by phytoplankton. Following induction to synthesize the degradation enzyme, bacteria were attracted to DMSP at levels occurring in seawater near senescing phytoplankton cells. In contrast, genetically identical cells without enzyme induction were not attracted to DMSP. Investigators are now testing whether the degradation enzyme, or a protein coinciding with it, functions as a chemoreceptor that mediates chemical attraction. Alternatively, the enzyme (or coincidental protein) might serve as a transporter for DMSP uptake from the environment across the periplasmic membrane. When combined with enzyme activity, bacterial attraction to DMSP should substantially increase the rate of DMS production and therefore play a critical role in biogeochemical sulfur cycling between dissolved organic matter in seawater and the global atmosphere.

SEE ALSO THE FOLLOWING ARTICLES

Fertilization, Mechanics of / Foraging Behavior / Hydrodynamic Forces / Larval Settlement, Mechanics of / Predation / Turbulence

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CHITONS

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Chitons are an ancient lineage of molluscs, found only in the sea, that are classified as class Polyplacophora of phylum Mollusca. They can be recognized by their eight overlapping shell plates, known as valves (six intermediate valves and two terminal valves at the head and tail), which are firmly anchored in a tough muscular girdle (Fig. 1). The dorsal surface of the girdle is occasionally
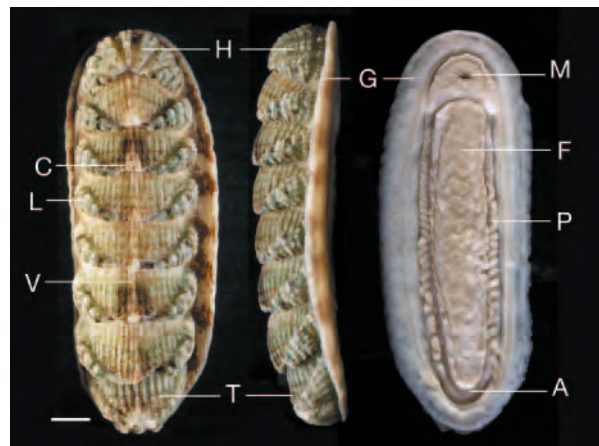

FIGURE 1 A chiton, *Callistochiton crassicostatus* (Monterey, California), in dorsal (left), lateral (center), and ventral (right) orientations. Abbreviations: V = one of eight valves, H = head (or first) valve, T = tail (or eighth) valve, C = central area, L = lateral area, G = girdle, M = mouth and oral region, F = foot, P = pallial groove and gills (ctenidia), A= anus, chiton in dorsal view, with labeled features. Scale bar = 2 mm. Photographs courtesy of A. Draeger.

nearly nude but is otherwise adorned with various scales, stout spines, elongate needles, hairs, branching setae, or dense microscopic granules (Fig. 2). Fossils of chitons, including some that are more than 500 million years old, suggest that throughout their history their lifestyle and appearance have not changed very much. Most of the more than 900 recognized species live on rocky habitats in intertidal to shallow subtidal habitats, where they are often common and ecologically important. Other species manage to inhabit the more sparse hard substrates found at greater depths, and some species have been dredged

FIGURE 2 Selected examples of different girdle ornamentation: (A) hairy and calcareous elements in *Stenoplax conspicua* (southern California); (B) clusters of spines at valve sutures in *Acanthochitona exquisita* (Gulf of California, Mexico); (C) imbricating scales in *Chiton virgulatus* (Gulf of California, Mexico); (D) setae with calcareous spicules in *Mopalia ciliata* (central California). Photographs A–C by the author; photograph D courtesy of A. Draeger.

from the deepest ocean trenches. Chitons usually attach firmly to hard substrates with a muscular foot, and they move by creeping with the aid of mucous secretions and by contractions of their foot.

FEEDING

Like many other molluscs, chitons feed with a thin strap bearing rows of teeth known as the radula. The anterior rows are used up and discarded or swallowed and replaced by new rows moving forward like a conveyor belt. Depending on the particular species, they scrape algal films off rocks, take bites of larger algal blades, eat encrusting colonial animals, or sometimes even ambush and eat mobile animals that come close enough to be trapped. The chiton radula is noteworthy because one pair of cusps in each row is hardened with magnetite, which provides these teeth with a coating harder than stainless steel. They are the only molluscs that have magnetite-coated teeth. In fact, they are the only organisms known to manufacture such vast quantities of magnetite.

