OCS Study
MMS 96-0045

# TAXONOMIC ATLAS OF THE BENTHIC FAUNA OF THE SANTA MARIA BASIN AND WESTERN SANTA BARBARA CHANNEL

FINAL REPORT
Volume 8 of 14

The Mollusca Part 1 — Aplacophora, Polyplacophora, Scaphopoda, Bivalvia, and Cephalopoda

U.S. Department of the Interior
Minerals Management Service
Pacific OCS Region

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The Mollusca Part 1 — Aplacophora, Polyplacophora, Scaphopoda, Bivalvia, and Cephalopoda

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## DISCLAIMER

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## TAXONOMIC DISCLAIMER

This report is not deemed nor intended to be a valid publication for the naming of new taxa as stipulated in the International Code of Zoological Nomenclature, Article 8b.

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**BACKGROUND**: The Taxonomic Atlas of the Santa Maria Basin and western Santa Barbara Channel is an extension of the benthic reconnaissance (Phase I) and monitoring programs (Phase II) that were conducted by the MMS since 1983. The organisms that were collected as part of those programs provide the material on which the Atlas is developed. In order to fully document the fauna collected by those programs, a series of 14 volumes will be prepared that provide keys, descriptions, and illustrations of the benthic fauna of the hard and soft substrate environments. A team of 40 experts on the fauna has been assembled to carry out this work and their contributions are distributed among the 14 volumes.

**OBJECTIVES**: The objectives of Volume 8 are to introduce the Phylym Mollusca. This volume treats the non-gastropod classes. The following 5 classes are treated in this volume: Aplacophora, Polyplacophora, Scaphopoda, Bivalvia, and Cephalopoda.

**DESCRIPTION**: Volume 8 treats the non-gastropod classes and includes the Aplacophora, Polyplacophora, Scaphopoda, Bivalvia, and Cephalopoda. The 5 chapters are organized into sections that include the morphology, taxonomic history, biology, keys of species, and descriptions of genera and species. Each species is fully illustrated with relevant characteristics labeled and identified.

**SIGNIFICANT CONCLUSIONS**: The keys, detailed descriptions, and illustrations to the 96 species treated in this volume represents a major contribution to molluscan systematics for the eastern Pacific Ocean. Many poorly know species are newly defined with new illustrations or photographs. Five new aplacophoran species are described, along with diagnoses for one new genus and four new species of bivalves.

**STUDY RESULTS**: The fauna of the Santa Maria Basin and western Santa Barbara Channel is evaluated from samples that were taken from depths of about 50 to 1,000 m. Organisms were collected from soft sediments using box cores and from rocks using manipulator arms of submersibles and remotely operated vehicles. The collections are organized into sets of vouchers from Phase I and II that have been made available to the team of investigators. Additional material from the bulk collections now archived with the Natural History Museum of Los Angeles County is also being examined. The total number of species treated in the entire Taxonomic Atlas (14 volumes) may exceed 1,300 species.

A total of 69 genera and 42 families are treated as part of Volume 8. The scope of this volume includes materials from the MMS surveys as well as additional material from the eastern Pacific accumulated by the authors. The authors have also examined most type specimens for each species and have produced a monograph that will be applicable to the entire marine environment of western North America. In this regard, this volume becomes the most important compilation on northeastern Pacific non-gastropod mollusks in the last century, in particular with the bivalves and aplacophorans. In addition, to being an important taxonomic contribution, this study is a valuable contribution to understanding the distribution and zoogeography of aplacophorans, chitons, scaphopods, bivalves, and cephalopods in the eastern Pacific. The ranges of many species are extended. Nine new species are here described for the first time.

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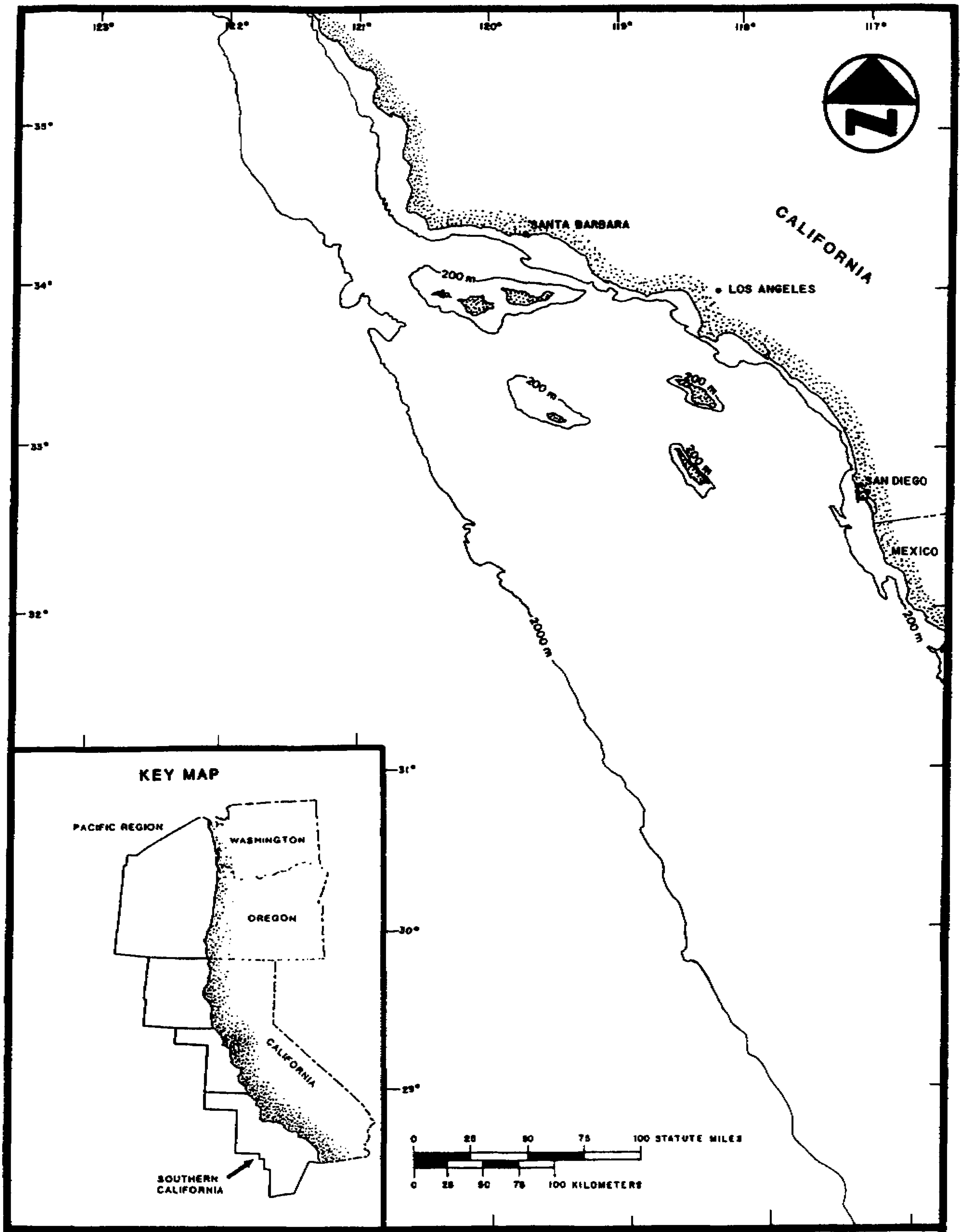

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Order Octopoda Leach, 1818

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# List of Acronyms

| | |
|---|---|
| ANSP | Academy of Natural Sciences, Philadelphia, Pennsylvania, USA. |
| BLM | Bureau of Land Management. |
| BMNH | The Natural History Museum, London, United Kingdom. |
| BRA | Refers to a station designation from the MMS Phase I Reconnaissance: Benthic Rocky, transect A/B. |
| BRC | Refers to a station designation from the MMS Phase I Reconnaissance: Benthic Rocky, transect C/D. |
| CAS | California Academy of Sciences, Department of Invertebrate Zoology, San Francisco, California, USA. |
| ICZN | International Code of Zoological Nomenclature. |
| LACM | Natural History Museum of Los Angeles County, Los Angeles, California, USA. |
| MCZ | Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA. |
| MMS | Minerals Management Service. |
| SCAMIT | Southern California Association of Marine Invertebrate Taxonomists. |
| SBMNH | Santa Barbara Museum of Natural History, Santa Barbara, California, USA. |
| SDNHM | San Diego Natural History Museum, San Diego, California, USA. |
| USNM | United States National Museum. A historical designation for the National Museum of Natural History (NMNH), Smithsonian Institution, Washington, D.C., USA. |

# 1. INTRODUCTION TO THE MOLLUSCA

by

Eugene V. Coan[1]

The living Mollusca are believed to be a monophyletic group of organisms that originated at least as early as the Lower Cambrian. Their shell-less ancestor was probably unsegmented and dorsoventrally flattened, and it lived in the ocean, scraping microorganisms off the substratum for food. Differentiation of the Mollusca into distinct classes occurred so long ago and probably at least in part among shell-less ancestors that relationships remain a topic of lively debate.

Key features of the living Mollusca, although not each present in all classes, include a hardened calcium carbonate shell, a unique feeding apparatus called a radula, an otherwise soft body that has as its external layer mantle tissue capable of secreting the shell, and a cavity invaginating the mantle that contains gills and openings to the digestive and reproductive systems.

The modern Mollusca are now divided into seven distinctive classes, each represented in the Santa Maria Basin and the Santa Barbara Channel.

The **Aplacophora** are divided into two subclasses the Chaetodermomorpha and the Neomenimorpha. The **Chaetodermomorpha** are cylindrical, wormlike mollusks from 2-140 mm in length. They have a radula but no shell, instead being covered by a chitinous cuticle with embedded imbricating scales. There is a posterior mantle cavity with a pair of bipectinate ctenidia. They are marine, mostly infaunal burrowers that feed on microorganisms and detritus. There are about 70 species.

The **Neomeniomorpha** are also wormlike, but are laterally compressed, with a ventral pedal groove. They are from 1-300 mm in length. Like the Chaetodermomorpha, they lack a shell, and only some have a radula. Their outer surface is covered with a cuticle and scales or spicules. There is a posterior mantle cavity, which lacks a gill but has secondary respiratory structures in some. They are marine and live on sediment or epizoic on cnidarians, upon which they feed. There are about 180 species.

The **Polyplacophora**, or chitons, are dorsoventrally flattened, elongate to ovate, from 3-400 mm in length. Their dorsal surface is covered by eight overlapping calcareous plates embedded in an encircling girdle. The girdle covers or almost covers the plates in a few species, and it is covered by spines, spicules or bristles. There is a broad ventral foot, surrounded by a narrow encircling mantle cavity with 6-88 pairs of gills. They are mostly grazing herbivores on hard substrata using their radula. There are more than 800 species.

The **Monoplacophora**, are similar in shape to limpet gastropods, but have not undergone torsion. There are eight pairs pedal muscles and 5-6 pairs of gills in the mantle cavity that surrounds the foot. These benthic marine animals make a living scraping substrata with their radula. There are as many as 20 living species from 200 m to abyssal depths. A single species has been reported in about 300 m in southern California.

The **Gastropoda**, or snails, are by far the most common class. They occur through the seas, as well as in freshwater and on land. A few marine taxa are entirely parasitic. They were primitively torted (the body mass being twisted relative to the foot), resulting in bilateral asymmetry. There is generally a single shell, coiled in most, limpet-like in several groups, and the shell has become lost in many different lineages. There

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is a radula in most taxa, which has become specialized for various tasks in different groups. The foot of most is used for creeping, but it is specialized for swimming in a few. The mantle cavity, moved anteriorly by torsion, has gills in primitive forms, but these are lost in some groups, replaced by secondary structures, or by a lung in land snails. There are about 35,000 species.

The **Scaphopoda**, also known as the tusk or tooth shells, is an exclusively marine group, members of which have an elongate, curved, tapered, tubular shell from 2-150 mm in length that is open at both ends. The group, which is bilaterally symmetrical, is entirely marine, occurring from shallow to deep water. There is a radula, and the wider anterior end has numerous, elongate contractile filaments called captacula, with which they capture benthic microorganisms. They can dig in soft substrata by means of a lobed foot. The mantle cavity is tubular, and they take water into and expel it from the posterior end, which extends above the substratum. There is no gill. There are approximately 300 species.

The **Bivalvia** are found in marine and freshwater environments. As the name implies, almost all species are enclosed in a pair of lateral valves that are hinged dorsally. Some groups are cemented to the substratum by one valve. In some groups, the animal cannot be enclosed within the paired valves, and in one group the entire animal is surrounded by a calcareous tube, with the tiny valves embedded on its surface. Primitive forms are benthic feeders, using collecting and sorting organs near the mouth called palms. In most, there are a pair of complex gills called ctenidia, which not only provide respiration but also strain and sort food particles from the water, which are then processed by much-reduced palps. The posterior end of the mantle cavity is modified into incurrent and excurrent siphons in many groups. In some offshore marine taxa, the ctenidia have become reduced and the mantle cavity modified for capture of prey as small crustaceans. There is no radula. There are about 8,000 species.

The **Cephalopoda** include the squids and octopods, and modern representatives with the single exception of *Nautilus* do not have an external shell but rather an internal calcareous or cartilaginous shell. They are bilaterally symmetrical, and the head-foot of most has 8-10 flexible tentacles with adherent suckers. There is a set of beaks in the mouth and a radula. The mantle cavity contains a pair of gills, and in squids a funnel from this cavity provides propulsion. There are about 600 carnivorous marine species, of which a number of shallow-water species are commercially important as food.

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# 2. CLASS APLACOPHORA

by

Amélie H. Scheltema[1]

## Introduction

The Aplacophora are a small class of marine Mollusca represented in the literature by fewer than 300 species worldwide. Most inhabit the deep-sea benthos from the edge of the continental shelf to hadal depths over 9,000 m, and nearly every deep-sea dredge or box core sample brings new species to light. All Aplacophora are free-living.

The class is comprised of two subclasses, the Neomeniomorpha or neomenioids (=Class Solenogastres, see Salvini-Plawen, 1985) and the Chaetodermomorpha or chaetoderms (=Class Caudofoveata). All Aplacophora are vermiform and covered by a cuticle in which are embedded innumerable spicules of aragonite. The animals range in size from 1 mm to over 30 cm, and in shape from nearly spherical to long and extremely narrow. Their molluscan affinities are clear from the presence of a radula and its supports, coelomic pericardial cavity around a heart with ventricle and usually paired auricles, ladderlike nervous system similar to that in chitons, and mantle cavity into which empty gametoducts and anus. As in other Mollusca, most of the body cavity is hemocoel. Fully expressed body-wall musculature consists of outer circular, two middle orthogonal, and inner longitudinal muscle layers. Neomenioids have an additional pair of ventral longitudinal bands, giving them their "new moon" shape.

In the creeping subclass Neomeniomorpha there is a ventral, longitudinal, ciliated ridge, or foot, within a furrow that begins from an anterior pedal pit just posterior to the mouth (Fig. 2.2C). This character separates them from the burrowing subclass Chaetodermomorpha in which a foot is lacking. Cephalization is only weakly expressed in neomenioids; indeed, sometimes the anterior end can be determined only from the posteriorly facing spicules along the foot furrow. Chaetoderms have a cuticular oral shield, often exposed, and fringing spicules around the posterior mantle cavity. In both groups the mantle cavity is small and posterior; in the chaetoderms it houses a pair of ctenidia (Fig. 2.14B). The gut is composed of a mouth, a pharynx with a radula (sometimes lacking in neomenioids) and salivary glands, a combined (neomenioids) or separate (chaetoderms) stomach and digestive gland, intestine, and anus.

The reproductive system, unique among mollusks, has a paired or fused gonad that empties directly into the pericardial cavity. The gametes pass posteriorly through the pericardium into U-shaped gametoducts that empty through the glandular lower limb into the mantle cavity.

Sensory elements in both subclasses consist of one or more dorsoterminal sense organs (Fig. 2.12B) In neomenioids, a vestibule with sensory papillae lies above the mouth, with which it usually shares a common opening (Fig. 2.2C).

General accounts of the group in English are Heath (1911), Hyman (1967), Salvini-Plawen (1985), Scheltema (in press), and Scheltema *et al.* (1994). A systematic account appears in Salvini-Plawen (1978) for Neomeniomorpha and in Boss (1982) for the whole class.

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## Reproduction and Development

The chaetoderms have a unique, derived ectaquasperm, or externally fertilizing sperm (Buckland-Nicks and Chia, 1989). Neomeniomorpha, on the other hand, have a primitive introsperm, that is, a filiform, internally fertilizing sperm (Buckland-Nicks and Scheltema, in prep.). External fertilization is thus presumed for chaetoderms, which are dioecious and have a simple reproductive tract, and internal fertilization for neomenioids, which are hermaphroditic and have a more complicated reproductive tract with seminal receptacles, sometimes seminal vesicles, and often copulatory spicules.

Development is lecithotrophic, the larvae called "pericalymma" or "test-cell" larvae. They are similar to the larvae of protobranch bivalves, with a ciliated, cellular test within which the juvenile develops. In aplacophorans the test is eventually engulfed by the expanding ectodermal layer (Thompson, 1960). A larva of one species was said to go through a stage with seven bands of spicules, reminiscent of chiton plaques (Pruvot, 1890).

## Phylogeny

The phylogenetic position of the Aplacophorans among the Mollusca is not certain. Their highly modified external worm shape and primitive-appearing internal anatomy have been interpreted as indicating that they are basal mollusks, with the chaetoderms the sister taxon to all other extant mollusks (Salvini-Plawen, 1985), or that they are progenetic aculiferans, sharing sister status to conchiferan mollusks with the Polyplacophora (Scheltema, 1993). In the latter case, the aplacophoran worm shape is considered to have evolved only once and the Chaetodermomorpha are said to be the more derived of the two subclasses, with loss of the foot, reduction in the nervous system, and a derived digestive system.

## Habitat and Behavior

Insofar as known, aplacophorans are carnivores or omnivores. Neomenioids mostly prey on Cnidaria, grasping their prey with the radula and sucking out tissue with a muscular pharynx (Scheltema and Jebb, 1994). Chaetoderms feed on foraminiferans or organic debris, the radula apparently used for capture. Only in the Prochaetodermatidae is the radula known to be used for rasping (Scheltema, 1981). Movement is extremely slow in all Aplacophora. Neomenioids creep on or within sediment on their ciliated, nonmuscular foot, or they wrap around hydroids or octocorals upon which they prey. Chaetoderms, on the other hand, burrow through the sediment by means of a hydrostatic skeleton.

