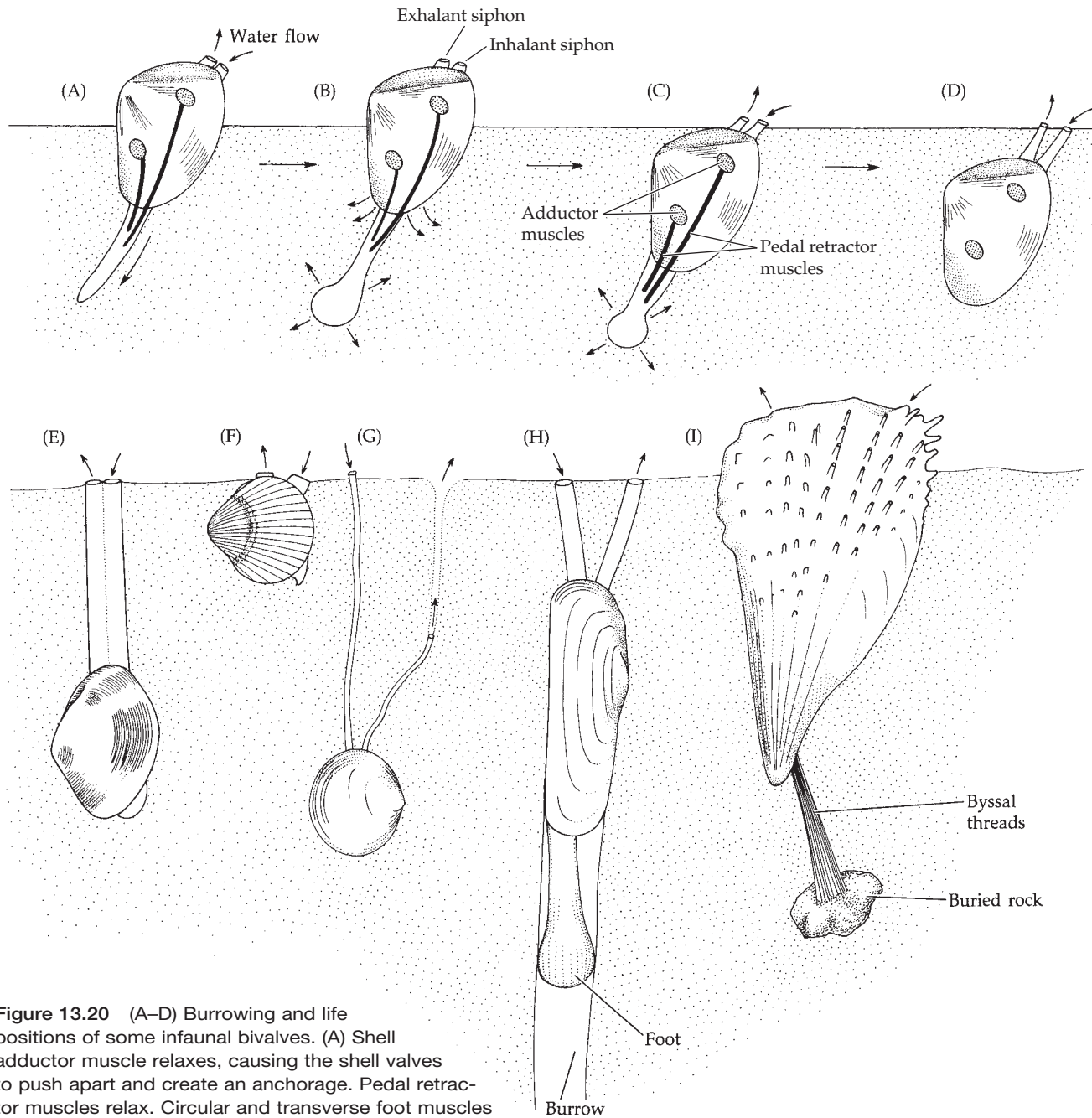
Figure 13.20 (A–D) Burrowing and life positions of some infaunal bivalves. (A) Shell adductor muscle relaxes, causing the shell valves to push apart and create an anchorage. Pedal retractor muscles relax. Circular and transverse foot muscles cotract, causing the foot to extend into the substratum. (B) Hemolymph is pumped into the tip of the foot, causing it to expand and form an anchorage. Siphons close and withdraw as the shell adductor muscles contract, closing the shell and forcing water out between the valves and around the foot. (C) Anterior and posterior pedal retractor muscles contract, pulling the clam deeper into substratum. (D) The shell adductor muscle relaxes to allow shell valves to push apart and create an anchorage in the new position. The foot is withdrawn. (E–I) Five bivalves in soft sediments; arrows indicate direction of water flow. (E) A deep burrower with long, fused siphons (*Tresus*). (F) A shallow burrower with very short siphons (*Clinocardium*). (G) A deep burrower with long, separate siphons (*Scrobicularia*). (H) The razor clam (*Tagelus*) lives in unstable sands and maintains a burrow into which it can rapidly escape. (I) The pen shell, *Atrina*, attaches its byssal threads to solid objects buried in soft sediments.

in mussels (Mytilidae) (Figure 13.21A,B), ark shells, and a number of other families including winged or pearl oysters (Pteriidae), and numerous other pteriomorphian bivalves including the Pinnidae and many Arcidae and Pectinidae. While the juveniles of many heterodont bivalves produce one or a few temporary byssal threads, a few species, such as the zebra mussel (*Dreissena*), remain byssally attached as adults.

The true oysters (Ostreidae) (including the edible American and European oysters) initially anchor as a settling veliger larva (called a **spat** by oyster farmers) by secreting a drop of adhesive from the byssus gland. Adults, however, have one valve permanently

cemented to the substratum, with the cement being produced by the mantle.

Byssal threads are secreted as a liquid by the **byssus gland** in the foot. The liquid flows along a groove in the foot to the substratum, where each thread becomes tightly affixed. The threads are emplaced by the foot; once attached they quickly harden by a tanning process, whereupon the foot is withdrawn. A byssal thread retractor muscle may assist the animal in pulling against its anchorage. Mussels have a small, finger-like foot whose principal function is generation and placement of the byssal threads. Giant clams (Cardiidae) initially attach by byssal threads, but usually lose these as they mature and become heavy enough not to be cast about

by currents (Figure 13.1N). In jingle shells (Anomiidae), the byssal threads run from the upper valve through a hole in the lower valve to attach to the substratum after which they become secondarily calcified. Byssal threads probably represent a primitive and persisting larval feature in those groups that retain them into adulthood, and many bivalves lacking byssal threads as adults utilize them for initial attachment during settlement.

Figure 13.21 More bivalves. (A) A "bed" of mussels (*Mytilus californianus*) attached by byssal threads (close up of two mussels). (B) A mussel (lateral view, with left valve removed). (C) Shell of the Mesozoic rudist clam *Coralliochama*. (D) The wood-boring bivalve (shipworm) *Teredo*. The pallets (only one is shown) are a pair of shelly plates that close over the siphons when they are retracted. (E) A shipworm-bored piece of driftwood (notice the thousands of small holes). (F) A pholad-bored rock. The pholad can be seen in its bore hole.

(A)

(B)

(C)

(D)

(E)

(F)

In many families of attached bivalves, such as mussels and true oysters, the foot and anterior end are reduced. This often leads to a reduction of the anterior adductor muscle (**anisomyarian condition**) or its complete loss (**monomyarian condition**).

Great variation occurs in shell shape and size among attached bivalves. Some of the most remarkable were the Mesozoic rudists, in which the lower valve was horn-like and often curved, and the upper valve formed a much smaller hemispherical or curved lid (Figure 13.21C). Rudists were large, heavy creatures that often formed massive reef-like aggregations, either by somehow attaching to the substratum or by simply accumulating in large numbers on the seabed, in "log jams." These accumulations of fossil shells provide the spaces in which oil deposits formed in sediments in many parts of the Middle East and Caribbean.

Some originally attached bivalves have evolved to live freely upon the sea floor (e.g., some Pectinidae and Limidae) (Figure 13.1M). Some are capable of short bursts of "jet-propelled" swimming, which is accomplished by quickly clapping the valves together.

The habit of boring into hard substrata has evolved in several different bivalve lines. In all cases, excavation begins soon after larval settlement. As the animal bores deeper, it grows in size and soon becomes permanently trapped, with only the siphons protruding out of the original small opening. Boring is usually by a mechanical process; the animal uses serrations on the anterior region of the shells to abrade or scrape away the substratum. Some species also secrete an acidic mucus that partially dissolves or weakens hard calcareous substrata (limestone, coral, large dead shells). Some species bore into wood, such as *Martesia* (Phaladidae), *Xylophaga* (Xylophagidae), and nearly all species in the family Teredinidae (*Bankia*, *Teredo*). Teredinids, with their long wormlike bodies, are known as shipworms because of the destruction that they can cause to the wooden hulls of ships (or to wood pier pilings). In the teredinids the shells are reduced to small anterior bulb-like valves that serve as the drilling apparatus (Figure 13.21D,E). Some pholads bore into soft stone (e.g., *Pholas*), or into other substrata (e.g., *Barnea*; Figure 13.21E). Some species in the family Mytilidae also are borers, such as *Lithophaga*, which bores by mechanical and possibly chemical means into calcareous rocks, shells of various other molluscs (including chitons), and corals, and the genus *Adula*, which bores into soft rocks.

Scaphopods are adapted to infaunal habitats, burrowing vertically by the same basic mechanism used by many bivalves (Figures 13.1L and 13.9). The elongate foot is projected downward into soft substrata, whereupon a rim in the distal part of the foot is expanded to serve as an anchoring device; contraction of the pedal retractor muscles pulls the animal downward.

Perhaps the most remarkable locomotory adaptation of molluscs is swimming, which has evolved in several different taxa in several different ways, including by valve flapping in scallops. In most others of these groups, the foot is modified as the swimming structure. In the unique caenogastropod group known as heteropods, the body is laterally compressed, the shell is greatly reduced, the foot forms a fin, and the animal swims upside down (Figure 13.7A–C). Swimming has evolved several times in the heterobranchs, including the pteropods (sea butterflies), where the parapodial extensions of the foot form two long lateral fins that are used like oars (Figure 13.7D,E). Some nudibranchs also swim by graceful undulations of flaplike parapodial folds along the body margin or by vigorous undulations of the body. Although not technically swimming, violet shells (*Janthina*) float about the ocean's surface on a raft of bubbles secreted by the foot, and some planktonic nudibranchs (e.g., *Glaucus*, *Glaucilla*) stay afloat by use of an air bubble held in the stomach!

The champion swimmers are, of course, the cephalopods (Figures 13.1J,K and 13.22). These animals have abandoned the generally sedentary habits of other molluscs and have become highly effective swimming predators. Virtually all aspects of their biology have evolved to exploit this lifestyle. Most cephalopods swim by rapidly expelling water from the mantle cavity. In the coleoid cephalopods the mantle has both radial and circular muscle layers. Contraction of the radial muscles and relaxation of the circular muscles draws water into the mantle cavity while reversal of this muscular action forces water out of the mantle cavity. The mantle edge is clamped tightly around the head to channel the escaping water through a ventral tubular **funnel**, or **siphon** (Figure 13.11B,C). The funnel is highly mobile and can be manipulated to point in nearly any direction, thus allowing the animal to turn and steer. Squids attain the greatest swimming speeds of any aquatic invertebrates, and several species can even leave the water and propel themselves many feet into the air. Most octopuses are benthic and lack the fins and streamlined bodies characteristic of squids. Although octopuses still use water-powered jet propulsion, they more commonly rely on their long suckered arms for crawling about the sea floor. Some octopuses have even been observed moving about upright on only two tentacles—bipedal locomotion! Cuttlefish are slower than squids, and often use their fins for forward swimming as well as stabilization and to assist in steering and propulsion.

Nautilus move up and down in the water column on a diurnal cycle, often traveling hundreds of meters in each direction. They can actively regulate their buoyancy by secretion and reabsorption of shell chamber gases (chiefly nitrogen) by the cells of the siphuncle. The unoccupied chambers of these shells are filled partly with gas and partly with a liquid called the **cameral fluid**. The septa act as braces, giving the shells enough strength to withstand pressures at depth. As discussed

earlier, each septum in nautiloid shells is perforated by a small hole, through which runs the siphuncle, which originates in the viscera and is enclosed in a porous calcareous tube. Various ions dissolved in the cameral fluid can be pumped through the porous outer layers into the cells of the siphuncular epithelium. When the cellular concentration of ions is high enough, the diffusion gradient thus created draws fluid from the shell chambers into the cells of the siphuncle while the fluid is replaced with gas. The result is an increase in buoyancy. By regulating this process, *Nautilus* may be able to remain neutrally buoyant at whatever depth they are. It was once thought that this gas–fluid "pump" mechanism allowed buoyancy changes sufficient to explain all the large-scale vertical movements of *Nautilus*, but density changes may not be the sole source of power for moving great distances up and down in the water column. *Nautilus* moves using jet propulsion by rapidly contracting its head, not by mantle muscle contraction.

Feeding

Two basic and fundamentally different types of feeding occur among molluscs: the first encompasses the feeding modes of most molluscs and includes micro- to macrophagy involving browsing and scraping, herbivory, carnivorous grazing and predation, while the second is suspension feeding (suspension microphagy). The basic mechanics of these two feeding modes are examined in Chapter 4. Here we briefly summarize the ways in which these feeding behaviors are employed by molluscs. In this section we also discuss a uniquely molluscan structure, the radula, which is used in microphagy, herbivory, and predation, and has become modified in a variety of unusual and interesting ways.

The buccal cavity may contain a pair of lateral jaws (or a single dorsal jaw), muscularized regions with chitinous plates that can be solid or composed of multiple small units. Molluscan jaws are highly variable. For example, in some heterobranchs the jaws can be quite complex, with distinct "teeth," in some carnivorous caenogastropods the jaws can be quite large, in cephalopods the jaws are modified to form the beak, and some lineages have no jaws at all including bivalves, which lack both jaws and radula.

The radula is usually a ribbon of recurved chitinous teeth (Figures 13.23–13.26). The teeth may be simple, serrate, pectinate, or otherwise modified. The radula often functions as a scraper to remove food particles for ingestion, although in many groups it has become adapted for other actions. A radula is present in the majority of the most primitive living molluscs and is therefore assumed to have originated in the earliest stages of molluscan evolution. In the aplacophoran groups the teeth, when present, may not be borne on a ribbon per se but on a relatively thin cuticle covering the foregut epithelium—perhaps the evolutionary forerunner of the ribbon-like radula. In some aplacophorans, the teeth form simple plates embedded in either side of the lateral foregut wall, while in others they form a transverse row, or up to 50 rows, with as many as 24 teeth per row.

(A)

Figure 13.22   Swimming cephalopods. (A) *Sepia*, the cuttlefish. (B) *Nautilus*. (C) *Vampyroteuthis*, a "vampire" squid, viewed from the side.

(B)

(C)

Figure 13.23 A generalized molluscan radula and associated buccal structures, at three "magnifications" (longitudinal section).

In gastropods and other molluscs (except bivalves) an **odontophore** projects from the floor of the pharynx or buccal cavity. It is a muscular structure bearing the complex tooth-bearing radular ribbon (Figure 13.23). The ribbon, called a **radular membrane**, is moved back and forth by sets of radular protractor and retractor muscles over cartilages encased in the odontophore (Figure 13.23). These cartilages are absent in many heterobranch gastropods. The radula originates in a **radular sac**, in which the radular membrane and new teeth are continually being produced by special cells called **odontoblasts**, to replace those lost by erosion during feeding. Measurements of radular growth indicate that up to five rows of new teeth may be added daily in some species. The odontophore itself is moved in and out of the buccal cavity during feeding by sets of odontophore protractor and retractor muscles, which also assist in applying the radula firmly against the substratum (Figures 13.23 and 13.24A,B).

The number of radular teeth ranges from a few to thousands and serves as an important taxonomic character in many groups. In some molluscs, the radular teeth are hardened with iron compounds, such as magnetite (in chitons) and goethite (in patellogastropods). Just as in many vertebrates, the radular teeth show adaptations to the type of food eaten. In vetigastropods (e.g., keyhole limpets, abalones, top shells), the **rhipidoglossate radulae** bear large numbers of fine marginal teeth in each row (Figures 13.25A and 13.26A). As the radula is pulled

over the bending plane of the odontophore, these teeth act like stiff brushes, sweeping small particles to the midline where they are caught on the recurved parts of the central teeth, which draw the particles into the buccal cavity. Most vetigastropods are intertidal foragers

Figure 13.24 Feeding in macrophagous molluscs.
(A) Cutting and scraping action of a gastropod radula.
(B) A boring gastropod, the moon snail *Natica*, with radula visible in the mouth and the boring gland exposed (oral view). (C) The Pacific chiton *Placiphorella velata* in feeding position, with raised head flap ready to capture small prey.
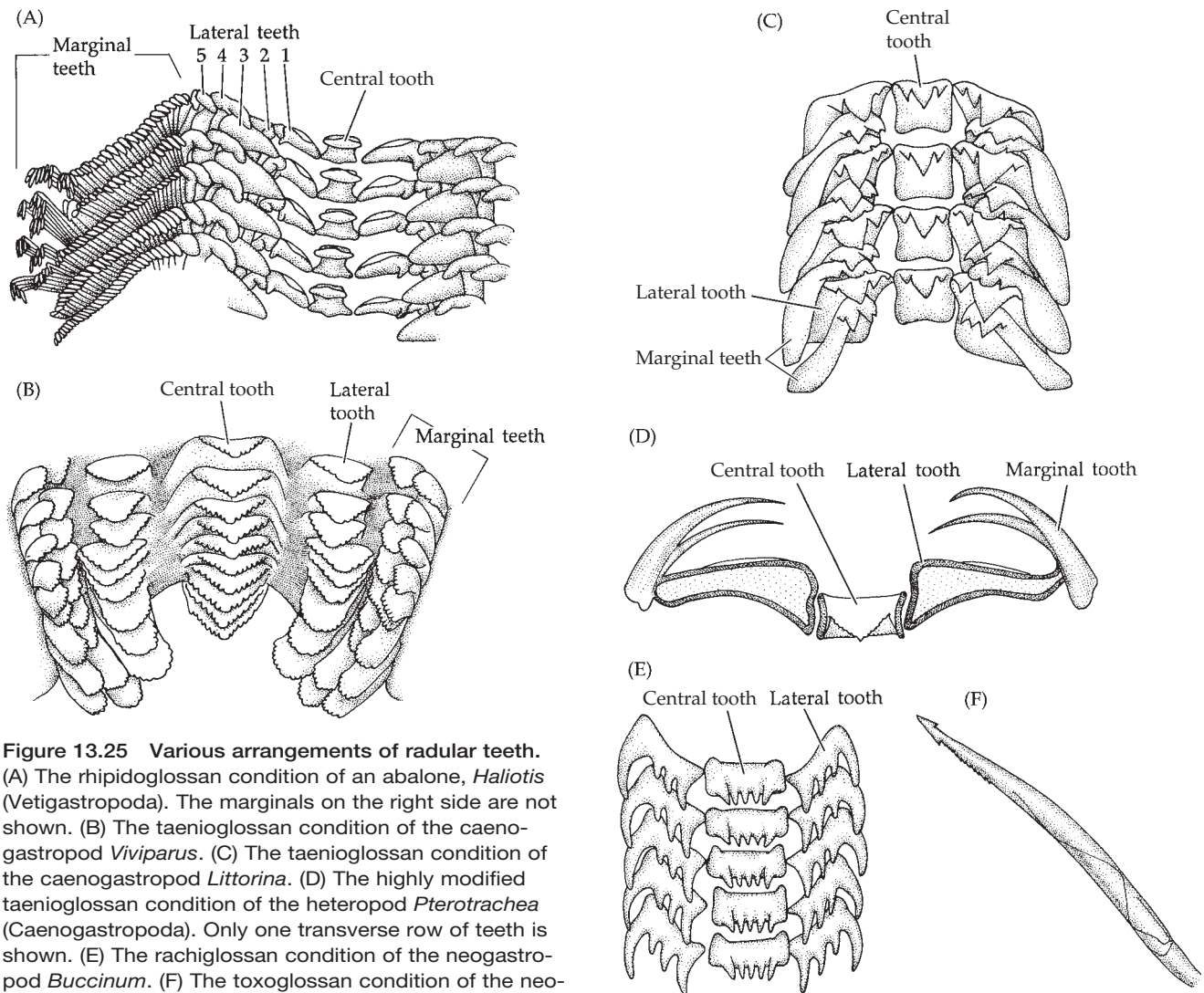
Figure 13.25 Various arrangements of radular teeth.
(A) The rhipidoglossan condition of an abalone, *Haliotis*
(Vetigastropoda). The marginals on the right side are not
shown. (B) The taenioglossan condition of the caeno-
gastropod *Viviparus*. (C) The taenioglossan condition of
the caenogastropod *Littorina*. (D) The highly modified
taenioglossan condition of the heteropod *Pterotrachea*
(Caenogastropoda). Only one transverse row of teeth is
shown. (E) The rachiglossan condition of the neogastro-
pod *Buccinum*. (F) The toxoglossan condition of the neo-
gastropod *Mangelia* (a single tooth).

that live on diatoms and other algae and microbes on
the substratum. In contrast, patellogastropods (e.g., lot-
tiid and patellid limpets) possess a **docoglossate radula**,
which is impregnated with iron and bear relatively few
teeth in each transverse row. Lottiid radulae, for exam-
ple, have only one, two, or no marginal teeth, and only
three pairs of lateral teeth per row (Figure 13.26B). The
mucous trails left by some limpets (e.g., homing species
such as the Pacific *Lottia gigantea* and *Collisella scabra*) ac-
tually serve as adhesive traps for the microalgae that are
their primary food resource).