The diet of many chitons consists of "diatom scuzz" scraped off rocks, but the largest chitons tend to take bites of large algal blades. Some chitons are specialists on particular marine plants (Fig. 3), scraping off the upper surface of coralline algal crusts (e.g., *Tonicella* spp.) or feeding on kelp (e.g., *Cyanoplax cryptica, C. lowei, Juvenichiton* spp., *Choriplax grayi*) or seagrasses (e.g., *Stenochiton* spp.). Even though chitons are important for their role as primary consumers of marine plants, many chitons feed predominantly on animals, for example, grazing on encrusting colonial animals in the low intertidal or on sponges or foraminifera in the deep sea or associated

FIGURE 3 Chitons that are specialist grazers, feeding on particular algal species. (A) *Tonicella lineata* (British Columbia, Canada) feeds on crustose coralline algae. Photograph by the author. (B) *Cyanoplax cryptica* (southern California) lives and feeds on the southern sea palm kelp, *Eisenia arborea*. Photograph by R. N. Clark and the author.

with deep sunken wood or even deep-sea hydrothermal vents. Perhaps most striking is the highly convergent broad body shape and predatory behavior of three only distantly related chiton genera, all in separate families: *Placiphorella, Loricella,* and *Craspedochiton* (Fig. 4).
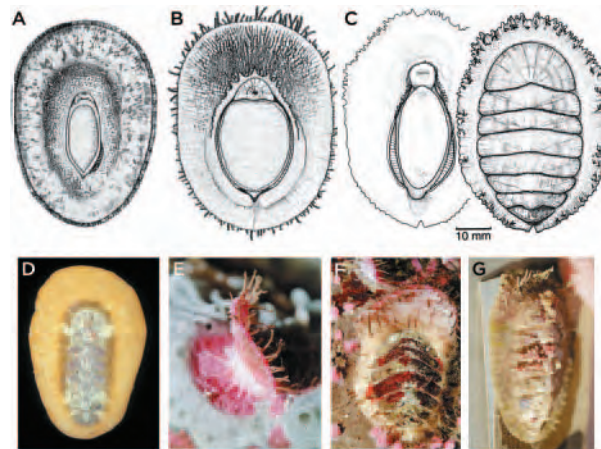

FIGURE 4 Convergent evolution of carnivorous feeding in three only distantly related chiton genera: *Placiphorella* (Mopaliidae), *Craspedochiton* (Acanthochitonidae), and *Loricella* (Schizochitonidae). (A) *Craspedochiton pyramidalis* (Japan), (B) *Placiphorella stimpsoni* (Japan); reprinted from Saito and Okutani 1992 (see Further Reading). (C) *Loricella angasi* (ventral and dorsal views, Western Australia); drawing by I. Grant, from Kaas *et al.* 1998 (see Further Reading). (D) *Craspedochiton productus* (South Africa), (E) *Placiphorella velata* (with oral hood raised, central California), (F) *P. velata* (central California), (G) *Loricella angasi* (Western Australia); photographs by the author. Members of all three genera have been shown to be ambush predators, with an expanded (especially anterior) girdle in comparison to their respective nearest nonpredatory relatives.