Life histories are unknown except partially for one deep-sea prochaetodermatid species from the Western North Atlantic that lives at 2,000 m depth. This species becomes sexually mature within one year (Scheltema, 1987).

## Aplacophora of the Santa Maria Basin and Santa Barbara Channel

Neomeniomorpha are represented in the Santa Maria Basin and Santa Barbara Channel MMS collections by only 4 species and 29 individuals, but there are 11 species and 116 individuals of Chaetodermomorpha. The family Chaetodermatidae, in particular, is represented by 9 species, with 3 further species known from the Southern California Bight but not present in the Santa Maria Basin samples examined here. This radiation is the greatest yet discovered for a chaetoderm fauna.

Excluding unnamed species represented by a single individual, depth distributions can be determined for 11 species as shown in Table 2.1. The divisions are based on the dendrogram figured in Blake (1993).

**Table 2.1.** Aplacophora of the Santa Maria Basin: Vertical Distribution

| Species | Inner Shelf | Outer Shelf | Upper Slope |
|---|---|---|---|
| ?*Gymnomenia minuta* | | | + |
| ?*Genitoconia mariensis* | + | + | |
| *Limifossor fratula* | | | + |
| *Chaetoderma argenteum* | | | + |
| *Chaetoderma californicum* | | | + |
| *Chaetoderma elegans* | + | | |
| *Chaetoderma nanulum* | | + | + |
| *Chaetoderma pacificum* | | | + |
| *Falcidens hartmanae* | | | + |
| *Falcidens longus* | + | | |
| *Falcidens macracanthos* | + | + | |
| *Spathoderma californicum* | | | + |

Three species can be considered as exclusively continental shelf species, whereas the majority, 9 species, are upper continental slope species. These vertical distributions parallel those known elsewhere, that is, that the Aplacophora are primarily creatures of the continental slope.

Several species occurring in the Santa Maria Basin have also been taken from depths greater than 1,000 m in the basin south of Santa Cruz Island (referred to as LACM under "Material examined"). These deep records are apparently due to slumping of the sediments, which carry animals with them into the basin.

## External and Hard-Part Morphology

### Body Shape

Neomeniomorpha may be round or oval in cross-section, the oval width greatest either dorsoventrally or laterally. Anterior and posterior ends may be rounded, pointed, slanted, or bulbous; either end may be the widest. The mouth/vestibule entrance may be open (Fig. 2.2C) or contracted in a specific manner (Fig. 2.3C).

The body is circular in cross-section in all chaetoderms, and may be of one width throughout (Fig. 2.7A), or, most usual, divided into two or more regions: anterium, often retracted; neck, usually separated from the trunk by an anterior constriction; anterior trunk; posterior trunk; and posterium. Anterior and posterior trunks may not be separate, or the anterior constriction may be lacking (cf. Figs.2.8A, 2.11A, 2.16A, and 1.20B). The oral shield may be large or small, circular or greater in one dimension than another, and pierced or cleft by the mouth opening; dorsally, the two lobes of the shield may be large (Fig. 2.9B) or small (Fig. 2.10B).

### Spicule Attitude and Form

Attitude of the numerous spicules of the body ranges from more or less upright (Figs. 2.8A; 2.9A, n, at) to adpressed against the body (Fig. 2.7A). They may lie parallel or at an angle to the anterior-posterior body axis (Figs. 2.9A, pt; 2.20 B, C) and may be only slightly or deeply buried in the cuticle. Many neomenioid species have several layers of spicules within a thick cuticle, but none were collected from the Santa Maria Basin. Spicules produce a sheen from dull to glossy or opalescent. They may be thinly or densely arranged along the body. The spicules around the mantle cavity in both neomenioids and chaetoderms have a distinctive pattern according to species.

Spicule morphology, like shell morphology in other mollusks, is of utmost taxonomic importance in determining species and often genera. Spicules are minute to large, ranging from 25 µm to more than 500 µm in length and from 1 µm to >10 µm in thickness. They are solid, flat or spherical in cross section, straight (Fig. 2.10E-G) or bent (Fig. 2.8F) or sinuous (Fig. 2.6D), oval (Fig. 2.2D) to elongate (Fig. 2.7D-F), and in neomenioids paddle- or hook-shaped or hollow (Fig. 2.4D). Spicules are often sculptured with ridges or grooves, and chaetoderm spicules may exhibit a distinct waist (Fig. 2.1B). Spicules from along the ventral furrow in neomenioids differ in shape from those on the rest of the body (Fig. 2.2D, E). Spicule morphology may differ between different regions of the body, particularly in the family Chaetodermatidae (Fig. 2.8E, H), and there may be more than one type of spicule present in particular body regions in both neomenioids and chaetoderms (Figs. 2.3E,G; 2.13F,L). The pattern formed by variations in spicule thickness and determination of greatest thickness are taxonomically important and can be determined from isochromes formed by birefringence colors (Fig. 2.1).

### Radula

As in other mollusks, the morphology of the radula is important for species and often generic or family determination. The primitive form of the radula in aplacophorans is distichous, that is, two teeth per row, and all chaetoderms have a distichous radula, albeit highly modified in the Chaetodermatidae. The radula in neomenioids may be distichous, monostichous (one tooth per row), or polystichous (many teeth per row).

### Copulatory Spicules

Many neomenioids have paired single, double, or multiple copulatory spicules formed within deep, modified pockets of the mantle cavity (Fig. 2.2F). Only exceptionally are they unpaired. They are of great taxonomic importance at the species level and are particularly useful in distinguishing closely related species.

## Collection and Preservation

Aplacophora are usually collected in samples taken by dredge, box core, or grab from the soft, level-bottom community. The best general fixation for such samples is buffered 10% formalin, with preservation in buffered 80% alcohol within 24 hours. The samples are then sorted after screening through a fine (.027 mm) sieve. Staining with Rose Bengal facilitates the sorting process. Living aplacophorans have been collected by several methods, according to habitat. Chaetoderms, all of which burrow in muds and silts, can be seen with the naked eye in grab samples that are washed through a 1- mm-mesh screen as they are collected. However, the chaetoderms need to be sufficiently large (about 2 cm) and numerous (1 or more organisms per grab) in order to make this procedure successful. Density in an area should be determined by previous quantitative sampling. Capture rates for aplacophorans can be about a dozen animals per hour with grabs taken and screened as rapidly as possible. Smaller chaetoderms and neomenioids can also be retrieved from dredge collections which are taken back to the laboratory, where they are carefully screened while the sediment is still fresh and the residue examined under a binocular microscope. The process is tedious as usually only a few animals are captured, but will bring results if collections are made in areas known to have aplacophorans present.

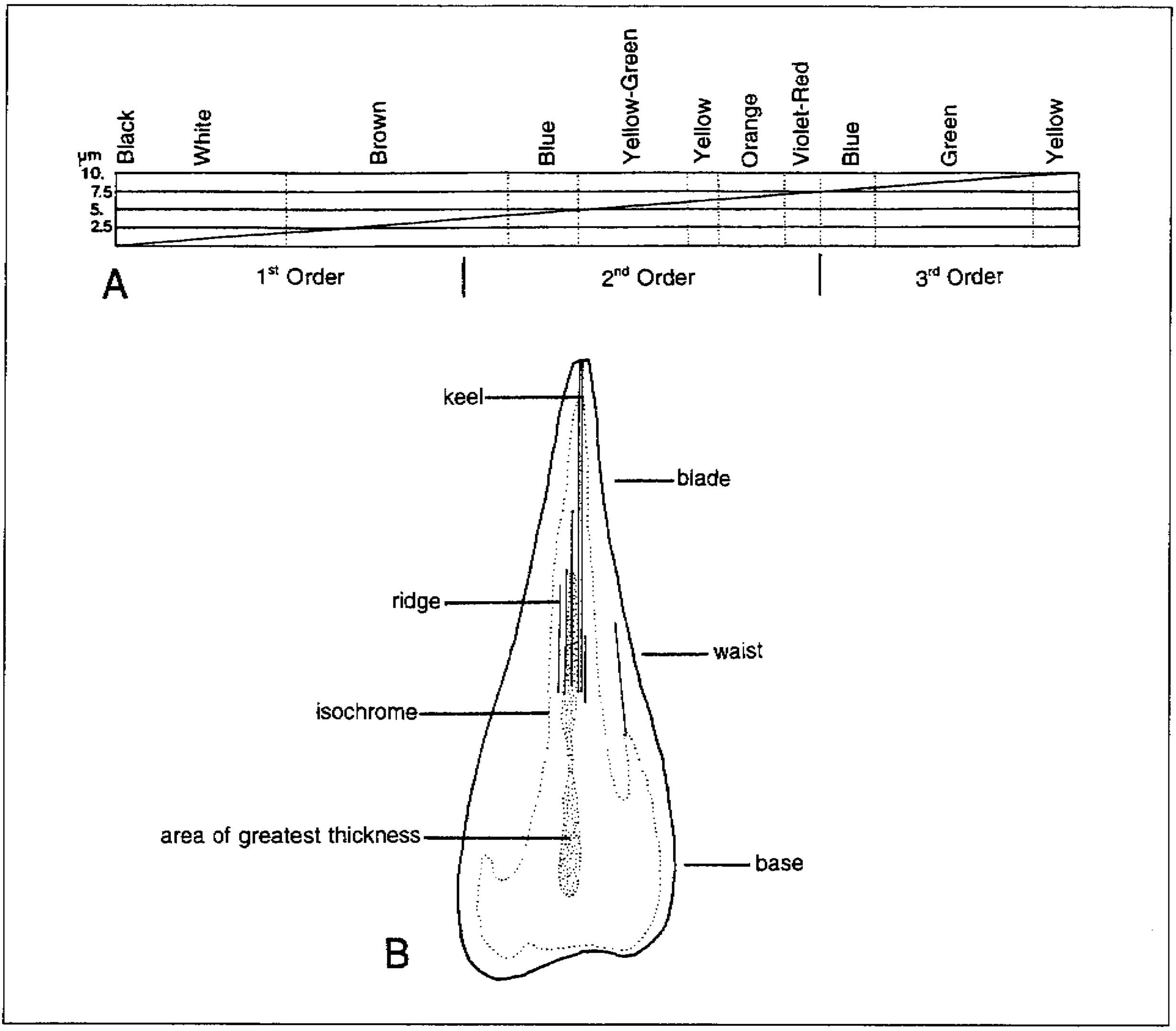

**Figure 2.1.** Spicule morphology: A, crystallographer's interference color chart showing birefringence of aragonite under cross-polarized light (diagonal line), thickness (ordinate), and colors (abscissa). The highest order of color for a spicule is determined when all light is extinguished except that passing through the spicule, starting at the black edge of spicule. The greatest thickness is illustrated in B by stippling. An isochrome between any two color bands is indicated by a dotted line and shows the pattern consequent upon varying thicknesses in the spicule. The base and blade of a spicule may or may not be set apart by an ill-defined waist. A spicule may be sculptured by a keel, indicated by a double line, or by ridges, shown with a single line.

Interstitial neomenioids, most of which are usually only about 1 mm long, can be retrieved from well-aerated, shallow-water, coarse sediments. The sediments are collected either by anchor dredge, by diving, or intertidally with a trowel in areas of swift tidal currents during spring low tide. The sediments are placed in buckets with several inches of aerated sea water and not disturbed for a day or two. The top few centimeters are then removed to a container, strongly agitated with a quantity of sea water, and the supernatant quickly poured through a fine screen. The residue is washed into a petri dish and examined under a dissecting microscope.

One tropical neomenioid genus, *Epimenia*, is so large (10-30 cm) that it can be collected by divers in its habitat, hard coral rock in areas of swift currents with alcyonarian corals. Observations have been made on living *Epimenia* collected this way (Scheltema and Jebb, 1994).

## Laboratory Methods

Taxonomic descriptions of Aplacophora have been based with few exceptions on preserved animals, and usually primarily from histologic sections. As the species descriptions herein demonstrate, hard parts and body shape are adequate for species identifications, although the higher classification of neomenioids, with their complicated reproductive systems and variety of salivary glands, depends on histologic sections.

### Body Characters

Measurements are made using dividers, measuring wheel, or digitizer on camera-lucida drawings of entire specimens, or on lines drawn through the axes of a camera-lucida image. A digitizer could also directly measure an image, although this method has not been used yet. Dimensions of the different body regions should be made for Chaetodermomorpha, and for Neomeniomorpha, relative differences between anterior and posterior widths and between dorsoventral height and lateral width should be noted. Because aplacophorans are contractile, and preserved specimens are nearly always contracted, length measurements are minimal for living individuals.

### Spicules

Temporary slides of spicules are made by placing an individual in a drop of glycerine in a depression slide and teasing off a few spicules with a needle or, if spicules are particularly resistant to being removed, with the end of a dissecting knife. In this manner, spicules can be removed from particular parts of the body. Permanent slides are made by first rinsing an individual in distilled water and then placing it in a drop of distilled water on a slide. After the spicules have been teased into the water-drop, they are thoroughly air-dried and permanently mounted with a histologic mountant and coverslip.

Spicules are drawn at as large a scale as possible under a compound microscope with the aid of a camera lucida and measured with an ocular micrometer. When solid spicules are placed between crossed polarizers of a light microscope[2], spicules produce bands of rainbow colors owing to the high birefringence of aragonite. The bands, or isochromes, are species specific in their topography, depending upon where and to what extent each spicule is thickened. The interference colors exhibited by a spicule can be compared to a crystallographer's chart relating birefringence, interference colors, and thickness, upon which is drawn a diagonal representing the birefringence of aragonite (Fig. 2.1A). By comparing the spicule colors to the colors on the interference color chart, one can determine the greatest thickness of the spicule. The microscope stage or lower polarizer should be rotated until the background extinguishes all light except that passing through the spicule. The thickest part(s) of the spicule and at least one isochrome are then traced.

### Radula

The entire buccal mass is dissected from an individual by means of a dorsal longitudinal cut and removed to a drop of hypochlorite (filtered household bleach) in a depression slide. In very small specimens, the entire anterior end may need to be dissected and placed in the hypochlorite. After the tissue has dissolved, the hypochlorite is drawn off with a pipette and the radula washed several times by adding and drawing off

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[2] Several types of microscopes are equipped with polarizing light, including differential interference contrast (Nomarksi) optics and petrographic microscopes.

distilled water. A drop of glycerine is then added to the slide and the radula drawn under a compound microscope with the aid of a camera lucida. If the radula is very small (cf. Figs. 2.2G, 2.3H), it should be placed in glycerine on a flat slide, covered with a coverslip, and examined at 100x under oil immersion. To make a permanent slide, the radula, cleared of tissue, is washed in a quantity of distilled water; the use of a small Stender dish works well. After a day, the radula is removed to a drop of CMPC-10 (a mountant miscible in water) containing a water miscible stain. A micropipettor can be used to pick up very small radulae. The preparation is allowed to harden for a day and then is covered with clear mountant and a cover slip.

### Copulatory Spicules

The posterior end of a neomenioid is cut free and placed in hypochlorite. When the tissue dissolves, the copulatory spicules can be teased out from the surrounding cuticle, washed, placed in glycerine, and drawn as described above for radula preparations. To make a permanent slide, the spicules are washed in a quantity of distilled water, and using a micropipettor placed on a slide to dry. They are then covered by a histological mountant and a coverslip.

## List of Species

## Subclass Neomeniomorpha

Family Gymnomeniidae

- ?***Gymnomenia minuta*** **Scheltema, new species**
- ?***Genitoconia mariensis*** **Scheltema, new species**

Family Dondersiidae

- *Heathia porosa* Heath
- ?*Nematomenia* sp.

Family undetermined

- Neomeniomorpha sp.

## Subclass Chaetodermomorpha

Family Limifossoridae

- *Limifossor fratula* Heath

Family Chaetodermatidae

- *Chaetoderma argenteum* Heath
- *Chaetoderma californicum* Heath
- *Chaetoderma elegans* **Scheltema, new species**
- *Chaetoderma hancocki* (Schwabl)
- *Chaetoderma marinelli* (Schwabl)
- *Chaetoderma nanulum* Heath
- *Chaetoderma pacificum* (Schwabl)
- *Chaetoderma scabrum* Heath
- *Falcidens hartmanae* (Schwabl)
- ***Falcidens longus*** **Scheltema, new species**
- ***Falcidens macracanthos*** **Scheltema, new species**
- ***Furcillidens*** *incrassatus* (Schwabl) **Scheltema, new genus**

Family Prochaetodermatidae

- *Spathoderma californicum* (Schwabl)

## Abbreviations Used in the Figures

an, anterium
ap, apophysis
at, anterior trunk
c, carina
fr, frontal
lat, lateral
lp, lateral projection
mc, opening of mantle cavity
m/v, opening of vestibule and mouth
n, neck
pos, posterium
pp, pedal pit
pt, posterior trunk
tp, triangular plate
vf, ventral furrow

## Key to the Species of Aplacophora in the Santa Maria Basin, Santa Barbara Channel, and Southern California Bight

1A. Cuticle interrupted by ventral longitudinal furrow .................................. Neomeniomorpha ...... 2
1B. Cuticle entire; oral shield present ............................................................. Chaetodermomorpha . 6

[Neomeniomorpha species are differentiated by spicule morphology exclusive of spicules lying beside the foot furrow]

2A. Spicules of 1 type ........................................................................................................ 3
2B. Spicules of 2 or more types ......................................................................................... 4

3A. Spicules rimmed ovals ........................................................................... ?*Gymnomenia minuta*
3B. Spicules broad, paddle-shaped ....................................................................... ?*Nematomenia* sp.