The radula of many caenogastropods is the **taenio-
glossate type**, in which there are only two marginal
teeth in each row, along with three other teeth (laterals
and central) (Figure 13.25B–D). In conjunction with the
elaboration of jaws, taenioglossate radulae are capable
of powerful rasping, which enables some littorid snails
to feed by directly scraping off the surface cell layers of
algae.

The most derived caenogastropods (Neogastro-
poda) usually have **rachiglossate radulae**, which lack

marginal teeth altogether (Figures 13.25E and 13.26C,D).
They use the remaining (one to three) teeth for rasping,
tearing, or pulling. These snails are usually carnivores
or carrion feeders although some members of one fam-
ily, the Columbellidae, are herbivores. Caenogastropods
of the families Muricidae and Naticidae eat other mol-
luscs by boring through the prey's calcareous shell
to obtain the underlying flesh. This ability to bore has
evolved entirely independently in the two groups. It is
mainly mechanical; the predator boring with its radula
while holding the prey with the foot. The boring activity
is complemented by the secretion of an acidic chemical
from a **boring gland** (also called the "accessory boring
organ"); the chemical is periodically applied to the drill
hole to weaken the calcareous matrix. The boring gland
of the neogastropod muricids is located on the foot
while that of the littorinimorph naticids is located on the
anterior end of the proboscis (Figure 13.24B). Boring gas-
tropods such as the American drill (*Urosalpinx*) and the
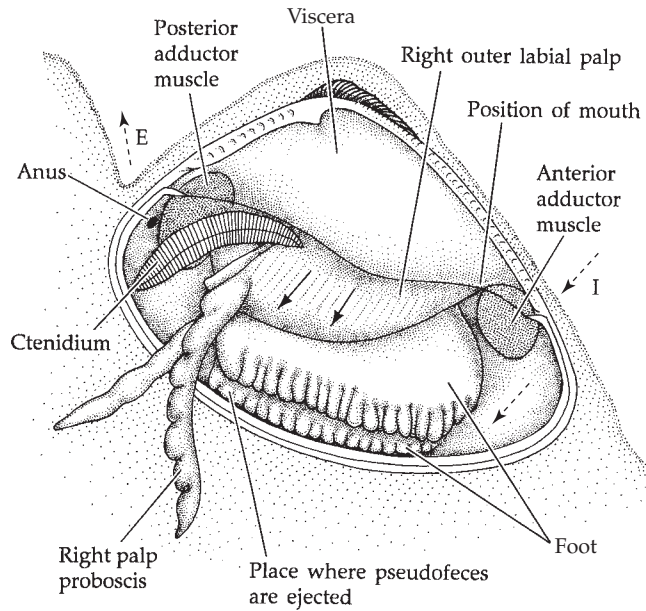Japanese drill (*Rapana*) cause a loss of millions of dollars
annually for oyster farms.

Figure 13.26   Gastropod radulae.
(A) A closeup view of the rhipidoglossate radula of the abalone *Haliotis rufescens* (Vetigastropoda). Note the many hook-like marginal teeth. (B) The docoglossate radula of a lottiid limpet. (C) The serrated central teeth of a rachiglossate radula from the muricid whelk *Nucella emargina-ta*, a neogastropod (Caenogastropoda) that preys on small mussels and barna-cles. (D) The worn radular teeth of *Nucella*. (E) The radula of the polycerid nudibranch *Triopha*, seen here in dorsal view as it rests in the animal.

Some carnivorous gastropods (e.g., *Janthina*) do not gnaw or rasp their prey, but swallow it whole. In these gastropods a **ptenoglossate radula** forms a cov-ering of strongly curved spines over the buccal mass. The prey is seized by the quickly extruded buccal mass and simply pulled whole into the gut. A some-what similar feeding method is seen in the carnivorous slug *Testacella*, where the hooked radula catches earth-worms that the slug consumes whole. The nudibranch *Melibe* (chapter opener photo) uses its large hood to sweep the water for copepods, amphipods, and other small planktonic prey.

A few gastropods have lost the radula altogether and feed by sucking body fluids from their prey, a habit seen, for example, in some nudibranchs. Pyramidellids do this with the aid of a hypodermic stylet (a modified jaw) on the tip of an elongate proboscis.

One of the most specialized feeding modes in gas-tropods is seen in the cone snails (*Conus*), and rela-tives. Their toxoglossate radula is formed from a few harpoon-like, venom injecting teeth that are probably modified marginal teeth. The teeth (Figure 13.25F) are discharged from the end of a long proboscis that can be extended very rapidly to capture prey, usually a fish, a worm, or another gastropod, which is then pulled into the gut (Figure 13.27). The venom is injected through the hollow, curved radular teeth by contraction of a

venom gland. A few Indo-West Pacific cones produce a potent neuromuscular toxin that has caused human deaths.

Among the most unusual gastropod feeding strate-gies are those that involve parasitism on fishes. For ex-ample, the neogastropod *Cancellaria cooperi* attaches to the Pacific electric ray and makes small cuts in the skin through which the proboscis is inserted to feed on the ray's blood and cellular fluids. Several other neogas-tropods parasitize "sleeping" reef fishes by inserting their proboscides into the host and sucking out fluids. Some other gastropods are known to parasitize vari-ous invertebrate hosts, notably the pyramidellids (on a variety of invertebrates, including other molluscs) and the Eulimidae on echinoderms, with the latter group including some internal parasites that have lost their shell and become wormlike.

Certain euthyneurans also show various radular modifications. Groups of "opisthobranchs" that feed on cnidarians, ectoprocts, and sponges, and those that scrape algae (e.g., aplysiids) usually have typical rasp-ing radulae. In sacoglossans, however, the radula is modified as a single row of lance-like teeth that can pierce the cellulose wall of filamentous algae, allowing the gastropod to suck out the cell contents. A similar type of feeding strategy is also seen in the microscopic lower heterobranch *Omalogyra*.

Figure 13.27 **Sequence of photographs of a cone shell (*Conus*) capturing and swallowing a small fish.** The proboscis is extended and swept back and forth above the substratum in search of prey; when a fish is encountered, a poison-charged tooth of the toxoglossan radula is fired like a harpoon; and the prey is quickly paralyzed and ingested.

Aeolid nudibranchs (Figure 13.7G) have a well-deserved reputation for their particular mode of feeding, in which portions of their cnidarian prey are held by the jaws while the radula rasps off pieces for ingestion. A similar mode of feeding has also been observed in the caenogastropod family Epitoniidae.

Many aeolid nudibranchs engage in a remarkable phenomenon called **kleptocnidae**. Some of the prey's nematocysts are ingested unfired, passed through the nudibranch's gut, and eventually transported to lobes of the digestive gland in dorsal finger-like extensions called **cerata** (singular, ceras) (Figure 13.32D,E). How the nematocysts undergo this transport without firing is still a mystery. Popular hypotheses are that mucous secretions by the nudibranch limit the discharge, or that a form of acclimation occurs (like that suspected to

occur between anemone fishes and their host anemones), or perhaps that only immature nematocysts survive, to later undergo maturation in the dorsal cerata. It may also be that, once the cnidocytes are digested, the nematocysts' firing threshold is raised, thereby preventing discharge. In any case, once in the cerata the nematocysts are stored in structures called cnidosacs and presumably help the nudibranch to fend off attackers. Discharge might even be under the control of the host nudibranch, perhaps by means of pressure exerted by circular muscle fibers around each cnidosac.

Some dorid nudibranchs also utilize their prey in remarkable ways. Many dorids secrete complex toxic compounds incorporated into mucus released from the mantle surface. These noxious chemicals act to deter potential predators. While some of these chemicals may be manufactured in some dorids, in most cases it appears that they are obtained from the sponges or ectoprocts on which they feed. Some species, such as the "Spanish dancer" nudibranch (*Hexabranchus sanguineus*), not only use a chemical from their prey (in this case a sponge) for its own defense, but deposit some of the noxious chemical on the egg mass, helping to protect the embryos until they hatch.

In polyplacophorans there are generally 17 teeth in each transverse row of the radula (a central tooth flanked by eight on each side). Most chitons are herbivorous grazers. Notable exceptions are certain members of the order Ischnochitonida (family Mopaliidae, e.g., *Mopalia*, *Placiphorella*), which are known to feed on both algae and small invertebrates. *Mopalia* consumes sessile invertebrates, such as barnacles, ectoprocts, and hydroids. *Placiphorella* captures live microinvertebrates (particularly crustaceans) by trapping them beneath its head-flap, a large anterior extension of the girdle (Figure 13.24C).

In monoplacophorans the radula consists of a ribbon-like membrane bearing a succession of transverse rows of 11 teeth each (a slender central tooth flanked on each side by five broader lateral teeth). Monoplacophorans are probably generalized deposit feeders that graze on minute organisms coating the substratum on which they live.

Cephalopods are predatory carnivores. Squids are some of the most voracious creatures in the sea, successfully competing with fishes. Octopuses are also active carnivores, preying primarily on crabs, bivalves and gastropods. Some species of *Octopus* bore through the shells of molluscan prey in a fashion similar to that of gastropod drills. Some even drill and prey upon their close relatives, the chambered nautiluses. They do not use the radula to drill, but instead use a rasp-like projection formed from the salivary papilla.

Using their impressive locomotor skills, most cephalopods hunt and catch active prey. Some octopuses, however, hunt "blindly," by tasting beneath stones with their highly sensitive suckers that are both

Figure 13.28 Arrangement of ctenidia in some bivalves (transverse sections) showing the following conditions: (A) protobranch, (B) lamellibranch, (C) septibranch.

mechano- and chemosensitive. In any event, once prey is captured and held by the arms, the cephalopod bites it with its horny beak (modified jaws) and injects a neurotoxin from modified salivary glands. This ability to quickly immobilize prey also helps prevent the soft-bodied cephalopod from being engaged in a potentially dangerous struggle.

Suspension feeding evolved in autobranch bivalves, and also several times in gastropods, and in most of these cases it involves modifications of the ctenidia that enabled the animal to trap particulate matter carried into the mantle cavity by incoming respiratory water current. The lamellar nature of molluscan gills exapted them for extracting suspended food particles. Increasing the size of the gills and the degree of folding also increased the surface area available for trapping particulate material. In suspension feeders, at least some of the gill and mantle cilia, which otherwise serve to remove potentially clogging sediment from the mantle cavity (as pseudofeces), are preadapted to transport particulate matter from the gills to the mouth region.

While collecting food on the gills has been adopted by autobranch bivalves and some groups of gastropods, other methods have also been employed. In the gill-less planktonic sea butterflies (pteropods), the ciliated "wings" or parapodia used for swimming (Figure 13.7D,E) also function as food-collecting surfaces or may cooperate with the mantle to produce large mucous sheets that capture small zooplankton. From the foot, ciliary currents carry mucus and food to the mouth. In some pteropods, the mucous sheet may be as large as 2 m across. Mucous sheet feeding is also employed by a few other gastropods including the intertidal limpet-like Trimusculidae and the vermetids (see below). However, the majority of suspension feeding gastropods, including a few vetigastropods such as the sand-beach trochids (*Umbonium, Bankivia*), the hot vent neomphalid (*Neomphalus*), and some marine caenogastropods (Calyptraeidae, e.g., *Crepidula*; Vermetidae,

e.g., *Vermetus*; Turritellidae, e.g., *Turritella*) and the freshwater Viviparidae (e.g., *Viviparus*). The ctenidial filaments in these filter feeders are much elongated and the mantle waste rejection cilia have evolved into a food collecting groove that runs to the mouth. The radula in suspension-feeding gastropods is somewhat reduced, serving mainly to pull mucus-bound food into the mouth. Some feed entirely by suspension feeding, others use browsing to supplement this method.

The wormlike shell of the vermetids is permanently affixed to the substratum and while some adopt ciliary food collecting, others combine this with mucous net collecting or use the latter method exclusively. A special pedal gland in the reduced foot produces copious amounts of mucus that spreads into the water column as a sticky plankton trap. Periodically the net is hauled in by the foot and pedal tentacles, and a new one is quickly secreted. *Thylacodes arenarius*, a large Mediterranean species, casts out individual threads up to 30 cm long, whereas the gregarious California species *Thylacodes squamigerus* forms a communal net shared by many individuals.

The radula apparently disappeared early in the course of bivalve evolution, and in living species there is no trace of this structure or even the buccal cavity that contained it. Most autobranch bivalves use their large ctenidia for suspension feeding but the more primitive bivalves in the subclass Protobranchia are not suspension feeders but engage in a type of deposit-feeding microphagy. Protobranchs live in soft marine sediments and maintain contact with the overlying water either directly (e.g., *Nucula*) or by means of siphons (e.g., *Nuculana*, *Yoldia*). The two ctenidia are small, conforming to the primitive molluscan bipectinate plan of an elongated axis carrying a double row of lamellae (Figures 13.28A and 13.29). Protobranchs feed by means of two pairs of large labial palps flanking the mouth. The two innermost palps are the short **labial palps**, and the two outermost palps are formed into tentacular processes called **proboscides** (each being called a **palp proboscis**), which can be extended beyond the shell (Figure 13.29). During feeding the

Figure 13.29 **Feeding in the primitive bivalve *Nucula* (Protobranchia).** The clam is seen from the right side, in its natural position in the substratum (right valve and right mantle skirt removed). Arrows show direction of ciliary currents in the mantle cavity and on the palps. Water currents are also shown in the (I) inhalant region and (E) exhalant region.

proboscides are extended into the bottom sediments. Detrital material adheres to the mucus-covered surface of the proboscides and is then transported by cilia to the labial palps, which function as sorting devices. Low-density particles are carried to the mouth; heavy particles are carried to the palp margins and ejected into the mantle cavity.

In the suspension feeding subclass Autobranchia, lateral cilia on the ctenidia generate a water current from which suspended particles are gleaned. Increased efficiency is achieved by various ctenidial modifications. The primary modification, seen in all living autobranch bivalves, has been the conversion of the original, small, triangular plates into V-shaped filaments with extensions on either side (Figures 13.28B and 13.30B). The arm of this V-shaped filament that is attached to the central axis of the ctenidium is called the descending arm; the arm forming the other half of the V is the ascending arm. The ascending arm is usually anchored distally by ciliary contacts or tissue junctions to the roof of the mantle, or to the visceral mass. Taken together, the two V-shaped filaments, with their double row of leaflets, form a W-shaped structure when seen in cross section.

Some pteriomorphian autobranch bivalves have **filibranch** ctenidia (e.g., mussels) wherein adjacent filaments are interlocked to one another by periodic clumps of specialized cilia, leaving long narrow slits in between (interfilament spaces) (Figure 13.30C,D). The spaces between the arms of the W's are exhalant suprabranchial chambers, which merge with the exhalant

area in the posterior mantle cavity to be discharged; the spaces ventral to the W's are inhalant and communicate with the inhalant area of the mantle edge. Many other bivalves have **eulamellibranch** ctenidia, which are similar to the filibranch design but neighboring filaments are fused to one another by actual tissue junctions at numerous points along their length. This arrangement results in interfilament pores that are rows of ostia rather than the long narrow slits of filibranchs (Figure 13.30B,E,F). In addition, the ascending and descending halves of some filaments may be joined by tissue bridges that provide firmness and strength to the gill.

Both filibranch and eulamellibranch ctenidia are used to capture food. Water is driven from the inhalant to the exhalant parts of the mantle cavity by lateral cilia all along the sides of filaments in filibranchs, or by special lateral ostial cilia in eulamellibranchs (Figure 13.30E–F). As the water passes through the interfilament spaces it flows through rows of frontolateral cilia, which flick particles from the water onto the surface of the filament facing into the current. These feeding cilia are called **compound cirri**; they have a pinnate structure that probably increases their catching power. Mucus presumably plays some part in trapping the particles and keeping them close to the gill surface, although its precise role is uncertain. Bivalve ctenidia are not covered with a continuous sheet of mucus, as occurs in many other suspension-feeding invertebrates (e.g., gastropods, tunicates, amphioxus). Once on the filament surface, particles are moved by frontal cilia toward a food groove on the free edges of the ctenidium, and then anteriorly to the labial palps. The palps sort the material by size and perhaps also by quality before passing the food to the mouth. Rejected particles fall off the gill or palp edges into the mantle cavity as **pseudofeces**. This "filtration" of water by bivalves is quite efficient. The American oyster (*Crassostrea virginica*), for example, can process up to 37 liters of water per hour (at 24°C), and can capture particles as small as 1 µm in size. Studies on the common mussels *Mytilus edulis* and *M. californianus* suggest that these bivalves maintain pumping rates of about 1 liter per hour per gram of (wet) body weight.

Members of the superfamily Tellinoidea (including Tellinidae and Semelidae) are deposit feeders, sucking up surface detritus with their long, mobile inhalant siphon (Figure 13.20G) and using the large labial palps to pre-sort the particles before ingesting them.

