Roper. C. F. E., M. J. Sweeney, C. E. Naun. 1984. FAO species catalogue. Volume 3. Cephalopods of the world. An annotated and illustrated guide to species of interest to fisheries. FAO Fish Synopsis 125(3): 1–277.

Verrill, A. E. 1883. Descriptions of two species of *Octopus* from California. Bulletin of the Museum of Comparative Zoology 11: 117–123.

Winkler, L. R., and L.M. Ashley. 1954. The anatomy of the common octopus of northern Washington. Walla Walla College Publications in Biological Science 10: 1–30.

Polyplacophora

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(Plates 352–354)

Chitons are conspicuous in intertidal and shallow subtidal habitats along much of the Pacific coast of North America, where they are often abundant and ecologically important members of the community (Dethier and Duggins 1984; Duggins and Dethier 1985). Indeed, the Pacific coast supports both an unusually high diversity of species and the largest-bodied chiton species in the world.

This diversity was relatively well known when the noted malacologist Allyn G. Smith wrote the chiton key in the previous edition of this manual. Nevertheless, many changes have occurred in our understanding of the diversity of the chiton fauna, nomenclatural advances have been introduced, and we have added more species that, although largely subtidal, find their upper limits in the lower intertidal zone. Most chitons found within 15 m (a depth readily accessible by scuba) may also be expected to occur occasionally in the intertidal. The number of recognized species has also increased due to morphological and molecular studies (see especially the worldwide monograph series by P. Kaas and R. A. Van Belle [1985–1994], and the publications of A. J. Ferreira, R. N. Clark, and D. J. Eernisse).

The following key and species list include some reassignments of genera and the revival of some older nominal species rescued from synonymy. Those that are higher-level changes are based on phylogenetic studies (D. J. Eernisse, unpublished; R. P. Kelly and D. J. Eernisse, unpublished; see also Kelly and Eernisse, 2007; Kelly et al., 2007), which have extended earlier worldwide phylogenetic (Okusu et al. 2003) and morphological analyses (review by Eernisse and Reynolds 1994; see also Buckland-Nicks 1995; Sirenko 1993; 1997; 2006).

Chitons are exclusively marine and relatively conservative in appearance and life styles. All chitons normally have eight shells, or **VALVES**, embedded in a tough but flexible mantle referred to as the **GIRDLE** (plate 352A, 352B). Rare specimens may have six, seven, or nine valves (Roth 1966, Veliger 9: 249–250). Chitons cling to rocks or other hard substrates with their muscular broad foot. Their anterior mouth is separated from the foot, but chitons lack a true head—a condition typical of mollusks except for gastropods and cephalopods. Alongside the foot are paired rows of interlocking **CTENIDIA** (referred to here as **GILLS**). Noting the length and position of each gill row and whether the size of gills decreases toward the posterior anus can aid in identification.

Most chitons (members of order Chitonida), including most in this key, have an **INTERSPACE** between the posterior ends of the left and right gill rows, and each gill row extends at least halfway to the anterior end of the groove alongside the foot. With this arrangement, each gill row functionally divides this pallial groove between the foot and girdle into outer inhalant and inner exhalant spaces because the gills have interlocking cilia, hanging curtainlike from the roof of each pallial groove. Cilia on each gill power water through the row and eject it at surprising velocities past the anus, allowing these chitons to have effective aquatic respiration despite their firm attachment to hard substrates (Yonge 1939).

When chitons are exposed during low tide, when oxygen is more abundant, they have a large surface area of gills with which to respire in air by direct diffusion, provided they are able to keep their gills moist. Chitons of the suborder Acanthochitonina (including Lepidochitonidae and Mopaliidae in this key) have an **ABANAL** gill arrangement in which the largest gill in each gill row is the most posterior. In contrast, members of the suborder Chitonina (Chaetopleuridae and Ischnochitonidae in this key) have an **ADANAL** gill arrangement with the largest gill away from the posterior end of the gill row.

Members of the mostly deep-water order Lepidopleurida (Leptochitonidae in this key, =Lepidopleuridae) are most readily distinguished by their posterior gill arrangement. As in Chitonina, their gill rows are adanal but they do not have an interspace. Instead, the left and right gill rows form a nearly continuous U-shaped arrangement adjacent to the anus. The respiratory mantle cavity, including all the gills, is restricted to the posterior one-third of the animal, resulting in a different and probably primitive functional arrangement with implications not well studied by Yonge (1939) or subsequent authors.

Chitons sense their surroundings with numerous sensory organs distributed on their girdle and across the upper surface of their valves. The presence of these shell organs, called **ESTHETES** (or **AESTHETES**), in the upper layer of valves known as the **TEGMENTUM** is unique to chitons among mollusks. Elsewhere (especially certain genera in tropical seas), esthetes are impressively modified as shell eyes (ocelli) large enough to be visible to the naked eye. Many Pacific coast species have photosensory esthetes, among those used for other sensory functions. Chitons also have many sensory organs among their diverse girdle ornamentation (Leise and Cloney 1982).

It is relatively easy to learn to recognize most chiton genera, whereas distinguishing species within some genera can be quite challenging. The shape of the girdle and the various structures on it provide many of the clues to species identification. Within chitons the girdle shape varies from merely a flexible skirt surrounding the valves, through various degrees of intrusion between the valves, to a covering completely enclosing the valves. The elements on the dorsal girdle surface (bare girdle, granules, scales, spicules, spines, fleshy bristles, or setae) are even more varied and useful for distinguishing species (plate 352C–352H). Closer examination is required to reveal finer diagnostic girdle element features: the organization of scales variously ranges from **IMBRICATING** (i.e., shingled and overlapping) (plate 352E, 352F), to scattered without apparent order, to scales sculptured with microscopic bumps and ridges; the distribution of spines (or setae) varies from scattered to specifically located at the valve sutures, and from individual structures to several structures gathered into tufts, and the setae usually bear further species-specific elaborations of the form of spicules and bristles, which often ornament individual setae. In particular, seta features are the most reliable morphological clues for identifying the 17 species of the most diverse genus in this key: *Mopalia* (plates 353, 354). These setae distinctions have been corroborated with molecular sampling (Kelly et al. 2007; R. P. Kelly and D. J. Eernisse, unpublished).

There are three structures of diagnostic importance on setae. First, setae emerge from a follicle in the girdle as a central supporting shaft, and this can have or lack a dorsal groove.

Second, there can be thinner flexible bristles borne on the shaft and attached either in the groove or in a matrix adhering to the shaft. Third, setae can have or lack rigid, sharp, fracturable mineral spicules, and these spicules can either be located directly on the shaft or be mounted on the end of short to long bristles. If one searches for bristles that are intact, and those found are carefully examined, this will reveal that most species of *Mopalia* have bristles with a spicule at their tip. Likewise, most species lack spicules or bristles on the ventral surfaces of the setae.

Setae are subject to erosion, fouling, and malformation. The setae chosen as models (plates 353, 354) reflect our experience with typical variation in setae due to erosion, and extremely high or low levels of erosion could lead to setae that differ from our key descriptions and drawings. For example, some species have setae with long shafts that we suspect are typically worn clean of bristles and spicules, but exceptionally uneroded setae might have bristles or spicules clear to the tip. Similarly, we have used the proportion of the length of the setal shaft versus the length of valve 5 tegmentum to distinguish some species, but these distinctions might not work well for the occasional animal subject to exceptionally high or low erosion. Such challenges can partly be avoided by examining a selection of setae from different regions of each animal's dorsal girdle surface.

Some environments generate biological and sediment fouling of the setae and valves, which can impede identification. Fouled preserved specimens can be cleaned with needle-pointed forceps and cautious brushing with fine-bristled brushes a few millimeters wide. For field identification of living animals, the jet from a pump-spray bottle filled with seawater aids in dislodging enough material to facilitate identification of familiar species.

The details of the bristles, spicules, and shaft of the setae are minute and are best viewed with a magnification of 50x or higher. With experience, a hand lens will usually suffice to identify species. However, very small *Mopalia* remain challenging: their setae often differ from the adult form.

Chiton valves are typically divided into regions, more pronounced in species with heavier sculpturing patterns, and these partly reflect the radiating or longitudinal rows of esthete sensory organs. Valves are of three types: the anterior or **HEAD** valve, six **INTERMEDIATE** valves, and posterior or **TAIL** valve. The dorsal surface of an intermediate valve can have as many as three distinctive symmetrical regions of sculpturing. The median longitudinal ridge is called the **JUGUM** (or **JUGAL RIDGE**), and the area along the ridge is referred to as the **JUGAL AREA** only if it is set off with distinctive sculpturing. Most chitons with a distinctive jugal area are more southern in California (e.g., *Acanthochitona* spp.), but *Oldroydia percrassa* is a local (albeit rare) exception. The jugum can be sharp-angled in chitons with a high profile or rounded when chitons are flat and broad. The apices of the valve can have or lack a pointed beak. On either side of the jugum is the **CENTRAL** area, extending to paired triangular **LATERAL** areas. The anterior portion of the tail valve has sculpturing similar to the central areas, often with longitudinal riblets or latticelike sculpturing. The posterior part of the tail valve has sculpturing like the lateral areas, often with radiating rows of **RIBS**, finer **RIBLETS**, or discrete nodules. The apex of the tail valve, called the **MUCRO** (or beak), requires special notice. In lateral view, chitons differ in the position of the mucro and in whether the **POST-MUCRONAL SLOPE** (from the mucro to the posterior shell margin) is concave, straight, convex, or even bulging.

The different patterns of pitting, ribbing, nodules, and growth lines alone are seldom sufficient to enable correct identifications. These seemingly fundamental aspects of the skeletal structure can display intraspecific variations in both the number and magnitude of features ornamenting the valves, as well as interspecific similarities in structure. Being aware of some causes for this variability is helpful. This variability results from the nature of the valve's growth, from environmental insults and from genetic variability within a species. Except for the posterior portion of the tail valve, valves grow primarily from their anterior and lateral edges, with the number of sculpturing elements (nodules, ribs, etc.) increasing as the animal grows. Valves are also subject to environmental factors from simple erosion and breakage to damage from encrusting organisms. Even individuals within a species of similar size and apparently pristine sculpture can show enough variability so valve sculpturing is not by itself sufficient for identification.