4A. With rodlike spicules .......................................................................................... Neomeniomorpha sp.
4B. With oval-shaped spicules ............................................................................................ 5

5A. Some oval-shaped spicules with elongate points ........................................ ?*Genitoconia mariensis*
5B. Some spicules elongate, paddle-shaped ................................................................. *Heathia porosa*

[Body shape is used to differentiate the first four species of Chaetodermomorpha. The remainder of the key is based on morphology of anterior trunk spicules at the anterior constriction]

6A. Body short, cylindrical, body regions not delimited ........................................... *Limifossor fratula*
6B. Body regions differentiated ............................................................................................ 7

7A. Posterium long, narrower than rest of body, anterior and posterior trunk not differentiated ......... 8
7B. Posterior trunk same width or wider than anterior trunk, trunk regions differentiated by attitude of spicules ............................................................................................................. 9

8A. Anterior constriction present ........ *Falcidens hartmanae*

8B. Neck and anterior trunk not differentiated by constriction, jaws present ..... *Spathoderma californicum*

9A. Neck and/or anterium greatly expanded, posterior trunk broad, >2x width short, narrow anterior trunk ........ *Furcillidens incrassatus*

9B. Body elongate, width of posterior trunk <2x width of anterior trunk ........ 10

10A. Some or all spicules deeply curved or sharply bent ........ 11

10B. Spicules flat or nearly so ........ 14

11A. Spicules of 2 dominant types, one type flat, longer than curved or bent spicules, thickest basally .... 12

11B. Spicules predominantly of 1 type ........ 13

12A. Shorter spicules bent, usually with many ridges, with abfrontal groove, radula cone straight ........ *Chaetoderma nanulum*

12B. Shorter spicules curved, ridge of keel single, isochromes pinched in below keel on midanterior spicules ........ *Chaetoderma scabrum*

13A. Spicules thickened in inverted V, <130 µm long ........ *Chaetoderma argenteum*

13B. Spicules large, thick ( 10 µm), up to 400 µm long, base broad, asymmetrical ........ *Chaetoderma californicum*

14A. Spicules widest medially, tapered basally ........ 15

14B. Spicules widest and more or less flared basally ........ 16

15A. Spicules ridged, thin (5 µm or less), body slender throughout, radula cone curved ........ *Chaetoderma elegans*

15B. Spicules thickest (to 8 µm) laterally or medially or both, ridges few or none, posterior trunk broader than anterior trunk, radula cone straight ........ *Chaetoderma pacificum*

16A. Spicules with few or no ridges, sparse, long (>450 µm), thick (>10 µm); posterior end "glandular," knoblike, anterior end usually greatly swollen ........ *Chaetoderma hancocki*

16B. Spicules with many parallel ridges ........ 17

17A. Spicules to 400 µm long, with abfrontal groove, ridged medially, thickest laterally, radula cone straight ........ *Falcidens macracanthos*

17B. Most spicules <250 µm long ........ 18

18A. Spicules flat, thickest laterally or medially, base of radula cone bulbous frontally ........ *Chaetoderma marinelli*

18B. Spicules somewhat curved, thickest laterally and medially in 3 longitudinal bands, radula cone narrow frontally ........ *Falcidens longus*

# Descriptions of Species

## Subclass Neomeniomorpha

Solenogastres Gegenbaur, 1878 [*partim*]; Salvini-Plawen (1967, 1985).

**Diagnosis.** Aplacophorans with ventral furrow within which lies a foot fold and with a more or less distinct pedal pit at anterior end of groove.

### Family Gymnomeniidae

Wireniidae Salvini-Plawen, 1978.

**Type Species:** *Gymnomenia pellucida* Odhner, 1921.

### Genus *Gymnomenia* Odhner, 1921

**Diagnosis.** Small, 5 mm or less in length, dorsoventrally flattened, tapered posteriorly, becoming terminally bulbous (Fig. 2.2A); with midgut sacculations visible through thin cuticle; mouth and vestibule surrounded, or nearly surrounded, by external fold (Fig. 2.2B, C); pedal pit evaginated and heavily ciliated (Fig. 2.2A, C); posterior end tapered to point in juveniles; spicules small, flat, thin ovals ridged around perimeter (Fig. 2.2D); radula small, mostly within radula sac, teeth with distichous hooks; ventral salivary glands opening through numerous ductules; copulatory spicules in paired bundles of a dozen or more.

### ?*Gymnomenia minuta* Scheltema, new species

Figure 2.2

**Material Examined.** Santa Maria Basin, Sta. R-3 (1); Sta. R-6 (5, **holotype**, USNM 860388; **paratype** LACM 2745); Sta. R-9 (20, **paratype** LACM 2746).

**Description.** A small species less than 2 mm long, spicular coat mossy rather than glistening (Fig. 2.2A). Opening to vestibule and mouth broad (Fig. 2.2C). Posterior bulbous in lateral view, mantle cavity opening small, round, with rounded prominences within (Fig. 2.2B). Oval spicules up to 25 µm long and 11 µm wide (Fig. 2.2D); spicules beside ventral furrow up to 47 µm long and 14 µm wide (Fig. 2.2E); all spicules 1 µm or less thick. Copulatory spicules in bundles of about 12, tips bent, staff either ridged or grooved, longest about 65 µm (Fig. 2.2F). Radula examined from 1 paratype: about 20 rows, total length 142 µm; teeth with distal hook, medial denticle, and small proximal denticle, length about 35 µm (Fig. 2.2G).

**Biology.** In silts and sandy silts with 16% or less clay and up to 34% sand; occurred at same stations as *Limifossor fratula*, *Chaetoderma nanulum*, *C. argenteum*, *Falcidens hartmanae*, and an unnamed species of Neomeniomorpha.

**Remarks.** The original description of *Gymnomenia* considered both radula and spicules to be lacking (Ohdner, 1921). However, the easily dissolved spicules (they are lacking on most of the specimens from the Santa Maria Basin) leave telltale lacunae in the cuticle as illustrated by Odhner, and the tiny radula was apparently destroyed in the sagittal sections upon which the original description was based.

Generic assignment is here based on similarity of spicules, body, and radula to numerous specimens of an undescribed but undoubted species of *Gymnomenia* off west Africa (Scheltema, 1981, figs. 1A, 2M,N, 4).

**Etymology.** From Latin *minutus*, small, this being a small species for the genus.

**Distribution.** An upper continental slope species so far known only from the Santa Maria Basin at 409-410 m, but collections still to be closely examined from the Southern California Bight have similar or perhaps the same species.

### Genus *Genitoconia* Salvini-Plawen, 1967

**Type Species:** *Genitoconia rosea* Salvini-Plawen, 1967.

**Diagnosis.** Small, seldom more than 5 mm in length, nearly round in cross-section, rounded anteriorly and posteriorly; pedal pit indistinct; edges of ventral furrow evaginated, forming a sharp V; cuticle thin, easily torn; spicular coat glossy; spicules thin, somewhat oval-shaped with rounded base and a distal point; midgut sacculations lacking; radula small, mostly within radula sac, teeth with distichous hooks; copulatory spicules in paired bundles of up to 20.

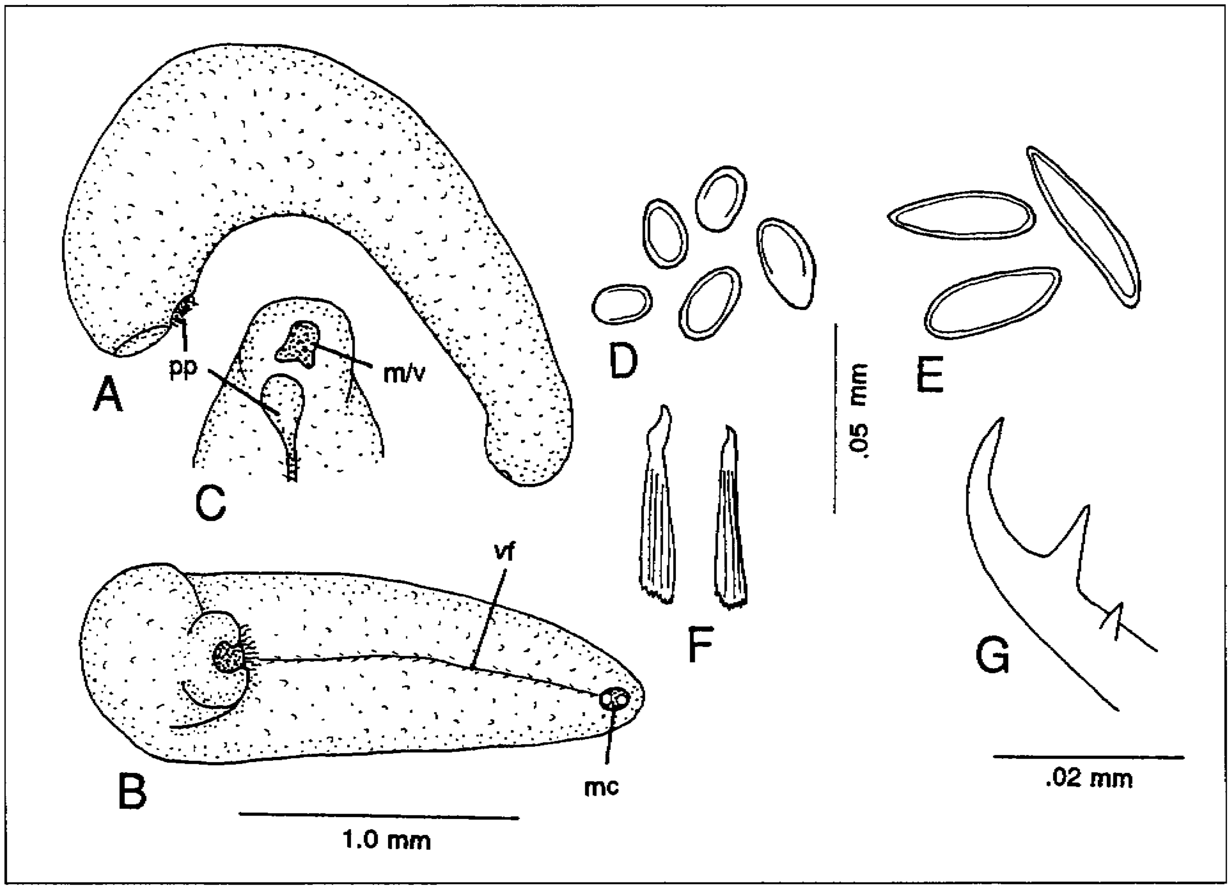

**Figure 2.2.** ?*Gymnomenia minuta* **Scheltema, new species**: A, B, holotype (USNM 860388), lateral and ventral views, anterior to left; C, ventral view of paratype (LACM 2745) showing mouth/vestibule opening and pedal pit; D, E, holotype spicules from body (D) and ventral furrow (E); F, 2 copulatory spicules, proximal ends eroded, from a bundle of about 12, specimen C; radula tooth, base not seen, from paratype (LACM 2746).

### ?*Genitoconia mariensis* Scheltema, new species

Figure 2.3

**Material Examined.** Santa Maria Basin, Sta. PJ-1 (3, **holotype** USNM 860389; **paratype** (LACM 2747); Sta. R-5 (4).

**Description.** Up to 4.4 mm long and 1.5 mm in diameter, anterior end slightly bulbous, widest at midbody (Fig. 2.3A); posterior mantle cavity wall flattened in lateral view (Fig. 2.3B); retracted mouth/vestibule Y-shaped (Fig. 2.3C). Spicules 1-2 μm thick, mostly ovals with short points, up to 52 μm long x 29 μm wide (Fig. 2.3E), but many others with points half spicule length, up to 79 μm long x 34 μm wide (Fig. 2.3G); spicules of foot furrow curved on one edge, recurved on other, 45 μm x 16 μm (Fig. 2.3F). Copulatory spicules numerous, slender, flat, ridged along edges, ridges meeting to form a solid, rounded, distal point (Fig. 2.3D); length not determined. Radula 100 μm long, denticles 31 μm long with distal hook, medial denticle, and shorter proximal denticle; edge away from denticles is recurved (Fig. 2.3H).

**Biology.** Taken from silt with 16% sand and sand with 40% silt, both with clay content of 12% or less. Collected at the same station as *Falcidens macracanthos.*

**Remarks.** This species is placed in the genus *Genitoconia* on the basis of body shape and glossiness, evaginated ventral furrow, lack of midgut sacculations, spicule morphology, bundles of copulatory spicules, and radula morphology.

**Etymology.** The ending *-ensis* means belonging to, i.e., the Santa Maria Basin.

**Distribution.** A continental shelf species so far known only from 145-154 m in the Santa Maria Basin, but like *Gymnomenia*, *Genitoconia* is a widespread genus (unpublished data), and some species of Gymnomeniidae have broad distributions.

## Family Dondersiidae

**Diagnosis.** With 2 types of solid spicules; radula monostichous (single tooth per row) with 1 or 2 pairs of denticles, the medial denticles fused at tips, or radula lacking.

### Genus *Heathia* Thiele, 1913

*Ichthyomenia* Heath, 1911.

**Type Species:** *Ichthyomenia porosa* Heath, 1911.

### *Heathia porosa* (Heath, 1911)

Figure 2.4

**Material Examined.** Southern California Bight, off San Diego, 900-976 m, **holotype** and **paratype** (*Albatross* Sta. 4400, 4402, CAS 021406, 021407, spicule slide and serial sections).

**Description.** According to Heath (1911): average length 16 mm, diameter 1.2 mm (Fig. 2.4A); posterior drawn into finger, "but in other cases it may become blunt and trumpet-shaped"; with numerous sensory pits ventrolaterally; radula lacking. All spicules thin, about 1 μm thick, of 2 types: short ovals drawn to point distally, with thickened rim and light striations, up to 20 x 11 μm (Fig. 2.4B), and long paddles with short, solid, proximal "handle" and longer, rimmed "scoop," up to 81 x 9 μm (Fig. 2.4D). Paddles located along foot furrow, lateral to foot-furrow spicules with which they are juxtaposed on the type slider, and which are elongate ovals up to 47 x 7 μm (Fig. 2.4C).

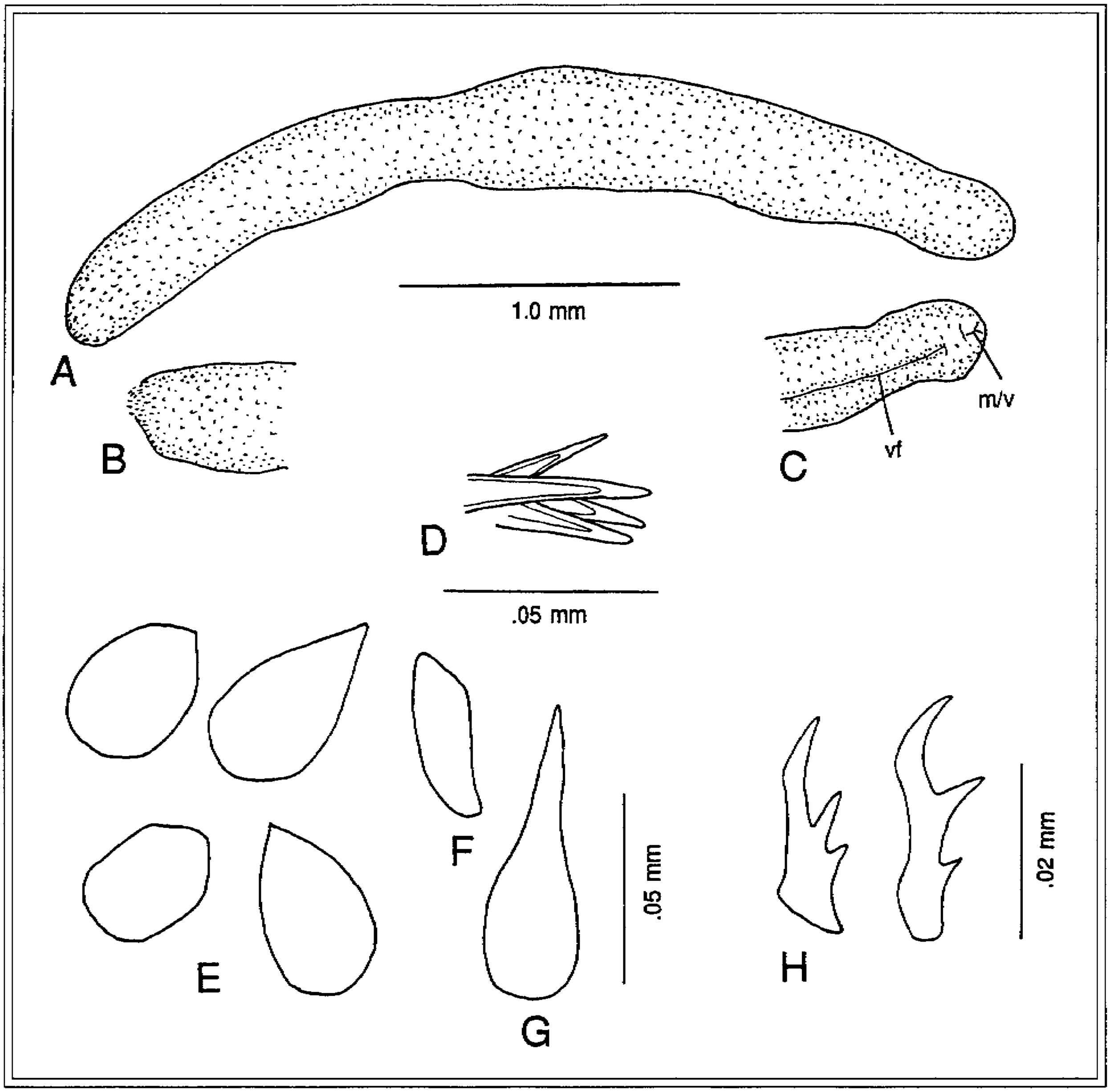

**Figure 2.3.** ***?Genitoconia mariensis*** **Scheltema, new species**: A, holotype (USNM 860389), dorsal view, anterior to right; the drawing does not do justice to the shining, glossy coat of spicules; B, paratype, posterior end, lateral view (LACM 2747); C, anterior end of A, ventral view; D, several copulatory spicules from B, proximal ends to left probably eroded; E, short-pointed spicules; F, spicule from foot furrow; G, long-pointed spicule; H, radula teeth from 2 different views.

**Remarks.** Specimens of Gymnomeniidae from off southern California are sometimes labeled *Heathia porosa* in museum collections.