Some members of the order Poromyata (Anomalodesmata) are known as septibranchs and are sessile predators and, unlike other autobranch bivalves, their gills are not used for feeding. Instead the ctenidia are very reduced and modified as a perforated but muscular septum that divides the mantle cavity into dorsal and ventral chambers (Figures 13.28C and 13.31A). The muscles are attached to the shell such that the septum can be raised or lowered within the mantle cavity. Raising the septum causes water to be sucked into the

(A)

Lateral cilia

Afferent branchial vessel

Axis

Efferent branchial vessel

(B)

Exhalant space

Shell

Mantle

Ostium

Tissue connection between adjacent filaments

Connection of filament to mantle

Afferent blood vessel

Ctenidial axis

Efferent blood vessel (to atrium of heart)

Inhalant space

Descending arm of ctenidial filament

Ascending arm of ctenidial filament

Inhalant space

Tissue connection between ascending and descending arms of same filament (= interlamellar junction)

Food groove

(C)

Ciliary tuft junctions

(D)

Frontal cilia

Frontolateral cilia

Lateral cilia

Ctenidial filament

Interfilament space

Exhalant space

Tissue junction

(E)

Ostia

(F)

Ostium

Ctenidial filament

Tissue junctions

Exhalant water space

Frontolateral cirri

Frontal cilia

Lateral cilia

Figure 13.30 Ctenidial structure in bivalve molluscs. In all drawings, solid arrows indicate the direction of water flow (from inhalant space, between ctenidial filaments, to exhalant space). (A) Section through part of the gill axis in a nuculanid protobranch, showing four alternating filaments (leaflets) on each side. Dashed arrows indicate direction of hemolymph flow in the filament. (B) Highly schematic cutaway view showing four ctenidial filaments, and their interconnections, on one side of the body of a eulamellibranch. (C) Lateral view of four ctenidial filaments of a filibranch. (D) Cross section through ascending and descending arms of four filibranch ctenidial filaments. (E) Lateral view of four filaments of a eulamellibranch. (F) Cross section through ascending and descending arms of four eulamellibranch ctenidial filaments. (G) Ctenidial filaments of the mussel *Mytilus californianus* showing ciliary junctions and interfilament spaces. (H) Frontal ciliary tracts on ctenidial filaments of *Mytilus*. (I) Ventral gill edge of *Mytilus* showing food groove.

(G)

(H)

(I)

Food groove

Figure 13.31   Feeding in the septibranch bivalve *Cuspidaria* **(Anomalodesmata).** (A) General anatomy of *Cuspidaria rostrata*. Arrows indicate water flow. (B) Siphon and sensory siphonal tentacles protruding from the substratum, but largely contracted. (C) Siphon extended, capturing a microcrustacean. (D) Details of the siphons and tentacles.

mantle cavity by way of the inhalant siphon; lowering the septum causes water to pass dorsally through the pores into the exhalant chamber. These movements also force hemolymph from mantle sinuses into the siphonal sinuses, thereby causing a rapid protrusion of the inhalant siphon, which can be directed toward potential prey (Figure 13.31B–D). In this fashion, small animals such as microcrustaceans are sucked into the mantle cavity, where they are grasped by muscular labial palps and thrust into the mouth; at the same time, the mantle tissue serves as the gas exchange surface.

While most pteriomorphians are restricted to epibenthic life, lacking siphons (Figure 13.21A, B), many heterodont bivalves live buried in soft sediments, where long siphons are utilized to maintain contact with the overlying water (Figures 13.8A and 13.20D–H).

Scaphopods consume foraminifera and other meiofauna taxa, diatoms, zooplankton, and interstitial detritus. Two lobes flank the head, each bearing numerous (up to several hundred) long, slender tentacles called **captacula** (Figures 13.9 and 13.13F). The captacula are extended into the substratum by metachronal beating of cilia on the small terminal bulb. Within the sediment organic particles and microorganisms adhere to the sticky terminal bulb; small food particles are transported to the mouth by way of ciliary tracts along the tentacles, while larger food items are transported directly to the mouth by muscular contraction of the captacula. A well-developed, large radula pulls the food into the mouth, perhaps partially macerating it in the process.

Several forms of symbiotic relationships have evolved within molluscs that are intimately tied to the host's nutritional biology. One of the most interesting of these relationships exists between many molluscs and sulfur bacteria. These molluscs appear to derive a portion of their nutritional needs from symbiotic, carbon-fixing sulfur bacteria, which usually reside on the host mollusc's gills. In some monoplacophorans (*Laevipilina antartica*) and gastropods (*Lurifax vitreus*, *Hirtopelta*) the bacteria are housed in special cavities called bacteriocytes in the mantle cavity. This mollusc–bacteria symbiosis has been recently documented from a variety of sulfide-rich anoxic habitats, including deep-sea hydrothermal vents, where geothermally produced sulfide is present, and from other reduced sediments, where microbial degradation of organic matter leads to the reduction of sulfate to sulfide (e.g., anoxic marine basins, seagrass bed and mangrove swamp sediments, pulp mill effluent sites, sewage outfall areas).

Members of some bivalve families, in particular the Solemyidae and Lucinidae, harbor sulfur bacteria in their enlarged gills which have the ability to directly oxidize sulfide. They do this by means of a special sulfide oxidase enzyme in the mitochondria. These bivalves inhabit reduced sediments where free sulfides are abundant. The ability to oxidize sulfide not only provides the bivalve with a source of energy to drive ATP synthesis, it also enables them to rid their body of toxic sulfide molecules that accumulate in such habitats. The nutrients obtained by this symbiosis are sufficient for the bivalve so, in solemyids, the gut is reduced or, in a few species, absent.

Another notable partnership exists between giant clams (*Tridacna*) and their symbiotic zooxanthellae (the dinoflagellate *Symbiodinium*). These clams live with

(A)

Mouth
Sphincter
Outer lip
Radular sac
Esophagus
Salivary glands
Esophageal bulb
Gland of Leiblein (modified esophageal gland)
Anus
Esophagus
Anal gland
Intestine
Stomach
Digestive gland

(B)

Buccal bulb
Salivary gland duct
Esophagus
Anus
Stomach
Salivary gland
Digestive gland
Intestine

(C)

Mucocyte
Gland cells
Support cells
Connective tissue

(D)

Cerata
Branch of digestive gland
Intestine
Anus
Rhinophores
Foregut gland
Anterior diverticulum of stomach
Salivary gland
Pharynx
Stomach
Salivary gland
Esophagus
Mouth
Digestive gland

(E)

Cnidosac
Sphincter
Branch of digestive gland
Epidermis

their dorsal side against the substratum, and they expose their fleshy mantle to sunlight through the large shell gape. The mantle tissues harbor the zooxanthellae. Many species have special lens-like structures that focus light on zooxanthellae living in the deeper tissues. A few other bivalves and certain sea slugs also maintain a symbiotic relationship with *Symbiodinium*. Several species of *Melibe*, *Pteraeolidia*, and *Berghia* harbor colonies of these dinoflagellates in "carrier cells" associated with their digestive glands. Experiments indicate that when sufficient light is available, host nudibranchs utilize photosynthetically fixed organic molecules produced by the alga to supplement their usual diet of prey. The dinoflagellates are probably not transmitted with the zygotes of the nudibranchs, each new generation thus requiring reinfection from the environment. A number

Figure 13.32 Molluscan digestive system. (A) The digestive system of the neogastropod (Muricidae). (B) The digestive system of the stylommatophoran land snail *Cornu*. (C) The histology of the intestinal wall of the gastropod *Tonna*. (D) A cladobranch nudibranch (*Embletonia*) in which large branches of the digestive gland fill the dorsal cerata. (E) A longitudinal section of the ceras of the aeolidid nudibranch *Trinchesia* showing the cnidosac where nematocysts (not shown) from this animal's cnidarian prey are stored. (F) Diagrammatic lateral view of the digestive tract and nearby organs of the unionoid clam *Anodonta*. (G) The digestive system of the cuttlefish *Eledone*. (H) The digestive system of the squid *Loligo*.

of aeolid nudibranchs accumulate zooxanthellae from their cnidarian prey. Some of the dinoflagellates end up inside cells of the nudibranch's digestive gland, but many others are released in the slug's feces, from where they may reinfect cnidarians. An even more remarkable phenomenon occurs in some members of another group of sea slugs, the Sacoglossa (e.g., *Placobranchus*). These sea slugs obtain functional chloroplasts from the green algae upon which they feed and incorporate them into their own tissues; the chloroplasts remain active for a period of time and produce photosynthetically fixed carbon molecules that are utilized by the hosts.

Still another unusual symbiosis occurs between an aerobic bacterium and the wood-boring marine shipworm bivalves (Teredinidae) (Figure 13.21D). Shipworms are capable of living on a diet of wood alone by harboring this cellulose-decomposing, nitrogen-fixing bacterium. The bivalve cultures the bacterium in a special organ associated with ctenidial blood vessels called the **gland of Deshayes**. The bacterium

breaks down cellulose and makes its products available to its host. Nitrogen-fixing bacteria occur as part of the gut flora in many animals whose diet is rich in carbon but deficient in nitrogen (e.g., termites). However, shipworms are the only animals known to harbor a nitrogen fixer as a pure (single species) culture in a specialized organ (similar to the host nodule–*Rhizobium* symbiosis of leguminous plants).

In addition to the above and myriad other feeding strategies of molluscs, some species (notably some bivalves and sea slugs) probably obtain a significant portion of their nutritional needs by direct uptake of dissolved organic material from seawater, such as amino acids.

Digestion

Molluscs possess complete, or through guts, a few of which are illustrated in Figure 13.32. The mouth leads inward to a buccal cavity, within which the radular apparatus and jaws (when present) are located (Fig-

Figure 13.33 The molluscan stomach and style sac. (A) A generalized stomach and style apparatus of an autobranch bivalve. The crystalline style rotates against the gastric shield, releasing digestive enzymes and winding up the mucus–food string to assist in pulling it from the esophagus. Food particles are sorted in the ciliated, grooved sorting area: small particles are carried (in part by the typhlosole) to the digestive glands for digestion; large particles are carried to the intestine for eventual elimination. (B) A cross section of a style sac.

ure 13.23). The esophagus is generally a straight tube connecting the foregut to the stomach. Various glands are often associated with this anterior gut region, including some that produce enzymes and others that secrete a lubricant over the radula that are usually called salivary glands. In many herbivorous species (e.g., certain eupulmonates, anaspideans [*Aplysia*], and some cephalaspideans), a muscular **gizzard** (unrelated to the jaws) may be present for grinding up tough vegetable matter. The gizzard may have chitinous, or even calcareous plates or teeth. The stomach usually bears one or more ducts that lead to the large glandular digestive gland (variously called the digestive diverticula, digestive caeca, midgut glands, liver, or other similar terms). Several sets of digestive glands may be present. The intestine leaves the stomach and terminates as the anus, which is typically located in the mantle cavity in or near the exhalant water flow.

Once food has entered the buccal cavity of most molluscs, it is carried in mucous strings into the esophagus and then to the stomach. In cephalopods and some predatory gastropods, chunks of food or whole prey are swallowed by muscular action of the esophagus. The food is stored in the stomach or in an expanded region of the esophagus called the "crop," as in octopuses and *Nautilus*, and many gastropods. In many bivalves and gastropods, the stomach wall bears a chitinous **gastric shield** and a ciliated, ridged **sorting area** (Figure 13.33). The posterior stomach region (anterior in gastropods) is a **style sac**, which is lined with cilia and in autobranch bivalves and in some gastropods

contains a **crystalline style** (Figure 13.33). This structure, which functions to aid in digestion, is a rodlike matrix of proteins and enzymes (often amylase) that are slowly released as the projecting end of the style rotates and grinds against the gastric shield that protects the otherwise delicate stomach wall. The gastric cilia and rotating style wind up the mucus and food into a string and draw it along the esophagus to the stomach. The style is produced by special cells of the style sac. The style of some bivalves is enormous, one-third to one-half the length of the clam itself. Particulate matter is swept against the stomach's anterior sorting region, which sorts mainly by size. Small particles are carried into the digestive glands, which arise from the stomach wall. Larger particles are passed along ciliated grooves of the stomach to the intestine. In more primitive bivalves (Protobranchia) and in many gastropods a crystalline style is absent but a style sac is often present, which contains a rotating mass of mucus mixed with particles that is termed a **protostyle**.

Extracellular digestion takes place in the stomach and lumina of the digestive glands, while absorption and intracellular digestion occur in the digestive gland cells and the intestinal walls. Extracellular digestion is accomplished by enzymes produced in foregut (e.g., salivary glands, esophageal pouches or glands, pharyngeal glands—sometimes called "sugar glands" because they produce amylase), the stomach, and the digestive glands. In primitive groups, intracellular digestion tends to predominate. In Solenogastres all digestive functions are accomplished in a uniform midgut lined by voluminous digestive and secretory cells. In most molluscs, ciliated tracts line the digestive glands and carry food particles to minute diverticula, where they are engulfed by phagocytic digestive cells of the duct wall. The same cells dump digestive wastes back into the ducts, to be carried by other ciliary tracts back to the stomach, from there to be passed out of the gut via the intestine and anus as fecal material. In most highly-derived groups (e.g., cephalopods and many gastropods), extracellular digestion predominates. Enzymes secreted primarily by the digestive glands

Figure 13.34 Hemolymph flow in a typical mollusc. Oxygenated hemolymph is pumped from the ventricle to the hemocoel, where it bathes the organs; eventually it drains into various channels and sinuses and then into the afferent branchial vessels, which enter the ctenidia. Oxygen is picked up in the ctenidia, and the hemolymph is then transported by the efferent branchial vessels to the left and right atria, through the ventricle, and then back to the hemocoel. Additional auxiliary pumping vessels occur in several taxa, particularly in active groups such as cephalopods.

and stomach digest the food, and absorption occurs in the stomach, digestive glands, and intestine.

Circulation and Gas Exchange

Although molluscs are coelomate protostomes, the coelom is greatly reduced. The main body cavity is, in most species, an open circulatory space or hemocoel, which comprises several separate sinuses, and a network of vessels in the gills, where gas exchange takes place. The blood of molluscs contains various cells, including amebocytes, and is referred to as hemolymph. It is responsible for picking up the products of digestion from the sites of absorption and for delivering these nutrients throughout the body. It usually carries in solution the copper-containing respiratory pigment hemocyanin. Some molluscs use hemoglobin to bind oxygen and many have myoglobin in the active muscle tissues, in particular those of the odontophore.

The heart lies dorsally within the **pericardial chamber**, and includes a pair of atria (often called auricles) and a single ventricle. In monoplacophorans and in *Nautilus* there are two pairs of atria, and in many gastropods there is only one (the left) that corresponds to the single gill. The atria receive the efferent branchial vessels, drawing oxygenated hemolymph from each ctenidium and passing it into the muscular ventricle, which pumps it anteriorly through a large anterior artery (the anterior or cephalic aorta). The anterior artery branches and eventually opens into various sinuses within which the tissues are bathed in oxygenated hemolymph. Return drainage through the sinuses eventually funnels the hemolymph back into the afferent branchial vessels. This basic pattern of molluscan

circulation is shown diagrammatically in Figure 13.34, although it is modified to various degrees in different classes (Figure 13.35). In some cephalopods the circulatory system is secondarily closed (Figure 13.35C).

Most molluscs have ctenidia. But many have lost the ctenidia and rely either on secondarily derived gills or on gas exchange across the mantle or general body surface. In the primitive condition the ctenidium is built around a long, flattened axis projecting from the wall of the mantle cavity (Figure 13.30A). To each side of the axis are attached triangular or wedge-shaped filaments that alternate in position with filaments on the opposite side of the axis (except in nucuid protobranchs, where they are opposite). This arrangement, in which filaments project on both sides of the central axis, is called the **bipectinate condition**. There is one gill on each side of the mantle cavity, sometimes held in position by membranes that divide the mantle cavity into upper and lower chambers (Figure 13.28A,B). Lateral cilia on the gill draw water into the inhalant (ventral) chamber, from which it passes upward between the gill filaments to the exhalant (dorsal) chamber and then out of the mantle cavity (Figure 13.30A).

Two vessels run through each gill axis. The afferent vessel carries oxygen-depleted hemolymph into the gill, and the efferent vessel drains freshly oxygenated hemolymph from the gill to the atria of the heart, as noted above. Hemolymph flows through the filaments

(A)

(B)

(C)

Figure 13.35 The circulatory systems of three molluscs. (A) A neogastropod *Buccinum* (hemolymph sinuses not shown). (B) A eulamellibranch unionid bivalve. (C) A squid, *Loligo*.

from the afferent to the efferent vessel. Ctenidial cilia move water over the gill filaments in a direction opposite to that of the flow of the underlying hemolymph in the branchial vessels. This countercurrent phenomenon enhances gas exchange between the hemolymph and water by maximizing the diffusion gradients of O_2 and CO_2 (Figure 13.30A). These presumed primitive bipectinate ctenidial gill conditions are expressed in several living groups, for example, in Caudofoveata, chitons, protobranch bivalves, and some gastropods.

As a result of torsion, gastropods evolved novel ways to circulate water over the gills before it comes into contact with gut or nephridial discharges. Some vetigastropods with two bipectinate ctenidia may accomplish this by circulating water in across the gills, then past the anus and nephridiopore, and away from the body via slits or holes in the shell. This circulation pattern is used by the slit shells (Pleurotomariidae) and the minute Scissurellidae and Anatomidae (Figure 13.36), abalones (Haliotidae) (Figure 13.1D), and volcano (or keyhole) limpets (Fissurellidae) (Figures 13.16H,I and 13.25A). Some specialists regard the Pleurotomariidae as "living fossils" that reflect an early gastropod character state since gastropods bearing slits are found amongst early gastropod fossils. Most other gastropods have lost the right ctenidium and with it the right atrium; inhalant water enters on the left side of the head and then passes through the mantle cavity and straight out the right side, where the anus and nephridiopore open. Other gastropods have lost both ctenidia and utilize secondary respiratory regions, either the mantle surface itself, expanded nephridial surfaces, or secondarily derived gills of one kind or another. Limpets of the genus *Patella* have rows of secondary gills in the mantle groove along each side of the body, superficially similar to the condition seen in chitons where multiple ctenidia are found.

In many gastropods one ctenidium is lost, e.g., patellogastropods, some vetigastropods, all neritimorphs and caenogastropods. In caenogastropods, the dorsal and ventral suspensory membranes seen in vetigastropod ctenidia are absent and the gill is attached directly to the mantle wall by the gill axis. The gill filaments on the attached side have been lost, while
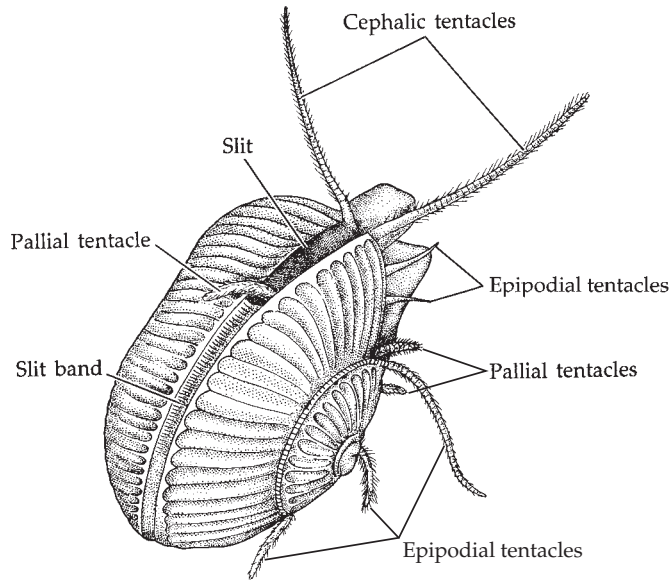
Figure 13.36 The slit-bearing vetigastropod *Anatoma*.

those of the opposite side project freely into the mantle cavity. This arrangement of filaments on only one side of the central axis is referred to as the **monopectinate (or pectinobranch) condition** (Figure 13.14D). Some caenogastropods have evolved inhalant siphons by extension and rolling of the anterior mantle margin (Figures 13.1E and 13.40A). In these cases the margin of the shell may be notched, or drawn out as a canal to house the siphon. The siphon provides access to surface water in burrowing species, and may also function as a mobile, directional organ used in conjunction with the chemosensory osphradium.