Although in this key we have largely avoided using characteristics that can only be viewed in disarticulated specimens, important additional characters may often include normally hidden features of the valves. For some species of similar appearance, knowing to search for these normally hidden valve features could be the most efficient route to positive identification. A preserved chiton can be disarticulated by slow heating in a beaker, starting with cold water and a monolayer of KOH pellets. The individual valves can then be carefully separated and rinsed. This will reveal that the valves have an upper exposed, and often colored, layer (the tegmentum) overlaying a thicker, often porous (or solid) intermediate layer, and an inner, porcelain **ARTICULAMENTUM** layer. In some species, the color of the articulamentum varies away from white and can help distinguish between species of similar appearance. In all but some ancient fossil chitons, the articulamentum layer extends anteriorly beneath the preceding valve as paired semi-circular to angular **EAVES** (or **SUTURAL LAMINAE** or **APOPHYSES**). The proportions of the tegmentum versus the eaves, as well as variances in the profile of the anterior and posterior margins of the valves, can also be of taxonomic value. In all but the most phylogenetically basal living chitons (e.g., *Leptochiton* spp.), this layer also extends laterally from the intermediate valves or distally from the terminal valves as **INSERTION PLATES** to anchor the valves firmly in the girdle. These can often be exposed without complete disarticulation by temporarily teasing the girdle tissue away from the valves at their dorsal margin.

Most chitons have **SLITS** in the insertion plates, which correspond to the innervation of the radiating rows of esthetes in the tegmental layer. Some keys to chitons (including the one in the previous edition of this volume) list a **SLIT FORMULA** expressing the number, or range of numbers, of slits observed in the head, each side of an intermediate, and tail valves, respectively. Their omission here reflects our opinion that these are not generally necessary or informative for species-level identifications, besides requiring disarticulation to observe.

Two features that are apparent at first glance are coloration and body proportions. These turn out to be of only modest utility for identifying species. Coloration and pattern can be striking in many of the chiton species. Unfortunately coloration and pattern are also strikingly variable within most species, and it is the exceptional case where color is diagnostic. The body proportions of length to width to height do provide clues, but the ratio of these proportions is not constant between species for some genera. Allometry, or shape change with size,
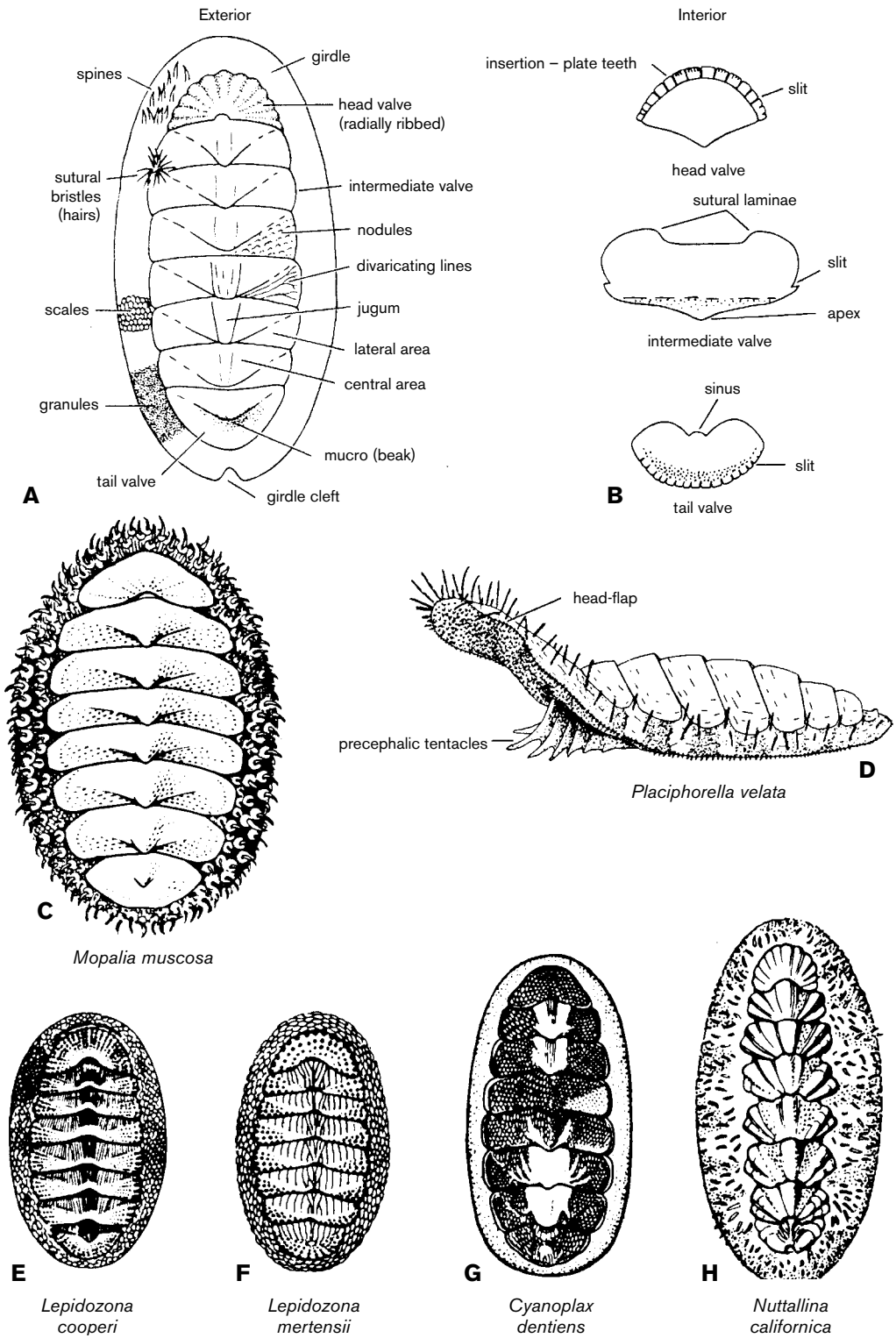
PLATE 352 Chitons: A, diagrammatic chiton showing girdle and shell ornamentation; B, terminology of valves; C, *Mopalia muscosa;* D, *Placiphorella velata;* E–H, other representative chitons (A, B, redrawn by Emily Reid after Yonge (1960); D, McLean, 1962; not to scale).

is another confounding factor as the proportions are often quite different for smaller chitons of any species. As a chiton grows, its cross-sectional profile tends to change from flattened to more peaked. In some species, the change is only a mild increase in proportional height, but in other species the change can be from a flat juvenile cross section to a nearly circular adult cross section. The outline of many species will also change from a rounded oval in juveniles to more elongated in large specimens. Finally, the addition of sculpturing can intensify as a chiton reaches adult size. For example, members of

A

Mopalia muscosa

B

Mopalia hindsii

C

Mopalia vespertina

D

Mopalia lionota

E1

E2

Mopalia lowei

F1

F2

Mopalia ferreirai

G

Mopalia porifera

H

Mopalia acuta
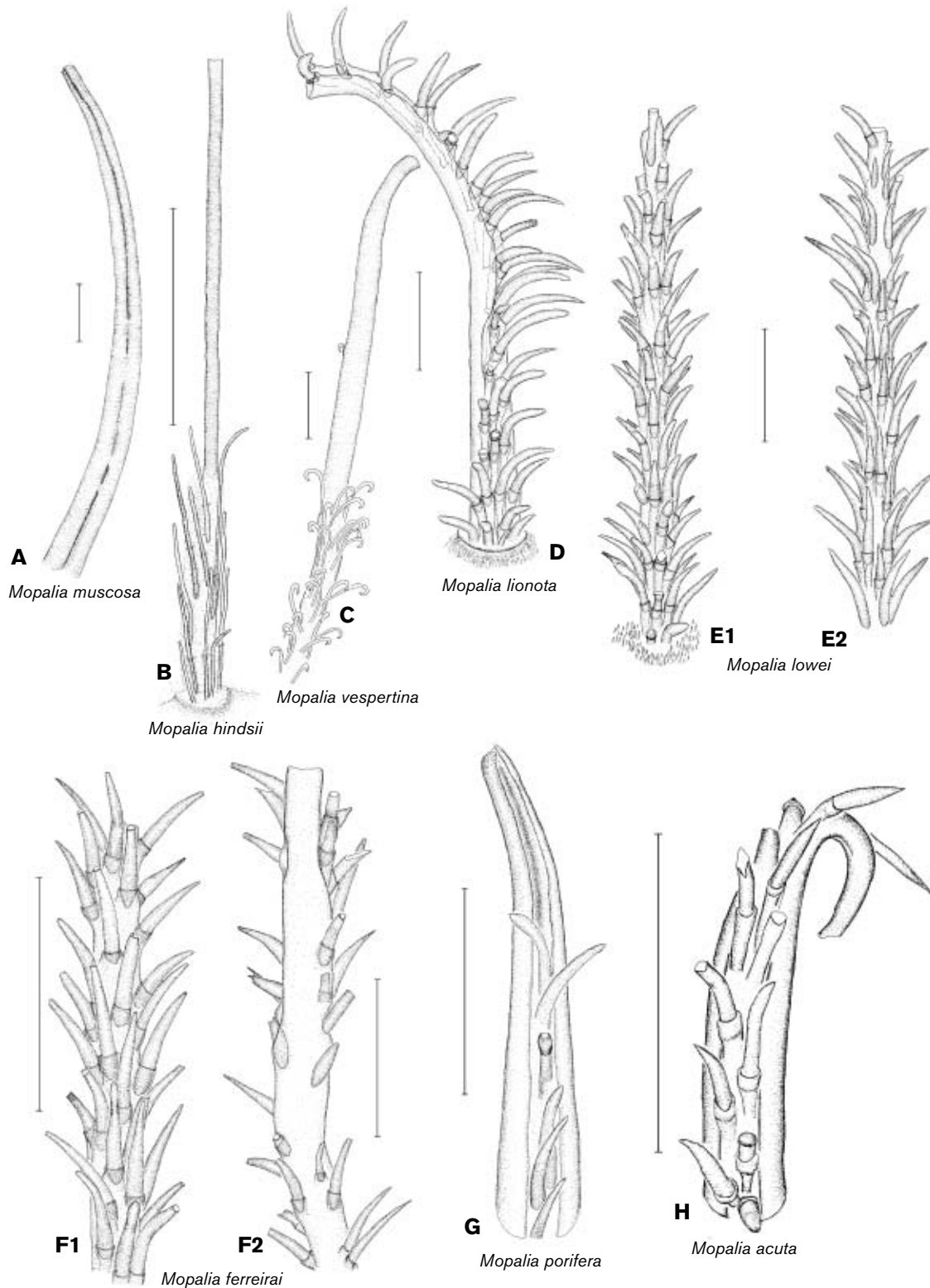
PLATE 353 *Mopalia* setae, species as labeled (original artwork by Anthony Draeger).