**Distribution.** Known only from type material off San Diego.

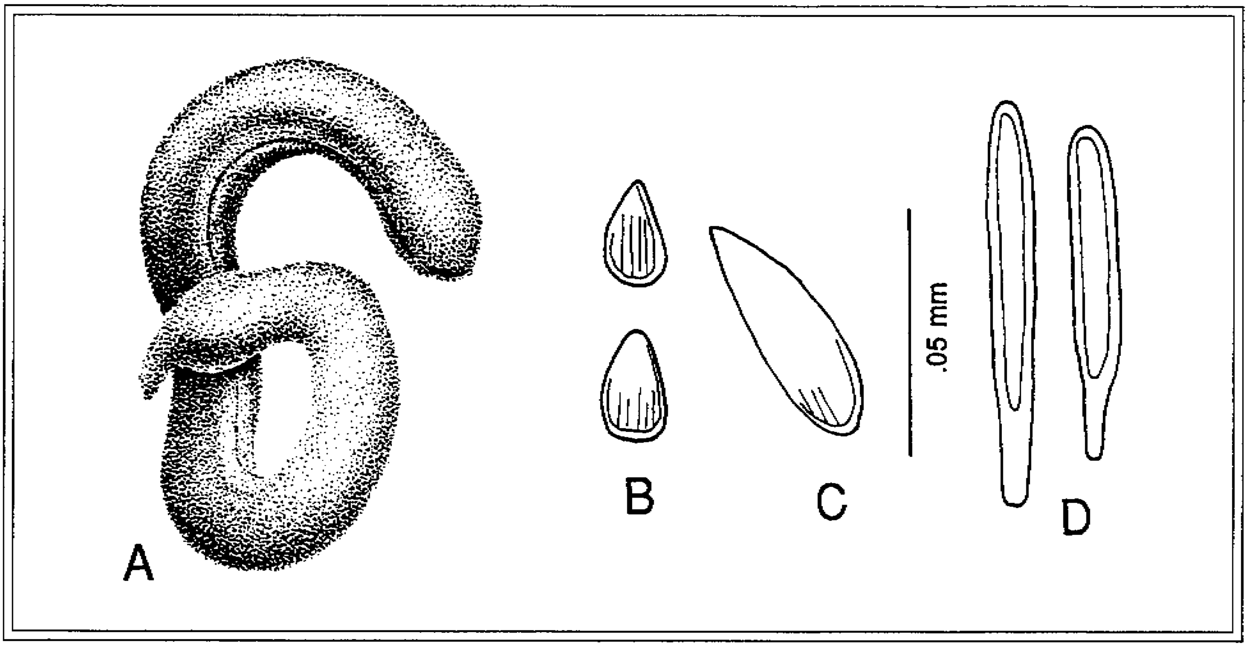

**Figure 2.4.** *Ichthyomenia* (= *Heathia*) *porosa* Heath: A, figure from Heath, 1911, plate 3, fig. 4; B-D, holotype spicules from body (B), foot-furrow (C), and lateral to foot-furrow (D).

### ?*Nematomenia* sp.

Figure 2.5

**Material Examined.** Santa Maria Basin, Sta. 1 (1).

**Description.** Length 5.3 mm, dorsoventral width 1.4 mm, body narrower than high; anterior and posterior ends slantingly truncated (Fig. 2.5A, B); with dorsal carina. Spicules paddle shaped, paddle thicker and forming shelf above handle (Fig. 2.5C, D); length to 65 µm, width to 32 µm, thickness 4 µm or less. Radula, if present, not known.

**Biology.** Collected from sand with some gravel; silt and clay together <25%.

**Remarks.** The single specimen is in poor condition. Based on spicule morphology of the paddles, even though a second spicule type was not discovered, it belongs to the genus *Nematomenia* Simroth, 1893, species of which live and feed on hydroids (see Pruvot, 1891, as *Dondersia*). This individual may have dropped off a hard-bottom, fouling prey organism and may not be part of the soft-bottom community.

**Distribution.** One locality at 98 m in the Santa Maria Basin.

### Neomeniomorpha sp.

Figure 2.6

**Material Examined.** Santa Maria Basin, Sta R-6 (1).

**Description.** A small species 2.8 mm long, 1.4 mm wide dorsoventrally, and very narrow laterally, between 1.2 and 1.3 mm, rounded anteriorly, pointed posteriorly (Fig. 2.6A-C). Pedal pit indistinct. Spicular coat dull. Spicules small, straight or curved or recurved solid rods and paddles, up to 52 µm long (Fig. 2.6D). Specimen not dissected; radula and copulatory spicules, if present, not known.

**Biology.** Found with an individual of *Gymnomenia minuta* in sandy silt with 34% sand. *Limifossor fratula*, *Chaetoderma argenteum*, and *Falcidens hartmanae* occur at the same station.

**Distribution.** Known only from a single specimen taken from the Santa Maria Basin at 410 m.

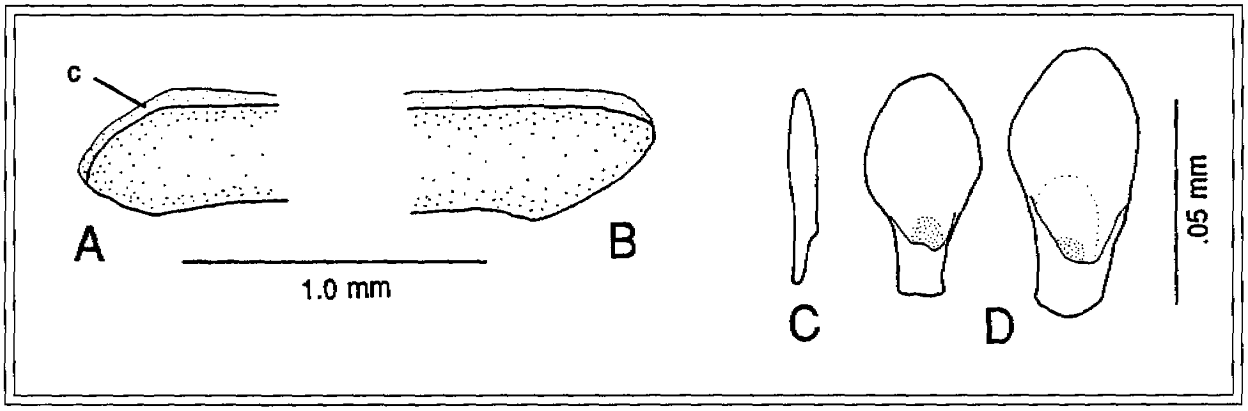

**Figure 2.5.** ?*Nematomenia* sp.: A, B, posterior and anterior ends, respectively, in lateral view showing dorsal carina, spicules not indicated; C, D, lateral and frontal views of spicules.

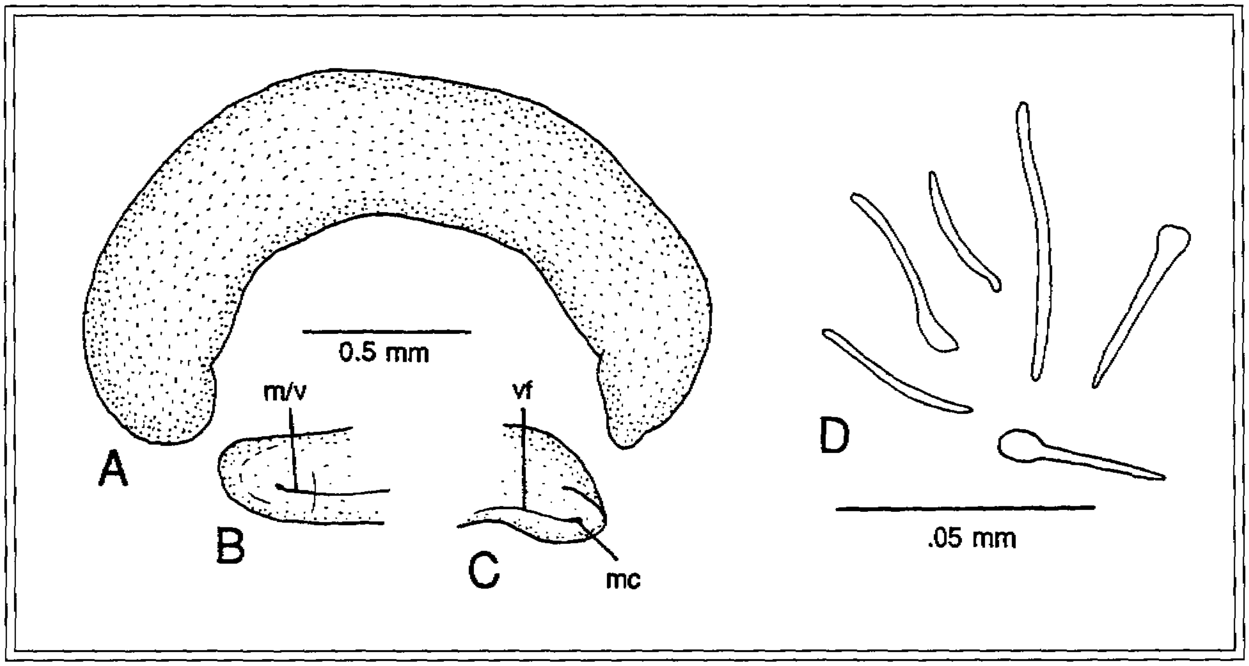

**Figure 2.6.** Neomeniomorpha sp.: A, entire specimen, anterior to left; B, C, ventral view of anterior and posterior ends, respectively; D, spicules of body.

## Subclass Chaetodermomorpha Pelseneer, 1906

Caudofoveata Boettger, 1956.

**Diagnosis.** Aplacophorans with cuticle entire and with an oral shield.

### Family Limifossoridae

#### Genus *Limifossor* Heath, 1904

**Type Species:** *Limifossor talpoideus* Heath, 1904.

**Diagnosis.** Short, broad, no divisions of body evident; spicules closely adpressed to body and thickly overlaid; oral shield divided; radula large, distichous with 20-30 rows, teeth heavily sclerotized, each tooth with a large lateral denticle and one or more smaller median denticles on a broad base.

#### ***Limifossor fratula* Heath, 1911**

Figure 2.7

*Limifossor fratula* Heath, 1911: 44, 72, pl. 2 fig. 6, pl. 4 fig. 13, pl. 35 figs. 1-5, 10, pl. 36 fig. 8.—Schwabl, 1963, 261-262.—Salvini-Plawen, 1992, 318, figs. 2, 12.

**Material Examined.** British Columbia, 181 m (1) (IOS).—Off Oregon, 200-600 m (12) (OSU).—California, Santa Maria Basin, Sta.26 (1, USNM); Sta. 106 (1, SBMNH); Sta. R-3 (1) (voucher, USNM); Sta. R-6 (1); Sta. R-9 (1).—Southern California Bight, south of Santa Cruz Island, 626-1,830 m (16) (LACM 76-252, 76-253, 76-257, 76-272, 76-271, 76-269, 76-268, 76-263); off San Diego, 468 m, **syntypes** (*Albatross* Sta. 4369, CAS 021401, 021402, spicule slide and serial sections, and wet specimen, MCZ).

**Description.** A short, stout species up to 7.4 mm long x 2.3 mm wide (to 10 mm long, Schwabl, 1963), length/width index 3.2-3.5 (Fig. 2.7A); mantle cavity distinctly set off from trunk by sharply reduced width; oral shield not known; dorsoterminal sense organ present, but not evident except in sectioned material. Spicules deeply embedded in cuticle over entire body and forming ring around mantle cavity. Spicules long, all 10 µm thick, slightly curved towards body, with very short, sharp keel at tapered distal end, taper more or less abrupt Fig. 2.7D-G); often longitudinally grooved on either side of raised medial section; narrowest from dorsoanterior region, up to 440 µm long and 58 µm wide (Fig. 2.7D); mid-dorsally and dorsoposteriorly to over 500 µm long and up to 87 µm wide (Fig. 2.7E, F); shorter ventrally, many <400 µm long, to 87 µm wide (Fig. 2.7G). Radula with up to 30 rows, lateral denticles up to 135 µm long, medial denticles single, up to 72 µm long, distance between inner edges of denticles at base 41 µm (Fig. 2.7B, C) to about 53 µm (holotype).

**Biology.** Most specimens taken from the Santa Maria Basin were from muddy silts with 66% or more silt and up to 31% clay; one specimen was collected from sandy silt having 34% sand. *Limifossor fratula* occurred at the same stations as *Chaetoderma nanulum*, *C. argenteum*, *Falcidens hartmanae*, *Gymnomenia minuta*, and an unnamed species of Neomeniomorpha; and in the Southern California Bight at the same stations as *F. longus*, *F. hartmanae*, *C. hancocki*, *C. marinelli*, *C. nanulum*, *C. elegans*, *C. scabrum*, *Spathoderma californicum*, and a species of *Psilodens*. Off Oregon, *L. fratula* is stouter, with a length/diameter index of 3:0 or less.

**Remarks.** Species of *Limifossor* are not easily confused with any other Chaetodermomorpha. *Limifossor* species are best differentiated from each other by body shape, i.e., length:width index, and radula morphology. Spicules of *L. fratula* are morphologically similar to those of *L. talpoideus* Heath, found from

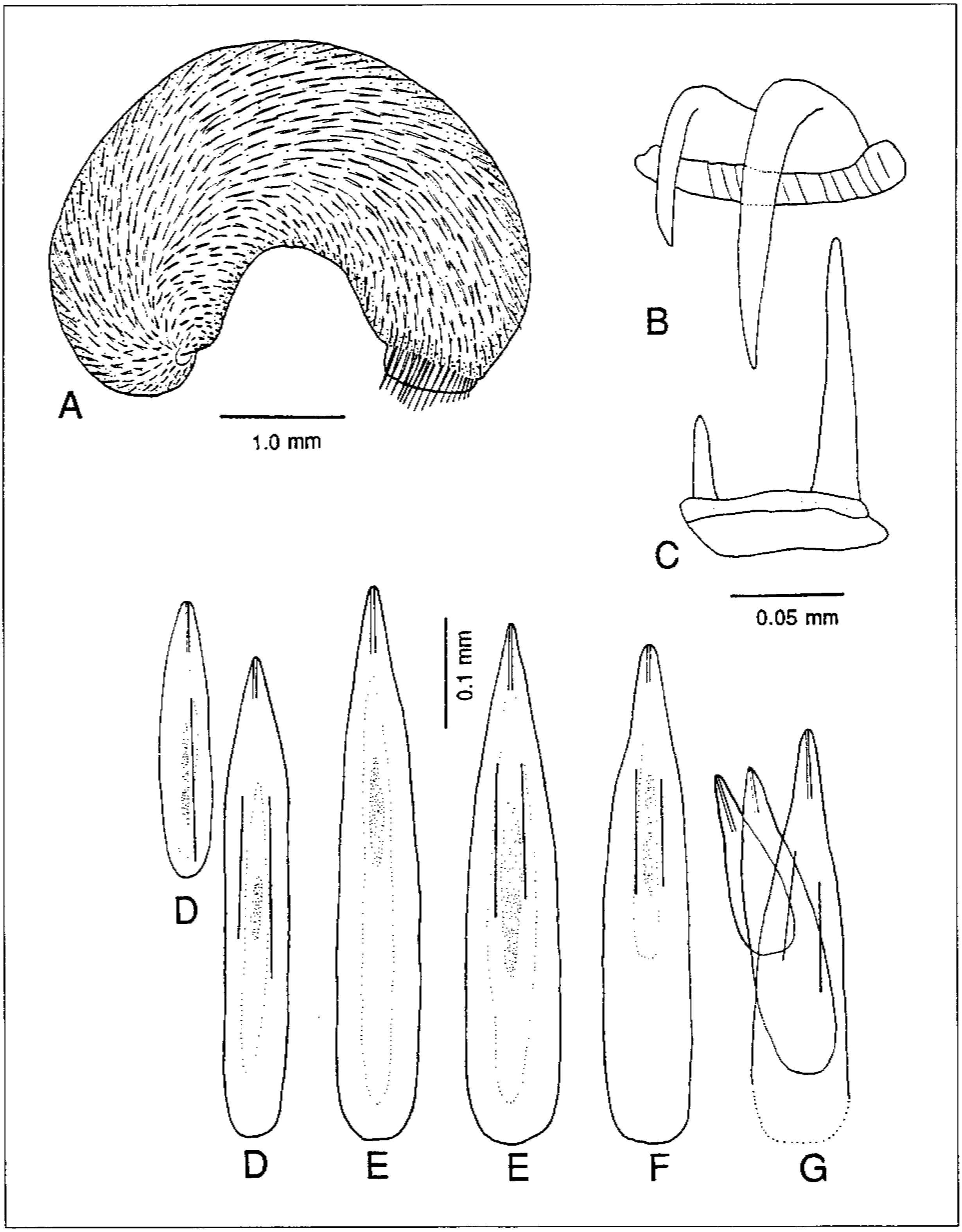

**Figure 2.7.** *Limifossor fratula* Heath: A, specimen from Santa Maria Basin (USNM); B, C, radula of A, dorsal (B) and frontal (C) view; D, E, G, spicules of A from dorso-anterior body (D), mid-dorsal trunk (E), and midventral trunk (G); F, spicule from syntype (CAS). Longitudinal lines here indicate grooves, not ridges.

southern Alaska perhaps as far south as off Oregon, but *L. talpoideus* is more slender (index up to 6.0) and each radula tooth has two medial denticles. *L. fratula* is the sole member of the genus known south of San Francisco.

**Distribution.** An upper continental slope species from off Oregon to Southern California Bight between 200-600 m, except to 1,830 m south of Santa Cruz Island. Schwabl (1963) reported a depth range in the Southern California Bight of 140-810 m.

## Family Chaetodermatidae

### Genus *Chaetoderma* Lovén, 1844

***Crystallophrisson* Möbius, 1875. Ivanov, 1981.**

**Type Species:** *Chaetoderma nitidulum* Lovén, 1844.

**Diagnosis.** With distinct body regions of neck, anterior trunk, posterior trunk, and posterium. Radula with paired denticles lying outside dome-shaped cuticular membrane covering buccal mass and with paired lateral projections extending from radula cone to dome-shaped membrane opposite base of denticles (Fig. 2.8J) (Scheltema, 1972; Scheltema *et al.*, 1991).

### *Chaetoderma argenteum* Heath, 1911

Figure 2.8

*Chaetoderma argentea* Heath, 1911: 43, 62-63, pl. 4 Fig. 7, pl. 26 figs. 1-7, pl 36 fig. 1, pl.37 fig. 6.

*Chaetoderma argenteum*: Scheltema *et al.*, 1991.

*Chaetoderma attenuata* Heath, 1911: 43, 55-59, pl. 4 figs. 3, 10, pl. 5 fig. 1, pl. 12 fig. 4, pl. 25 figs. 1-10, pl. 36 fig. 2, pl. 37 fig. 8.