All heterobranchs have lost the typical ctenidia but some have a plicate, or folded, gill that has been considered by some to be a reduced ctenidium, but is now considered to be a secondary structure that has reformed in much the same location as the original ctenidial gill. Trends toward detorsion, loss of the shell, and reduction of the mantle cavity occur in many heterobranchs, and the process has apparently occurred several times within this group. Some nudibranchs have evolved secondary dorsal gas exchange structures called **cerata** or, in some nudibranchs, secondary gills that surround the anus (Figures 13.7F–J).

Wholly terrestrial gastropods lack gills and exchange gases directly across a vascularized region of the mantle, usually within the mantle cavity, the latter arrangement usually referred to as a **lung**. In marine, freshwater and terrestrial eupulmonates, the edges of the mantle cavity have become sealed to the back of the animal except for a small opening on the right side called a **pneumostome** (Figure 13.37A) that is controlled by a sphincter muscle (except in siphonariid limpets). Instead of having gills, the roof of the mantle cavity is highly vascularized. By arching and flattening the mantle cavity floor, air is moved into and out of the lung.

In chitons the mantle cavity is a groove extending along the ventral body margin and encircling the foot (Figure 13.4B). A large number of small bipectinate ctenidial gills lie laterally in this groove. The mantle is held tight against the substratum, largely enclosing

(A)

(B)

Figure 13.37 Land snails (Heterobranchia: Eupulmonata). (A) A terrestrial slug (*Arion lusitanicus*), showing the pneumostome that opens to the "lung" (Stylommatophora: Limacidae). (B) Terrestrial helicid snails (Stylommatophora: Helicidae) during summer dormancy in Sicily.

this groove except on either side at the anterior end to form incurrent channels, and in one or two places at the posterior end to form excurrent areas. Water enters the inhalant region of the mantle groove lateral to the gills, then passes between the gills into the exhalant region along the sides of the foot. Moving posteriorly, the current passes over the gonopores, nephridiopores, and anus before exiting (Figure 13.4B).

In bivalves the capacious mantle cavity allows the ctenidia to develop a greatly enlarged surface area, serving in most autobranch species for both gas exchange and feeding. Many of the morphological modifications of bivalve gills are described above in discussion of suspension feeding. In addition to the folded, W-shaped ctenidial filaments seen in many bivalves (Figure 13.28B), some forms (e.g., oysters) have plicate ctenidia. A plicate ctenidium has vertical ridges or folds, each ridge consisting of several ordinary ctenidial filaments. So-called "principal filaments" lie in the grooves between these ridges and their cilia are important in sorting particles from the ventilation and feeding currents. The plicate condition gives the ctenidium a corrugated appearance and further increases the surface area for feeding and gas exchange.

In spite of these modifications, the basic system of circulation and gas exchange in bivalves is similar to that seen in gastropods (Figure 13.35B). In most bivalves, the ventricle of the heart folds around the gut, so the pericardial cavity encloses not only the heart but also a short section of the digestive tract. The large mantle lines the interior of the valves and provides an additional surface area for gas exchange, which in some groups may be as important as the gills in this regard. For example, in lucinid bivalves where the gills are full of symbiotic bacteria, folds on the mantle act as a secondary gill, and in septibranchs, which have very reduced gills, the mantle surface is the principal area of gas exchange.

Most autobranch bivalves lack respiratory pigments in the hemolymph, although hemoglobin occurs in a few families and hemocyanin is found in protobranchs.

Scaphopods have lost the ctenidia, heart, and virtually all vessels. The circulatory system is reduced to simple hemolymph sinuses, and gas exchange takes place mainly across the mantle and body surface. A few ciliated ridges occur in the mantle cavity that may assist in maintaining water flow. A few tiny gastropods and at least one small monoplacophoran species lack a heart altogether.

No doubt associated with their large size and active lifestyle, cephalopods have a more developed circulatory system than other molluscs, and in the highly active decapodiforms (squid and cuttlefish) it is effectively closed, with many discrete vessels, secondary pumping structures, and capillaries (Figures 13.11C, 13.12B, and 13.35C). The result is increased pressure and efficiency of hemolymph flow and delivery. In most cephalopods, the pumping of blood into the ctenidia is assisted by muscular accessory branchial hearts, which boost the low venous pressure as the hemolymph enters the gills. The gills are not ciliated and their surface is highly folded, increasing their surface area for greater gas exchange necessary to meet the demands of their high metabolic rate.

In the Solenogastres, gills are absent but the mantle cavity surface may be folded or form respiratory papillae. Caudofoveates have a single pair of bipectinate ctenidia in the mantle cavity. Monoplacophoran gills are well-developed but weakly muscular and ciliated, and only have lamellae on one side of the gill axis; they occur as three to six pairs, aligned bilaterally within the mantle groove. The gills of monoplacophorans are thought to be modified ctenidia that vibrate and ventilate the groove where gas exchange occurs.

Excretion and Osmoregulation

The basic excretory structures of molluscs are paired tubular nephridia (often called kidneys) that are primitively similar to those of annelids. Typical nephridia are absent in the aplacophoran groups. Three, six, or seven pairs of nephridia occur in monoplacophorans, two pairs in the nautiloids, and a single pair in all other molluscs (except where one is lost in higher gastropods) (Figure 13.14). The nephrostome typically opens into the pericardial coelom via a renopericardial duct, and the nephridiopore discharges into the mantle cavity, often near the anus (Figures 13.14 and 13.34). In molluscs, the pericardial fluids (primary urine) pass through the nephrostome and into the nephridium, where selective resorption occurs along the tubule wall until the final urine is ready to pass out the nephridiopore. The pericardial sac and heart wall act as selective barriers between the open nephrostome and the hemolymph in the surrounding hemocoel and in the heart. Mollusc nephridia are rather large and saclike, and their walls are often greatly folded. In many species, afferent and efferent nephridial vessels carry hemolymph to and from the nephridial tissues (Figure 13.38). Sometimes a bladder is present just before the nephridiopore and sometimes a ureter forms a duct to carry urine well beyond the nephridiopore.

In many molluscs urine formation involves pressure filtration, active secretion, and active resorption. Aquatic molluscs excrete mostly ammonia, and most marine species are osmoconformers. In freshwater species the nephridia are capable of excreting a hyposomotic urine by resorbing salts and by passing large quantities of water. Terrestrial gastropods conserve water by converting ammonia to uric acid. Land snails are capable of surviving a considerable loss of body water, which is brought on in large part by evaporation and the production of the metabolically expensive slime trail. They often absorb water from the urine in the ureter. In many gastropods (e.g., neritimorphs,
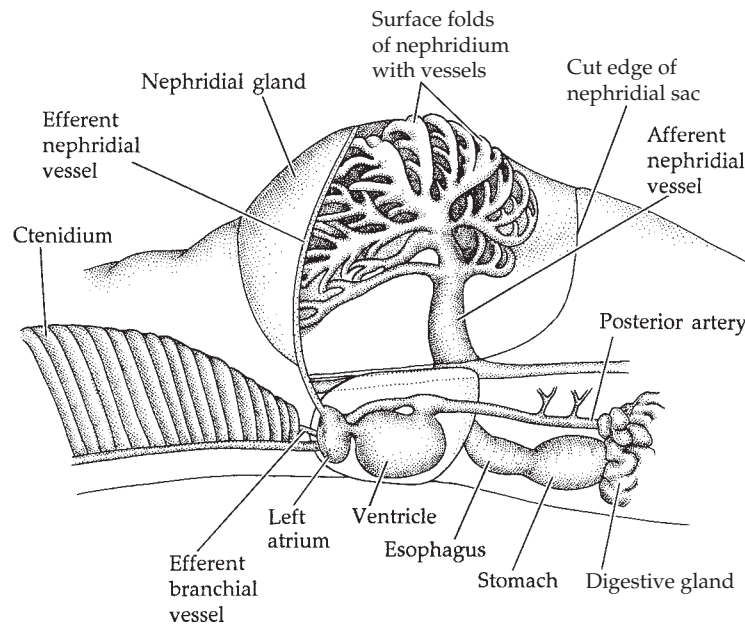
Figure 13.38 **The nephridium and nearby organs of *Littorina* (cutaway view).** The nephridial sac has been slit open.

way of renopericardial canals and empty via nephridiopores into the mantle cavity. However, the nephridia bear enlarged regions called **renal sacs**. Before reaching the branchial heart, a large vein passes through the renal sac, wherein numerous thin-walled evaginations, called **renal appendages**, project off the vein. As the branchial heart beats, hemolymph is drawn through the renal appendages, and wastes are filtered across their thin walls into the nephridia. The overall result is an increase in excretory efficiency over the simpler arrangement present in other molluscs.

The fluid-filled nephridia of cephalopods are inhabited by a variety of commensals and parasites. The epithelium of the convoluted renal appendages provides an excellent surface for attachment, and the renal pores provide a simple exit to the exterior. Symbionts identified from cephalopod nephridia include viruses, fungi, ciliate protists, rhombozoans, trematodes, larval cestodes, and juvenile nematodes.

caenogastropods, and heterobranchs), torsion is accompanied by loss of the adult right nephridium; in neritimorphs and caenogastropods, a small remnant contributes to part of the gonoduct. Some gastropods have lost the direct connection of the nephrostome to the pericardial coelom. In such cases the nephridium is often very glandular and served by afferent and efferent hemolymph vessels, and wastes are removed largely from the circulatory fluid.

In bivalves, the two nephridia are located beneath the pericardial cavity and are folded in a long U-shape. In autobranch bivalves, one arm of the U is glandular and opens into the pericardial cavity; the other arm often forms a bladder and opens through a nephridiopore in the suprabranchial cavity. In protobranchs, the unfolded walls of the tube are glandular throughout. The nephridiopores may be separate from or joined with the ducts of the reproductive system. In the latter case, the openings are urogenital pores.

In patellogastropods and vetigastropods and some other molluscs, the gonoduct fuses with the renopericardial canal, and the nephridiopore functions as a urogenital pore and discharges both excretory wastes and gametes. In some cases, as in one monoplacophoran, a few bivalves and in some vetigastropods, the urogenital pore may become glandular. In many bivalves and chitons the nephridium and gonad have separate ducts.

In monoplacophorans and chitons, the nephridia open into the exhalant regions of the mantle grooves; in scaphopods, the paired nephridia open near the anus. In most gastropods the nephridiopores open directly into the mantle cavity but in some, such as in stylommatophoran pulmonates, there is an elongate ureter that opens outside the enclosed lung (mantle cavity).

Cephalopods retain the basic nephridial plan, in which the nephridia drain the pericardial coelom by

Nervous System

The molluscan nervous system is derived from the basic protostome plan of an anterior circumenteric arrangement of ganglia and paired ventral nerve cords. In molluscs, the more ventral and medial of the two pairs of nerve cords are called the **pedal cords** (or ventral cords); they innervate the muscles of the foot. The more lateral pair of nerves are the **visceral cords** (or lateral cords); they serve the mantle and viscera. Transverse commissures interconnect these longitudinal nerve cord pairs, creating a ladderlike nervous system. This basic plan is seen in the aplacophorans and polyplacophorans (Figure 13.39). The molluscan nervous system lacks the segmentally arranged ganglia of annelids and arthropods.

In the "simplest" molluscs—such as aplacophorans, monoplacophorans, and polyplacophorans—ganglia are poorly developed (Figure 13.39). A simple nerve ring surrounds the anterior gut, often with small cerebral ganglia on either side. Each cerebral ganglion, or the nerve ring itself, issues small nerves to the buccal region and gives rise to the pedal and the visceral nerve cords. Most other molluscs have more well-defined ganglia. Their nervous systems are built around

(A)

(B)
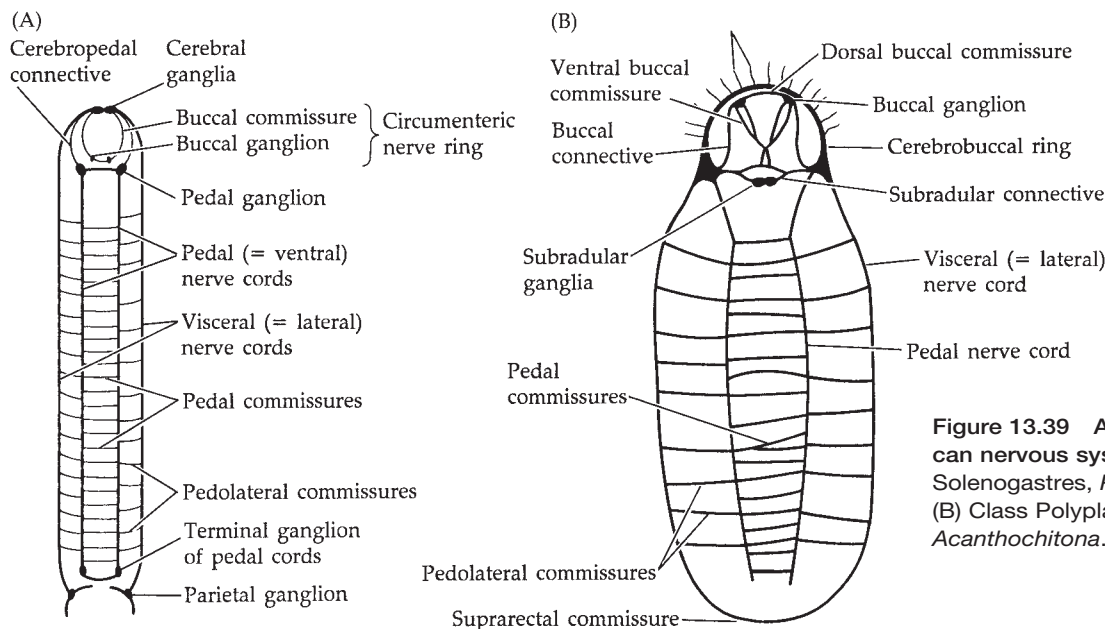
Figure 13.39 Aculiferan mollus-
can nervous systems. (A) Class
Solenogastres, *Proneomenia*.
(B) Class Polyplacophora,
Acanthochitona.

three pairs of large ganglia that interconnect to form a partial or complete nerve ring around the gut (Figures 13.40 and 13.41). Two pairs, the cerebral and pleural ganglia, lie dorsal or lateral to the esophagus, and one pair, the pedal ganglia, lies ventral to the gut, in the anterior part of the foot. In cephalopods, bivalves, and advanced gastropods, the cerebral and pleural ganglia are often fused. From the cerebral ganglia, peripheral nerves innervate the tentacles, eyes, statocysts, and general head surface, as well as buccal ganglia, with special centers of control for the buccal region, radular apparatus, and esophagus. The pleural ganglia give rise to the visceral cords, which extend posteriorly, supplying peripheral nerves to the viscera and mantle. The visceral cords eventually join a pair of esophageal (= intestinal, = pallial) ganglia and from there pass on to terminate in paired visceral ganglia. The esophageal ganglia or associated nerves innervate the gills and osphradium, and the visceral ganglia serve organs in the visceral mass. The pedal ganglia also give rise to a pair of pedal nerve cords that extend posteriorly and provide nerves to muscles of the foot.

As described above, due to torsion, the posterior portion of the gastropod nervous system is twisted into a figure eight, a condition known as streptoneury (Figure 13.40A,B). In addition to twisting the nervous system, torsion brings the posterior ganglia forward. In many advanced gastropods this anterior concentration of the nervous system is accompanied by a shortening of some nerve cords and fusion of ganglia. In most detorted gastropods the nervous system displays a secondarily derived bilateral symmetry and more or less untwisted visceral nerve cords—a condition known as euthyneury (Figure 13.40C).

In bivalves, the nervous system is clearly bilateral, and fusion has usually reduced it to three large, distinct ganglia. Anterior cerebropleural ganglia give rise

to two pairs of nerve cords, one extending posterodorsally to the visceral ganglia, the other leading ventrally to the pedal ganglia (Figure 13.41). The two cerebropleural ganglia are joined by a dorsal commissure over the esophagus. The cerebropleural ganglia send nerves to the palps, anterior adductor muscle, and mantle. The visceral ganglia issue nerves to the gut, heart, gills, mantle, siphon, and posterior adductor muscle.

The degree of nervous system development within the Cephalopoda is unequaled among invertebrates. The paired ganglia seen in other molluscs are not recognizable in cephalopods, where extreme cephalization has concentrated ganglia into lobes of a large brain encircling the anterior gut (Figure 13.42A). In addition to the usual head nerves originating from the dorsal part of the brain (more or less equivalent to the cerebral ganglia), a large optic nerve extends to each eye via a massive optic lobe. In most cephalopods, much of the brain is enclosed in a cartilaginous cranium. The pedal lobes supply nerves to the funnel, and anterior divisions of the pedal ganglia (called brachial lobes) send nerves to each of the arms and tentacles, an arrangement suggesting that the funnel and tentacles are derived from the molluscan foot. Octopuses may be the "smartest" invertebrates, for they can be quickly taught some rather complex memory-dependent tasks.

Squid and cuttlefish (Decapodiformes) have a rapid escape behavior that depends on a system of giant motor fibers that control powerful and synchronous contractions of the mantle muscles. The command center of this system is a pair of very large first-order giant neurons in the lobe of the fused visceral ganglia. Here, connections are made to second-order giant neurons that extend to a pair of large stellate ganglia. At the stellate ganglia, connections are made with third-order giant neurons that innervate the circular muscle fibers of the mantle (Figure 13.42D). Other nerves extend

(A)

(B)

(C)
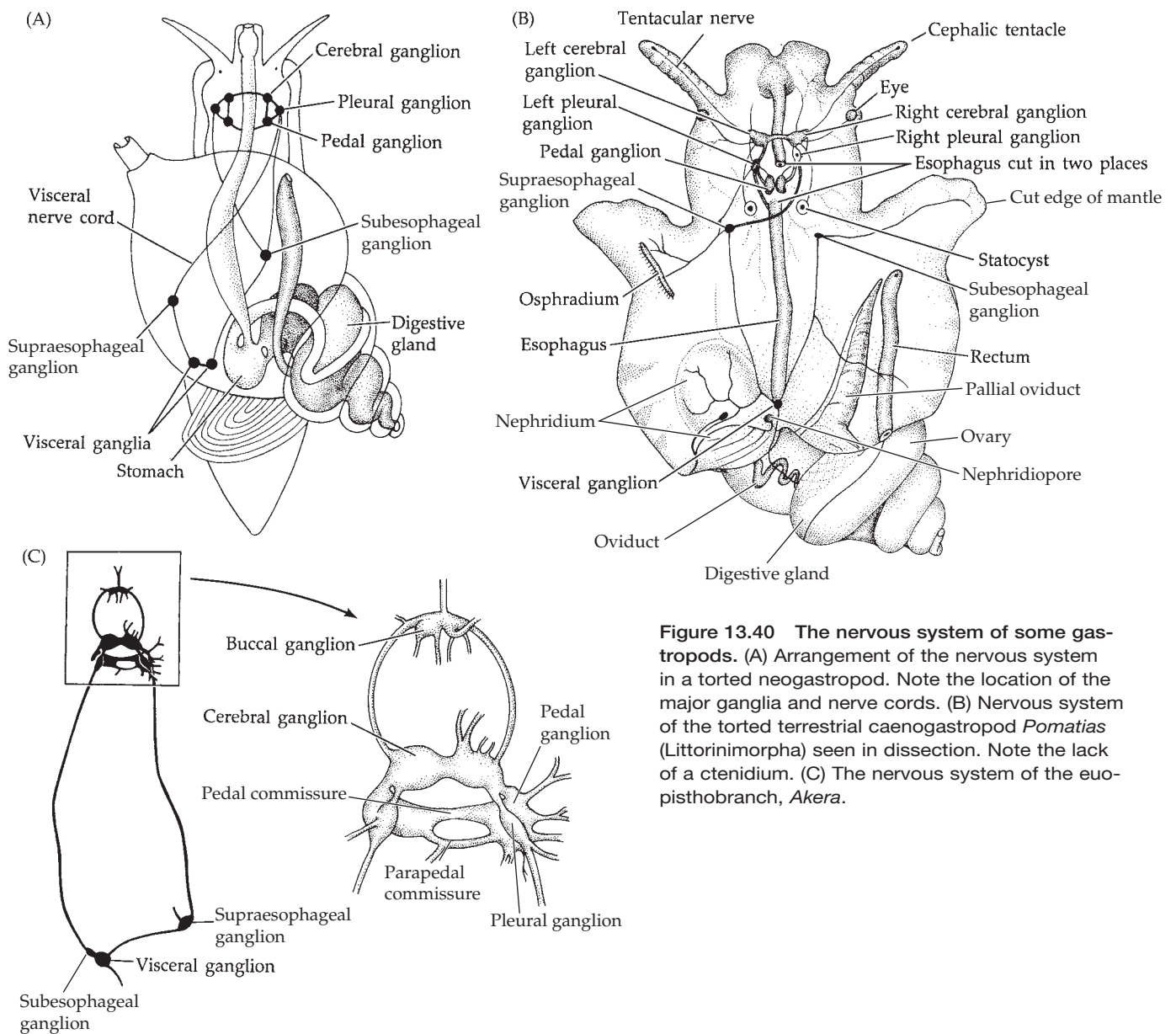
Figure 13.40   The nervous system of some gastropods. (A) Arrangement of the nervous system in a torted neogastropod. Note the location of the major ganglia and nerve cords. (B) Nervous system of the torted terrestrial caenogastropod *Pomatias* (Littorinimorpha) seen in dissection. Note the lack of a ctenidium. (C) The nervous system of the euopisthobranch, *Akera*.

posteriorly from the brain and terminate in various ganglia that innervate the viscera and structures in the mantle cavity.