RESPIRATION

For respiration, most molluscs have a pair of gills (or ctenidia), sometimes reduced to a single gill, but chitons have entire rows of interlocking gills hanging from the roof of the pallial groove along each side of their foot. Members of the mostly deepwater Lepidopleurida (e.g., *Leptochiton;* Fig. 5, left) have a continuous semicircular arrangement of gills surrounding the anus, and this arrangement is likely primitive; however, more familiar chitons (Chitonida) have gill rows on either side of the foot, separated by an interspace between the ends of the rows (Fig. 5, right). The latter arrangement more effectively divides the outer and inner pallial groove into inhalant and exhalant spaces, respectively. Chitons use small hemoglobin proteins called myoglobins in tissues associated with feeding structures, but for delivering oxygen throughout their body they use a circulatory copper-based respiratory protein called hemocyanin. This
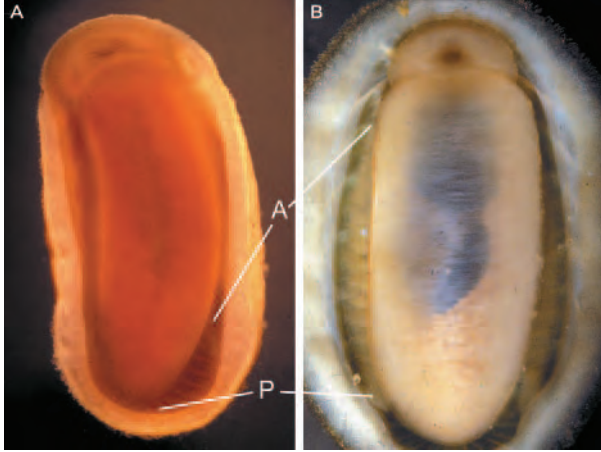
FIGURE 5 Ventral views of chitons from Washington, each about 1 cm in length, with contrasting arrangements of gill rows. Left: *Leptochiton rugatus* (Lepidopleurida: Leptochitonidae) with posterior gill rows that form a continuous semicircle of gills. Right: *Cyanoplax dentiens* (Chitonida: Lepidochitonidae) has lateral gill rows with an interspace at the posterior end. For each, the line points to the anterior (A) or posterior (P) end of one of the paired gill rows. Note: The red coloration of the foot and gills of *L. rugatus* is due to tissue hemoglobins, and this is the only chiton species for which these are known (Eernisse *et al.* 1988). Photographs by the author.

functional protein is unique to molluscs and is not related to a different copper-based respiratory protein found in arthropods, despite having the same name.

Underwater, an impressive respiratory current exits past a chiton's anus, generated by the numerous cilia on each gill. Oxygen is relatively more abundant in air than in water, so a large chiton sprawled with its gills partly exposed at low tide could be effectively involved in aerial respiration, provided that its gills do not dry out.

BEHAVIOR, NERVOUS SYSTEM, AND SENSORY ORGANS

A chiton's mouth is associated with the radula and a tonguelike subradular organ, but chitons really do not have a head. In this sense, they are typical molluscs; unlike the familiar subgroup of molluscs that includes snails and octopuses with a head, typically well equipped with a brain, tentacles, and eyes. The chiton has none of these, but even without a brain a chiton still manages to behave in an adaptive manner. For example, when touched, a chiton rapidly responds by clamping down on its attachment with powerful muscles in its foot and girdle and attached to its valves, and so resists being pried off a rock with amazing tenacity. To maintain such a tight grip indefinitely would be a waste of energy. Instead, a chiton chooses when and where to cling the tightest. Chitons will often move to feed or to seek shelter. For example,

a chiton can move with surprising speed when the rock it is on is overturned as it seeks to crawl back under the rock. When moving, it is at its most vulnerable to losing its grip when it might be surprised by an unusually large wave, a shorebird's beak, or human fingers. Even when dislodged, many species are able to escape from a would-be predator by rolling in a tight ball, like a common garden isopod (roly-poly, pillbug, sowbug). Such behavior allows them to be picked up by a passing wave and rolled out of harm's way, later to uncurl when conditions are safer. Some chitons (e.g., *Callistochiton* spp.) seem to spontaneously detach without provocation when a rock is overturned.

Many species show striking diurnal (daily cycle) patterns of activity, usually remaining hidden under a rock or wedged into a depression by day, and foraging by night when visual predators are not a threat. Tropical intertidal chitons of the genus *Acanthopleura* are well known to display homing behavior, possibly retracing the chemical cues in their own trails of mucus to return to the safe haven of their own home depression, which they also can aggressively defend, excluding other chitons. Particular members of *Nuttallina* (Fig. 6) are especially effective burrowers on soft sandstones and collectively can riddle the midshore with deep burrows. No one has studied how these chitons manage to make a home depression.

FIGURE 6 *Nuttallina fluxa* (southern California) creates a home depression in soft sandstones. Photograph by the author.

The most interesting aspect of a chiton's nervous system has to do with the many nerve bundles that innervate the upper (tegmentum) layer of each valve, leading to the primary complex sensory organs found in a chiton. These numerous shell organs and their supporting nervous tissue make the upper partly mineralized and partly

living shell layer of chitons different from the shell of other molluscs, or from other animals with calcium carbonate skeletons in general. All chitons have esthetes, or small shell organs, and these were also present early in their evolutionary history during the Paleozoic Era (543 to 250 million years ago).