*Chaetoderma montereyensis* Heath, 1911: 43, 61-62, pl. 4 figs. 4, 8, 14, 17, pl. 27 figs. 1, 2, 4-11, pl. 37 figs. 2, 3.

*Chaetoderma montereyense*: Salvini-Plawen, 1993.

*Chaetoderma* sp. Buckland-Nicks and Chia, 1989.

**Material Examined.** Southeast Alaska, Behm Canal, 148-203 m, holotype (*Albatross* Sta. 4231, CAS 021392, spicule slide and serial sections); Stikine R. delta, Stephens Passage, and Kasaan Bay, 90-362 m (7) (holotype of *C. attenuata*, *Albatross* Sta. 4250, CAS 021393, spicule slide and serial sections; and 6 paratypes, MCZ).—British Columbia, off SW Vancouver Island, 100-200 m (96) (IOS); Observatory Inlet, 400-600 m, (36) (IOS); Saanich inlet, 90 m (4) (IOS).—off Oregon coast, 150-200 m (11) (OSU).—California, Monterey Bay, 70-640 m (31) (**lectotype** of *C. montereyensis*, *Albatross* Sta. unknown, CAS 021397, spicule slide and serial sections; **paratypes** and presumed **syntypes**, MCZ).—Santa Maria Basin, Sta. 19 (1, SBMNH); Sta. 59 (1, USNM); Sta. 85 (1); Sta. R-3 (11); Sta. R-6 (7) (vouchers, USNM); Sta. R-9 (3).

**Description.** Greatest length to more than 40 mm; anterior trunk longer and narrower than posterior trunk, narrower than or same width as neck, wrinkled when greatly contracted, with dense, furry coat of short, upright spicules; posterior trunk up to 2.0 mm in diameter (Fig. 2.8A). Posterior end roundly truncated, with short, bushy terminal spicules; posterior mantle cavity wall covered with spokelike spicules (Fig. 2.8A, C). Oral shield nearly circular, often retracted, up to 1.1 mm wide by 1.0 mm high, with deep, wide dorsal cleft, dorsal lobes large (Fig. 2.8B). Anterior constriction deep, dorsoterminal sense organ obvious. All spicules widest basally, up to more than 10 μm thick; neck spicules curved, most narrow, thickest medially at flared

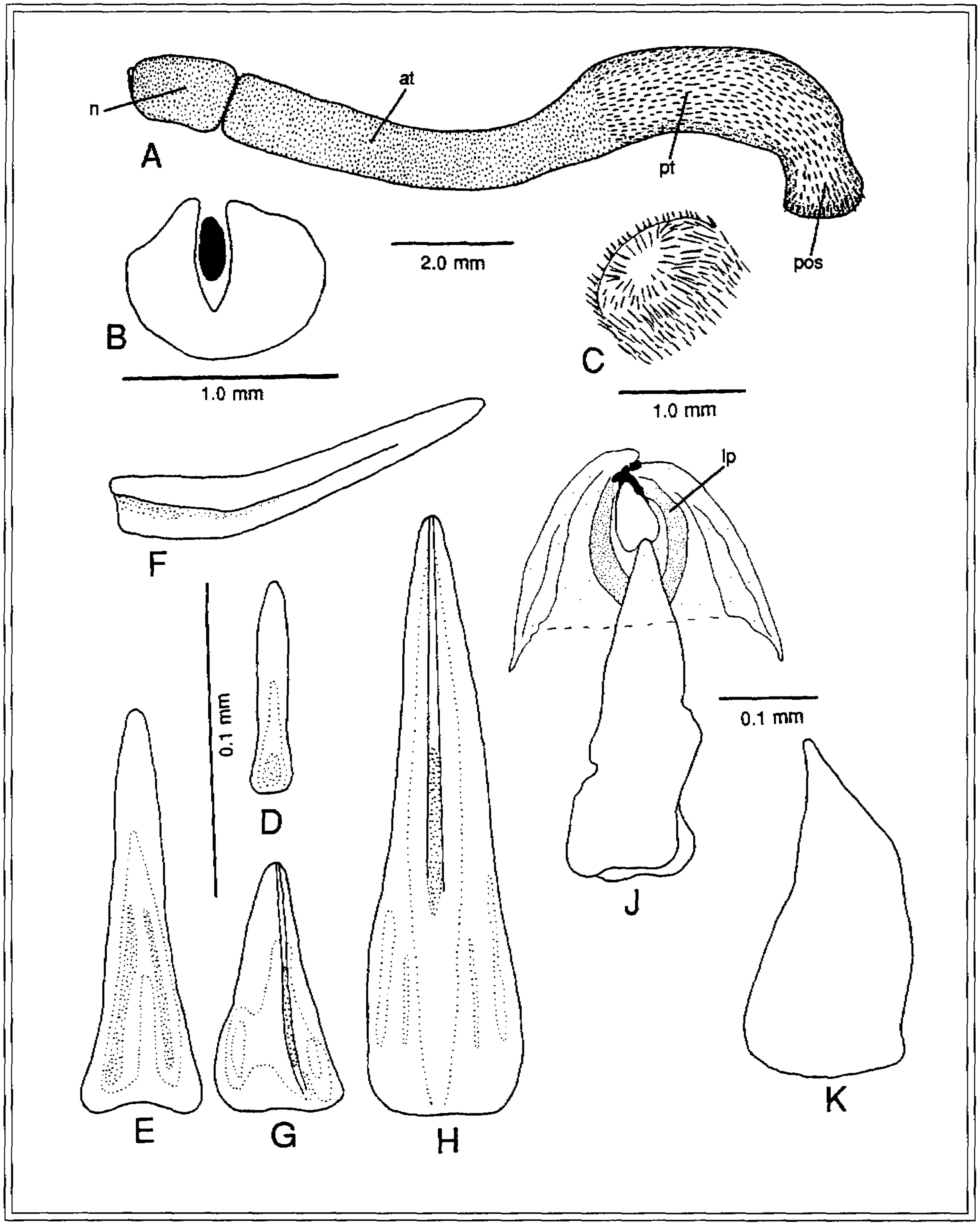

**Figure 2.8.** *Chaetoderma argenteum* Heath: A, specimen from Santa Maria Basin (USNM); B, oral shield of presumed syntype of *C. montereyensis* (MCZ); C, posterium of specimen A; D-H, spicules of specimen B, from neck (D), anterior trunk at constriction (E, F), posterior region of anterior trunk (G), and mid-posterior trunk (H); J, K, radula of specimen A, frontal view (J) and lateral view of cone (K), frontal to right.

base, <100 µm long, up to 25 µm wide (Fig. 2.8D); anterior trunk spicules diagnostic, bent and abfrontally grooved (Fig. 2.8F), basally flared and up to 40 µm wide, thickest on each side with isochromes often meeting in an inverted V, length greatest near anterior constriction, up to 130 µm in length (Fig. 2.8E), decreasing to 90 µm at the midpoint and to 80 µm next to posterior trunk, spicules nearest posterior trunk sharply keeled (Fig. 2.8G); posterior trunk spicules flat, tapered, sharply keeled, with 1 or more lateral ridges on each side and numerous fine axial striations on base, from 170 µm long anteriorly to 265 µm posteriorly, up to 60 µm wide, thickest medially at keel (Fig. 2.8H). Radula cone large, deeply curved laterally (Fig. 2.8J, K), 510 µm long, 140 µm wide frontally, and 190 µm wide laterally in largest specimen examined, tapered distally in lateral view to narrow end; lateral projections narrow, long, up to 250 µm; denticles 30 to 60 µm long; cuticular dome one-half length of cone.

**Biology.** *Chaetoderma argenteum* was collected from Santa Maria Basin in silty sands with 48% sand, in silts, and in muddy silts with up to 24% clay. A juvenile came from the Santa Barbara Channel, south of the usual range, in a very muddy silt with 30% clay. In British Columbia, it occurs in fine and muddy silts. Species found at the same stations as *C. argenteum* in the Santa Maria Basin were *C. nanulum*, *Falcidens macracanthos*, *F. hartmanae*, *Limifossor fratula*, *Gymnomenia minuta*, and an unnamed species of Neomeniomorpha; off Oregon and British Columbia it was found with *Limifossor* cf. *talpoideus* and *Falcidens longus*.

**Remarks.** Specimens from British Columbia provided material for the first published account of spermiogenesis in a chaetoderm aplacophoran (Buckland-Nicks and Chia, 1989).

The synonymy of *C. montereyense* (but not *C. attenuatum)* with *C. argenteum* has recently been questioned based on the presence of a smaller pericardial cavity in the type of *C. argenteum* and in one paratype of *C. attenuatum*, and small differences in the manner in which muscle fibers of the ctenidial retractors divide in *C. argenteum* and *C. montereyense* (Salvini-Plawen, 1993). Pericardial size can be related to age (the type of *C. argenteum* is a juvenile) or, probably, to reproductive state, as eggs must pass from the gonad through the pericardium to the outside in spawning individuals. Muscle fibers can split in divergent ways even on two sides of an individual. Therefore, the differences given are not considered here to be more than individual, or at the most population, differences.

**Distribution.** Primarily an upper continental slope species from off Pt. Conception, California, to southeast Alaska, between 70-640 m.

### *Chaetoderma californicum* Heath, 1911

Figure 2.9

*Chaetoderma californica* Heath, 1911: 43, 64-66, pl. 4 fig. 6, pl. 31 figs. 1-4, 7, 8, 10, pl. 35 fig. 11, pl. 37 fig. 14.

**Material Examined.** California, Santa Maria Basin, Sta. 56 (1) (voucher, USNM).—Off San Diego, 1,112-1,200 m, **holotype** (*Albatross* Sta. 4381, CAS 021394, spicule slide and serial sections). Possibly the same species from off the Farallon Islands, 2,623-2,750 m (47).—off Oregon, 800-2,800 m (2).

**Description.** A robust species up to 24 mm long (holotype) and 2.3 mm wide at posterior trunk (Fig. 2.9A); anterior trunk shorter than posterior trunk, narrowest at anterior constriction, slightly wider than neck, with densely arranged, large upright spicules; neck with short spicules; anterium short; posterior trunk rough, with large spicules; posterium truncated, spicules extending beyond mantle cavity wall, which has spokelike spicules not easily discernible through heavy encrustations (Fig. 2.9C). Oral shield wider than high, 1.85 x 1.65 mm, with short dorsal cleft, dorsal lobes large (Fig. 2.9B). Anterior constriction covered by anterior trunk spicules; dorsoterminal sense organ indistinct. All spicules with greatest thickness much greater than 10 µm and very long except on neck; neck spicules narrow, with short keel and broad base, up to 153 µm long and 36 µm wide (Fig. 2.9E); anterior trunk spicules bent (Fig. 2.9G, lateral view), base long,

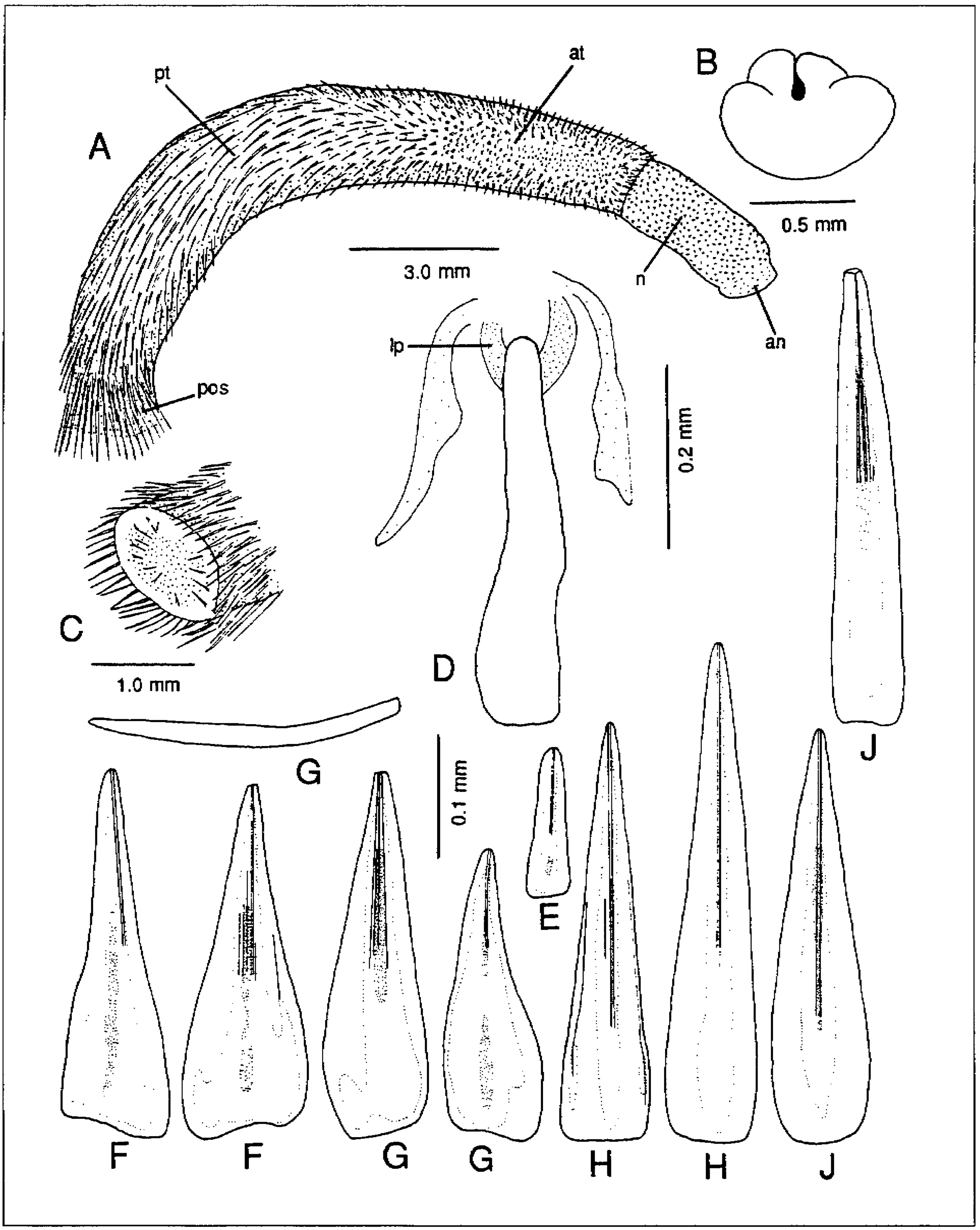

**Figure 2.9.** *Chaetoderma californicum* Heath: A, specimen from Santa Maria Basin (USNM); B, oral shield of A; C, posterium of A; D, radula reconstructed from holotype sections (CAS); E, G, J, spicules of specimen A, from neck (E), anterior trunk at constriction (G, lateral view above), and mid-posterior trunk (J); F, H, spicules from anterior (F) and posterior (H) trunk of holotype.

broad, asymmetrical, distal ends either narrow (Fig. 2.9F) or, in individual from Santa Maria Basin, both broad and narrow (Fig. 2.9G), thickest medially, keeled from distal end to midpoint, usually with several ridges, spicule length from 230 to 400 μm long, width from 80 μm (Santa Maria Basin) to 100 μm (holotype); posterior trunk spicules keeled from distal end to midpoint, base flat (most spicules of holotype, Fig. 2.9H left) or rounded (most spicules in Santa Maria Basin individual, Fig. 2.9J below), most holotype spicules symmetrical, with lateral ridges and keel without ridges, most Santa Maria Basin spicules without lateral ridges but with ridged keel, many with asymmetrical base. One radula examined, from holotype in serial sections; cone length about 475 μm long, frontal width about 85 μm, lateral projections about 50 μm long (Fig. 2.9D).

**Biology.** Taken in the Santa Maria Basin from a well-sorted sediment with 33% sand, 47% silt, and 19% clay.

**Remarks.** *Chaetoderma californicum* is distinguishable from other southern California species by its large, thick, asymmetrical spicules. The species is probably also present off the Farallon Islands and the Oregon coast; however, there is enough variation in spicule morphology that identification of the more northern specimens is not yet certain. The variation may due to the calcification process that produces great spicule thickness in combination with irregular shape.

**Distribution.** A continental slope species found off southern California between 900-1,200 m; possibly to 3,000 m off the Farallones Islands and Oregon coast.

### *Chaetoderma elegans* Scheltema, new species

Fig. 2.10

**Material Examined.** California, Santa Maria Basin, Sta. 21, **paratype** (USNM 860390).—Southern California Bight, south of Santa Cruz Island, 33°45.85'N, 119°39.25'W, 1,808 m, **holotype** (LACM 2748).

**Description.** Long (holotype 31.6 mm), slender, anterior trunk shaggy, up to twice as long as posterior trunk (Fig. 2.10A). Neck bent at 90° angle, narrower than or same diameter as anterior trunk at constriction. Anterior trunk up to 1.0 mm in diameter at constriction, wider posteriorly, to 1.4 mm becoming same width as opaque posterior trunk. Posterium rounded, bulblike, spicules bushy, dorsoterminal sense organ indistinct (Fig. 2.10C). Oral shield wider than high, 1.50 x 1.40 mm (paratype), dorsal lobes small, dorsally cleft (Fig. 2.10B). Spicules flat, thin, 5 μm or less thick, with those of trunk with parallel sides, rounded or straight base, sharp narrow keel, and few to several parallel ridges, easily dislodged from preserved specimens (Fig. 2.10F, G). Spicules of neck narrow, arrow- to nearly rod-shaped, thickened symmetrically or asymmetrically, up to 86 μm long x 16 μm wide x 5 μm thick (Fig. 2.10D); anterior trunk spicules both at constriction (Fig. 2.10E) and midpoint (Fig. 2.10F) with keel medial or offset laterally, up to 225 μm long x 35 μm wide x 3.5 μm thick, thickened at keel and ridges; mid-posterior trunk spicules up to 205 x 42 x 5 μm, except a few broader, up to 54 μm wide (Fig. 2.10G). Radula small, curved in lateral view, cone 220 μm long, frontal width 50 μm, lateral width 85 μm (Fig. 2.10H, J), dome-shaped piece 140 μm long, denticles (broken) >20 μm, lateral projections about 50 μm; cuticle of dome strongly cuticularized in part.