For several decades neurobiologists have utilized the giant axons of *Loligo* as an experimental system for the study of nerve physiology and mechanics, and much of our fundamental knowledge of how nerve cells work is based on squid neurology. The sea hare *Aplysia*, and some eupulmonate snails have also been used in the same fashion and, although they lack giant axons, they possess exceptionally large neurons and ganglia that can be easily impaled with microelectrodes to discover the physiological secrets of such systems.

Sense Organs

With the exception of the aplacophorans, molluscs possess various combinations of sensory tentacles, photoreceptors, statocysts, and osphradia.
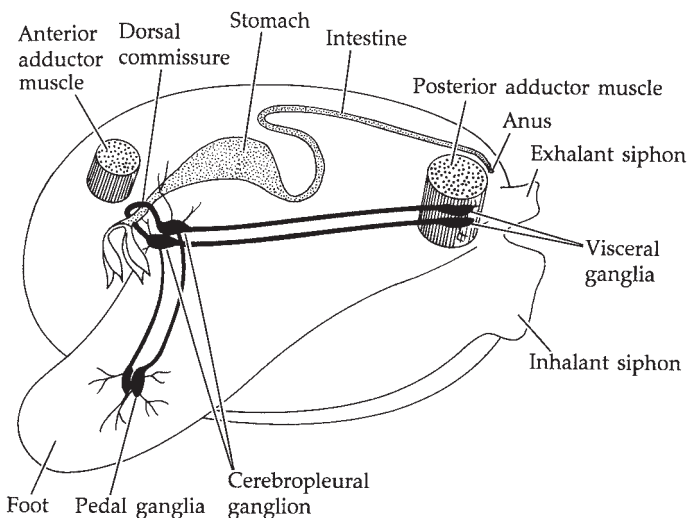
Figure 13.41   The reduced and concentrated nervous system of a typical autobranch bivalve.

(A)
Eyeball
Optic lobe
Optic gland
Optic tract
Nerves to hind part of body
Vertical lobe
Frontal lobe
Superior buccal lobe
Supraesophageal complex
Nerves to buccal region
Esophagus
Optic nerves (cut)
Subesophageal complex
Statocyst of left side
Pedal lobe
Brachial lobe
Brachial nerves to arms

(B)
Interconnecting nerve
Brachial nerves
Buccal nerves
Esophageal ganglia
Optic tract
Optic lobe
Optic nerves
Stellate nerve
Infundibular nerve
Eye
Stellate ganglion
Visceral nerve
Visceral ganglion

(C)
Tentacle (brachial) nerve
Superior buccal ganglion
Optic lobe
Brachial ganglion
Cerebral ganglion
Olfactory nerve
Pallial nerve (= giant nerve)
Stellate ganglion
Fin nerves
Branchial ganglion

(D)
First-order giant nerve cells
Second-order giant cells
Third-order giant cells
Proximal (finer) third-order axons
Distal (thicker) third-order axons
Brain
Magnocellular lobe
Pallioviseral center
Stellate ganglion

Figure 13.42 **The highly developed nervous system of cephalopods.** (A) The brain of an octopus. The lobes of the supraesophageal complex approximately correspond to the cerebral and buccal ganglia of other molluscs while the subesophageal complex comprises the fused pedal and pleurovisceral ganglia. About 15 structurally and functionally distinct pairs of lobes have been identified in the brain of octopuses. (B) Nervous system of an octopus. (C) Nervous system of a squid (*Loligo*). (D) Giant fiber system of a squid. Note that the first-order giant neurons possess an unusual cross connection, and that the third-order giant neurons are arranged so that motor impulses can reach all parts of the mantle-wall musculature simultaneously (as a result of the fact that impulses travel faster in thicker axons).
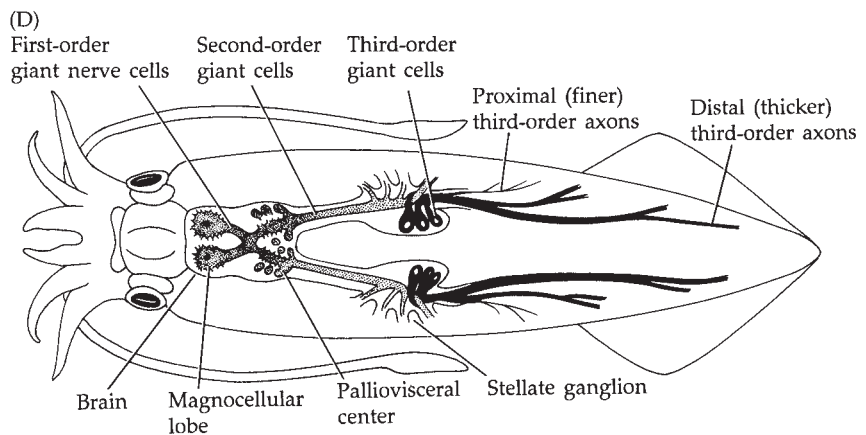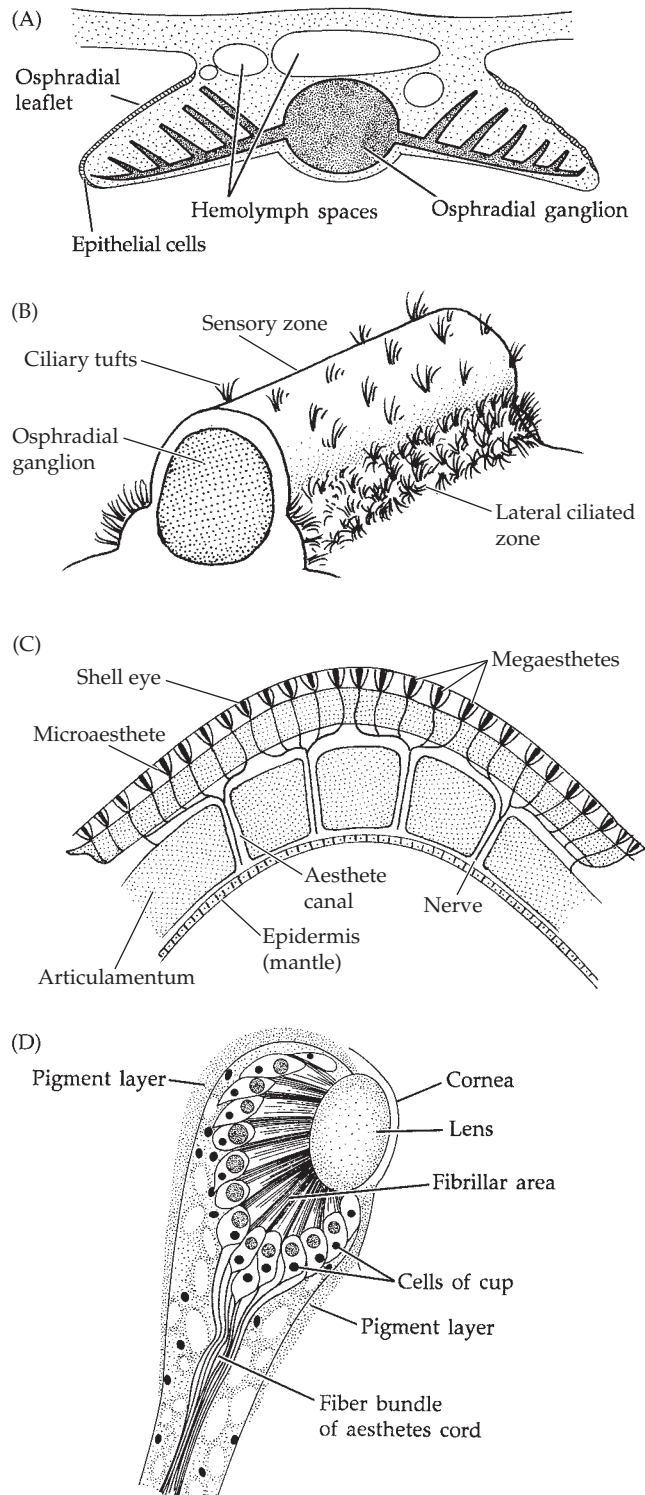
Figure 13.43 Two sensory organs of molluscs: osphradia and aesthetes. (A) Cross section of a bipectinate osphradium of the caenogastropod *Ranella* showing two leaflets. (B) Part of the osphradium of a littorinimorph caenogastropod such as *Littorina*. (C) One valve of a polyplacophoran (*Tonicia*). The aesthetes extend to the shell surface through megalopores and micropores. (D) Eye-bearing aesthetes (longitudinal section) in a megalopore of a chiton (*Acanthopleura*).

Osphradia are patches of sensory epithelium, located on or near the gills, or on the mantle wall (Figures 13.40B and 13.43A,B). They are chemoreceptors, and their cilia can also assist in mantle cavity ventilation in some caenogastropods. Little is known about the biology of osphradia, and their morphology and histology differs markedly within the phylum and even within some classes such as the gastropods.

In vetigastropods, a small osphradium is present on each gill; in those gastropods that possess one gill, there is only one osphradium, and it lies on the mantle cavity wall anterior and ventral to the attachment of the gill itself. Osphradia are reduced or absent in gastropods that have lost both gills, that possess a highly reduced mantle cavity, or that have taken up a strictly pelagic existence. Osphradia are best developed in benthic predators and scavengers, such as neogastropods and some other caenogastropods.

Most gastropods have one pair of sensory cephalic tentacles, but eupulmonates and many sea slugs possess two pairs. Many vetigastropods also have epipodial tentacles on the margin of the foot or mantle and there are also epipodial sense organs present (Figure 13.5A,C). The cephalic tentacles may bear eyes as well as tactile and chemoreceptor cells. Many nudibranchs have a pair of branching or folded anterior dorsal chemoreceptors called **rhinophores** (Figure 13.7F,G).

The primitive patellogastropods have simple pigment-cup eyes, while the more advanced gastropods have more complex eyes with a lens and often a cornea (Figure 13.44A,B,D). Most gastropods have a small eye at the base of each cephalic tentacle, but in some, such as the conch *Strombus* and some neogastropods, the eyes are enlarged and elevated on long stalks. The stylommatophoran and systellommatophoran pulmonates also have eyes placed on the tips of special optic tentacles and, in stylommatophorans, these tentacles have become olfactory organs.

Gastropods typically produce a mucopolysaccharide slime trail as they crawl. In many species the trail contains chemical messengers that other members of the species "read" by means of their excellent chemoreception. These chemical messengers may be simple trail markers, so one animal can follow or locate another, or they may be alarm substances that serve to warn others of possible danger on the path ahead. For example, when the carnivorous cephalaspidean sea slug *Navanax* is attacked by a predator, it quickly releases a yellow chemical mixture on its trail that causes other members of the species to abort their trail-following activity. Laboratory experiments have shown that at least one nudibranch (*Tritonia diomedea*) possesses geomagnetic orientation to the Earth's magnetic field. Motile gastropods usually possess a pair of closed statocysts near the pedal ganglia in the anterior region of the foot that contain either a single large statolith or several **statoconia** (much smaller particles).

Scaphopods lack eyes, tentacles, and osphradia typical of the epibenthic and motile molluscan groups. The captacula may function as tactile (as well as feeding) structures. Sense organs are found in the mantle edge surrounding the ventral aperture and at the dorsal water intake opening.

Bivalves have most of their sensory organs along the middle lobe of the mantle edge where they are in contact with the external environment (Figure 13.15C). These receptors may include mantle tentacles, which can contain both tactile and chemoreceptor cells. Such tentacles are commonly restricted to the siphonal areas, but in some swimming clams (e.g., *Lima*, *Pecten*) they may line the entire mantle margin. Paired statocysts usually occur in the foot near the pedal ganglia, and are
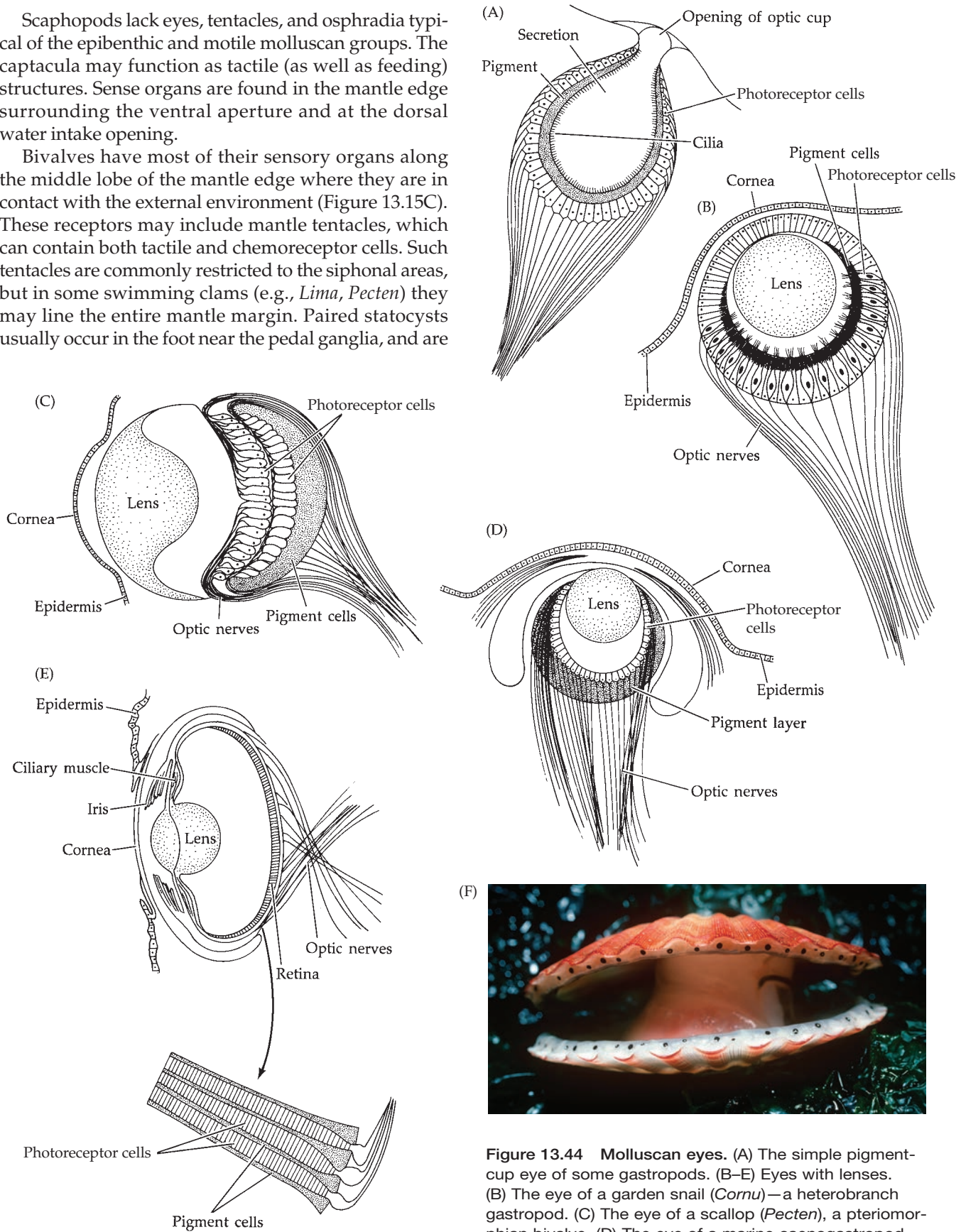
Figure 13.44 Molluscan eyes. (A) The simple pigment-cup eye of some gastropods. (B–E) Eyes with lenses. (B) The eye of a garden snail (*Cornu*)—a heterobranch gastropod. (C) The eye of a scallop (*Pecten*), a pteriomorphian bivalve. (D) The eye of a marine caenogastropod (*Littorina*). (E) The eye of an octopus (*Octopus*). (F) The queen scallop *Aequipecten opercularis*, showing its dark eyes along the mantle edges.

of particular importance in georeception by burrowing bivalves. Mantle eyes may also be present along the mantle edge or on the siphons and have evolved independently in a number of bivalve groups. In the spiny oyster *Spondylus* and the swimming scallop *Pecten*, these eyes are "mirror eyes" with a reflective layer (the **tapeum**) behind paired retinas. This layer reflects light back into the eye giving these bivalves a separate focal image on each retina–one from the lens and the other from the mirror. (Figure 13.44C–E). The bivalve osphradium lies in the exhalant chamber, beneath the posterior adductor muscle.

Chitons lack statocysts, cephalic eyes, and tentacles. Instead, they rely largely on two special sensory structures. These are the **adanal sensory structures** in the posterior portion of the mantle cavity and the **aesthetes**, which are a specialized system of photoreceptors unique to the class Polyplacophora. Aesthetes occur in high numbers across the dorsal surface of the shell plates. They are mantle cells that extend into the minute vertical canals (megalopores and micropores) in the upper tegmentum of the shell (Figure 13.43C,D). The canals and sensory endings terminate beneath a cap on the shell surface. Little is known about the functioning of aesthetes, but they apparently mediate light-regulated behavior. In at least one family (Chitonidae), some of them are modified as simple lensed eyes. The outer mantle surface of the girdle of many chitons is liberally supplied with tactile and photoreceptor cells (Figure 13.43D).