Callistochiton of similar length can vary dramatically in the prominence of their ribs and bulging tail valves, and juveniles barely exhibit these sculpturing features. For these reasons, we have tried to use characteristics that are evident regardless of the chiton's age. However, this key generally describes adult animals, and juveniles can be challenging to identify.

Chitons feed with a ribbon of teeth, or **RADULA**. Radular properties are relatively conservative within chitons compared to the tremendous variation found in gastropods. Chitons typically have 17 teeth in each row and up to hundreds of rows of teeth. The main (**MAJOR LATERAL** or **SECOND LATERAL**) paired teeth are the primary working teeth and, in chitons, are always

A
Mopalia ciliata

B
Mopalia kennerleyi

C
Mopalia spectabilis

D
Mopalia imporcata

E
Mopalia lingosa

F
Mopalia sinuata

G
Mopalia cirrata

H
Mopalia plumosa

I
Mopalia swanii
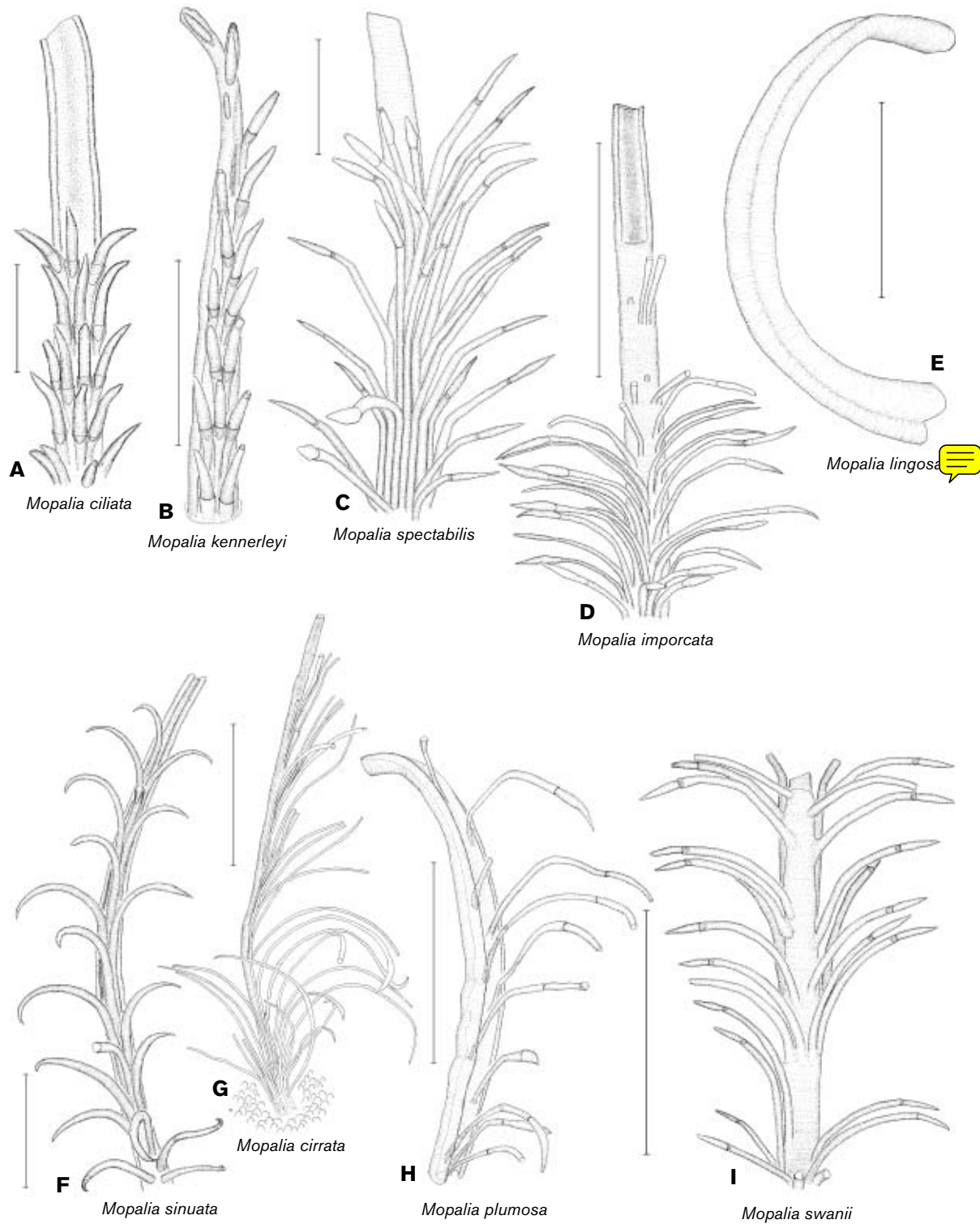
PLATE 354 *Mopalia* setae, species as labeled (original artwork by Anthony Draeger).

covered with black shiny magnetite, an iron mineral harder than stainless steel. The number or shape of their cusp(s) varies somewhat with species, partly reflecting variation in their diet.

Like limpets, many chiton species scrape diatoms or other microscopic algae off rock surfaces. Some chitons are more specialized. For example, certain *Tonicella* species feed on en-crusting coralline algae. Other, especially large, chitons will take bites of fleshy algae. One local shallow-water chiton, *Placiphorella velata* (plate 352D), is an ambush predator, trap-ping small prey such as amphipods with a rapid lowering of its unusually large anterior girdle, modified as an extended head flap, but its radula is only somewhat shorter than most, without

much tooth specialization. Radular characters are not employed in this key because central to northern California and Oregon chitons mostly belong to a few families that show relatively little radular variation, and those not belonging to these families are more easily distinguished by external features such as girdle ornamentation, gill arrangement, or valve sculpturing patterns.

Most chitons can be quite difficult to remove from rocks without injury, especially if they have been alerted to a threat, as could occur from a mere passing shadow, their being touched, or from being uncovered by the turning of a rock. Typically, a chiton can be safely removed from a rock by surprising it with a sudden "dig" with a pointed tool directed into the rock under the foot. Alternatively, especially for chitons found underneath rocks with a smooth undersurface, one can wait for the chiton to start crawling (in either direction) at which point one can more easily slide it laterally and dislodge it. A few species (e.g., *Callistochiton* spp.) will readily detach themselves and drop, curled up, from an overturned rock, often before they are noticed. Once chitons are removed from their attachment, most (but not all) can effectively roll up into a ball, remaining tightly in this position until, conceivably, a wave has rolled them to a new safe position, where they can unroll, extend their foot for a new attachment, and escape.

It is important to flatten specimens before they are placed in preservative. It is much easier to study a flat specimen than one that has curled when put into the preserving fluid. Fortunately, this can be accomplished with a little extra effort and patience. Attempting to force curled chitons flat is futile, but if they are left undisturbed in clean aerated seawater they eventually unroll and attach themselves to the sides of the container, from which they can be swiftly slid, placed on a "chiton stick," and immediately bound into place. The chiton stick may be a tongue depressor or any similar flat strip of wood, and its width should be wider than that of the chiton. Plastic flats can be used in place of wood, but plastic is less porous than wood and thus tends to prevent the penetration of alcohol to the chiton's undersurface. Strips of nylon (i.e., pantyhose) are porous to ethanol and perform well for binding the chiton firmly to the stick, especially if the ends of the stick have been broken to expose a jagged edge that will naturally catch the nylon to hold it in place.

To produce a correctly preserved and flattened specimen, orient each chiton with its long axis parallel to that of the stick and tightly stretch the nylon strips along the longitudinal axis of its body, securing the chiton flat against the stick. With small specimens, the nylon strip can effectively cover several valves; with larger specimens, it may be necessary to use wider strips or several wraps per valve. Once wrapped, the chiton can simply be dropped into ethanol and unwrapped after it is no longer responsive. Methods that call for placing the chiton in hot water to relax the specimen before dehydration should be avoided because they could damage the specimen's DNA, but a magnesium chloride solution that is isotonic with seawater is an effective relaxant.

Alcohol is a generally useful preservative agent for chitons, with other preservatives useful for particular cases, such as initial buffered formaldehyde or (better) cold buffered glutaraldehyde fixation for the study of internal anatomy or gametes. Ethanol is preferable to isopropanol primarily because the former is better for potential DNA extraction, and for this same reason an initial high percentage of ethanol (95%–100%) is generally preferred to more dilute solutions. However, some workers have reported that subsequent trans-

fer and storage in a more dilute concentration (70%–80%) will help avoid the girdle elements becoming brittle. Likewise, although we have found it generally unnecessary or even less desirable for specimens stored in alcohol, others (see Berry, 1961; Burghardt and Burghardt, 1969; Hanselman, 1970) have advocated adding 1%–2% of glycerol to improve the flexibility of the specimen, or even higher amounts if the specimen will be stored dry. Glycerol dry preservation is not trustworthy for molecular study, but specimens for morphological comparisons might be more conveniently handled and housed when dry. There are successful collections produced this way. The recipes and procedures involved with glycerin preservation are more complicated than for ethanol storage, and anyone interested in this preservation mode should first examine several recipes to determine the most appropriate.

Unfortunately, neither method of preservation retains a flawlessly natural appearance. Color is the aspect that most conspicuously suffers in many but not all species from either preservation method, and photographs of the live or freshly fixed specimens are currently the only recourse if accurate records of coloration are important. Lamb and Hanby (2005) provide excellent images of living representatives of most of the species in this key.