**Biology.** *Chaetoderma elegans* was taken from a sandy silt (21% sand, 75% silt, 4% clay) in the Santa Maria Basin. The species was not found with other aplacophorans in the Santa Maria Basin, but occurred at the same station as *C. nanulum* south of Santa Cruz Island.

**Remarks.** The long, slender body and thinness of spicules distinguish *C. elegans* from *C. pacificum*, which has a broader body, radula without a curve, longer, thicker spicules on the posterior trunk, and often longer anterior trunk spicules; and from *Falcidens longus*, which has basally flared, thicker anterior trunk spicules and joined radula denticles.

**Etymology.** From Latin *elegans*, elegant, as the species seems elegant in its slenderness.

**Distribution.** Known from a single specimen from the Santa Maria Basin at 49 m and one from the basin south of Santa Cruz Island at 1,808 m.

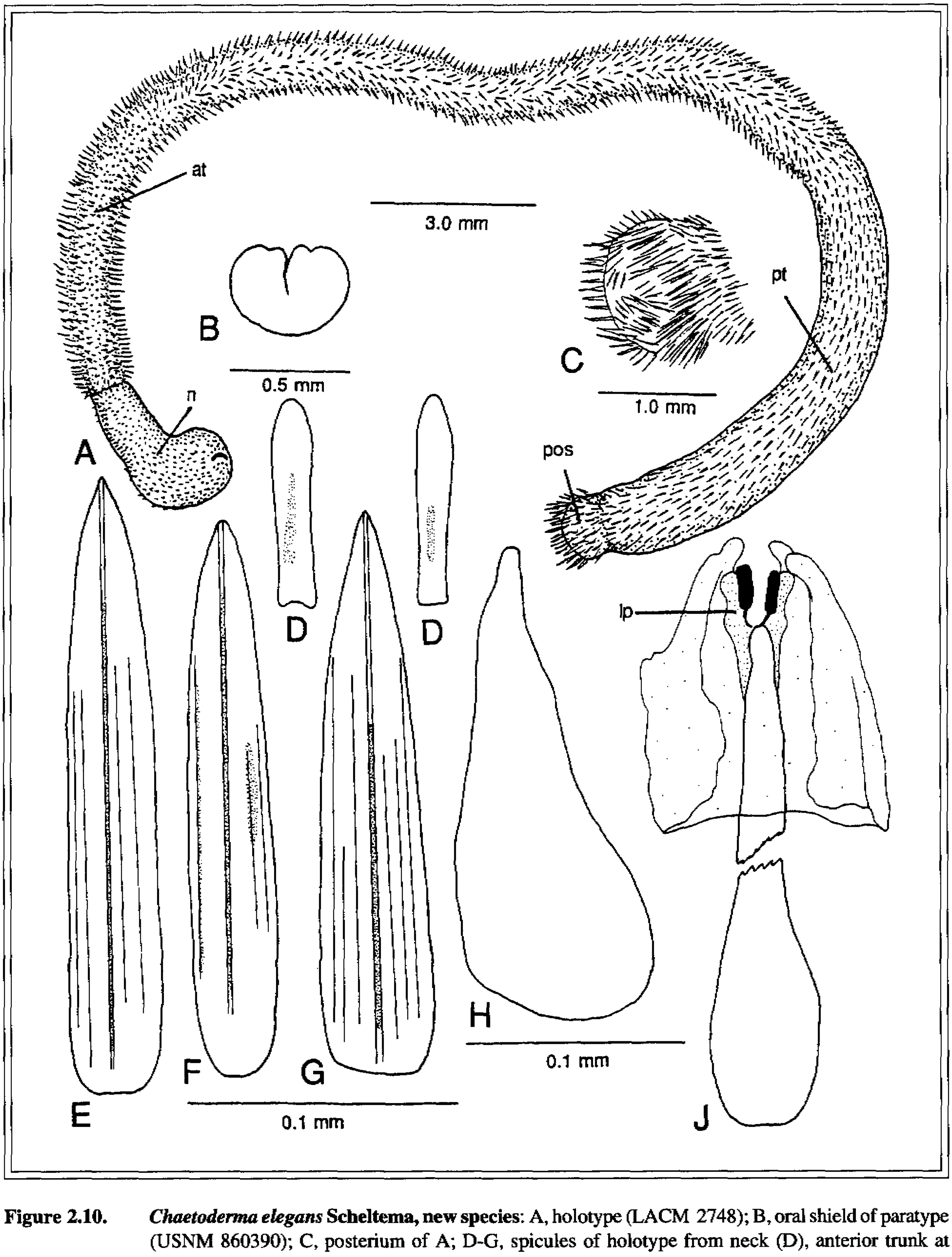

**Figure 2.10.** ***Chaetoderma elegans*** **Scheltema, new species**: A, holotype (LACM 2748); B, oral shield of paratype (USNM 860390); C, posterium of A; D-G, spicules of holotype from neck (D), anterior trunk at constriction (E), mid-anterior trunk (F), and mid-posterior trunk (G): H, J, radula of paratype, lateral view of cone (H), frontal to left, and frontal view (J) (cone broke after drawing H).

## *Chaetoderma hancocki* (Schwabl, 1963)

Figure 2.11

*Crystallophrisson hancocki* Schwabl, 1963: 272-273, figs. 14, 15.

*Crystallophrisson inflatum* Schwabl, 1963: 276-277, figs. 21, 22.

?*Crystallophrisson rectum* Schwabl, 1963: 278-279, figs. 25, 26.

*Crystallophrisson riedli* Schwabl, 1963: 274, Sta. 2352 only.

**Material Examined.** Southern California Bight: San Pedro Basin, 504-803 m (14) (**lectotype**, LACM 2093; **lectotype** and **paralectotype** of *Cr. inflatum*, LACM 2097 and LACM 2098; LACM 53-158; LACM 77-204, 77-275, 77-203, 77-276, 77-202, 77274).—south of Santa Cruz Island, 833-1,830 m (18) (LACM 76-252, 76-253, 76-258, 76-271, 76-270, 76-269).

**Description.** A distinctive long, slender species up to 45 mm long x 2.0 mm wide at posterior trunk, often greatly swollen anteriorly, knoblike posterior end, spicules large, anterior trunk shaggy with spicules sparsely scattered (Fig. 2.11A). Anterior trunk longer than posterior trunk; anterium and neck divided by deep constriction; spicules of anterior trunk easily dislodged; posterior wall of mantle cavity extending without spicules beyond spiculose body wall, ending in a round, glandular-appearing protuberance with dumbbell-shaped opening (Fig. 2.11D, E). Oral shield large, width and height nearly equal, up to 1.90 x 1.80 mm, with short dorsal cleft and large dorsal lobes (Fig. 2.11B, C). Anterior constriction deep, with dorsoterminal sense organ obvious, long, extending from outer body wall onto protruded, glandular posterior mantle cavity wall. Spicules long, flat, with little or no sculpturing; type 1 spicules (Fig. 2.11H, K, N, O) with or without parallel ridges on basal half, often with narrow medial keel, thickest medially, up to 8 µm thick, flared basally on neck and anterior trunk, more than 200 µm long x 60 µm wide on neck, up to 300 x 60 µm on anterior trunk at constriction, >300 x 55-60 µm on mid-anterior and mid-posterior trunk, ridges most numerous on posterior trunk; type 2 spicules (Fig. 2.11J, L, M) usually without sculpturing, lateral edges slightly convex, longer and thicker than type 1 spicules from same region, neck spicules thickest medially and up to 250 x 52 x 10 µm, trunk spicules thickest laterally, with thickenings joining distally in inverted V, up to >450 x 60 x >10 µm. Trunk spicules commonly with one lateral edge at base more curved than other (Fig. 2.11M-O). Radula cone large, curved, up to 520 µm long, frontal and lateral widths nearly equal, 150 and 165 µm, respectively, lateral projections short, teeth small (30 µm), dome extending from one-third to two-fifths cone length (Fig. 2.11F, G).

**Biology.** Qualitative descriptions of the sediment in which *Chaetoderma hancocki* has been found are sticky or oozy muds and clay. The species has been found at the same stations as *Chaetoderma nanulum*, *C. scabrum*, ?*C. marinelli*, *Falcidens hartmanae*, *F. longus*, *Limifossor fratula*, *Spathoderma californicum*, and *Psilodens* sp.

**Remarks.** *Crystallophrisson inflatum* Schwabl is synonymized with *Chaetoderma hancocki* (Schwabl) based on similarity of body morphologies in the two lectotypes and single paralectotype of *Cr. inflatum*. Although spicules are now entirely lacking on the lectotype of *Chaetoderma hancocki*, a few remain on the lecto- and paralectotypes of *Crystallophrisson inflatum* and can be compared to spicules from recently collected specimens and Schwabl figures for both (1963, figs. 14, 21). The small radula denticles were considered to be lacking in the original descriptions of both *Chaetoderma hancocki* and *Crystallophrisson inflatum* (Schwabl, 1963).

**Distribution.** Off southern California on the upper continental slope between 508-1,830 m. The species has not been found north of Pt. Conception and was not in the Santa Maria Basin collections.

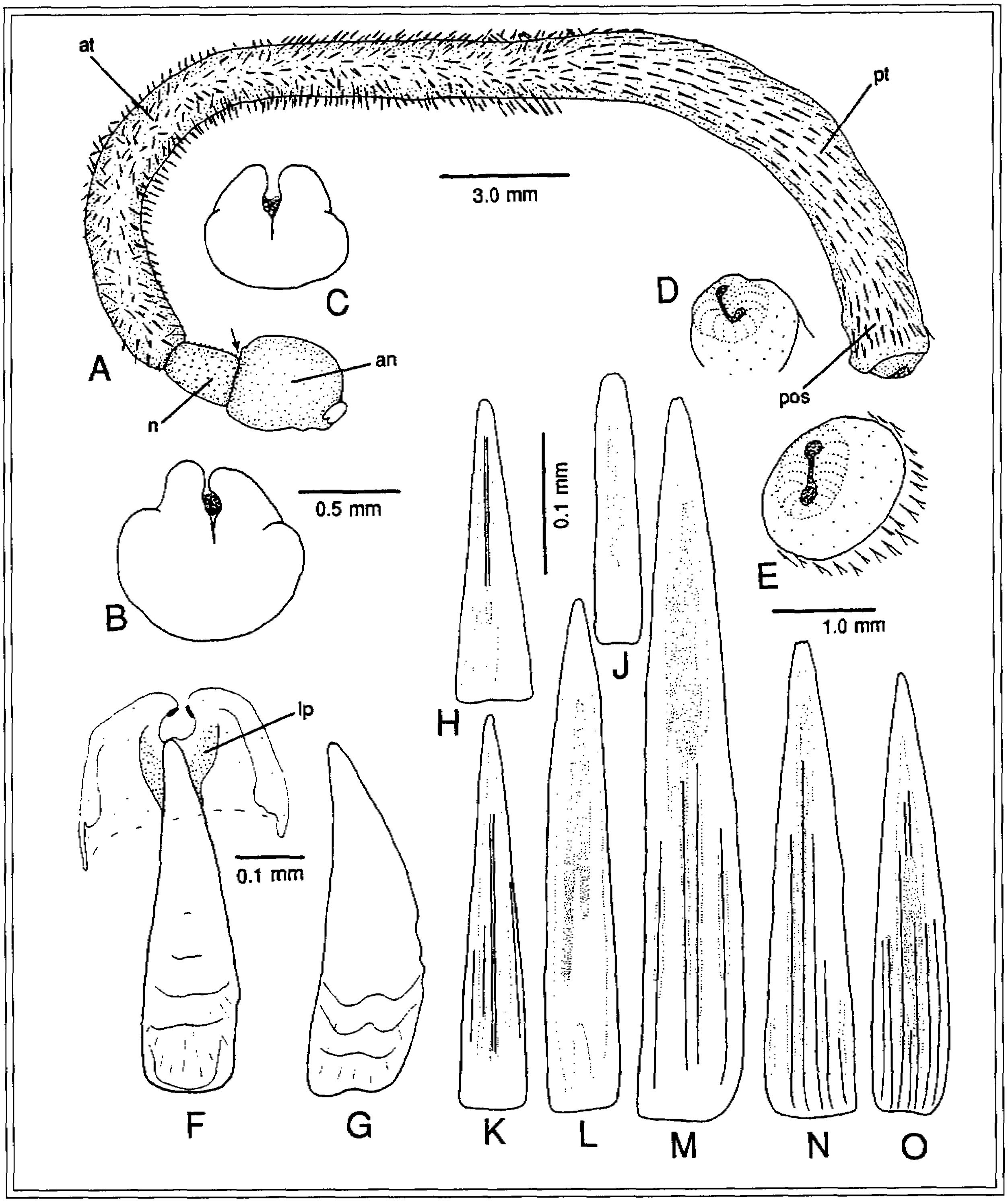

**Figure 2.11.** *Chaetoderma hancocki* (Schwabl): A, specimen from San Pedro Basin (LACM 77-203, 77-276), deep constriction between anterium and neck indicated by arrow; B, C, oral shield of specimen A (B) and lectotype (C, LACM 2093); D, E, posterium of lectotype (D) and specimen A (E); F, G, radula of specimen from San Pedro Basin (LACM 77-204, 77-275), frontal view (F) and lateral view of cone (G), frontal to right; H-O, spicules of specimen A (H-L, O) and lectotype of *Cr. inflatum* (M, N) from neck (type 1, H, type 2, J), anterior trunk (type 1, K, type 2, L) and posterior trunk (type 1, M, type 2, N, O).

## ***Chaetoderma marinelli* (Schwabl, 1963)**

Figure 2.12

*Crystallophrisson marinelli* Schwabl, 1963: 277-278, figs. 23, 24.

**Material Examined.** Southern California Bight: off San Diego, 47-64 m (5) (SD Sta. A-2, A-10 [voucher, LACM], B-1, B-5).—San Pedro Basin, 29 m **lectotype** (LACM 2099); 1 specimen from type station, not syntype (LACM 53-94); 1 specimen identified by Schwabl as *C. pacificum*, 50 m (LACM 2102).

**Description.** A large species up to nearly 40 mm x 3.3 mm in posterior trunk diameter (lectotype); other specimens 20-30 mm long x 1- to 2 mm posterior trunk width. Neck narrower posteriorly than anteriorly except when fully contracted as in Figure 2.12A. Anterior trunk shaggy, about same length as posterior trunk. Posterium rounded, somewhat bulbous, with short terminal spicules and, in large lectotype, spiculeless collar around mantle cavity; dorsoterminal sense organ obvious (Fig. 2.12B). Oral shield dorsally cleft, nearly spherical, up to 1.1 mm in width, with large dorsal lobes (Fig.2.12C). Spicules of both anterior and posterior trunk with many parallel ridges, posterior trunk spicules usually shorter than those of anterior trunk. Neck spicules narrowly or broadly arrowhead-shaped on smaller specimens (Fig. 2.12D), nearly rod-shaped on large lectotype (Fig. 2.12E), asymmetrically thickened except in broad spicules, up to 120 µm long x 23 µm wide x 7 µm thick; anterior trunk spicules flat, keeled, most thickened laterally only, but also medially, or both, base striaght to slightly flared, lateral edges often appear thickened in plain transmitted light, up to 260 x 40 x 9 µm (Fig. 2.12F, H); mid-posterior trunk spicules somewhat curved towards body, lateral edges straight, thickest at keel and sometimes at adjacent ridge, less than 225 µm long, up to 40 µm wide x 7.5 µm thick (Fig. 2.12G, J). Radula cone large, up to 370 µm long, proximally bulbous and curved in lateral view, width up to 145 µm frontally and 174 µm laterally, dome-shaped cuticle up to 232 µm long, denticles up to 35 µm long (Fig. 2.12K, L).

**Biology.** Probably a shallow-water species occurring at <65 m. Found with *Falcidens longus* at some stations. Sediment type not known.

**Remarks.** *Chaetoderma marinelli* can be confused with *C. pacificum*, *Falcidens macracanthos*, and *F. longus*. The anterior trunk spicules of *C. marinelli* are similar to, but shorter than those of *F. macracanthos*, and the radulae differ. The species is differentiated from *C. pacificum* by the many ridges and flared base present on anterior trunk spicules, by the shorter mid-posterior trunk spicules, and by the flared proximal end of the radula cone; neck spicules in both species are thickened asymmetrically. It differs from *F. longus* by radula morphology and by the flat, basally less flared anterior trunk spicules which are predominantly laterally thickened.