Like the rest of their nervous system, the sense organs of cephalopods are highly developed. The eyes are superficially similar to those of vertebrates (Figure 13.44E), and these two types of eyes are often cited as a classic example of convergent evolution. The eye of a coleoid cephalopod such as *Octopus* sits in a socket associated with the cranium. The cornea, iris, and lens arrangement is much like that of vertebrate eyes. Also as in vertebrates, the lens is suspended by ciliary muscles but has a fixed shape and focal length. An iris diaphragm controls the amount of light entering the eye, and the pupil is a horizontal slit. The retina comprises closely packed, long, rodlike photoreceptors whose sensory ends point toward the front of the eye; hence the cephalopod retina is the direct type rather than the indirect type seen in vertebrates. The rods connect to retinal cells that supply fibers to the large optic ganglia at the distal ends of the optic nerves. Unlike the eyes of vertebrates, the coleoid cornea probably contributes little to focusing because there is almost no light refraction at the corneal surface (as there is at an air–cornea interface). The coleoid eye accommodates to varying light conditions by changes in the size of the pupil and by migration of the retinal pigment. Coleoid eyes form distinct images (although octopuses are probably quite nearsighted) and experimental work suggests that they do not see colors other than as different shades of grey, although they can detect polarized light. In addition,

coleoids can discriminate among objects by size, shape, and vertical versus horizontal orientation. The eyes of *Nautilus* are rather primitive relative to the eyes of coleoids. They lack a lens, and are open to the water through the pupil. They are thought to function in the same way that a pinhole camera does.

Coleoids have complex statocysts that provide information on static body position and on body motion. Those of *Nautilus* are relatively simple. In addition, the arms of coleoids are liberally supplied with chemosensory and tactile cells, especially on the suckers of benthic octopuses, which have extremely good chemical and textural discrimination capabilities. *Nautilus* is the only cephalopod with osphradia.

Cephalopod Coloration and Ink

Coleoid cephalopods are noted for their striking pigmentation and dramatic color displays. The integument contains many pigment cells, or chromatophores, most of which are under nervous control. Such chromatophores can be individually rapidly expanded or contracted by means of tiny muscles attached to the periphery of each cell. Contraction of these muscles pulls out the cell and its internal pigment into a flat plate, thereby displaying the color; relaxation of the muscles causes the cell and pigment to concentrate into a tiny, inconspicuous dot. Because these chromatophores are displayed or concealed by muscle action, their activity is extremely rapid and coleoid cephalopods can change color (and pattern) almost instantaneously. Chromatophore pigments are of several colors—black, yellow, orange, red, and blue. The chromatophore color may be enhanced by deeper layers of iridocytes that both reflect and refract light in a prismatic fashion. Some species, such as the cuttlefish *Sepia* and many octopuses, are capable of closely mimicking their background coloration (Figure 13.12E) as well as producing vivid contrasting colors (Figure 13.12F,G). Many epipelagic squids show a dark-above, light-below countershading similar to that seen in pelagic fishes. Most coleoids also undergo color changes in relation to behavioral rituals, such as courtship and aggression. In octopuses, many color changes are accompanied by modifications in the surface texture of the body, mediated by muscles beneath the skin— something like elaborate, controlled "gooseflesh."

In addition to the color patterns formed by chromatophores, some coleoids are bioluminescent. When present, the light organs, or photophores, are arranged in various patterns on the body, and in some cases even occur on the eyeball. The luminescence is sometimes due to symbiotic bacteria, but in other cases it is intrinsic. The photophores of some species have a complex reflector and focusing-lens arrangement, and some even have an overlying color filter or chromatophore shutter to control the color or flashing pattern. Most luminescent species are deep-sea forms, and little is known about the role of light production in their

lives. Some appear to use the photophores to create a countershading effect, so as to appear less visible to predators (and prey) from below and above. Others living below the photic zone may use their glowing or flashing patterns as a means of communication, the signals serving to keep animals together in schools or to attract prey. The flashing may also play a role in mate attraction. The fire squid, *Lycoteuthis*, can produce several colors of light: white, blue, yellow, and pink. At least one genus of squid, *Heteroteuthis*, secretes a luminescent ink. The light comes from luminescent bacteria cultured in a small gland near the ink sac, from which ink and bacteria are ejected simultaneously.

In most coleoid cephalopods, a large ink sac is located near the intestine (Figure 13.32H). An ink-producing gland lies in the wall of the sac, and a duct runs from the sac to a pore into the rectum. The gland secretes a brown or black fluid that contains a high concentration of melanin pigment and mucus; the fluid is stored in the ink sac. When alarmed, the animal releases the ink through the anus and mantle cavity and out into the surrounding water. The cloud of inky material hangs together in the water, forming a "dummy" image that serves to confuse predators. The alkaloid nature of the ink may also act to deter predators, particularly fishes, and may interfere with their chemoreception.

Like virtually all other aspects of coleoid biology, the ability to change color and to defend against predators are part and parcel of their active hunting lifestyles. In the course of their evolution, coleoid cephalopods abandoned the protection of an external shell, becoming more efficient swimmers but also exposing their fleshy bodies to predators. The evolution of camouflage and ink production, coupled with high mobility and complex behavior, played a major role in the success of these animals in their radical modification of the basic molluscan body plan.

Reproduction

Primitively, molluscs are mostly gonochoristic, with a pair of gonads that discharge their gametes to the outside, either through the nephridial plumbing or through separate ducts. In species that free-spawn, fertilization is external and development is indirect. Many molluscs with separate gonoducts that store and transport the gametes also have various means of internal fertilization. In these forms, direct and mixed life history patterns have evolved.

Caudofoveata are gonochoristic with paired gonads, while Solenogastres are hermaphroditic with a pair of gonads (Figure 13.45). In both aplacophoran groups the gonads discharge gametes by way of short gonopericardial ducts into the pericardial chamber, from which they pass through gametoducts to the mantle cavity. In the Solengastres fertilization is internal and the young are sometimes brooded, while in the Caudofoveata the gametes are discharged into the surrounding seawater
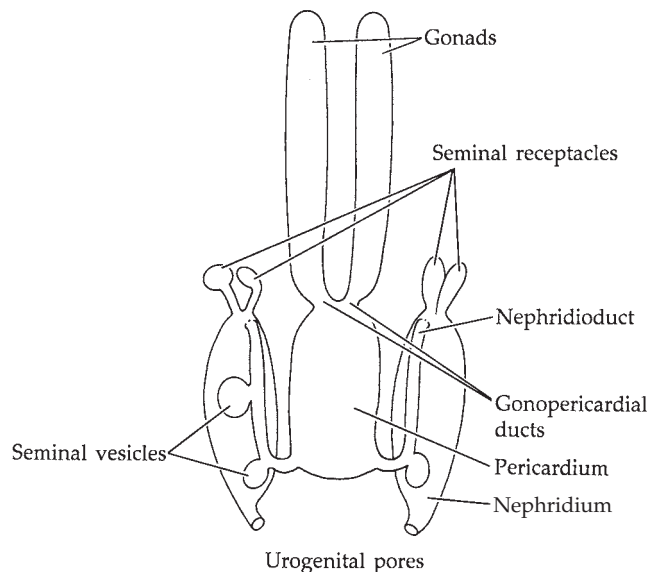
Figure 13.45   A solenogaster urogenital system.

where fertilization occurs. Monoplacophorans possess two pairs of gonads, each with a gonoduct connected to one of the pairs of nephridia (Figures 13.3D and 13.14E). One tiny monoplacophoran species, *Micropilina arntzi,* is a hermaphrodite and broods its embryos in its mantle cavity.

Most chitons are gonochoristic, although a few hermaphroditic species are known. In chitons, the two gonads are fused and situated medially in front of the pericardial cavity (Figure 13.4F). Gametes are transported directly to the outside by two separate gonoducts. The gonopores are located in the exhalant region of the mantle groove, one in front of each nephridiopore. Fertilization is external but can occur in the mantle cavity of the female. The eggs are enclosed within a spiny, buoyant membrane and are released into the sea individually or in strings. A few chitons brood their embryos in the mantle groove, and in one species (*Callistochiton viviparous*) development takes place entirely within the ovary.

In living gastropods, one gonad has been lost and the remaining one is usually located with the digestive gland in the visceral mass. The gonoduct is developed in association with the right nephridium in patellogastropods and vetigastropods (Figure 13.46A) while in neritimorphs and caenogastropods a vestige of the right nephridium is incorporated in the oviduct. In cases where the right nephridium is still functional in transporting excretory products, as in the patellogastropods and vetigastropods, the gonoduct is properly called a urogenital duct, because it discharges both gametes and urine.

Gastropods may be gonochoristic or hermaphroditic, but even in the latter case usually only a single gonad (an ovotestis) exists, although a few heterobranchs have separate male and female gonads (e.g.,
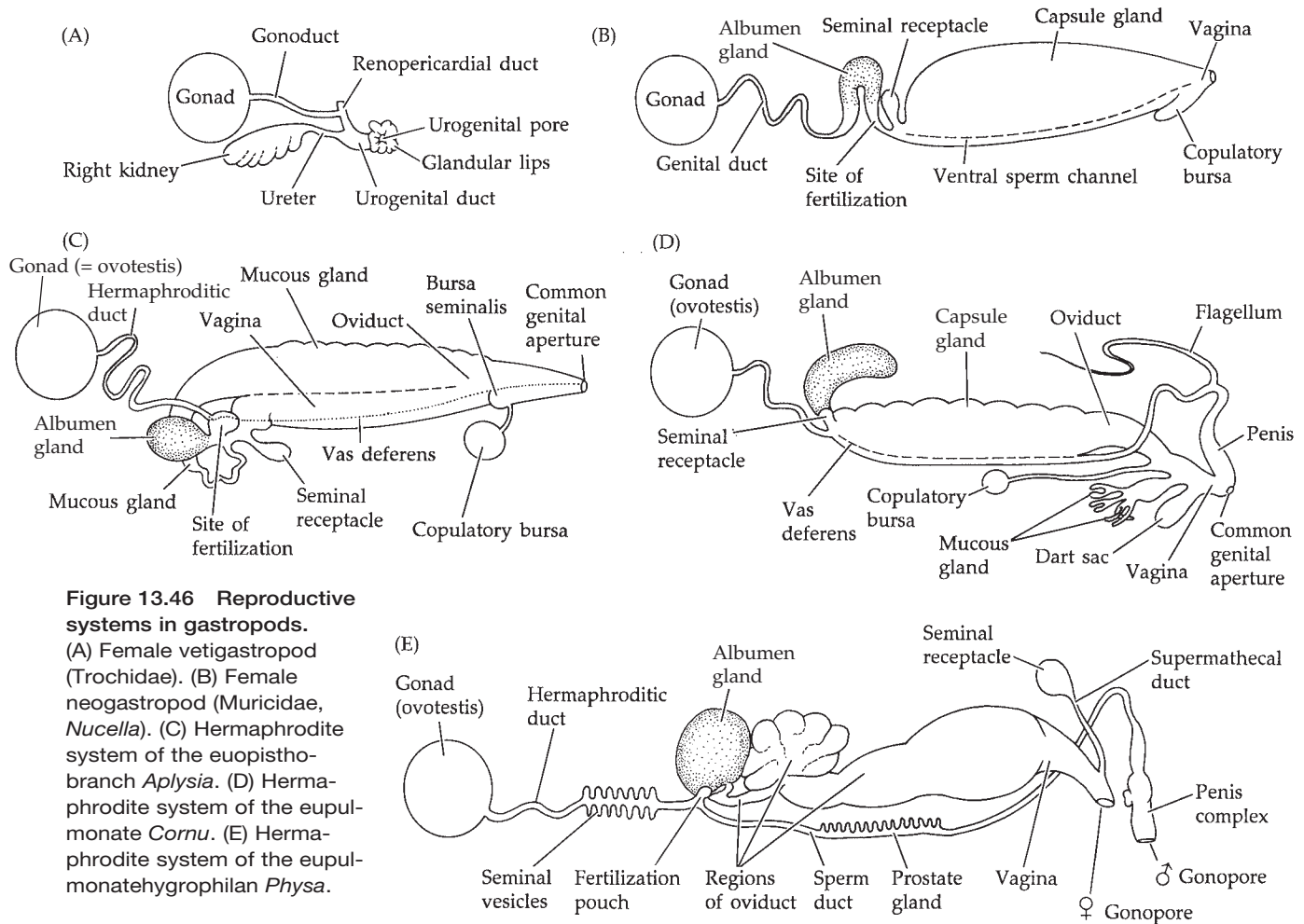
Figure 13.46 Reproductive systems in gastropods.
(A) Female vetigastropod (Trochidae). (B) Female neogastropod (Muricidae, *Nucella*). (C) Hermaphrodite system of the euopisthobranch *Aplysia*. (D) Hermaphrodite system of the eupulmonate *Cornu*. (E) Hermaphrodite system of the eupulmonatehygrophilan *Physa*.

Omalogyra and in the mathildid *Gegania valkyrie*), while others are protandric. The commitment of the right nephridial plumbing entirely to serving the reproductive system was a major step in gastropod evolution. The isolation of the reproductive tract allowed its independent evolution, without which the great variety of reproductive and developmental patterns in gastropods may never have been realized.

In many gastropods with isolated reproductive tracts, the female system bears a ciliated fold or tube that forms a vagina and oviduct (or pallial oviduct). The tube develops inwardly from the mantle wall and connects with the genital duct. The oviduct may bear specialized structures for sperm storage or egg case secretion. An organ for storing received sperm, the seminal receptacle often lies near the ovary at the proximal end of the oviduct. Eggs are fertilized at or near this location prior to entering the long secretory portion of the oviduct. Many female systems also have a copulatory bursa, usually at the distal end of the oviduct, where sperm are received during mating. In such cases the sperm are later transported along a ciliated groove in the oviduct to the seminal receptacle, near where fertilization takes place. The secretory section of the oviduct may be modified as an albumin gland

and a mucous or capsule gland. Many heterobranchs lay fertilized eggs in jelly-like mucopolysaccharide masses or strings produced by these glands. Most terrestrial pulmonates produce a small number of large, individual, yolky eggs, which are often provided with calcareous shells. Other pulmonates brood their embryos internally and give birth to juveniles. Many caenogastropods produce egg capsules in the form of leathery or hard cases that are attached to objects in the environment, thereby protecting the developing embryos. A ciliated groove is often present to conduct the soft egg capsules from the female gonopore down to a gland in the foot, where they are molded and attached to the substratum.

The male genital duct, or vas deferens, may include a prostate gland for production of seminal secretions. In many gastropods the proximal region of the vas deferens functions as a sperm storage area, or seminal vesicle. In many caenogastropods, neritimorphs, and lower heterobranchs the males have an external penis to facilitate transfer of sperm (Figures 13.6B and 13.47), and internal fertilization takes place prior to formation of the egg case. The penis is a long extension of the body wall usually arising behind the right cephalic tentacle. In these groups with a cephalic penis, most

(A)

(B)

(C)

(D)
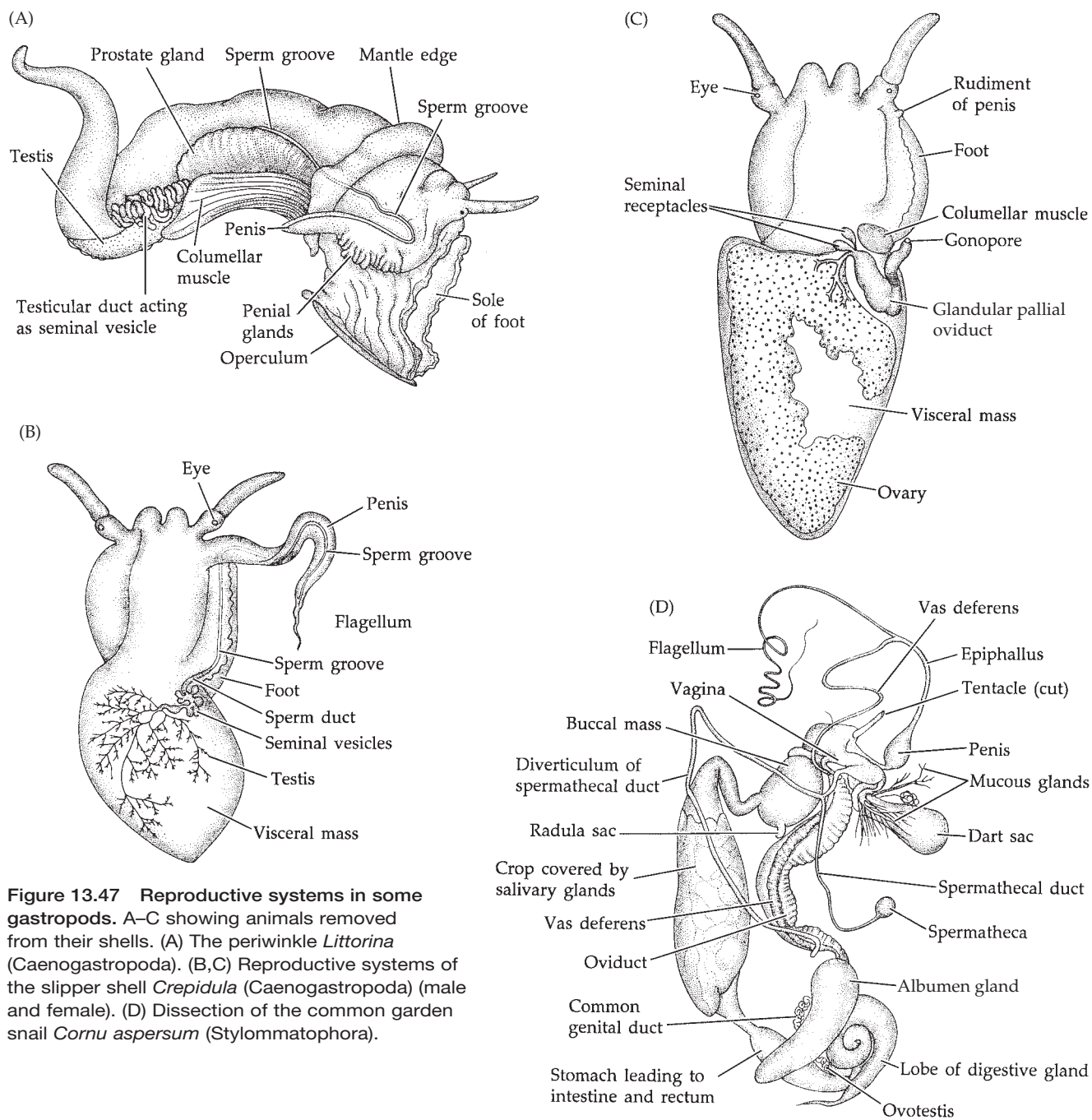
Figure 13.47 Reproductive systems in some gastropods. A–C showing animals removed from their shells. (A) The periwinkle *Littorina* (Caenogastropoda). (B,C) Reproductive systems of the slipper shell *Crepidula* (Caenogastropoda) (male and female). (D) Dissection of the common garden snail *Cornu aspersum* (Stylommatophora).

of the glandular parts of the reproductive system lie within the mantle cavity or may extend back alongside the nephridium. In most euthyneurans these parts of the reproductive system have migrated into the body cavity and the penis has become a retractile, internal structure. Sperm transfer in some gastropods involves the use of spermatophores either involving a penis or without one in the case of the cerithiomorph groups, and some others. In some, large parasperm are used to transport the normal sperm.