Key to the Intertidal and Shallow Water Chitons from Central California to Oregon

1. Valves completely concealed by thick, red-brown, velvety girdle (juveniles <10 mm in length are yellow and have the tiny apices of valves exposed); length often exceeds 20 cm . . . . *Cryptochiton stelleri*
— Valves exposed 2
2. Girdle black, leathery, covering about two-thirds of each valve, exposed areas roughly diamond shaped; length up to 13 cm . . . . *Katharina tunicata*
— Girdle otherwise and not covering most of valves 3
3. Gill rows without an interspace and restricted to posterior one-third of animal; insertion plates absent 4
— Gill rows with an interspace, and extending to the anterior at least halfway along each side of the foot; insertion plates present and visible when valves are disarticulated 6
4. Girdle extends more than halfway into the sutures between valves and has conspicuous spicules; valves thick; jugum raised, anteriorly extended relative to forward edge of a valve's tegmentum; sculpture thickened and indistinct; sculpture on all valves increasingly inflated with increasing body size; color dull brown tinged toward tan or gray; rare in intertidal; length to 3.4 cm . . . . *Oldroydia percrassa*
— Girdle not extending noticeably between the valves, girdle spicules present or absent; valves thin, jugal area not raised or extended toward anterior; sculpture (if present) of radial and longitudinal rows of granules; length <2 cm 5
5. Color of valves brown with darker specks; profile varying from flattened in small specimens to conspicuously arched in large animals; color of foot cream to only slightly pinkish; dorsal girdle surface with numerous scattered spicules much longer than other girdle elements . . . . *Leptochiton nexus*
— Color of valves cream, tan, or orange; valves curved and relatively high in profile; color of foot reddish or "liver colored," dorsal girdle surface without scattered long spicules

.... *Leptochiton rugatus*

6. Tail valve conspicuously longer than head valve 7
— Tail valve smaller or about equal in length to the head valve.. 8
7. Foot of living animal cream; valves whitish or tan, streaked or speckled with brown or greenish; girdle minutely granular (like fine sand paper), at 80x girdle scales with 10–14 laterally oriented ridges visible; can exceed 8 cm .... *Stenoplax heathiana*
— Foot of living animal orange (except in juveniles <1.5 cm); valves purple and reddish tones with brown or white speckles; girdle scales very fine, giving girdle leathery appearance; at 80x, these scales lack visible sculpture; can exceed 8 cm .... *Stenoplax fallax*
8. Dorsal girdle covered with closely packed conspicuous scales 9
— Dorsal girdle appears fleshy or gritty, with or without tiny stout corpuscles, more elongate spicules, or setae (hairs or bristles) 16
9. End valves and lateral areas of intermediate valves with very prominent radial ribs (one to two on lateral areas) 10
— End valves and lateral areas of intermediate valves with at most riblets or rows of tubercles, pustules or granules (two to many on lateral areas) 12
10. Animal small, not exceeding 8 mm, oval in outline; central areas with even, netlike reticulation; color yellowish or tan (very rare) .... *Callistochiton connellyi*
— Animal larger, to 3 cm or more; elongated in outline; central areas with longitudinal ribs crossed by finer cross ribs 11
11. Head valve with nine to 10 ribs, lateral areas of intermediate valves with two ribs topped by rounded pustules; tail valve inflated, in adults posterior ribbed area very swollen and "rolled" forward (juveniles are much flatter with much less prominent sculpturing); color tan, brown, or cream .... *Callistochiton palmulatus*
— Head valve with seven ribs, lateral areas of intermediate valves with a single heavy rib; tail valve with pointed, posterior mucro (juveniles are much flatter with more central mucro and much less prominent sculpture) .... *Callistochiton crassicostatus*
12. Central and radial areas of valves granular or with weak riblets... 13
— Central areas prominently ribbed (usually with both longitudinal and lateral cross ribs); radial areas with ribs, or rows of pustules or nodules 14
13. Central areas with numerous fine longitudinal riblets; when animal flat, total length of all valves about 2.5x width of valve 4 tegmentum, body elongate; coloration monochrome olive, slate grey, or (rarely) sky blue; length to 4.5 cm .... *Lepidozona regularis*
— Central areas granular, lacking longitudinal riblets; when animals flat, total valve length about 2x the width of valve 4 tegmentum, body broadly oval; color pattern highly variable, colors green, black, blue, white; length to 3 cm .... *Lepidozona radians*
14. Dorsal girdle scales smooth or with only very faint ribbing; scattered scales conspicuously mammillated; radial areas with rows of pustules or nodules; color variable, often with reddish or purplish tones, but also with uniform or mottled orange, with or without symmetrical anterior and posterior curved markings, or maculated with white, yellow, tan, or brown tones; length to 5 cm....... *Lepidozona mertensii*

— Dorsal girdle scales conspicuously ribbed and never mammillated.................................... 15
15. Radial areas with rows of pustules or nodules; color uniform gray-green or occasionally brown; length to about 4 cm .... *Lepidozona cooperi*
— Radial areas with two to six ribs or riblets, with considerable variation in strength of the sculpture; color and pattern extremely variable; length to 2.5 cm .... *Lepidozona scrobiculata*
16. Girdle fleshy, often sandy or leathery in appearance, lacking any noticeable setae or spicules 17
— Girdle bearing spines, spicules, or setae............. 27
17. Valves orange or pinkish with alternating colored lines (in life, some lines may be brilliant blue) 18
— Valves not orange or pinkish, and lacking alternating colored lines...................................... 21
18. Head valve with dark maroon or black lines extending the full length of the lined pattern (with similar markings on intermediate valves) 19
— Head valve lacking or with only partial dark maroon or black lines 20
19. Lines more or less longitudinal, with concentric alternating colored lines on head valve forming a distinctive "arrowhead" or "arch" shape, but without zigzags; slope of tail valve usually straight or slightly convex; length to 5 cm .... *Tonicella lineata*
— Lines with zigzag patterns, with concentric zigzags on head valve; slope of tail valve concave; length to 5 cm....... .... *Tonicella lokii*
20. Lines on central areas of intermediate valves expanding to large flamelike markings, concentric lines on head valve similar in color to valve background color and difficult to see; slope of tail valve concave; 30 × 18 μm dorsal girdle scales crowded to touching at 60×; length to 1.5 cm (rare in intertidal) .... *Tonicella venusta*
— Lines not expanding into flamelike markings, head valve usually with conspicuous concentric zigzag lines in two colors; slope of tail valve variable; 20 × 10 μm dorsal girdle scales dispersed (not touching) at 60×; length to 2.5 cm .... *Tonicella undocaerulea*
21. Uneroded portions of valves have generally regular granular sculpturing except on their lateral edges, where somewhat larger wartlike pustules are superimposed between the more regular granules, best viewed at 40× when valves are dry 22
— Uneroded portions of valves have regular granular sculpturing extending to the extreme margins of lateral valves, where there are no superimposed wartlike pustules 23
22. Intermediate valves scarcely if at all beaked (or often eroded where beak would be); color usually olive to dark green, occasionally maroon, often with black sub-apical stripes; gills extending entire length of foot, 28–35 plumes per side; length to 4 cm .... *Cyanoplax hartwegii*
— Valves prominently beaked; color green with white, black, and/or blue specks or streaks; found only in sea caves or under *Nuttallina californica*; gills extending about 80% of foot length, about 11–20 plumes per side; length rarely exceeding 1.2 cm .... *Cyanoplax caverna*
23. Head valve with prominent radial ribs; valves pale yellowish or tan; found exclusively on the holdfasts of *Macrocystis pyrifera*; length to 2.5 cm (rare) ...... *Cyanoplax lowei*
— Head valve lacking radial ribs, color and habitat not as above 24

24. Slope of tail valve distinctly concave; shell interior white 25
— Slope of tail valve more or less straight to somewhat convex; shell interior blue 26
25. Valves typically rusty orange with ultramarine irregular spots, but portions of one or more valves can be solid in color; body outline oval-elongate; length rarely exceeding 1.4 cm . . . . *Cyanoplax berryana*
— Valves variable in color, often tan, black, green, or orange with white or black speckles; body outline oval; length to 1.5 cm . . . . *Cyanoplax keepiana*
26. Valves uniformly dark brown to black or can have a few white streaks, but central areas often eroded to underlying bluish shell layer; mucro nearly terminal, slope convex; girdle uniformly dark brown to black, like the valves, rough appearing because corpuscules vary in length; restricted to midintertidal, length to 1.6 cm . . . . . . *Cyanoplax thomasi*
— Valves extremely variable in color and pattern, often reddish, brown, or greenish tones with blue-green, whitish, or dark specks, spots, or streaks; mucro subcentral to central, slope more or less straight; girdle with light and dark banding or uniformly dark, with corpuscules of similar length; mid- to especially low intertidal; length occasionally >2.0 cm but more normally to 1.6 cm . . . . *Cyanoplax dentiens*
27. Valves with longitudinal and radial rows of well-spaced rounded granules; girdle with scattered fine glassy spicules visible under magnification; color often orange, reddish, green, yellow, or brown; tail valve typically black or dark brown with white central stripe; length to 1.8 cm . . . . *Chaetopleura gemma*
— Valves and girdle not as above, girdle bearing spines or flexible setae 28
28. Girdle covered densely with stout, sharp spines 29
— Girdle bearing various forms of simple or complex setae 31
29. Valves (when not eroded) dark brown or black, sometimes with white subjugal stripes; gills extending nearly 100% of foot length; length to 5 cm . . . . *Nuttallina californica*
— Valves not black, gills extending 80% or less of foot length 30
30. Exposed portion of intermediate valves about twice as wide as long; color brown, white, yellow, or pink tones; gills extending about 75%–80% of foot length; length to 3.5 cm . . . . *Nuttallina fluxa*
— Exposed portion of intermediate valves about as long as wide; color brown or pink-orange tones; gills extending less than 75% of foot length; length to 3.5 cm . . . . *Nuttallina* sp.
31. Girdle greatly expanded anteriorly; setae scaled; valves very wide and much shorter than wide, variously colored with brown, pink, blue, tan, and green; length to 5 cm . . . . *Placiphorella velata*
— Girdle not expanded anteriorly, setae not scaled; valves not short and wide. 32
32. Valves smooth appearing, microgranular; sculpture, if present, only in the form of longitudinal ribs on central areas that are especially conspicuous when valves are dry; largest setae located chiefly near valve junctures and around posterior girdle, setae can be scarce with girdle nearly bare; girdle never with posterior slit 33
— Valves variously sculptured; head valve often with 10 radial ribs, including two flanking each posterior margin of the valve and the other eight corresponding at the valve margin to slits in the hidden eaves (articulamentum) anchoring the valves in the girdle; setae simple to complex, scattered