**Distribution.** A continental shelf species in the Southern California Bight from 30-64 m.

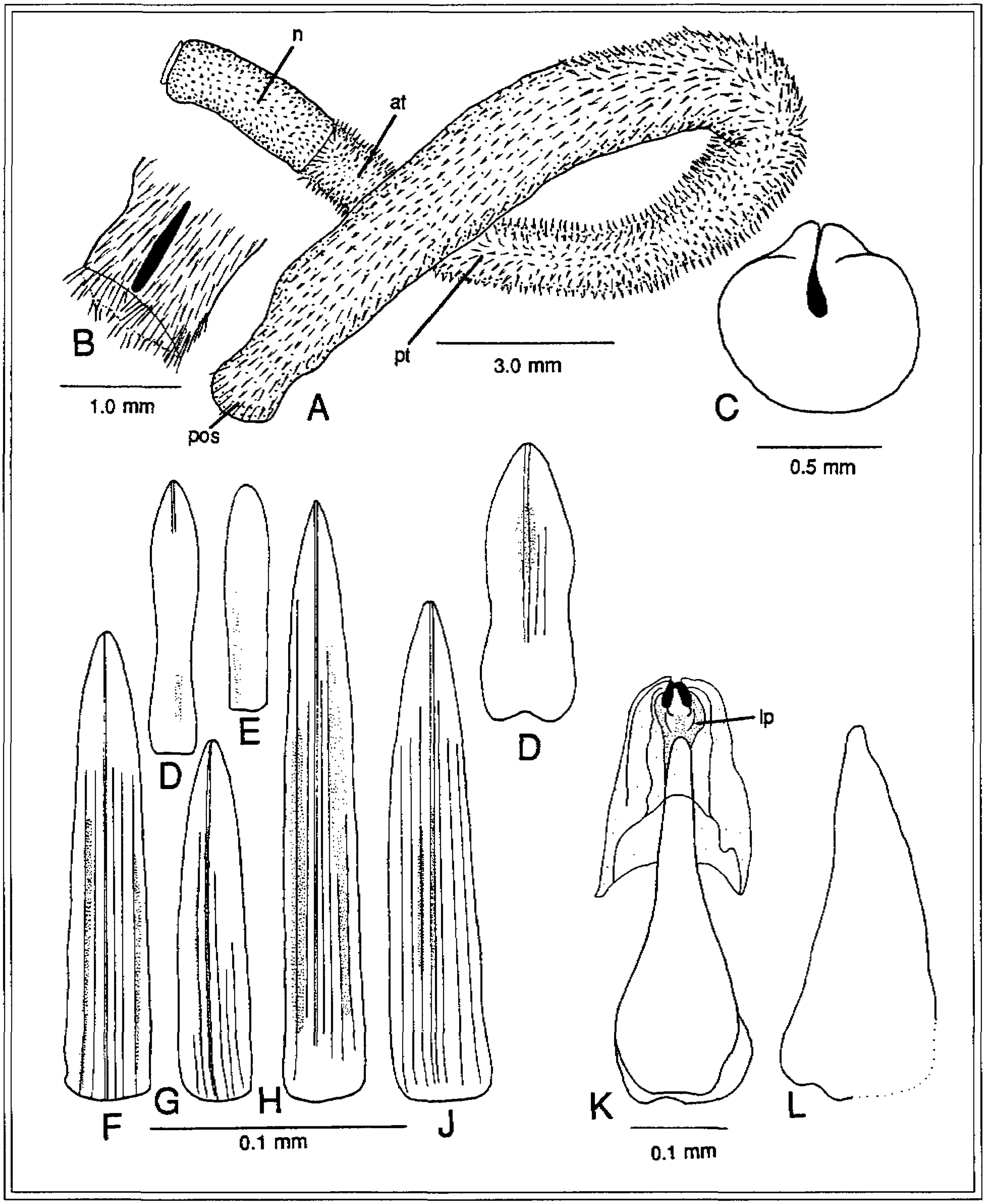

**Figure 2.12.** *Chaetoderma marinelli* (Schwabl): A, specimen from off San Diego (LACM); B, posterium of specimen A showing dorsoterminal sense organ (black); C, oral shield of lectotype (LACM 2099); D-J, spicules of lectotype (E-G) and specimen A (D, H, J) from neck (D, E), anterior trunk at constriction (F, H), and mid-posterior trunk (G, J), posterior trunk spicules slightly oblique showing curve towards body; K, L, radula of specimen A, frontal view (K) and lateral view, frontal to right, broken at base (L).

### *Chaetoderma nanulum* Heath, 1911

Figure 2.13

*Chaetoderma nanula* Heath, 1911: 66-67, pl. 4 figs. 1, 12, pl. 27 fig. 3, pl. 28 figs. 7, 10-12, pl. 37 fig. 18.
*Crystallophrisson riedli* Schwabl, 1963: 274-276, figs. 19, 20.
*Crystallophrisson rubrum* Schwabl, 1963: 280, figs. 27, 28.
*Crystallophrisson scabrum* (Heath): Schwabl, 1963: 269 [extant material from AHF Sta. 2418].

**Material Examined.** California, Santa Maria Basin, Sta. 16 (4) (vouchers, USNM); Sta. 54 (5, SBMNH); Sta. 60 (2); Sta. 61 (2); Sta. R-2 (1); Sta. R-3 (7, USNM); Sta. R-7 (1).—Southern California Bight, Santa Barbara Channel, 337 m (1) (LACM 77-279); south of Santa Cruz Island, 833-1,843 m (24) (LACM 76-252, 76-253 [voucher, LACM], 76-257, 76-258, 76-271, 76-270, 76-269, 76-268, 76-263, 76-262); San Pedro Basin, 333 m (6) (AHF Sta. 2418, as *Crystallophrisson scabrum* in Schwabl, 1963); 558 m, **lectotype** and **paralectotype** *Crystallophrisson riedli* (LACM 2105, 2106); 250-504 m (7) (LACM 77-293, 77-203, 77-276, 77-260).—off San Diego, 468 m, **holotype** (*Albatross* Sta. 4369, CAS 021398, spicule slide and serial sections).

**Description.** A species greatly variable in body and spicule size. One individual from Santa Maria Basin (Sta. R-7) 44 mm long; all others examined 15 mm or less. Anterior trunk shaggy, about equal to or shorter than posterior trunk plus posterium, slightly narrower than neck (Fig. 2.13A, B); posterior trunk up to 3.7 mm wide, usually <3 mm; anterior trunk only slightly less wide than posterior trunk. Oral shield wider than high, up to 1.65 × 1.40 mm, with short dorsal cleft and small dorsal lobes (Fig. 2.13C). Posterior end truncate, ringed by long spicules; few spicules on posterior mantle-cavity wall (Fig. 2.13D). Anterior constriction and dorsoterminal sense organ obvious. Spicules thick, those on anterior trunk of 2 distinctive types. Neck spicules long, bent, arrowhead- to rod-shaped, often ridged, usually thickest basally but also medially, or both, often asymmetrical, up to 130 µm long × 30 µm wide × 10 µm thick (Fig. 2.13E). Spicules of anterior trunk of 2 main types: type 1 bent outward, flared basally below a waist, thickest basally at broad ridged keel over an abfrontal groove, bearing sharp lateral ridges (Fig. 2.13F, J); some with narrow keel (Fig. 2.13H); greatest spicule dimensions not correlated with body length except in individuals <4 mm long, largest spicules ranging from 152-240 µm long, 50-75 µm wide, and up to 10 µm or more thick (Fig. 2.13 cf. F, G, H); type 2 spicules longer than type 1 spicules, flat, thickest laterally, or medially, or both, waist scarcely or not evident, ridges faint, size variable as for type 1 spicules, ranging from 185-390 µm long, 30-70 µm wide, and up to 10 µm or more thick (Fig. 2.13K, L). Mid-posterior trunk spicules flat, with sharp keel and ridge along each side running nearly to base, with shorter ridges between the lateral ridges and edge of spicule, thickest at keel, isochromes symmetrical around keel, up to 300 µm long, 60 µm wide, and 10 µm thick, usually shorter than type 2 anterior trunk spicules (Fig. 2.13M). Radula cone straight, nearly as wide frontally as laterally, up to 475 µm long, 115 µm in frontal width, and 140 µm in lateral width; lateral projections up to 70 µm long; denticle length up to 55 µm; cuticular dome extending one-half length of cone or less, slightly to greatly tanned distally.

**Biology.** *Chaetoderma nanulum* was collected from a wide range of silty, sandy, and muddy sediments in the Santa Maria Basin, with the sand content ranging from 2% to 59%, the silt fraction from 33% to 85%, and the clay fraction from 8% to 30%. It was the only aplacophoran species to occur at Sta. R-7 in the oxygen minimum zone (see Blake, 1993: Vol. 1, p. 26). The great variability in morphology and habitat may indicate that a species complex is involved here under a single species name. *Chaetoderma nanulum* was taken in the Santa Maria Basin at the same stations as *Chaetoderma pacificum*, *C. argenteum*, *Limifossor fratula*, *Falcidens hartmanae*, and *Gymnomenia minuta* and, in addition to these, in the Southern California Bight at the same stations as *Spathoderma californicum*, *Chaetoderma hancocki*, *C. elegans*, *C. scabrum*, *Falcidens longus*, and a species of *Psilodens*.

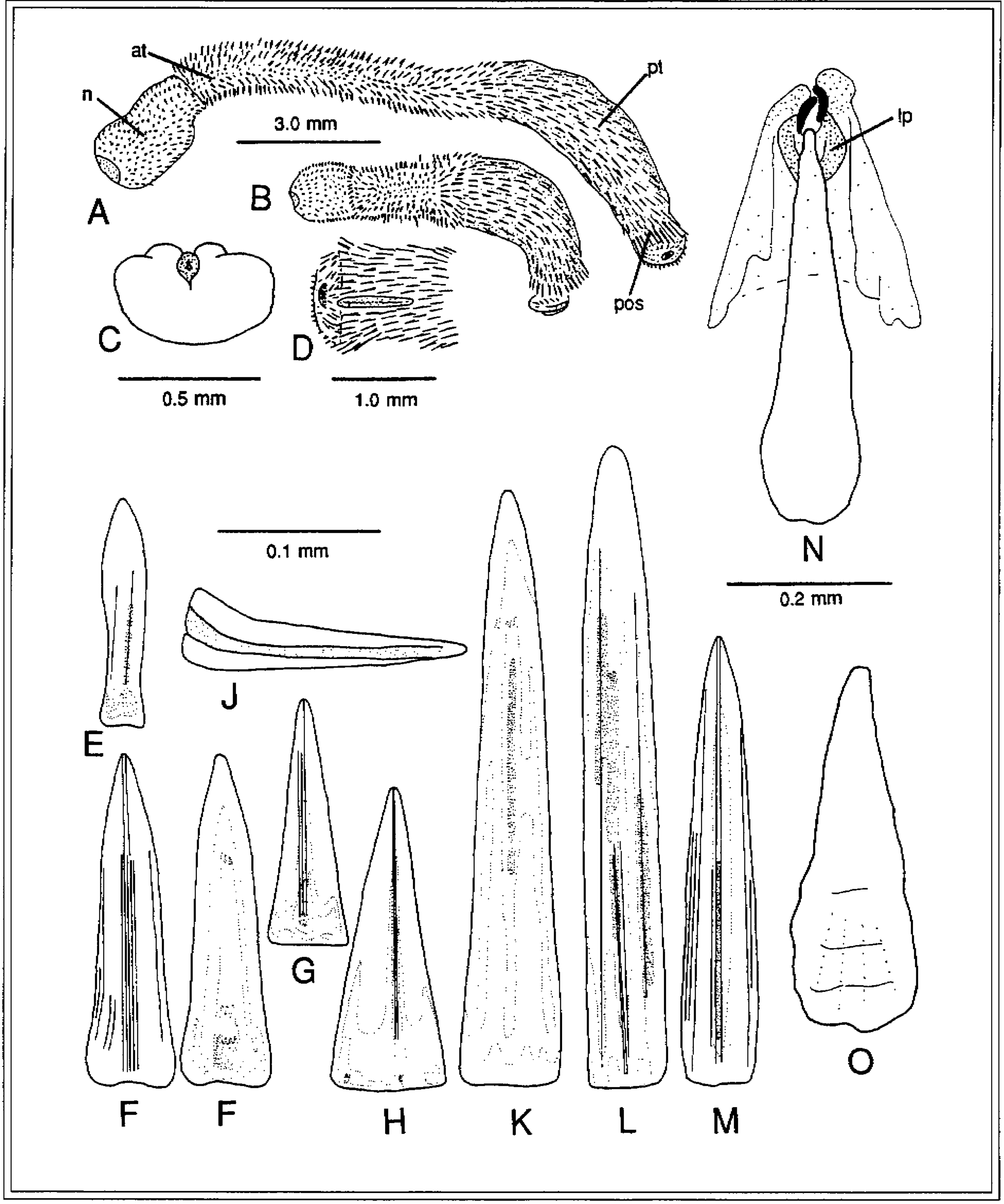

**Figure 2.13.** *Chaetoderma nanulum* Heath: A, specimen from San Pedro Basin (LACM 77-293); B, small individual from Santa Barbara Basin (USNM); C, oral shield of large individual from Santa Barbara Basin (USNM); D, posterium of specimen A showing dorsoterminal sense organ (stippling); E, neck spicule of large individual; F-H, type 1 spicules of anterior trunk from: holotype (F, CAS), specimen A (G), specimen from south of Santa Cruz Island (H), and 44-mm individual (Sta. R-7, USNM)(J); K, L, type 2 spicules of anterior trunk from holotype (K) and 44-mm individual(L); M, posterior trunk spicule from holotype; N, O, frontal and lateral views of radula of specimen from south of Santa Cruz Island (LACM 76-553).

**Remarks.** Only *Chaetoderma scabrum* has similar anterior trunk spicules; however, *C. nanulum* type 1 spicules have a heavily ridged keel, and type 2 spicules are blunter distally and thickest laterally and medially. Posterior trunk spicules in *C. nanulum* are narrower than those in *C. scabrum* and have a sharp keel to the base and lateral ridges.

Three specimens labeled *Crystallophrisson riedli* Schwabl are extant, all with few or no spicules. One, from AHF Sta. 2352, is cf. *Chaetoderma hancocki* (Schwabl). Of the two specimens from Sta. 2150, one was chosen as the lectotype from its similarity in body form and measurements to Schwabl's illustration (1963, Fig. 30)(LACM no. 2105). The second specimen, distorted and without spicules, may or may not be the same species (LACM no. 2106). Synonymy of *Cr. riedli* with *C. nanulum* Heath is based on body measurements, shape of the mantle cavity wall, and morphology of spicules from the posterior end.

*Crystallophrissom rubrum* Schwabl was described from a single specimen apparently no longer extant. It was found at Sta. 2150 with *Cr. riedli*, from which it was differentiated on the basis of its purple color, but there is great similarity between these two species in the illustrations of the spicules (Schwabl, 1963, Figs. 19, 27) and of the animals (Figs. 20, 28), as well as in the written descriptions. *Cr. rubrum* is therefore here considered a probable synonym of *C. nanulum*, its purple color due to diet and not a species character.

**Distribution.** An outer continental shelf-upper continental slope species of the Santa Maria Basin and Southern California Bight between about 160-650 m, except to 1,843 m in the deep basin south of Santa Cruz Island.

### *Chaetoderma pacificum* (Schwabl, 1963)

Fig. 2.14

*Crystallophrisson nitidulum* var. *pacificum* Schwabl, 1963: 273-274, figs. 16-18.

**Material Examined.** California, Santa Maria Basin, Sta. 60 (1) (USNM).—Southern California Bight, south of Santa Cruz Island, 1,464 m (1) (LACM); San Pedro Basin, 22-279 m, **lectotype** (LACM 2100) and **paralectotypes** (LACM 2101 [probable, spicules lacking], 2103, 2104); off San Diego, 62-80 m (2) (SD Sta. A-4, A-15).

**Description.** A large species up to 30 mm long x 2.5 mm in posterior trunk diameter (Fig. 2.14A). Neck more slender posteriorly than anteriorly when not fully contracted. Anterior trunk shaggy, spicules often dislodged in preserved specimens, same length as or only 2 to 3 mm longer than posterior trunk. Posterium somewhat bulbous, with short terminal spicules and spiculeless collar around mantle cavity opening; dorsoterminal sense organ obvious (Fig. 2.14B). Oral shield dorsally cleft, with large dorsal lobes, wider than high, up to 1.0 x 1.7 mm (Fig 2.14C). Spicules long, flat, only those of posterior trunk with many parallel ridges (Fig. 2.14F-H). Neck spicules slightly arrowhead- to rod-shaped, up to 118 μm long but usually <100 μm, base narrow, up to 18 μm wide, and up to 7.5 μm thick, usually thickened asymmetrically (Fig. 2.14F); anterior trunk spicules with parallel sides and slightly tapered base, up to 300 μm long x 35 μm wide x 8 μm thick, most >200 μm long, keeled but with few or no ridges, thickest laterally, or medially, or both, shorter than ridged mid-posterior trunk spicules (Fig. 2.14G); 2 types of spicules predominant on mid-posterior trunk, one similar to anterior trunk spicules, the other longer, ridged, and broad, up to 400 x 55 x 10 μm, many >300 μm long by 7.5-8 μm thick (Fig. 2.14H). Radula large, cone straight in lateral view, up to 425 μm long, 90 μm wide frontally, and 150 μm wide laterally; denticles to 40 μm long; cuticular dome to 275 μm long; lateral projections broad, to about 60 μm long (Fig. 2.14D. E).

**Biology.** *Chaetoderma pacificum* was collected with *C. nanulum* in the Santa Maria Basin from a sandy silt with 33% sand and 15% clay. In the Southern California Bight the species was found with *Limifossor fratula* and *Falcidens longus*.

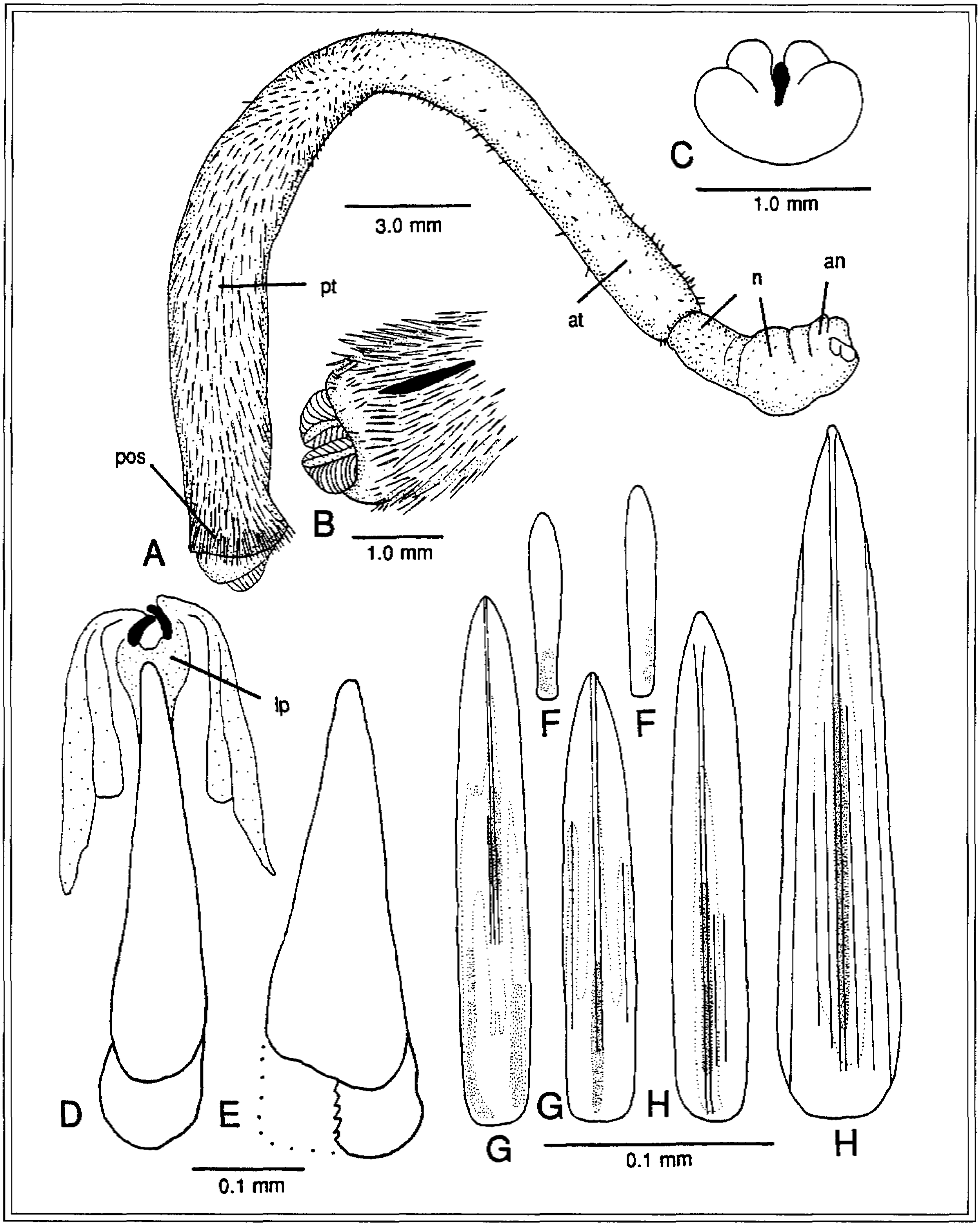

**Figure 2.14.** *Chaetoderma pacificum* (Schwabl): A-H, specimen from Santa Maria Basin (USNM). A, entire specimen; B, posterium, mantle cavity open and ctenidia extended, dorsoterminal sense organ black; C, oral shield; D, frontal view of radula; E, lateral view of radula cone, frontal to left, base broken; F-H, spicules from neck (F), anterior trunk at constriction (G), and mid-posterior trunk (H).