In addition to esthetes, some specific lineages of chitons also have considerably larger ocelli organs, and these are clearly photosensory. For example, some chitons normally clamp down to the rock when a potential predator (or scientist) creates a shadow over their body, but they lose this shadow response when their ocelli are covered with opaque material. Ocelli likely evolved separately in the families Schizochitonidae and Chitonidae.

REPRODUCTION

Chitons generally have separate sexes and spawn sperm or eggs from a simple gonad through paired gonopores near the posterior end of the pallial grooves alongside their foot. Spawning is often highly synchronous but is not necessarily exactly correlated with a particular stage of the lunar or annual solar cycle. Populations separated by some distance can be out of synchrony with each other. Chitons sometimes aggregate and simultaneously spawn (e.g., the giant gumboot chiton, *Cryptochiton stelleri*).

Normally gametes are free-spawned and exit past the anus, carried by normal respiratory currents into the plankton. Chiton embryos have typical spiral cleavage, leading to a trochophore larva (Fig. 7B) that hatches from the egg capsule normally within about two days. The trochophore is capped with a sensory plate with an apical tuft of cilia, and more flagella forming a band around the middle known as the prototroch. The rapidly beating prototroch propels the speedy larva through the plankton, but it is not involved in feeding as in some animals with a trochophore larva. Chiton trochophores depend entirely on the yolk supplied in the egg and are thus non-feeding, or lecithotrophic.

Although free spawning is most common, females from about five percent of all chiton species instead brood their eggs (Figs. 7A, 8A–C), with embryonic and larval development completed within the pallial groove of the brooding mother, sometimes with embryos sticking together in rod-shaped broods (Fig. 8B). A few species (e.g., *Stenoplax heathiana*) are known to lay benthic strings of jelly-like egg masses. Unlike a free-spawned embryo, a brooded or benthic-egg-mass embryo hatches as a late-stage larva and already has a creeping foot (Fig. 7A). Such a "crawl-away" larva is at least potentially capable of remaining near its mother.
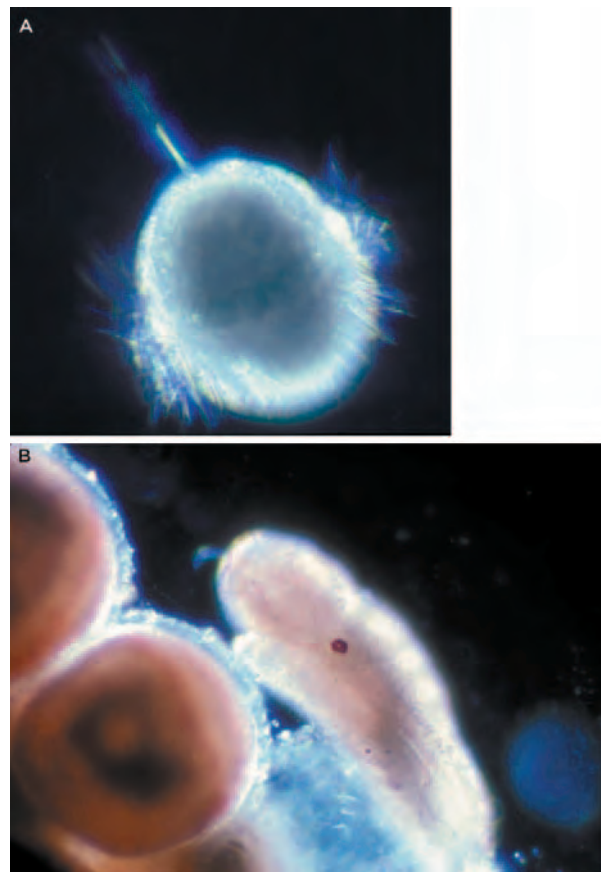

FIGURE 7 Contrast between stages of hatching in embryos of a free-spawner and a brooder. (A) Free-spawner *(C. hartwegii)* embryo hatches at early stage to a trochophore larva, topped with apical tuft and surrounded by prototroch flagella used for locomotion. (B) Brooder *(Cyanoplax thomasi)* larva just hatched and creeping over still unhatched embryos. In comparison to early-stage larva, this late-stage trochophore has already developed its foot so that it can crawl away; it has paired eyespots, and uncalcified shell precursors are visible on its dorsal surface. Photographs by the author.