or profuse; girdle with or without posterior slit 34
33. Valves microscopically granular; lateral areas not defined; color red, orange, or green speckled with blue, pale green and gray; setae with single row of recurved bristles (often restricted to area around posterior two valves); length usually <2 cm . . . . *Dendrochiton flectens*
— Lateral areas of intermediate valves raised; central areas with longitudinal ribs most conspicuous when valves are dry; setae plumose; coloration highly variable, often speckled with pink, green, gray, orange and/or brown; length usually <1.2 cm. . . . . *Dendrochiton thamnoporus*
34. Setae abundant, coarse, dark brown, simple stiff bristles; valves coarsely sculptured, dark brown, sometimes with gray mottling or white subjugal stripes; animals shorter than 1.5 cm can have spicules in the setal groove; body length to 8 cm (plate 353A) . . . . *Mopalia muscosa*
— Setae not as above 35
35. Setae extremely fine, hairlike 36
— Setae not fine and hairlike 37
36. Central area of valves with fine longitudinal riblets or lirae cut by growth lines; lateral areas granulose; setae profuse, very fine, often bearing short, extremely fine bristles (plate 353B); common in exposed rocky intertidal; length can exceed 6 cm. . . . . *Mopalia hindsii*
— Central areas with netlike reticulation (sometimes obsolete); lateral areas faintly granulose to smooth, bounded by a row of weak, spaced, rounded granules; setae fine, bearing short, strongly recurved bristles; rare and only subtidal in California; length can exceed 6 cm (plate 353C) . . . . *Mopalia vespertina*
37. Setae with white or yellow-tinged spicules, which are located directly on the shaft or are mounted on a short bristle that is usually less than twice the length of the spicule (plates 353D–353H, 354A, 354B) 38
— Setae either with long, soft, and flexible chitinous bristles that are usually tipped with a minute calcareous spicule, or setae recurved and devoid of bristles or spicules (plate 354C–354I) 44
38. Setae as long or longer than valve 5 tegmentum, thick, bearing numerous long, white or yellow-tinged spicules, with or without stalks 39
— Setae one-half to three-quarters as long as valve 5 tegmentum, most spicules close to the shaft but those in curved portions of the setae can be supported away from shaft on bristles 40
39. Jugal areas smooth (or nearly smooth); setae with two (occasionally three to four) rows of curved, sharply pointed white spicules arising from the upper side (plate 353D); color grayish green, sometimes with black or rarely red or white subjugal markings; length usually <2 cm . . . . *Mopalia lionota*
— Jugal areas not smooth; setae bearing sharply pointed white or yellow tinged spicules entirely encircling the shaft; color greenish tones, with dark (rarely colorful) markings; length usually <3 cm (plate 353E) . . . . *Mopalia lowei*
40. Setae without dorsal groove, short (to about 2 mm), bearing five irregular rows of spicules, three along the dorsal side, and one on each edge; ventral surface of setae bare; valves variously colored and patterned with rose, lavender, blue, orange, white, and gray (plate 353F). . . . . *Mopalia ferreirai*
— Setae with trough-shaped dorsal groove, but trough can be shallow and setae straplike, bearing one to four longitudinal

rows of spicules 41

41. Setae trough shaped, sparsely distributed in two or three alternating rows and especially prominent at valve sutures; setae bear a single (occasionally double) row of slender spicules (plate 353G); valve color green with black subjugal stripes or markings; length to 2.5 cm. . . . . *Mopalia porifera*

— Setae not restricted to two or three alternating rows, more numerous; spicules in two to three (or four) rows; valve color various 42

42. Posterior girdle notch absent; unbroken setae tapered, tip width one-half or less of base width; somewhat recurved; seta length generally less than one-half the length of the valve 5 tegmentum; proximal part of setae with two alternating rows of short-stalked, stout spicules, distal portions usually bare; color pattern highly variable, often streaked, speckled or mottled with red, purple, green, pink, gray, and blue; length rarely exceeding 3 cm (plate 353H) . . . . *Mopalia acuta*

— Posterior girdle notch present; unbroken setae not tapering strongly 43

43. Setae straplike or a broad shallow trough, bearing three (or four) rows of sharply pointed stalked white spicules along the dorsal side, stalks about one to 1.5 times the length of the spicules; spicules usually restricted to the proximal one-third of shaft; color and pattern highly variable, often green, with red, orange, blue, or white markings; length to 6 cm (plate 354A). . . . . *Mopalia ciliata*

— Setae slender, trough shaped or cylindrical, bearing two rows of slender stalked white spicules; on cylindrical setae, stalks and spicules can lie entirely within the setal groove; on curved setae, stalks can diverge from the groove and rise as rows of spicule-tipped bristles, the bristles about two (or three) times the length of the spicules; color and pattern variable, often green tones with reddish, black, yellow, or white markings; length to 6 cm (plate 354B) . . . . *Mopalia kennerleyi*

44. Setae with four or more rows of bristles. 45

— Bristles absent or in one to three rows on setae 46

45. Setae with four or more conspicuous rows of coarse bristles, proximal half of bristles clinging to the setae in crowded parallel alignment often obscuring the setal shaft, distal half of bristles angling away from setae at acute angles, tending to form tiers; head valve with radial rows of pustules, lateral area of valves set off by an indistinct row of pustules; valves light green or olive, with red flecks and brilliant blue zigzag lines, sometimes valves are partially or completely suffused with orange (plate 354C) . . . . *Mopalia spectabilis*

— Setae with slender, usually recurved, bristles in numerous indistinct rows, setal shaft visible between bristles, bristles angled away from the setal shaft at their attachment point; head valve heavily corded with prominent, usually nodulose, radial ribbing and lateral areas set off by similar prominent ribbing; valve color generally beige/brown but varies from white to pastel orange; length usually <1.5 cm (plate 354D) . . . . *Mopalia imporcata*

46. Setae lacking bristles, recurved, trough shaped (plate 354E; sparse, slender bristles exist on chitons <2.5 cm); valve sculpture smooth except for subdued rhomboid pitting, more pronounced in larger individuals; color pattern streaked or feathered with gray-brown and green, or white and black with occasional burgundy accents; length to 7 cm. . . . . *Mopalia lignosa*

— Setae with one to three rows of conspicuous bristles. 47

47. Bristles on setae robust with base of bristles roughly one-third the width of setae, recurved, tapering to spiculeless point, setae one to two times as long as valve 5 and bearing two to three bristle rows; valves smooth, with reticulation of deep pitting; radial ribs distinct, smooth or faintly beaded, rib of posterior edge of intermediate valves obsolete; color mottled with red, dark brown, white, or blue-green; length to 2 cm (plate 354F). . . . . . . *Mopalia sinuata*

— Bristles on setae slender, minimally tapering. 48

48. Setae with abundant long (often curled) filamentous bristles in a single row within the dorsal groove; setae two to three times as long as valve 5; central areas with strong longitudinal ribbing and weaker cross ribbing, radial ribs prominent, nodulose, posterior edge of valves with longitudinally elongate nodules; color mottled with brown, white, and dark green; length to about 2 cm (plate 354G) . . . . *Mopalia cirrata*

— Setae generally with two rows of bristles, placed laterally along the setal shaft; radial ribbing and longitudinal ribs of central area reduced or obsolete. 49

49. Jugal sculpture of distinct regular pitting, similar to that of adjacent central area; lateral one-third of anterior edge of valve 5 tegmentum angles away from posterior edge of valve 4 at 10–20 degrees; setae usually profuse, about one-half to one time as long as tegmentum of valve 5, dorsal groove either broad and bearing two irregular alternating rows of long bristles or narrow with bristles in a single line; color gray-white, pale blue, or burgundy, maculated with dark brown or black; length usually <3.5 cm (plate 354H) . . . . *Mopalia plumosa*

— Central area sculpture of indistinct to distinct regular pitting, diminishing to fine longitudinal ridges at the jugum; lateral anterior one-third of valve 5 tegmentum edge angles away from posterior edge of valve 4 at 30–40 degrees; setae very fine, less than half length of valve 5 tegmentum, often sparsely scattered, bearing two rows of fine, often opposite, laterally diverging, curved bristles; color and pattern variable, with one or more valve portions often colored uniformly or marked with orange, green, yellow, brown, and other colors; length to 6 cm (plate 354I) . . . . *Mopalia swanii*

List of Species

Unless otherwise indicated, habitats range from middle and low intertidal into the subtidal at depths of up to about 15 m (about 50 ft). The following list also includes species that are more typical of warm temperate southern California that are not in the key, even though occasional reports exist for central California. With relatively few exceptions, the above key will also serve adequately for the Pacific Northwest, the outer Channel Islands, and the northern Baja coast. The faunas of the Channel Islands and of the cold upwelling region south of Ensenada, near Punta Banda and Punta Santo Tomás, resemble the fauna of central California more than they do southern California, although there is an interesting mix of the two faunal elements.

The following classification to families represents a conservative estimate of phylogenetic affinities based on mitochondrial DNA sequence comparisons (unpublished research by DJE and collaborators). The composition of Lepidochitonidae and Mopaliidae is very robust in these molecular analyses but differs substantially from recent classifications. For simplicity's sake, we

have elected to either not use subgenus names or to elevate them to generic status, despite the possibility that their recognition might reflect an accurate phylogenetic pattern of nesting.

The late Donald Abbott (1987) presented sketches of the anatomy and functional morphology of *Nuttallina californica, Mopalia muscosa, Katharina tunicata, Cyanoplax hartwegii,* and *Lepidozona mertensii* from the Monterey Peninsula.