With both simultaneous and sequential hermaphrodite gastropods, copulation is the rule—either with one individual acting as the male and the other as the female, or with a mutual exchange of sperm between the two. Sedentary species, such as territorial limpets and slipper shells, are often protandric hermaphrodites. In slipper shells (*Crepidula*), individuals may stack one atop the other (Figure 13.48), with the more recently settled individuals being males on top of the stack, females on the bottom. Each male (Figure 13.47B) uses its long penis to inseminate the females (Figure 13.47C) below. Males that are in association with females tend to remain male for a relatively long period of time. Eventually, or if isolated from a female, the male develops into a female. Female slipper shells cannot switch back to males, because the masculine reproductive system degenerates during the sex change.
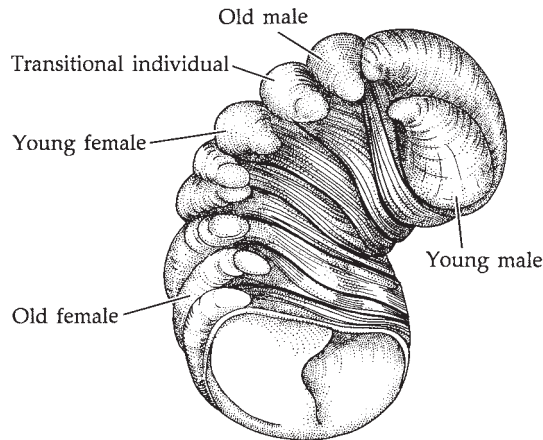
Figure 13.48 A stack of *Crepidula fornicata*, a slipper shell (Caenogastropoda) displaying sequential hermaphroditism.

Most eupulmonates are simultaneous hermaphrodites, although protandric hermaphrodites sometimes occur. In most simultaneous hermaphrodite euthyneurans a single complex gonad, the ovotestis, produces both eggs and sperm (Figures 13.46C–E and 13.47D) with the mature gametes leaving the ovotestis via the hermaphroditic duct. Euthyneuran reproductive systems are amazingly complex and varied in their plumbing and structure, and sometimes have separate male and female gonopores, or only a single common gonopore (Figure 13.46D,E).

Distinct precopulatory behaviors occur in a few groups of gastropods. These primitive courtship routines are best documented in land pulmonates and include behaviors such as oral and tentacular stroking, and intertwining of the bodies. In some pulmonates (e.g., the common garden snail, *Cornu*, formerly *Helix*) the vagina contains a dart sac, which secretes a calcareous harpoon. As courtship reaches its crescendo, and a pair of snails is intertwined, one will drive its dart into

Figure 13.49 Reproductive systems in a coleoid cephalopod, the squid *Loligo*. (A) Female and (B) male.

the body wall of the other, perhaps as a means of sexually arousing its partner.

Most bivalves are gonochoristic and retain the primitively paired gonads. However, the gonads are large and closely invested with the viscera and with each other, so an apparently single gonadal mass results. The gonoducts are simple tubes, and fertilization is usually external, although some marine and most freshwater species brood their embryos for a time. In primitive bivalves, the gonoducts join the nephridia and gametes are released through urogenital pores. In many advanced bivalves, the gonoducts open into the mantle cavity separately from the nephridiopores. Hermaphroditism occurs in some bivalves, including shipworms and some species of cockles, oysters, scallops, and others. Oysters of the genus *Ostrea* are sequential hermaphrodites, and most are capable of switching sex in either direction.

Cephalopods are almost all gonochoristic, with a single gonad in the posterior region of the visceral mass (Figures 13.11C, 13.12B, and 13.49). The testis releases sperm to a coiled vas deferens, which leads anteriorly to a seminal vesicle. Here various glands assist in packaging the sperm into elaborate spermatophores, which are stored in a large reservoir called **Needham's sac**. From there the spermatophores are released into the mantle cavity via a sperm duct. In females the oviduct terminates in one oviducal gland in squids, and two in octopuses. This gland secretes a protective membrane around each egg.

The highly developed nervous system of cephalopods has facilitated the evolution of some very sophisticated precopulatory behaviors, which culminate in the transfer of spermatophores from the male to the female. Because the oviducal opening of females is deep within the mantle chamber, male coleoids use one of their arms as an intromittent organ to transfer the spermatophores. These modified arms are called **hectocotyli** (Figures 13.12D and 13.49B). In squids and cuttlefish the right or left fourth
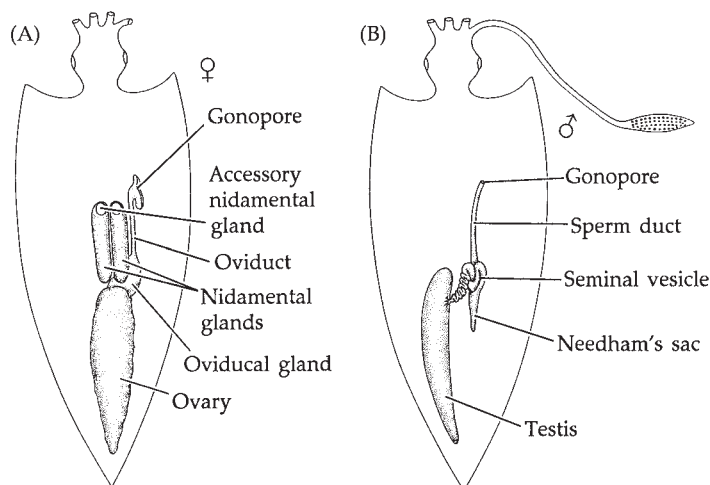
arm is used; in octopuses it is the right third arm. In *Nautilus* four small arms form a conical organ, the **spadix**, that functions in sperm transfer. Hectocotylus arms have special suckers, spoonlike depressions, or superficial chambers for holding spermatophores during the transfer, which may be a brief or a very lengthy process.

Each spermatophore comprises an elongate sperm mass, a cement body, a coiled, "spring-loaded" ejaculatory organ, and a cap. The cap is pulled off as the spermatophore is removed from the Needham's sac in squids or by uptake of seawater in octopuses. Once the cap is removed, the ejaculatory organ everts, pulling the sperm mass out with it. The sperm mass adheres by means of the cement body to the seminal receptacle or mantle wall of the female, where it begins to disintegrate and liberate sperm for up to two days.

Precopulatory rituals in coleoid cephalopods usually involve striking changes in coloration, as the male tries to attract the female (and discourage other males in the area). Male squids often seize their female partner with the tentacles, and the two swim head-to-head through the water. Eventually the male hectocotylus grabs a spermatophore and inserts it into the mantle chamber of his partner, near or in the oviducal opening. Mating in octopuses can be a savage affair. The exuberance of the copulatory embrace may result in the couple tearing at each other with their sharp beaks, or even strangulation of one partner by the other as the former's arms wrap around the mantle cavity of the latter, cutting off ventilation. In many octopuses (e.g., *Argonauta*, *Philonexis*) the tip of the hectocotylus arm may break off and remain in the female's mantle chamber.[7]

As the eggs pass through the oviduct, they are covered with a capsule-like membrane produced by the oviducal gland. Once in the mantle cavity, various kinds of **nidamental glands** may provide additional layers or coatings on the eggs. In the squid *Loligo*, which migrates to shallow water to breed, the nidamental glands coat the eggs within an oblong gelatinous mass, each containing about 100 eggs. The female holds these egg cases in her arms and fertilizes them with sperm ejected from her seminal receptacle. The egg masses harden as they react with seawater and are then attached to the substratum. The adults die after mating and egg laying. Cuttlefish deposit single eggs and attach them to seaweed or other substrata. Many open-ocean pelagic coleoids have floating eggs, and the young develop entirely in the plankton. Octopuses usually lay grapelike egg clusters in dens in rocky areas, and many species care for the developing embryos by protecting them, and aerating and cleaning

them by flushing the egg mass with jets of water. Octopuses and squids tend to grow quickly to maturity, reproduce, and then die, usually within a year or two. The pearly nautilus, however, is long-lived (perhaps to 25–30 years), slow growing, and able to reproduce for many years after maturity.

One of the most astonishing reproductive behaviors among invertebrates occurs in members of the pelagic octopod genus *Argonauta*, known as the paper nautiluses. Female argonauts use two specialized arms to secrete and sculpt a beautiful, coiled, calcareous shell into which eggs are deposited (Figure 13.17B). The thin-walled, delicate shell is carried by the female and serves as her temporary home and as a brood chamber for the embryos. The much smaller male often cohabits the shell with the female.

Development

Development in molluscs is similar in many fundamental ways to that of the other spiralian protostomes. Most molluscs undergo typical spiral cleavage, with the mouth and stomodeum developing from the blastopore, and the anus forming as a new opening on the gastrula wall (protostomous). Cell fates are also typically spiralian, including a 4d mesentoblast.

By the end of the 64-cell stage, the distinctive molluscan cross is formed by a group of apical micromeres ($1a^{12}$–$1d^{12}$ cells and their descendants, with cells $1a^{112}$–$1d^{112}$ forming the angle between the arms of the cross) (Figure 13.50). This configuration of blastomeres appears to be unique to the Mollusca. Beyond these generalities, a great deal of variation occurs in molluscan cleavage. As detailed studies are conducted on more and more species, the phylogenetic implications of these variations are being evaluated.
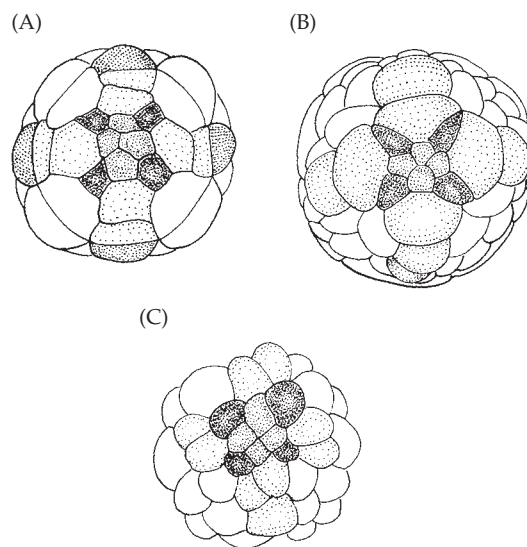
Figure 13.50 The "molluscan cross" of developing embryos. (A) Gastropoda (*Lymnaea*). (B) Polyplacophora (*Stenoplax*). (C) Aplacophora (*Epimenia*).

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[7]The detached arm was mistakenly first described as a parasitic worm and given the genus name *Hectocotylus* (hence the origin of the term).

(A)
Apical tuft
Apical plate
Prototroch
Stomodeum/blastopore

(B)
Apical tuft
Prototroch
Telotroch

(C)
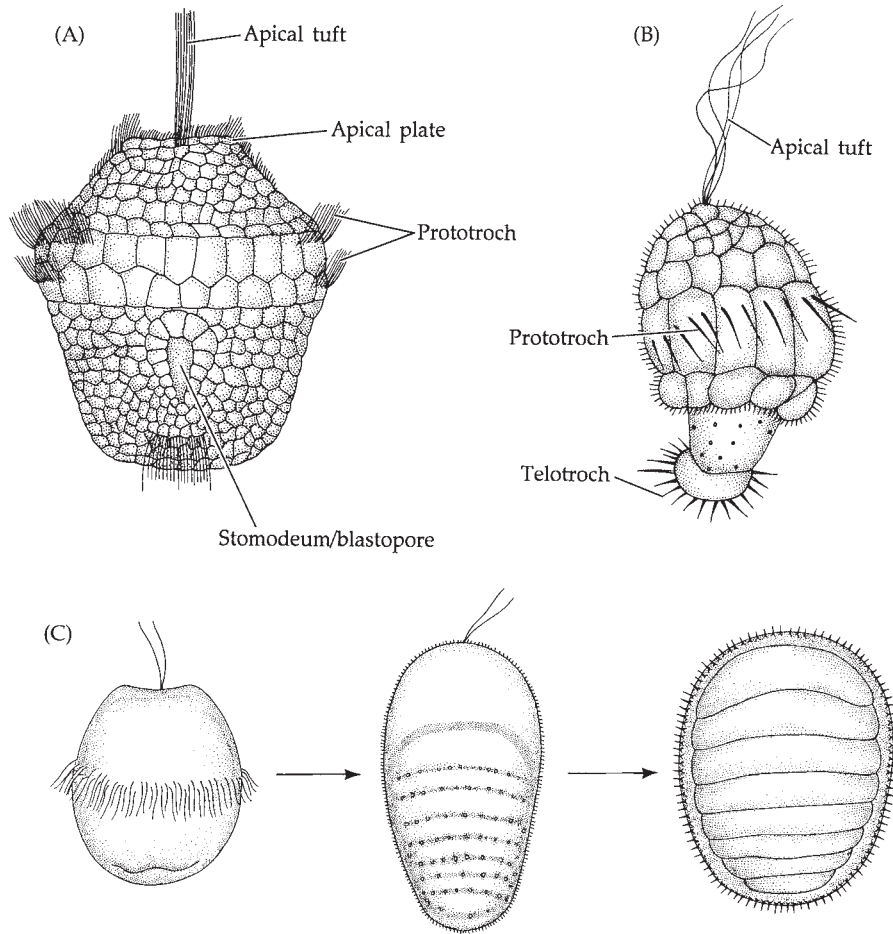
Figure 13.51 Molluscan trochophore larvae. (A) Generalized molluscan trochophore larva. (B) Trochophore of a solengaster aplacophoran. (C) Metamorphosis of a polyplacophoran from trochophore to juvenile.

Development may be direct, mixed, or indirect. During indirect development, the free-swimming trochophore larva that develops is remarkably similar to that seen in annelids (Figure 13.51). Like the annelid larva, the molluscan trochophore bears an apical sensory plate with a tuft of cilia and a girdle of ciliated cells—the prototroch—just anterior to the mouth.

In some free-spawning molluscs (e.g., chitons and Caudofoveata), the trochophore is the only larval stage, and it metamorphoses directly into the juvenile (Figure 13.51C). Solenogasters usually have a so-called "test cell larva," where a bell-shaped larval test encloses parts of the developing animal. But in other groups (e.g., gastropods and bivalves), the trochophore is followed by a uniquely molluscan larval stage called a veliger (Figure 13.52). The **veliger larva** may possess a foot, shell, operculum, and other adult-like structures. The most characteristic feature of the veliger larva is the swimming organ, or **velum**, which consists of two large ciliated lobes developed from the trochophore's prototroch. In some species the velum is also a feeding organ and is subdivided into four, five, or even six separate lobes (Figure 13.52C). Feeding (planktotrophic) veligers capture particulate food between opposed prototrochal and metatrochal bands of cilia on the edge of the velum, others are non-feeding

(lecithotrophic) and live on yolk reserves. Eventually eyes and tentacles appear, and the veliger transforms into a juvenile, settles to the bottom, and assumes an adult existence.

Like gastropods, some bivalves have long-lived planktotrophic veligers, whereas others have short-lived lecithotrophic veligers. Many widely distributed species have very long larval lives that allow dispersal over great distances. A few bivalves have mixed development and brood the developing embryos in the suprabranchial cavity through the trochophore period; then the embryos are released as veliger larvae. Some marine and freshwater clams have direct development, as for example in the freshwater family Sphaeriidae where embryos are brooded between the gill lamellae and juveniles shed into the water when development is completed. Several unrelated marine groups have independently evolved a similar brooding behavior (e.g., *Arca vivipara*, some Carditidae, etc.).

In the freshwater mussels (Unionida), the embryos are also brooded between the gill lamellae, where they develop into veligers highly modified for a parasitic life on fishes, thereby facilitating dispersal. These parasitic larvae are called **glochidia** (Figure 13.52E). They attach to the skin or gills of the host fish by a sticky mucus, hooks, or other attachment devices. Most glochidia

lack a gut and absorb nutrients from the host by means of special phagocytic mantle cells. The host tissue often forms a cyst around the glochidium. Eventually the larva matures, breaks out of the cyst, drops to the bottom, and assumes its adult life.

Among the gastropods, only the patellogastropods and vetigastropods that rely on external fertilization have retained a free-swimming trochophore larva. All other gastropods suppress the trochophore or pass through it quickly before hatching. In many groups embryos hatch as veligers (e.g., many neritimorphs,

caenogastropods and heterobranchs). As with bivalves, some of these gastropods have planktotrophic veligers that may have brief or extended (to several months) free-swimming lives. Others have lecithotrophic veligers that remain planktonic only for short periods

Figure 13.52 Molluscan veliger larvae. (A,B) Side and front views of the veliger larva of a caenogastropod snail. (C) A caenogastropod veliger with four velar lobes. (D) Generalized bivalve veliger. (E) Glochidium larva of a freshwater unionoidean bivalve. (F) Late veliger of a scaphopod (*Dentalium*).
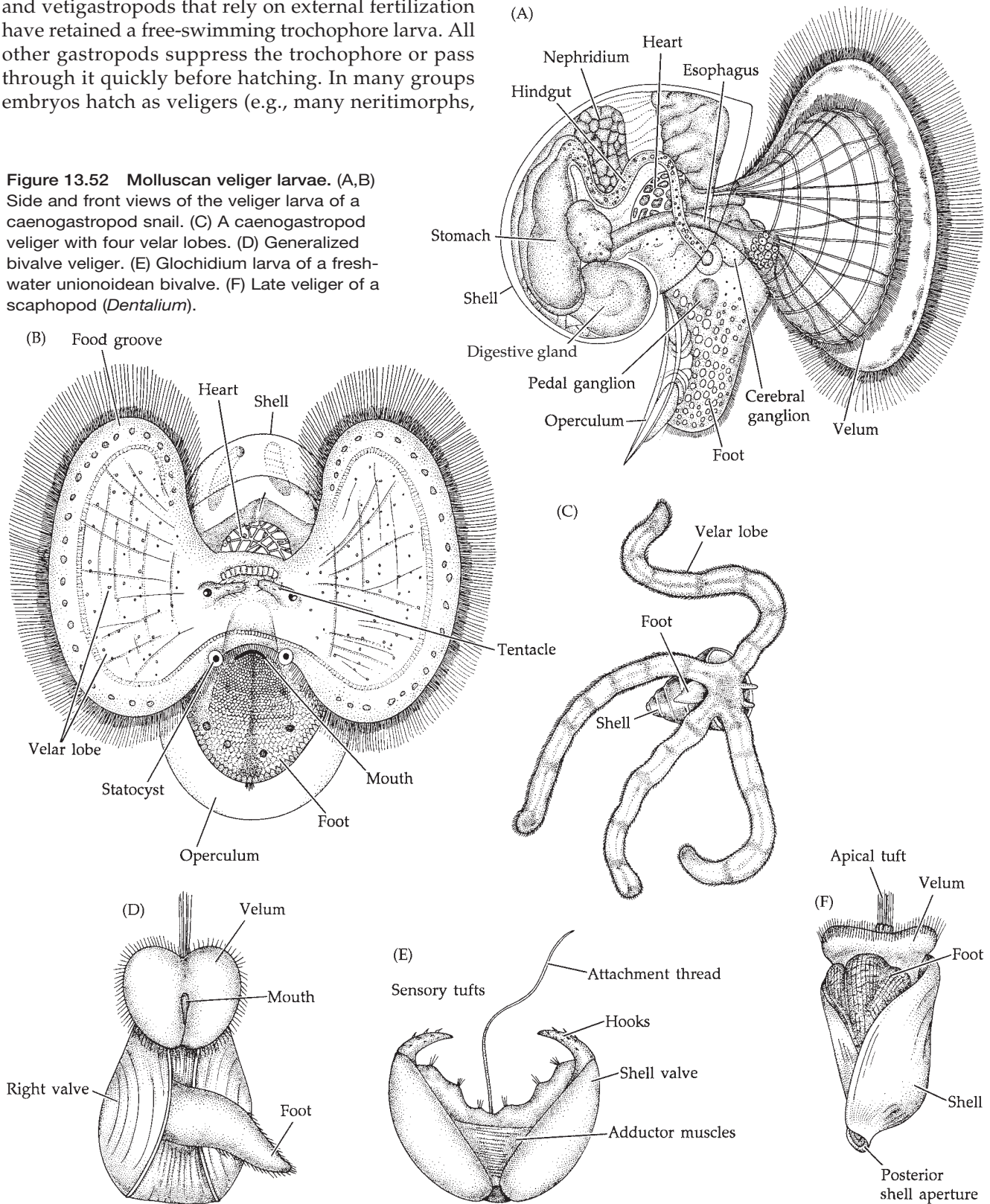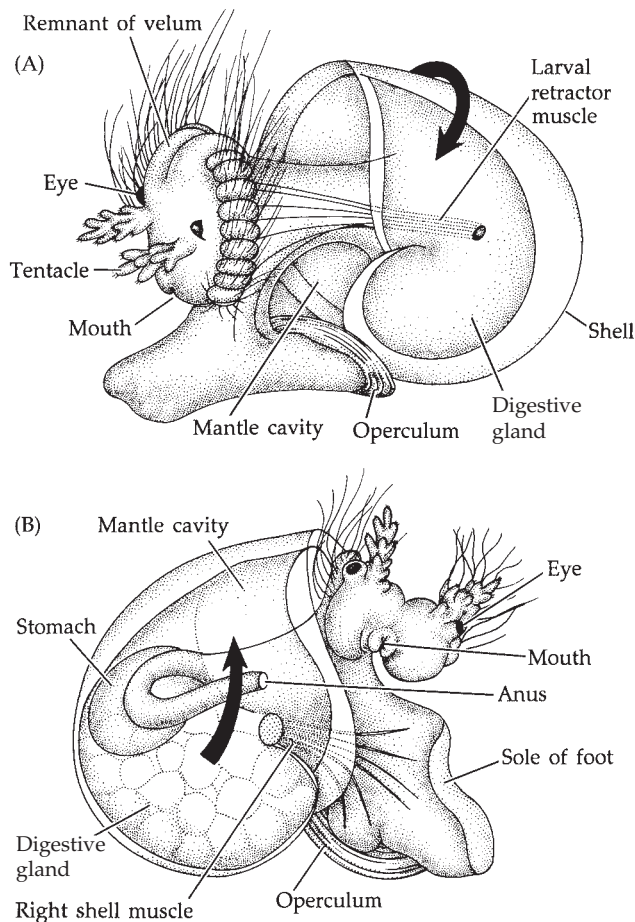
Figure 13.53 Settled larva of the abalone (*Haliotis*) undergoing torsion. (A) Left-side view after about 90° of torsion, with mantle cavity on the right side. (B) Torsion continues as the mantle cavity and its associated structures twist forward over the head.

embryo that develops within the egg case. Early cleavage is meroblastic and eventually produces a cap of cells (a discoblastula) at the animal pole. The embryo grows in such a way that the mouth opens to the yolk sac, and the yolk is directly "consumed" by the developing animal (Figure 13.54).