Because most species do not seem to undergo metamorphosis spontaneously in cultures maintained in filtered seawater, the cues that promote larval settlement and metamorphosis are mostly unknown. Metamorphosis is not very dramatic but does involve some important changes, including the immediate start of biomineralization of the valves (Fig. 8D vs. 8E) and radula, the latter also apparent from the active feeding of newly metamorphosed juveniles. The prototroch and apical tuft are cast off, and the larva soon transforms from elongate to oval in body outline about 0.5 mm in length (Fig. 8F). At first there are only seven calcareous valves, with the tail (eighth) valve typically added up to a month or so later. One carryover from the larval stage is the retention of two bright red "larval" eyespots on the ventral surface (Fig. 8F); these do not correspond to the adult shell organs, and they persist for only about a month before they are lost.
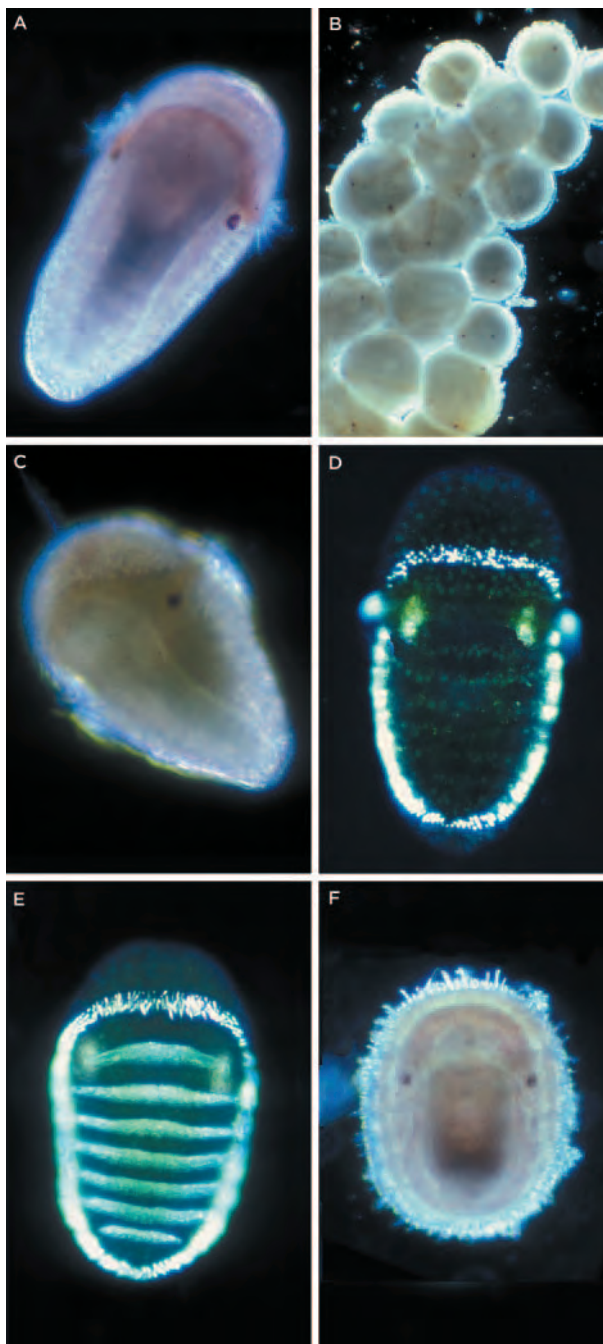
FIGURE 8 Selected chiton developmental states through metamorphosis. (A) Ventral view of newly hatched late-stage trochophore larva of the brooder *Cyanoplax thomasi* (compare with Fig. 7A); (B) brooded embryos already at late trochophore stage before hatching, *C. fernaldi;* (C) newly hatched late-stage trochophore larva of brooder *C. fernaldi*. (D) Dorsal view of late-stage trochophore larva of free spawner *Mopalia lignosa,* using polarized light to emphasize already calcified girdle spicules (paired eyespots and more indistinct prototroch cilia also are bright in this polarized view); (E) dorsal view of recently metamorphosed *M. lignosa* juvenile as in (D) but now also with newly calcified valves; (F) ventral view of recently metamorphosed *C. fernaldi* juvenile, with prominent paired red larval eyespots. Photographs by the author.