LEPTOCHITONIDAE

Leptochiton rugatus (Pilsbry, 1892). Occasional individuals can be found under rocks well submerged into sand or mud, especially those in shallow warm mid-zone pools near the shore; subtidally especially at 8 m–12 m, or within kelp holdfasts. The red foot and gills are from tissue hemoglobins (Eernisse et al. 1988).

Leptochiton nexus Carpenter, 1864. Rarely collected and primarily subtidal. This species is not rare but has the cryptic habit of living on the side and top surfaces of rocks that are well covered by sand.

Oldroydia percrassa (Dall, 1894) [alternatively placed in separate family, Protochitonidae, by Sirenko (1997), together with an undescribed West Coast *Deshayesiella* sp. from >15 m (R. N. Clark and B. Sirenko, unpublished)]. Rare, under rocks resting on soft substrate but not silt (5 m–10 m) and from granitic ridge under rocks resting on a mixture of course gravel and finer sediment (22 m–24 m).

*Hanleyella oldroydi (Dall, 1919). Subtidal, >15 m.

CHAETOPLEURIDAE

Chaetopleura gemma Dall, 1879 (assigned to subgenus *Pallochiton* by Kaas and Van Belle, 1985–1994, volume 3). Common on top and sides of rocks throughout Monterey Peninsula kelp forest down to 10 m.

ISCHNOCHITONIDAE

Stenoplax fallax (Carpenter in Pilsbry, 1892). Primarily subtidal. Along Monterey Peninsula, juveniles <1.5 cm are often under thin layers of sediment on top of rocks, while adults are buried below the sand line along the sides of rocks.

Stenoplax heathiana Berry, 1946 (assigned to subgenus *Stenoradsia* by Kaas and Van Belle, 1985–1994, volume 3). Intertidal down to 7 m under rocks well submerged in sand. Named for Harold Heath who, as a Stanford University professor at Hopkins Marine Station, pioneered the study of California chitons, including an extensive cell lineage study of this species (Heath, 1899). This species is unusual in spawning a sticky egg mass from which crawl-away larvae emerge (Haderlie and Abbott, 1980). Look for the tiny commensal snail *Vitrinella oldroydi* in the mantle cavity. See Andrus and Legard 1975 (habitat); Linsenmeyer 1975, Veliger 18 Supplement: 83–86 (behavior); Putman 1990, Veliger 33: 372–374 (diet).

Stenoplax conspicua (Pilsbry, 1892) (assigned to subgenus *Stenoradsia* by Kaas and Van Belle, 1985–1994, volume 3). Rare north of southern California, where it is common under rocks in a similar habitat to *S. heathiana.* May be preyed upon by octopus, which drill small holes through the plates (Pilson and Taylor 1961, Science 134: 1366–1368). Abbott and Haderlie (1980) note that tiny snails in the genera *Teinostoma* and *Vitrinella* may occur under the girdle.

Lepidozona cooperi (Dall, 1879) (=*Ischnochiton cooperi*). Most common from the low intertidal to 8 m, under rocks and hidden beneath sediment deposits on rocky surfaces. For a review of the genus, see Ferreira (1978).

Lepidozona radians (Pilsbry, 1892) (=*Ischnochiton radians*) Recognized as distinct herein; formerly (e.g., Ferreira, 1978) considered a synonym of the somewhat more northern (Alaska to Washington) and more uniformly tan-colored or reddish *L. interstincta* (Gould, 1852) (=*Ischnochiton interstinctus*). *L. radians* is highly variable in its coloration pattern and is found at shallower depths and in somewhat more exposed habitats, and its range is from southeastern Alaska to northern Baja. Molecular distinctions have also been found (DJE and R. P. Kelly, unpublished). Occasional in the intertidal but most common between 5 m–13 m (ranging deeper) under rocks and hidden beneath sediment deposits on rocky surfaces.

Lepidozona mertensii (Middendorff, 1847). Common in the intertidal to about 8 m, but ranging deeper, on bottom and sides of rocks. See Helfman 1968, Veliger 10: 290–291 (ctenostome bryozoan *Farella elongata* on ventral surface of girdle).

*Lepidozona pectinulata (Carpenter *in* Pilsbry, 1893) [=*L. californiensis* (Berry, 1931)]. Rare north of southern California, where it is common under rocks in the low intertidal.

Lepidozona regularis (Carpenter, 1855) (=*Ischnochiton regularis*). Assigned to subgenus *Tripoplax* by Kaas and Van Belle, 1985–1994, volume 4. Relatively rare, sometimes occurring under smooth cobbles in high energy shores.

*Lepidozona retiporosa (Carpenter, 1864). Rare in <15 m.

*Lepidozona scabricostata (Carpenter, 1864). Rare in <15 m and not likely north of southern California.

Lepidozona scrobiculata (von Middendorff, 1847) [=*Lepidozona sinudentata* (Carpenter in Pilsbry, 1892)]. Most common from 5 m–10 m, under rocks and shells on sand.

*Lepidozona willetti (Berry, 1917). Rare in <15 m.

Callistochiton connellyi Willett, 1937. Apparently a rare small species, known to occur in the intertidal. See Ferreira (1979) for a review of the genus.

Callistochiton crassicostatus Pilsbry, 1893. Especially common under rocks in shallow subtidal habitats.

Callistochiton palmulatus Dall, 1879. Especially common under rocks in sandy to silty shallow subtidal habitats; juveniles lack the bulging terminal valves typical of adults.

LEPIDOCHITONIDAE

Cyanoplax berryana (Eernisse, 1986) (=*Lepidochitona berryana*). Especially common in sandy flat shelves on the top and sides of rocks at 0 m–3 m; not known north of San Mateo County.

Cyanoplax caverna (Eernisse, 1986) (=*Lepidochitona caverna*). A small hermaphroditic chiton that normally appears to self-fertilize its brooded embryos (or is parthenogenetic), only locally common and with limited known range between Santa Cruz and San Luis Obispo Counties (Eernisse 1988). Sometimes found nestled in the pallial groove of the larger *Nuttallina californica,* even while brooding, creating Russian doll–like layers of nested chitons (Gomez 1975, Veliger 18 Supplement: 28–29 mistakenly as *C. dentiens*; Eernisse 1986).

Cyanoplax dentiens (Gould, 1846) (=*Lepidochitona dentiens*). Very common species, especially from the low intertidal to about 1 m, on the top and sides of rocky outcrops and boulders between central California and Alaska. Often overlooked because of its small size and cryptically variable color patterns.

* = Not in key.

This species is easy to confuse with other members of the genus (Eernisse 1986; 1988). See Piercy 1987 (habitat, feeding).

Cyanoplax hartwegii (Carpenter, 1855) (=*Lepidochitona hartwegii*). Common under the rockweed *Silvetia compressa* as well as in mid-intertidal tide pools, from Santa Cruz to northern Baja California. See DeBevoise (predation by seastars and crabs); Lyman (behavior); Robb (diet), Andrus and Legard (habitat), McGill (osmotic stress), and Connor (ecology), all in Veliger 18 Supplement, 1975.

Cyanoplax keepiana (Berry, 1948) (=*Lepidochitona keepiana*). Found in warm protected pools under small stones, only rarely observed north of Cayucos.

Cyanoplax lowei (Pilsbry, 1918) (=*Cyanoplax fackenthallae* Berry, 1919). Found exclusively amongst the holdfasts of the giant kelp, *Macrocystis pyrifera*, but rarely collected.

*Cyanoplax cryptica (Kues, 1974). Found exclusively on the southern sea palm kelp, *Eisenia arborea*. Originally proposed as subspecies of *Cyanoplax dentiens*; not known north of Catalina Island.

Cyanoplax thomasi (Pilsbry, 1898) (=*Lepidochitona thomasi; =Nuttallina thomasi*). A brooder with separate sexes, only locally abundant in mid-intertidal rocky cracks or under barnacle hummocks; known from the Monterey Peninsula to the southern Big Sur coastline. Closely related to the Pacific Northwest to southeastern Alaska *C. fernaldi* (Eernisse, 1986), which reproductively resembles *C. caverna* in being a selfing (or parthenogenetic) hermaphroditic brooder.

Nuttallina californica (Reeve, 1847). Extremely common mid-intertidal species. Rare north of central California or south of Point Conception, California, but does occur as far south as northern Baja California. See Moore (predation by gulls), Nishi (feeding), Robbins (respiration), Andrus and Legard (habitat), Gomez (association with *Cyanoplax*), Linsenmeyer (behavior), Piper (physiology), Simonsen (osmotic stress), all in Veliger 18 Supplement, 1975.

Nuttallina fluxa (Carpenter, 1864) [=*Nuttallina scabra* (Reeve, 1847), see Piper 1984]. Rare north of southern California, where it is common in mid- to low intertidal habitats, including home depressions when the substrate is sandstone.

Nuttallina sp. of Piper, 1984. More common in southern California, but does occur at central California localities with sandstone shelves, where it forms home depressions in the low intertidal.

MOPALIIDAE

Placiphorella velata Dall, 1879. Can entrap small prey beneath anterior girdle flap (McLean 1962, Proc. Malacol. Soc. London 35: 23–26). Occasionally found in the intertidal but more common at 5 m–10 m on sides and bottoms of rocks.

*Placiphorella mirabilis Clark, 1994. Greater than 15 m. See Clark 1994, Veliger 37: 290–311.

Katharina tunicata (Wood, 1815). Occurs with *Nuttallina californica* in central California; lives among corallines and mussels on exposed rocks from the Big Sur coastline to Alaska. See Giese et al. 1959 (reproduction); Tucker and Giese 1959 (shell repair); Nimitz and Giese 1964, Quart. J. Micr. Sci. 105: 481–495 and Lawrence and Giese 1969, Physiol. Zool. 42: 353–360 (both, chemical changes in reproduction and nutrition); Himmelman 1978, J. Exp. Mar. Biol. Ecol. 31: 27–41 (reproduction); Piercy 1987 (habitat, feeding); Stebbins 1988, Veliger 30: 351–357 (population structure, tenacity); Rostal and Simpson 1988, Veliger 31: 120–126 (salinity); Dethier and Duggins 1984, Amer.