Molluscan Evolution and Phylogeny

The phylogenetic details of molluscan evolution have yet to be thoroughly elucidated. The phylum is highly diverse, and many named taxa below the class level are known to be polyphyletic or paraphyletic. The existence of a good fossil record (primarily of shells) has been both a blessing and a curse as efforts to trace the evolutionary history of molluscs have often been frustrated by the limited and sometimes confusing dataset provided by molluscan shells.

Until fairly recently, the idea of a "hypothetical ancestral mollusc" (affectionately known as HAM) was popular, the nature of which derived largely from early work of the eminent British biologist and "Darwin's Bulldog" T. H. Huxley. Detailed and sometimes highly imaginative descriptions of this hypothetical ancestral mollusc were proposed by various workers, even including speculations on its physiology, ecology and behavior (see Lindberg and Ghiselin 2003). The usefulness of HAM in molluscan evolutionary studies was questioned as zoology moved into an era of explicit phylogenetic analysis (i.e., cladistics). Thus, most workers now avoid the pitfalls of *a priori* construction of a

(sometime less than a week). Planktotrophic veligers feed by use of the velar cilia, whose beating drives the animal forward and draws minute planktonic food particles into contact with the shorter cilia of a food groove. Once in the food groove, the particles are trapped in mucus and carried along ciliary tracts to the mouth.

Almost all pulmonates and many caenogastropods have direct development, and the veliger stage is passed in the egg case, or capsule. Upon hatching, tiny snails crawl out of the capsule into their adult habitat. In some neogastropods (e.g., certain species of *Nucella*), the encapsulated embryos cannibalize on their siblings, a phenomenon called **adelphophagy**; consequently, only one or two juveniles eventually emerge from each capsule.

It is usually during the veliger stage that gastropods undergo torsion (see previous discussion of torsion), when the shell and visceral mass twist relative to the head and foot (Figures 13.18 and 13.53). As we have seen, this phenomenon is still not fully understood, but it has played a major role in gastropod evolution.

Cephalopods produce large, yolky, telolecithal eggs. Development is always direct, the larval stages having been lost entirely during evolution of the yolk-laden

Figure 13.54 Juvenile coleoid cephalopod attached to and consuming its sac of yolk.

hypothetical ancestor, and instead analyze the evolutionary history of molluscs by phylogenetic inference. Although morphological analyses of molluscan relationships have differed in some details, the phylogenetic relationships resulting from this work have been similar. In contrast, more recent molecular analyses of molluscan relationships have produced several alternative trees depending on the molecular data type and analytical methods. Based on these recent phylogenetic studies, the probable molluscan common ancestor was small (~5 mm long), with a dorsal shell or cuticle, and a flattened ventral surface on which the animal moved by ciliary gliding. Our phylogeny (Figure 13.55) summarizes some current thinking on molluscan evolution. The characters used to construct the cladogram

are enumerated in the figure legend and briefly summarized in the following discussion. The nodes on the cladogram have been lettered to facilitate the discussion.

Exactly where the molluscs arose within the spiralian clade, and their kinship to other spiralian phyla, are still matters of much debate. While some workers treat them as descendant from a segmented ancestor, most do not. We support the idea that molluscs arose from a schizocoelomate, nonsegmented precursor. Recent molecular studies (see References: Molluscan Evolution and Phylogeny) have suggested different sister-group relationships for the molluscs, though commonly the annelids are nested within these putative sister clades. However, as with many of the spiralian

Figure 13.55   A cladogram depicting a conservative view of the phylogeny of the Mollusca based on current hypotheses (see Sigwart and Lindberg 2015 for alternative molluscan phylogenies). The numbers on the cladogram indicate suites of synapomorphies defining each hypothesized line or clade.
Synapomorphies of the phylum Mollusca defining node *a*: (1) reduction of the coelom and development of an open hemocoelic circulatory system; (2) dorsal body wall forms a mantle; (3) extracellular production of calcareous sclerites (and/or shell) by mantle shell glands; (4) ventral body wall muscles develop as muscular foot (or foot precursor); (5) radula; (6) chambered heart with separate atria and ventricle; (7) increase in gut complexity, with large digestive glands; (8) ctenidia.
Synapomorphies of the Aculifera (Aplacophora + Polyplacophora) defining node *d*: (9) sclerites.
Synapomorphies of the Aplacophora (Caudofoveata +

Solenogastres) **defining node *e*:** (10) vermiform body; (11) foot reduced; (12) gonads empty into pericardial cavity, exiting to mantle cavity via U-shaped gametoducts; (13) without nephridia.
Synapomorphies of Caudofoveata: (14) calcareous sclerites of the body wall form imbricating scales; (15) complete loss of foot.
Synapomorphies of Solenogastres: (16) posterior end of reproductive system with copulatory spicules; (17) loss of ctenidia.
Synapomorphies of Polyplacophora: (18) shell with 8 plates (and with 8 shell gland regions), articulamentum layer, and aesthetes; (19) multiple ctenidia; (20) expanded and highly cuticularized mantle girdle that "fuses" with shell plates.
Synapomorphies of the Conchifera defining node *b*: (21) presence of a well-defined single shell gland region and larval shell (protoconch); (22) shell univalve (of a single piece; note: the bivalve shell is derived from the univalve condition); (23) shell of basically three-layers (periostracum, prismatic layer, lamellar or crossed layer); (24) mantle margin of three parallel folds, each specialized for specific functions; (25) statocysts; (26) viscera concentrated dorsally.
Synapomorphies of Monoplacophora: (27) 3–6 pairs ctenidia; (28) 3–7 pairs nephridia; (29) 8 pairs pedal retractor muscles; (30) 2 pairs gonads; (31) 2 pairs heart atria.
Synapomorphies of Gastropoda: (32) torsion; (33) cephalic tentacles; (34) operculum.
Synapomorphies of Bivalvia: (35) bivalve shell and its associated mantle and (in autobranch bivalves) ctenidial modifications; (36) loss of radula; (37) byssus (autobranchs); (38) lateral compression of body; (39) adductor muscles; (40) ligament.
Synapomorphies of the cephalopod–scaphopod line defining node *c*: (41) ano-pedal flexure; (42) new neuro-anatomical features, including cerebral ganglia fusion and position.
Synapomorphies of Cephalopoda: (43) expansion of the coelom and closure of the circulatory system; (44) septate shell; (45) ink sac (in coleoids); (46) siphuncle; (47) beak-like jaws; (48) foot modified as prehensile arms/tentacles and funnel (=siphon); (49) development of large brain.
Synapomorphies of Scaphopoda: (50) tusk-shaped, shell open at both ends; (51) loss of heart and ctenidia; (52) captacula.
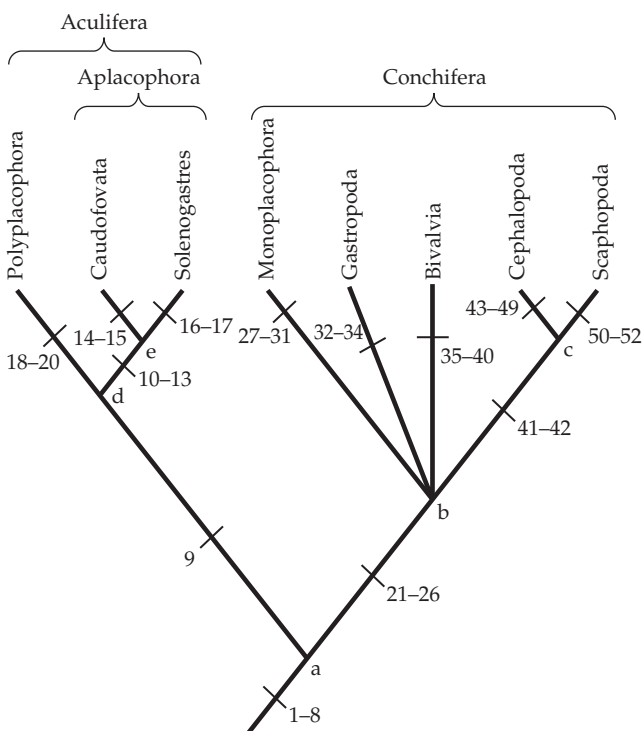
phyla, identification of the mollusc sister group remains a work in progress. Molluscs are clearly allied with the other spiralian protostomes (Platyhelminthes, Nemertea, Annelida), which are characterized by developmental features such as spiral cleavage, 4d mesentoblast, and trochophore-like larvae. But precisely where in the spiralian lineage they arose remains problematic.

The major steps in the evolution of what we generally think of as a "typical" mollusc—that is, a shelled mollusc, also remains controversial. Previous scenarios have often argued that this step took place after the origin of the aplacophorans, perhaps as molluscs adapted to active epibenthic lifestyles. These steps centered largely on the elaboration of the mantle and mantle cavity, the refinement of the ventral surface as a well-developed muscular foot, and the evolution of a consolidated dorsal shell gland and solid shell(s) in place of independent calcareous sclerites.

The description of a solenogaster larva by Pruvot in 1890, in which the dorsal surface was said to bear seven transverse bands of sclerites (described as "composite plates," reminiscent of chitons), led some workers to postulate that aplacophorans and polyplacophorans might be sister-groups; a relationships confirmed by several recent phylogenomic studies (e.g., Kocot et al. 2011). However, the discovery of a possible aplacophoran fossil having seven dorsal shell plates from Silurian deposits in England (*Acaenoplax*), as well as "footless" chitons (*Kulindroplax* and *Phthipodochiton*), have further confused the polarity of the aplacophoran-chiton character transformation. Adding to the confusion, there are fundamental differences between the shells of polyplacophorans and those of all other molluscs, an observation suggesting that the chitons and aplacophorans may stand alone as a unique radiation off the early molluscan line. Three hypotheses have been offered to explain this "shell problem" in molluscan evolution: (1) The multiplate shell may have been ancestral, the single-shell condition having evolved by coalescence of plates. (2) The single shell may have been ancestral, and the multiplate forms arose by subdivision of the single shell. (3) The single-shell and multishell designs arose independently from a shell-less ancestor, perhaps by way of sclerite consolidation. The presence of eight pairs of pedal retractor muscles in both polyplacophorans and monoplacophorans has been taken as evidence in favor of the first explanation. Acceptance of the first hypothesis suggests that the ancestor at node *a* in the cladogram in Figure 13.55 was a multivalved chiton-like creature. Acceptance of the second hypothesis implies that the ancestor at node *a* was a univalved, monoplacophoran-like ancestor. The third hypothesis postulates that the ancestor at node *a* lacked a solid shell altogether.

The primitive mantle and foot arrangement was probably somewhat similar to that in living polyplacophorans or monoplacophorans—that is, a large flattened sole was surrounded by a mantle groove.

Because of their small size, specialized respiratory structures were probably not required in the first molluscs and gas exchange was through the dorsal epidermis. However, with the origin of the cuticle-covered mantle or dorsal shell covering this surface, posterior, specialized respiratory structures (ctenidia) originated and became associated with excretory and reproductive pores in a posterior mantle cavity. This arrangement would have been modified at least twice; in both the polyplacophorans and monoplacophorans the mantle cavity was lost as it became continuous with the expanded mantle groove alongside the foot and the ctenidia multiplied and extended anteriorly in the mantle groove. Secondary modifications of the shape of the foot and other features in bivalves and scaphopods allowed most of these animals to exploit infaunal life in soft sediments, and both of these taxa are highly adapted to sediment burrowing. However, these modifications are clearly convergent and scaphopods share other characters, including ano-pedal flexure, with cephalopods. Gastropods also undergo ano-pedal flexure, but this could be convergent according to some molecular studies. Scaphopods are also the last class of molluscs to appear in the fossil record (about 450 Ma, Late Ordovician).

Monoplacophorans share the character of a single (univalve) shell with other molluscs (other than bivalves and chitons). They also share a similar shell structure and a host of other features. The only synapomorphies defining the monoplacophorans seem to be their repetitive organs (multiple gills, nephridia, pedal muscles, gonads, and heart atria). The question of whether this multiplicity arose uniquely in the monoplacophorans or represents a symplesiomorphic retention of ancestral features from some unknown metameric ancestor (below node *a* on the cladogram) has not been resolved (see discussion below) and will likely require developmental studies on monoplacophorans to finally settle the question.

The bivalve line in the cladogram is defined by the presence of 2 shell valves, adductor muscles, reduction of the head region, decentralization of the nervous system and associated reduction or loss of certain sensory structures, and expansion and deepening of the mantle cavity.

Cephalopods are highly specialized molluscs and possess a number of complex synapomorphies. Primitive shelled cephalopods are represented today by only six species of *Nautilus*, although thousands of fossil species of shelled nautiloid cephalopods have been described. This highly successful molluscan class probably arose about 450 million years ago. The nautiloids underwent a series of radiations during the Paleozoic, but were largely replaced by the ammonoids after the Devonian period (325 million years ago). The ammonoids, in turn, became extinct around the Cretaceous–Tertiary boundary (65 million years

ago). The origin of the coleoid cephalopods (octopuses, squids, and cuttlefish) is obscure, possibly dating back to the Devonian. They diversified mainly in the Mesozoic and became a highly successful group by exploiting a very new lifestyle, as we have seen.

The issue of ancestral metamerism in molluscs has been debated since the discovery of the first living monoplacophoran (*Neopilina galatheae*) in 1952. However, monoplacophorans are not the only molluscs to express serial replication or to have repeated organs reminiscent of metamerism (or "pseudometamerism," as some prefer to call it). Polyplacophorans have many serially repeated gills in the mantle groove and also typically possess eight pairs of pedal retractor muscles and eight shell plates. The two pairs of heart atria, nephridia, and ctenidia in *Nautilus* (and two pairs of retractor muscles in some fossil forms) have also been regarded by some workers as primitive metameric features.

The question is whether or not organ repetition in these molluscs represents vestiges of a true, or fundamental, metamerism in the phylum. If so, they represent remnants of an ancestral metameric body plan and may indicate a close relationship to annelids. On the other hand, organ repetition in certain molluscan groups may be the result of independent convergent evolution and not an ancestral molluscan attribute at all. And, nothing like the teloblastic metameric development of annelids is seen in molluscs. The genetic/evolutionary potential for serial repetition of organs is not uncommon and occurs in other non-annelid bilaterian phyla as well, e.g., Platyhelminthes, Nemertea, and Chordata.

The origin of molluscs themselves remains enigmatic. The excellent fossil record of this phylum extends back some 500 million years and suggests that the origin of the Mollusca probably lies in the Precambrian. Indeed, the late Precambrian fossil *Kimberella quadrata*, once thought to be a cnidarian, has been argued to have molluscan features, including perhaps a shell and muscular foot. However, recent examination of hundreds of specimens now suggests *Kimberella* more likely belongs to an extinct spiralian group.

The various ideas on the origin of the molluscs fall into three categories: molluscs were derived from (1) a free-living flatworm (Platyhelminthes) ancestor, (2) a nonsegmented coelomate protostome ancestor, or (3) a segmented ancestor, perhaps even a common ancestor with the annelids. The first hypothesis, known as the "turbellarian theory," was originally based upon the supposed homology and similarity in mode of locomotion between molluscs and flatworms by means of a "ventral mucociliary gliding surface." It suggests that either the molluscs were the first coelomate protostomes, or that they share a common ancestor with the first coelomates. However, most contemporary workers argue that the large pericardial spaces present in primitive molluscs (e.g., aplacophorans, monoplacophorans, polyplacophorans) point to a coelomate rather than an acoelomate (platyhelminth) ancestry, and the turbellarian theory enjoys little favor today.

The second theory advanced by Scheltema in the 1990s suggested that sipunculans (now placed within the Annelida) and molluscs might be sister groups, sharing, among other things, the unique "molluscan cross" during development. However, the idea that sipunculan embryogeny includes a molluscan cross blastomere configuration is no longer strongly supported. Scheltema also suggested that certain features of the sipunculan pelagosphera larva may be homologous to some molluscan structures. Indeed, molluscs share most of their typical spiralian features with the sipunculans, as well as the echiurids and other annelids (e.g., spiral cleavage, schizocoely, trochophore larvae). This leads to the third hypothesis, that molluscs and annelids are closely related and that molluscs might have arose from a segmented coelomate ancestor. Perhaps the three most striking synapomorphies distinguishing modern molluscs from annelids and most other spiralians are: the reduction of the coelom and the concomitant conversion of the closed circulatory system to an open hemocoelic one; the elaboration of the body wall into a mantle capable of secreting calcareous sclerites or shell(s); and, the unique molluscan radula. Identifying the sister group to the Mollusca remains a work in progress.

Selected References

The field of malacology is so large, has had such a long history, and has so embraced the mixed blessings of contributions from amateur shell collectors, that dealing with the literature is a daunting task. Many molluscs are of commercial importance (e.g., *Haliotis*, *Mytilus*, *Loligo*) and for these groups hundreds of studies appear annually; others are important laboratory/experimental organisms (e.g., *Loligo*, *Octopus*, *Aplysia*) and many papers are also published on these groups. New taxonomic monographs on various groups or geographical regions also appear each year, as do countless shell guides and coffee-table books. Distilling all of this into a small set of key references useful for entry into the professional literature is difficult; the list below is our attempt to do so.

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