FOSSIL RECORD

By the Late Cambrian Period (after 500 million years ago), chitons were already quite diverse and probably were important grazers on the then common cyanobacterial reefs. Particular fossils from earlier in the Cambrian or even the latest Precambrian (560 to 543 million years ago) that were previously considered as enigmatic "Problematica" or assigned to other phyla such as Annelida or Brachiopoda have recently been instead considered as close relatives of chitons. The range of fossils that are included within the chiton "crown group" has also been expanded by discoveries of exceptionally well-preserved articulated fossils, whereas most chiton fossil species are known only from separated valves. An Ordovician (approximately 450 millions of years ago) chiton, *Echinochiton dufoei,* is an example of an early chiton that had the normal eight valves but also had surprisingly gigantic spines on its girdle (Fig. 9). Other Paleozoic chitons probably had less dramatic smooth girdles.
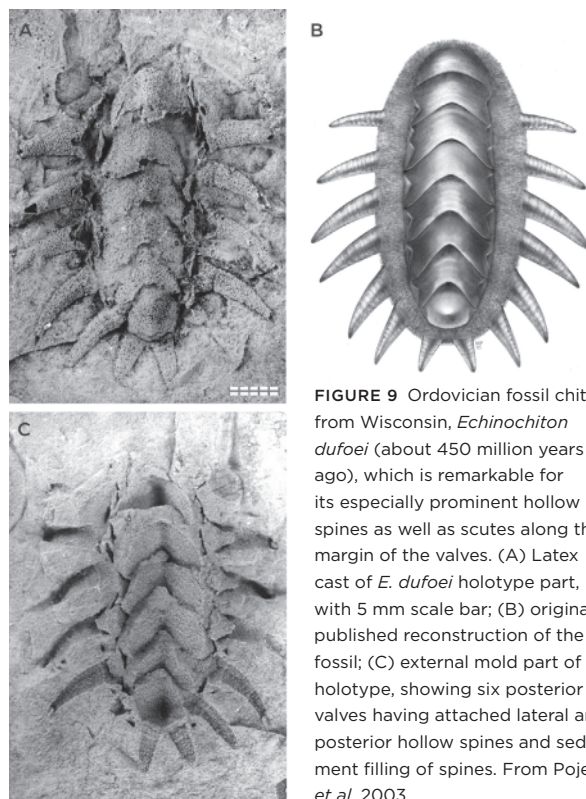

FIGURE 9 Ordovician fossil chiton from Wisconsin, *Echinochiton dufoei* (about 450 million years ago), which is remarkable for its especially prominent hollow spines as well as scutes along the margin of the valves. (A) Latex cast of *E. dufoei* holotype part, with 5 mm scale bar; (B) originally published reconstruction of the fossil; (C) external mold part of holotype, showing six posterior valves having attached lateral and posterior hollow spines and sediment filling of spines. From Pojeta *et al.* 2003.

PHYLOGENY AND CLASSIFICATION

There is general agreement that chitons are a monophyletic group. Most also agree that chitons are the sister taxon of a grouping that includes most other molluscan classes, known as Conchifera, including gastropods, cephalopods,

bivalves, and scaphopods. Together, chitons plus conchiferans constitute a molluscan subgroup known as Testaria. The only molluscs that are generally not considered part of Testaria are two lineages of wormlike "aplacophoran" molluscs; however, the position of these is controversial. Most have considered aplacophorans as basal molluscs, usually as two separate lineages outside of Testaria, but some others have instead argued that aplacophorans are a monophyletic sister taxon of chitons.

Recent progress in morphological and molecular analysis of genealogical relationships within chitons has substantially improved understanding of living and fossil chiton relationships. Most familiar living chiton species belong to Chitonida, which share derived similarities in shell, gill, and egg hull, sperm, and molecular traits. Other living chitons are mostly restricted to deep water and belong to Lepidopleurida (e.g., *Leptochiton;* Figs. 5A, 10). Within Chitonida, combined shell, sperm, egg, and molecular analyses support the basal position of Callochitonidae within Chitonida (e.g., *Callochiton*). Particular derived sperm and egg hull features support the monophyly of all remaining members of Chitonida, which likewise is subdivided into two well-supported lineages: Chitonina and Acanthochitonina. This division corresponds to fundamental differences between both the pattern of sculpturing for an extracellular hull surrounding spawned eggs and also the particular arrangement of gill addition in the ontogeny of chitons. Members of Chitonina have spiny egg hulls and have retained a primitive "adanal" gill arrangement (Fig. 1C), with gills added both posterior and anterior of the first pair of gills to appear in ontogeny, which appear just

posterior to paired renal openings. Acanthochitonina have cuplike or conelike egg hulls and derived abanal gill placement, with gills added only anterior to the first pair. In adults, if the last gill in each row is also the largest, the arrangement is abanal (Fig. 5B). In addition to these egg hull and gill arrangement features, both Chitonina and Acanthochitonina are strongly supported by molecular evidence. Within each of these taxa, most families and genera are well delimited, but relationships among these are not.