Nat. 124: 205–219 (ecology); Markel and DeWreede 1998, Mar. Ecol. Prog. Ser. 166: 151–161 (impact on kelp *Hedophyllum*).

Tonicella lineata (Wood, 1815). Much rarer than the next species in the central California intertidal but not uncommon at 3 m–8 m and by far the most common intertidal and shallow subtidal member of the genus from northern California to Alaska. Feeds on the upper layer of persistent coralline crustose algae, keeping other organisms from attaching. See Piercy 1987 (habitat, feeding); Clark 1999 (for discussion of literature prior to 1999 and proper species attributions).

Tonicella lokii Clark, 1999. The most common of four lined chiton species in the intertidal of central California; formerly confused with the previous species.

Tonicella undocaerulea Sirenko, 1973. Rare in the intertidal in central California; most common on top and sides of rocks at 12 m–17 m; our species is probably not the same as the one originally described from the northwestern Pacific, based on mitochondrial DNA distinctions (DJE, unpublished; see also Clark 1999).

Tonicella venusta Clark, 1999. Most common on top and sides of rocks at 13 m–18 m.

Cryptochiton stelleri (von Middendorff, 1847). A northern species found south to Monterey; intertidal throughout much of its range, but more commonly subtidal from 3 m–13 m around Monterey Peninsula. Occasionally found south to the Channel Islands, although it has been found in Native American middens from cold upwelling regions of northern Baja California (Emerson, 1956). See Heath 1897, Proc. Acad. Nat. Sci. Phil. 1897: 299–302 (juvenile morphology); Okuda 1947, J. Fac. Sci. Hokkaido Univ. Zool. 9: 267–275 (postlarval development); Tucker and Giese 1959 (shell repair); Tucker and Giese 1962, J. Exp. Zool. 150: 33–43 (reproduction); MacGinitie and MacGinitie 1968, Veliger 11: 59–61 (food, growth, age, external cleaning); Webster 1968, Veliger 11: 121–125 (commensals; Palmer and Frank 1974, Veliger 16: 301–304 (growth); McDermid 1981 Veliger 23: 317–320 (association with epizoic red alga *Pleonosporium*). Talmadge (1975, Veliger 17: 414) reported that the carnivorous snail *Ocinebrina lurida* makes pits on the dorsal surface of *C. stelleri*, rasping down to the flesh under the valves.

Dendrochiton flectens (Carpenter, 1864). [=*Basiliochiton heathii* (Pilsbry, 1898)] Mostly subtidal, 5 m–10 m, common on all sides of rocks, occasionally in low intertidal.

Dendrochiton thamnoporus (Berry, 1911). Common on the Monterey Peninsula on top and sides of rocks from 4 m–15 m; rare in low intertidal.

Mopalia acuta (Carpenter, 1855). Formerly confused with *M. plumosa*, in part (see below). Lowest intertidal to subtidal under rocks and shells on sand and beneath the sand line on larger rocks. Most abundant on Monterey Peninsula at 5 m–13 m.

Mopalia ciliata (Sowerby, 1840). Locally common in low intertidal, under overhangs and in crevices to about 10 m on all sides of rocks; rare north of Monterey Bay. See Fitzgerald 1975, Veliger 18 Supplement: 37–39 (movement, phototactic responses); Piercy 1987 (habitat, feeding).

Mopalia cirrata Berry, 1919. Subtidal in California.

*Mopalia egretta Berry, 1919. Rare in central California; >15 m.

Mopalia ferreirai Clark, 1991. Subtidal in California at 5 m–15 m, on top and sides of rocks.

Mopalia hindsii (Sowerby in Reeve, 1847). Most common in the mid intertidal to 2 m on exposed coasts, often found deep in crevices or on the walls of sea caves. See Giese et al. 1959 (reproduction); Tucker and Giese 1959 (shell repair); Andrus and Legard 1975 (habitat); Himmelman 1980 (reproduction,

* = Not in key.

British Columbia); Piercy 1987 (habitat, feeding); Rostal and Simpson 1988, Veliger 31: 120–126 (salinity).

Mopalia imporcata Carpenter, 1865. Subtidal in California, especially at about 8 m–12 m, or apparently somewhat deeper in canyons, but occurs in the intertidal further north.

Mopalia kennerleyi Carpenter, 1864. Recognized as distinct herein; formerly considered a synonym of *Mopalia ciliata;* rare south of San Francisco Bay. Himmelman 1980 (reproduction, British Columbia, as *M. ciliata*).

Mopalia lignosa (Gould, 1846). Common under rocks in intertidal. Around Monterey Peninsula, populations extend below 10 m in the kelp forests. See Fulton 1975 (diet), Watanabe and Cox (reproduction), Andrus and Legard (habitat), Lebsack (physiology), Linsenmeyer (behavior), all in Veliger 18 Supplement, 1975; Himmelman 1980 (reproduction, British Columbia).

Mopalia lionota Pilsbry, 1918. Of the many species of *Mopalia* with dense setae, this is probably the most heavily ornamented. Most common from the low intertidal to about 3 m, especially in the granite and sand channel habitat in Monterey.

Mopalia lowei Pilsbry, 1918. Subtidal in California, especially from 5 m–10 m on all sides of rocks.

Mopalia muscosa (Gould, 1846). A familiar high- to low-intertidal chiton often covered with algae. Its stiff setae and oval shape distinguish it from the superficially similar but narrower members of *Nuttallina,* which also differ in bearing spines on close inspection. See Fitzgerald (movement, phototactic responses), Smith (behavior), Watanabe and Cox (reproduction), Andrus and Legard (habitat), and Westersund (movement), all in Veliger 18 Supplement, 1975; Monroe and Boolootian 1965, Bull. So. Calif. Acad. Sci. 64: 223–228 (reproduction); Himmelman 1980 (reproduction, British Columbia); Leise 1984, Zoomorphology 104: 337–343 (metamorphosis); Piercy 1987 (habitat, feeding). See also Barnawell (1960), who found that *Mopalia muscosa, M. ciliata,* and *M. hindsii* include bryozoans, hydroids, and barnacles in their diets.

*Mopalia phorminx Berry, 1919. Greater than 15 m.

Mopalia plumosa Carpenter in Pilsbry, 1893. Recognized as distinct herein; formerly considered a synonym of *Mopalia acuta*. Ranges from low intertidal to 7 m in Monterey Bay.

Mopalia porifera Pilsbry, 1893. More common in northern Baja California.

Mopalia sinuata Carpenter, 1864. Subtidal in California, most common on the upper surfaces of rocks, from 8 m downward.

Mopalia spectabilis Cowan and Cowan, 1977. Subtidal in California, under rocks at 7 m–12 m. See Cowan and Cowan 1977, Syesis 10: 45–52.

Mopalia swanii Carpenter, 1864. Rare south of Oregon.

Mopalia vespertina (Gould, 1852) (=*Mopalia laevior* Pilsbry, 1918). Includes *M. hindsii recurvans* Barnawell, 1960. Rare in central California, usually on sides and top of rocks at 3 m–15 m.

References

Abbott, D. P. 1987. Observing marine invertebrates. G. H. Hilgard, ed. Stanford, CA: Stanford University Press, 380 pp.

Andrus, J. K., and W. B. Legard. 1975. Description of the habitats of several intertidal chitons (Mollusca: Polyplacophora) found along the Monterey Peninsula of central California. Veliger 18 (supplement): 3–8.

Barnawell, E. B. 1960. The carnivorous habit among the Polyplacophora. Veliger 2: 85–88.

Berry, S. S. 1917, 1919. Notes on West American chitons—I and II. Proc. Calif. Acad. Sci. (4) 7: 229–248 and 9: 1–36.

* = Not in key.

Berry, S. S. 1961. Chitons, their collection and preservation, pp. 44–49. In How to collect shells. 2nd ed. American Malacological Union.

Buckland-Nicks, J. 1995. Ultrastructure of sperm and sperm-egg interaction in Aculifera: implications for molluscan phylogeny. Mémoires du Muséum national d'Histoire naturelle 166: 129–153.

Burghardt, G. E., and L. E. Burghardt. 1969. A collector's guide to west coast chitons. San Francisco Aquarium Society, Special Publication 4, 45 pp.

Clark R. N. 1991. A new species of *Mopalia* (Polyplacophora: Mopaliidae) from the northeast Pacific. Veliger 34: 309–313.

Clark R. N. 1999. The *Tonicella lineata* (Wood, 1815) species complex (Polyplacophora: Tonicellidae), with descriptions of two new species. American Malacological Bulletin 15: 33–46.

Clark R. N. 2004. On the identity of von Middendorff's *Chiton sitchensis* and *Chiton scrobiculatus*. Festivus 36: 49–52.

Dethier, M. N., and D. O. Duggins. 1984. An "indirect commensalisms" between marine herbivores and the importance of competitive hierarchies. Am. Nat. 124:205–219.

Duggins, D. O., and M. N. Dethier. 1985. Experimental studies on herbivory and algal competition in a low intertidal habitat. Oecologia 67: 183–191.

Eernisse, D. J. 1986. The genus *Lepidochitona* Gray, 1821 (Mollusca: Polyplacophora) in the northeastern Pacific Ocean (Oregonian and Californian provinces). Zoologische Verhandelingen 228: 3–52.

Eernisse, D. J. 1988. Reproductive patterns in six species of *Lepidochitona* (Mollusca: Polyplacophora) from the Pacific coast of North America. Biological Bulletin 174: 287–302.

Eernisse, D. J. 1998. Class Polyplacophora, pp. 49–73. In Taxonomic atlas of the benthic fauna of the Santa Maria Basin and the Western Santa Barbara Channel. Volume 8. The Mollusca, Part 1: Aplacophora, Polyplacophora, Scaphopoda, Bivalvia and Cephalopoda. P. V. Scott and J. A. Blake, eds. Santa Barbara, CA: Santa Barbara Museum of Natural History.

Eernisse, D. J., and P. D. Reynolds. 1994. Chapter 3. Polyplacophora, pp. 56–110. In Microscopic anatomy of invertebrates, Volume 5, Mollusca 1. New York: Wiley-Liss.

Eernisse, D. J., N. B. Terwilliger, and R. C. Terwilliger. 1988. The red foot of a lepidopleurid chiton: Evidence for tissue hemoglobins. Veliger 30: 244–247.

Emerson, W. K. 1956a. Upwelling and associated marine life along Pacific Baja California, Mexico. Journal of Paleontology 30: 393–397.

Ferreira, A. J. 1978. The genus *Lepidozona* (Mollusca: Polyplacophora) in the temperate eastern Pacific, Baja California to Alaska, with the description of a new species. Veliger 21: 19–44.

Ferreira, A. J. 1979. The genus *Callistochiton* Dall, 1879 (Mollusca: Polyplacophora) in the eastern Pacific, with the description of a new species. Veliger 21: 444–466.

Ferreira, A. J. 1982. The family Lepidochitonidae Iredale, 1914 (Mollusca: Polyplacophora) in the northeastern Pacific. Veliger 25: 93–138.

Giese, A. C., J. S. Tucker, and R. A. Boolootian 1959. Annual reproductive cycles of the chitons *Katharina tunicata* and *Mopalia hindsii*. Biol. Bull. 117: 81–88.

Haderlie, E. C., and D. P. Abbott. 1980. Polyplachophora: the chitons, pp. 412–428. In Intertidal invertebrates of California. Morris, R. H., D. P. Abbott, and E. C. Haderlie, eds. Stanford, CA: Stanford University Press.

Hanselman, G. A. 1970. Preparation of chitons for the collector's cabinet. Of Sea and Shore 1: 17–22.

Heath, H. 1899. The development of *Ischnochiton*. Zool. Jahrb., Abt. Anat. Ontog. Tiere 12: 567–656.

Himmelman, J. H. 1980. Reproductive cycle patterns in the chiton genus *Mopalia* (Polyplacophora). Nautilus 94: 39–49.

Hyman, L. H. 1967. The Invertebrates: Mollusca I, Vol. VI. McGraw-Hill, pp. 70–142.

Kaas, P., and R. A. Van Belle, 1985–1994. Monograph of living chitons. Vols. 1–5. E. J. Brill/Dr W. Backhuys, Leiden.

Kelly, R. P., and D. J. Eernisse. 2007. Southern hospitality: A latitudinal gradient in gene flow in the marine environment. Evolution, 61.

Kelly. R. P., I. N. Sarkar, D. J. Eernisse, and R. Desalle. 2007. DNA barcoding using chitons (genus *Mopalia*). Molecular Ecology Notes 7.

Lamb, A., and B. P. Hanby. 2005. Marine life of the Pacific Northwest: a photographic encyclopedia of invertebrates, seaweeds and selected fishes. Madeira Park, B.C., Canada: Harbour Publishing.

Leise, E. M., and R. A. Cloney. 1982. Chiton integument: ultrastructure of the sensory hairs of *Mopalia muscosa* (Mollusca: Polyplacophora). Cell and Tissue Research 223: 43–59.

Lowenstam, H. A. 1962. Magnetite in denticle capping in Recent chitons (Polyplacophora.) Bull. Geol. Soc. Amer. 73: 435–438.

Okusu, A., E. Schwabe, D. J. Eernisse, and G. Giribet. 2003. Towards a phylogeny of chitons (Mollusca: Polyplacophora) based on combined analysis of five molecular loci. Organisms Diversity and Evolution 3: 281–302.

Omelich, P. 1967. The behavioral role and the structure of the aesthetes of chitons. Veliger 10: 77–82.

Piercy, R. D. 1987. Habitat and food preferences in six Eastern Pacific chiton species (Mollusca: Polyplacophora). Veliger 29: 388–393.

Pilsbry, H. A. 1892–1894. Polyplacophora (Chitons). Manual of Conchology 14, 350 pp.; 15, 133 pp.

Piper, S. C. 1984. Biology of the marine intertidal mollusc *Nuttallina*, with special reference to vertical zonation, taxonomy and biogeography (electrophoresis, growth, movement). Ph.D. Dissertation, University of California, San Diego, 698 pp.

Sirenko, B. I. 1993. Revision of the system of the order Chitonida (Mollusca: Polyplacophora) on the basis of correlation between the type of gills arrangement and the shape of the chorion processes. Ruthenica 3: 93–117.

Sirenko, B. I. 1997. The importance of the development of articulamentum for taxonomy of chitons (Mollusca, Polyplacophora). Ruthenica 7: 1–24.

Sirenko, B. 2006. New outlook on the system of chitons (Mollusca: Polyplacophora). Venus 65: 27–49.

Smith, A. G. 1960. Amphineura. In Treatise on invertebrate paleontology. Part I, Mollusca 1, pp. 41–76. R. C. Moore, ed. Univ. Kansas Press and Geol. Soc. Amer.

Smith, A. G. 1966. The larval development of chitons (Amphineura). Proc. Calif. Acad. Sci. (4) 32: 433–446.

Smith, A.G. 1977. Rectification of West Coast chiton nomenclature (Mollusca: Polyplacophora). Veliger 19: 215–258.

Strathmann, M., and D. J. Eernisse. 1987. Phylum Mollusca, Class Polyplacophora, pp. 205–219 in The Friday Harbor Labs Handbook of Marine Invertebrate Embryology. Seattle: Univ. of Wash. Press.

Thorpe, S. R., Jr. 1962. A preliminary report on spawning and related phenomena in California chitons. Veliger 4: 202–210.

Tomlinson, J., D. Reilly, and R. Ballering. 1980. Magnetic radular teeth and geomagnetic responses in chitons. Veliger 23: 167–170.

Tucker, J. S., and A. C. Giese. 1959. Shell repair in chitons. Biol. Bull. 116: 318–322.

Yonge, C. M. 1939. On the mantle cavity and its contained organs in the Loricata (Placophora). Quart. J. Micro. Sci. 81: 367–390.

Yonge, C. M. 1960. General Characters of Mollusca, pp. 3–36. In Treatise on invertebrate paleontology. Part I. Mollusca 1. R.C. Moore, ed. New York: Geol. Soc. Amer.; Lawrence: University of Kansas Press.

Gastropoda

Shelled Gastropoda

JAMES H. McLEAN

(Plates 355–373)

The gastropods are the largest class of mollusks and exhibit enormous diversity in form and habitat. Limpets, top shells, abalone shells, periwinkles, slipper shells, and whelks are well known to observers of tide pool animals. The beauty of many gastropod shells, especially from tropical regions, has long made them favored objects for collections. Our relatively advanced knowledge of the taxonomy of the gastropods is in large part due to the interest of amateur shell collectors.

This section deals with those gastropods with external shells that occur between Oregon and Point Conception, California, other than the patellogastropod limpets (see separate text by David Lindberg), all species of *Littorina* (separate text by David Reid) and pelagic gastropods (separate text by Roger Seapy and Carol Lalli). As in the 1975 text, shelled opisthobranchs are included, which are also treated separately by Gosliner and Williams.*****

Gastropods possess a muscular foot for creeping or burrowing, a head with sensory tentacles and eyes, and a characteris-

*This section is revised from 1975 text by James T. Carlton and Barry Roth.

tic rasping radula (absent in some). As in all mollusks, the mantle secretes the shell and provides, in the pallial cavity, a shelter for the gills (**CTENIDIA**). A hallmark of the gastropods that sets them apart from other mollusks is the phenomenon of **TORSION**, which occurs early in development. Torsion consists of a 180° counterclockwise rotation of the visceral mass upon the head and foot; the result is that the mantle cavity, ctenidia, and anus, which were originally at the rear, come to lie just above the head. Torsion in its fullest expression characterizes the prosobranch grade (meaning front gills), in which the ctenidia lie anteriorly and the nervous system is twisted into a crude figure 8 (the **STREPTONEUROUS** condition). Other groups of gastropods have tended to modify the extreme effects of torsion, one change being a straightening out of the nervous system to the **EUTHYNEUROUS** condition. Euthyneury has been attained in two ways: in opisthobranchs, the body has "unwound" itself in **DETORSION**; in the pulmonates, the body has retained much of its torsion, but the central nervous system has straightened out by condensation into a ring of ganglia around the esophagus.

Torsion is not the same thing as the coiling of the shell and visceral hump of most gastropods. Coiling serves to strengthen the shell, but it is lost in limpetlike gastropods, land slugs, and nudibranchs, which as adults have reduced or lost the shell and flattened the visceral hump. Coiling is not unique to the gastropods; it is also found in the cephalopod *Nautilus* and many extinct, shelled cephalopods.

CLASSIFICATION

Higher classification of gastropods has undergone fundamental changes in the 30 years since the 1975 publication of the last edition of *Light's Manual*. In that work, the prevailing classification was followed in which the divisions for the class Gastropoda were the subclasses Prosobranchia, Opisthobranchia, and Pulmonata; the prosobranchs were further subdivided into the orders Archaeogastropoda, Mesogastropoda, and Neogastropoda. That classification scheme is now considered to have been based on recognition of grades of complexity. The basic hypotheses of gastropod phylogeny have been greatly altered by the application of cladistic methodology and molecular genetics (see Introduction to Mollusca).

The classification system adopted here was introduced by consensus during the 1990s, in papers by Lindberg, Haszprunar, and Ponder and other authors who preceded the publication of the two mollusk volumes for the monumental *Fauna of Australia* (Beesley et al., 1998). A general phylogeny for Mollusca was presented in simplified form and reiterated by Lindberg, Ponder and Haszprunar (2004) in their section on Mollusca for the *Tree of Life* volume.

The two major divisions for the class Gastropoda are the subclasses **EOGASTROPODA** (represented by the living Patellogastropoda) and **ORTHOGASTROPODA** (containing all other gastropods), now placed within five monophyletic clades. These five groups are the superorders: **VETIGASTROPODA**, **NERITOGASTROPODA**, **COCCULINIDA**, **CAENOGASTROPODA**, and **HETEROBRANCHIA**.

The eogastropod superorder Patellogastropoda is treated separately by Lindberg. Two of the five orthogastropod superorders are not represented in the intertidal of Oregon and central California: the Neritogastropoda, which are mostly tropical, and the Cocculinida, which occur offshore in deep water.