ECOLOGY

Chitons are often important members of rocky intertidal communities. For example, the "black Katy" chiton, *Katharina tunicata* (Fig. 11), is a large herbivore that is abundant and conspicuous on rocky shores from northern California to Alaska. With lower densities of grazers, the algal turf grows so profusely that those grazers that are present are less successful than if grazers were more common. At high densities, *K. tunicata* becomes a competitive dominant species in its community. *K. tunicata* keeps the kelp *Alaria marginata* at extremely low densities, but when it is excluded this alga forms a monodominant covering of the same habitat.

FIGURE 11 *Katharina tunicata* (foreground and background, Washington, about 8 cm length) is a competitive dominant grazer along much of the northwestern North American coast that is also a traditional subsistence food source for some Native Alaskans. Other grazers, such as the coralline alga specialist limpet, *Acmaea mitra* (center), benefit from the presence of high densities of *K. tunicata* (see text). Photograph by the author.

FIGURE 10 *Leptochiton rugatus* (central California, about 1 cm length) is representative of the mostly deep-water order Lepidopleurida, although this species often occurs on the underside of rocks in the intertidal. Photograph by the author.

Other species of chitons occur in densities comparable to those of *K. tunicata* on various temperate and tropical shores but, unlike *K. tunicata,* they more normally retreat to under rocks or otherwise are hidden from sight during daylight hours.

SEE ALSO THE FOLLOWING ARTICLES

Fossil Tidepools / Homing / Molluscs / Rhythms, Nontidal

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CIRCULATION

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Circulation is a general term that describes the movement of fluids within an animal. In most, but not all organisms, it refers to the movement of a transport medium (termed blood or hemolymph) through specialized conduits. At its most complex, the circulatory or cardiovascular system consists of a transport fluid, a series of conduits or vessels, and one or more pumping organs (hearts). Circulatory systems range in complexity from simple open systems to the high-pressure closed systems typical of the vertebrates. The circulatory system is a communication system providing a vital link between specialized organs and the tissues.

FUNCTIONS OF THE CIRCULATORY SYSTEM

Gases, nutrients, and wastes move in and out of cells by diffusion. In unicellular animals and some of the lower multicellular animals, this can be accomplished by diffusion directly across the body wall. In most multicellular animals the process of diffusion from the external environment into individual cells would be far too slow to maintain cellular activities. The circulatory system has evolved to transport substances from the external environment to individual body cells and vice versa.

The circulatory system carries oxygen from the respiratory organs (gills or lungs) to the cells and transports carbon dioxide from the cells to be expelled from the body. Oxygen is usually transported on specialized carrier pigments, which can be intracellular or extracellular; smaller amounts are carried in solution. Carbon dioxide can be carried in solution or bound up in various chemical forms such as bicarbonate. Once nutrients have been processed by the digestive system, they have to be transported to individual cells. Once inside the cell, oxygen is used to break down nutrients for energy and growth. Metabolic wastes produced by cellular activities are toxic to the system and are transported to specialized organs for excretion.

In complex multicellular animals the circulatory system acts as a conduit for hormone transport. Hormones are a control system allowing communication between various areas of the body. An array of hormones regulates ion levels and maintain the volume and pressure of the circulatory system. The blood itself is also an important buffer system, regulating pH of the extracellular fluids.

In homeothermic (warm-blooded) animals and some poikilothermic (cold-blooded) animals the circulatory system is important for distribution of heat and maintenance of body temperature. The circulatory system also serves as a proliferation and storage area for specialized cells. These cells function in the defense (immune system) and repair of the body (e.g., clotting, tissue regeneration).

Finally, in many invertebrates a fluid-filled system provides rigidity to the body, thus functioning as a skeletal system. Such hydrostatic skeletons are important for movement or extension of various structures. For example, echinoderms move by use of tiny tube feet. These tube feet are extended by pumping fluid into them via the water