**Remarks.** *Chaetoderma pacificum* is differentiated from *C. marinelli* by (1) length of mid-posterior trunk spicules, which are more than 250 μm in *C. pacificum*; (2) relative lengths of trunk spicules: those from the anterior constriction are shorter than those from the mid-posterior trunk in *C. pacificum* and longer in *C. marinelli*; and (3) in *C. marinelli*, anterior trunk spicules bear many parallel ridges and are basally flared, whereas in *C. pacificum*, they have few to no ridges and are slightly tapered basally. Anterior trunk spicules are similar in shape to, but thicker than, those in *C. elegans*; greater body width and uncurved radula cone of *C. pacificum* readily distinguish the two species.

**Distribution.** A continental shelf species taken from off San Diego north to the Santa Maria Basin from 22 to 280 m, except to 1,464 m south of Santa Cruz Island.

### *Chaetoderma scabrum* Heath, 1911

Figure 2.15

*Chaetoderma scabra* Heath, 1911: 44, 63-64; pl. 4 figs. 2, 16, pl. 29 figs. 6, 7, 9-11, pl. 30 figs. 1, 3, pl. 37 fig. 19.

**Material Examined.** Central California, off Monterey Bay, 1,568 m, **holotype** (*Albatross* Sta. 4538, CAS 021400, spicule slide and serial sections).—Southern California Bight, south of Santa Cruz Island, 833 m (1) (LACM 76-271); 1,101 m (1) (LACM 76-270); northwest of San Nicolas Island, depth unknown (2) (LACM 77-238); San Pedro Basin, 504 m (1) (LACM 77-203, 77-276).

**Description.** Similar in appearance to *C. nanulum*. Greatest length 18 mm; anterior trunk shaggy, shorter than posterior trunk, narrower than neck and posterior trunk; diameter of posterior trunk up to 2.7 mm (Fig. 2.15A). Expanded oral shield nearly circular, 1.80 × 1.90 mm, pierced by mouth opening (Fig. 2.15B). Posterior end rounded, bushy (Fig. 2.15C). Anterior constriction obvious, dorsoterminal sense organ narrow but distinct. Neck spicules bent, with waist, thickest usually both basally and medially, <200 μm long, up to 60 μm wide, and 10 μm or more thick (Fig. 2.15D). Anterior trunk spicules near anterior constriction of two types: type 1 narrowly keeled, curved, basally flared, thickest medially and laterally at base, up to 300 μm long × 90 μm wide × 10 μm or more thick (Fig. 2.15E); type 2 spicules long, without sharp keel, flared basally, thickest either medially, or basally, or both, up to 420 × 90 × >10 μm (Fig. 2.15F). Spicules of mid-anterior trunk with isochromes pinching inwards between thickened base and blade, a character diagnostic for this species; sides convex, with keel and short lateral ridges, up to 290 x 70 × 10 μm (Fig. 2.15G, H); spicules of mid-posterior trunk to 420 x 80 × 10 μm, isochromes around keel bulged outwards. Radula with curved cone 425 μm long, widths 100 ìμm frontally, 150 μm laterally, denticles 30 μm, lateral projections 100 μm; dome heavily tanned distally, extending nearly one-half length of cone (Fig. 2.15K, L).

**Biology.** Sediment type unknown. Found at the same stations as *Chaetoderma hancocki*, *C. nanulum*, and *Falcidens hartmanae*.

**Remarks.** *Chaetoderma scabrum* resembles *C. nanulum* in body dimensions and similarity of type 1 spicules near the anterior constriction. However, in *C. scabrum*, type 1 spicules lack the broad, ridged keel found in *C. nanulum*. Spicules from the mid-anterior and posterior trunks and type 2 spicules at the anterior constriction have little resemblance between the two species. *C. scabrum* is further differentiated by a pierced, circular oral shield, bushy posterior end, and curved radula cone. Five of the specimens identified by Schwabl (1963) as *C. scabrum* are extant (LACM 53-76); they belong to *C. nanulum*.

**Distribution.** An Upper Slope species from off southern California between Monterey Bay and San Pedro Basin between 504-1,568 m; none occurred in the samples from the Santa Maria Basin.

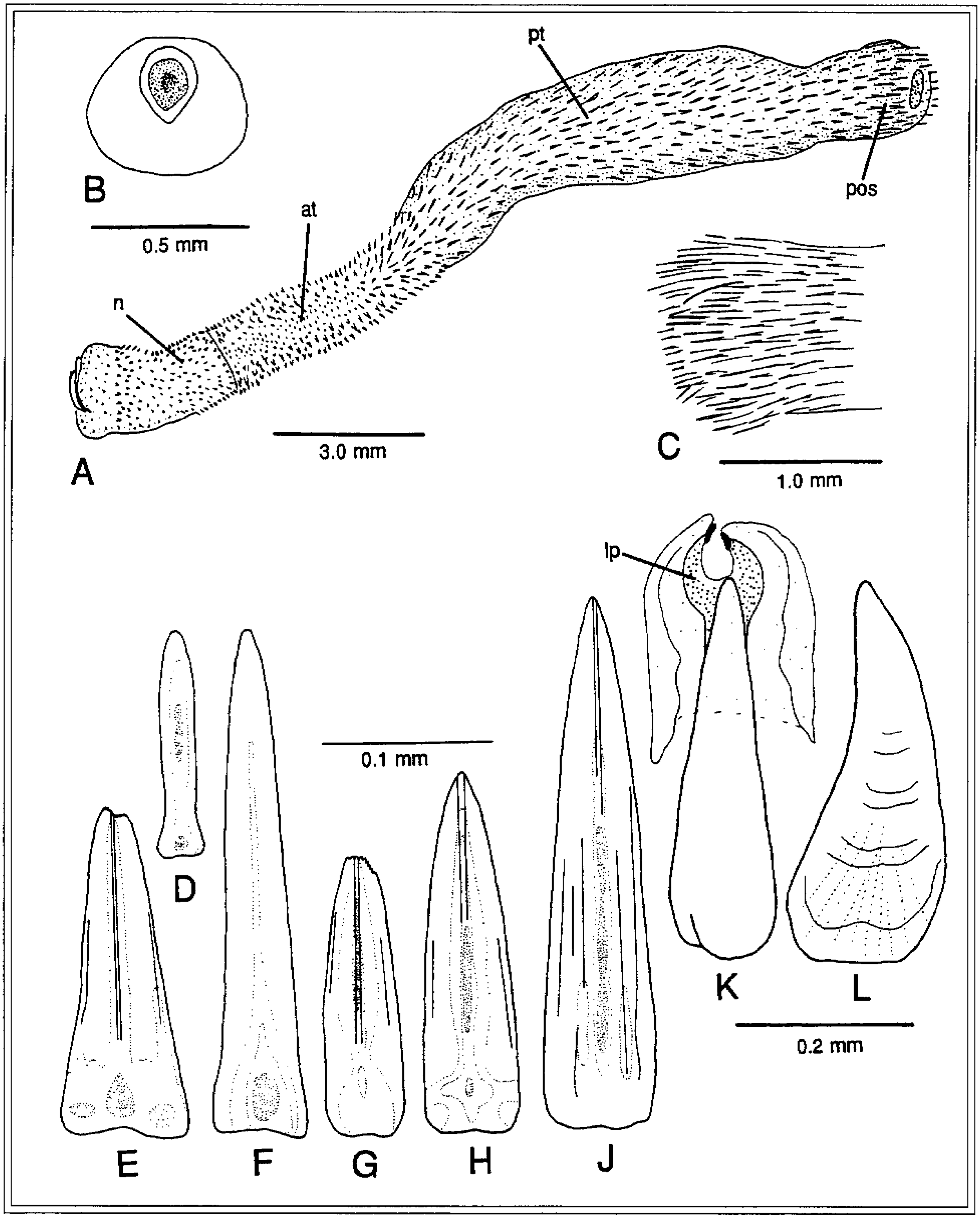

**Figure 2.15.** *Chaetoderma scabrum* Heath: A, individual northwest of San Nicolas Island (LACM 77-238); B, oral shield, individual from San Pedro Basin; C, posterium of A; D-J, spicules from neck (D), anterior trunk near constriction type 1 (E) and type 2 (F), mid-anterior trunk (G, H), and mid-posterior trunk (J), all from individual A except spicule G from holotype; K, L, frontal and lateral views of radula of individual A, front of radula cone to right in L.

### Genus *Falcidens* Salvini-Plawen, 1968

*Chaetoderma*. Ivanov, 1981 (Not Lovén, 1844).

**Type Species:** *Falcidens crossotus* Salvini-Plawen, 1968.

**Diagnosis.** With characters of the family. Radula with paired sickle-like denticles on a cuticular spring attached to the radular cone and with a triangular back plate (Fig. 2.16C, D); cuticle of buccal mass paired lateral membranes (Scheltema, 1972).

### *Falcidens hartmanae* (Schwabl, 1961)

Fig. 2.16

*Crystallophrisson hartmani* Schwabl, 1961: 258-277, figs. 1-10; 1963, 269-271, figs. 11, 12.

**Material Examined.** California, Santa Maria Basin and Santa Barbara Channel, Sta. 63 (2) (vouchers, USNM); Sta. 92 (3, SBMNH); Sta. R-3 (1); Sta. R-6 (1); Sta. R-9 (2, USNM).—Southern California Bight, South of Santa Cruz Island, 1,101-1,843 m (11) (LACM 76-252, 76-253, 76-270, 76-268, 76-262); San Pedro Basin, 558 m, **paralectotype** (LACM 2095); 324 m, **lectotype** (LACM 2094); San Diego Trough, 1,166-1,241 m, 32°25'-27'N, 117°28'W (11) (SIO, Rokop Sta. R-17, R-36, R-47).

**Description.** A distinctive species up to 11 mm long with broad trunk up to nearly 4 mm wide and narrow, tail-like posterium up to nearly 6 mm long (Fig. 2.16A), often heavily encrusted posteriorly with yellow-brown substance. Anterium usually evident, often large and balloon-like. Neck short, set off from combined anterior and posterior trunk by distinct, though shallow, anterior constriction. Neck and posterium spicules extending out from body; trunk spicules flat-lying, parallel to body axis. Single row of long spicules surrounding mantle cavity; posterior mantle cavity wall flat. Oral shield surrounding mouth opening, lobes scarcely evident (Fig. 2.16B). Spicules of anterium short, broad, blunt, lacking ornamentation (Fig. 2.16F). Neck spicules long, broad, bluntly rounded to somewhat pointed distally, base short, flat or slightly indented proximally; some with slight waist; thickened and often ridged distally in inverted V; up to 145 μm long, 60 μm wide,and 7 μm thick in ridges (Fig. 2.16G). Trunk spicules narrower and thinner than neck spicules, bluntly rounded distally, curved towards body, with single keel or double ridges, up to 170 μm long, 38 μm wide, and 6 μm thick in ridges (Fig. 2.16H). Spicules of posterium similar to those of trunk, but thinner, up to 4 μm, and with single sharp keel and a sharp ridge along edges. Radular cone straight, up to 360 μm long, frontal width to 60 μm, lateral width more than twice frontal width, up to 135 μm (Fig. 2.16E); lateral membranes up to 200 μm long; denticles up to 40 μm long (Fig. 2.16C,D,E); triangular plate with 2 little denticles and a pair of apophyses (Fig. 2.16D).

**Biology**. *Falcidens hartmanae* has been collected in silts with up to 34% sand or up to 21% clay. It has been taken at the same stations in the Santa Maria Basin as *Chaetoderma argenteum*, *C. nanulum*, *Limifossor fratula*, *Gymnomenia minuta*, and an unnamed species of Neomeniomorpha. In the Southern California Bight it has also been collected with *C. pacificum*, *C. hancocki*, and *Falcidens longus*.

**Remarks.** This species is distinctive. In Schwabl's (1963) description, the spicules labeled "b" in Figure 11 are from the trunk, and those labeled "d" are a mixture from the neck and posterium. The greatest length given, 18 mm, may be of a distorted specimen with the posterium stretched.

**Distribution.** Southern California on the upper continental slope from about 300-1,200 m, except to 1,843 m south of Santa Cruz Island. A similar species with a smaller radula and larger spicules occurs at 1,200 m and deeper off the Farallon Islands and at shallower depths off the Oregon coast.

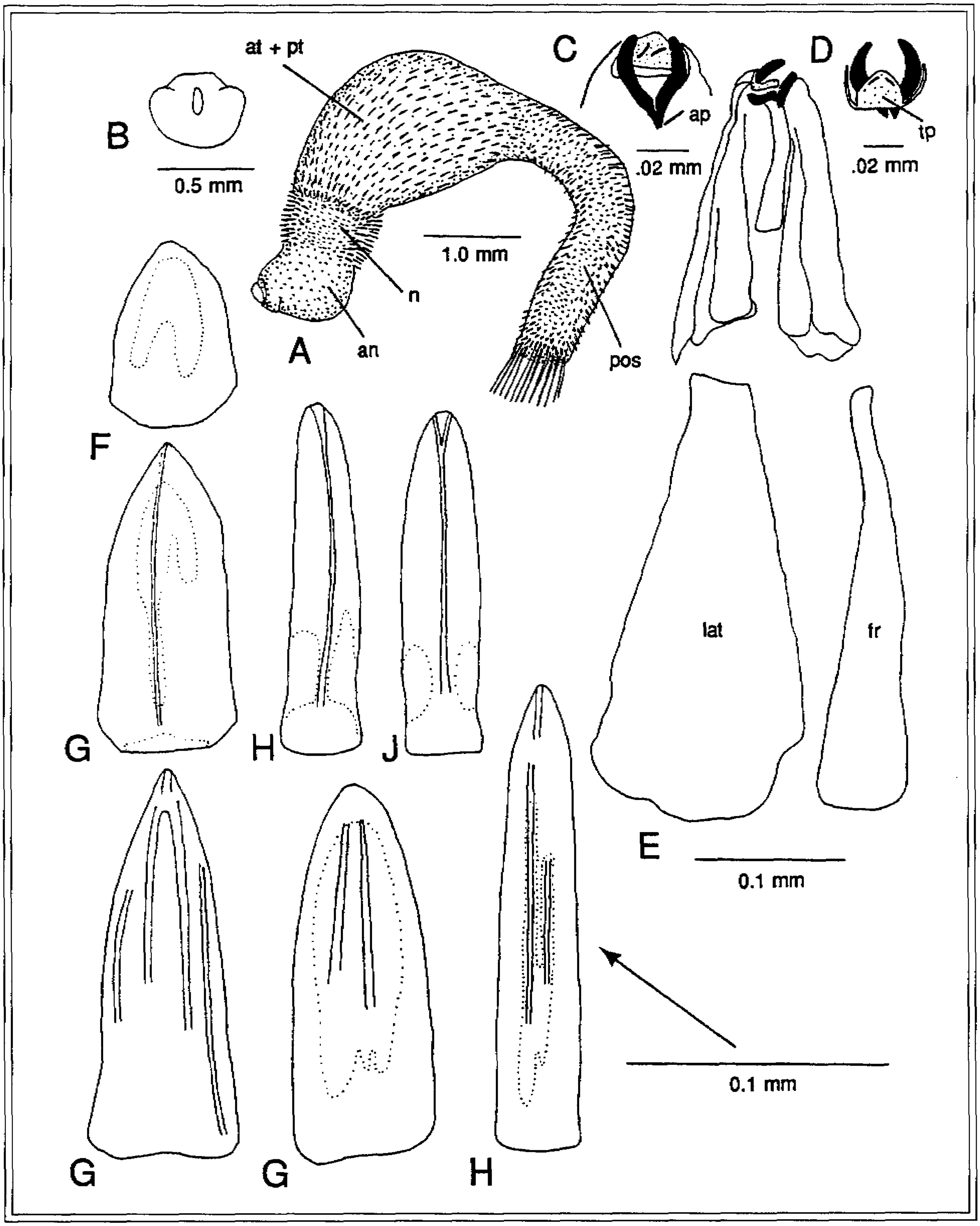

**Figure 2.16.** *Falcidens hartmanae*: A, specimen from Santa Maria Basin (USNM); B, oral shield of specimen A; C, D, E, radula of specimens from, respectively, Southern California Bight, San Diego Trough, and Santa Barbara Basin (USNM) (denticles and triangular plate broken); F-H, spicules from anterium (F), neck (G), trunk (H), and posterium (J); F, G upper, H upper, J from specimen A; G lower left from San Diego Trough; G, H, lower right, from Southern California Bight. Arrow: scale for spicules.

### *Falcidens longus* Scheltema, new species

Figure 2.17

**Material Examined.** California, Santa Maria Basin, Sta. R-4 (5) (**holotype**, USNM 860391; **paratype** LACM 2749); Sta. R-1 (8); Sta. R-8 (22).—Southern California Bight, south of Santa Cruz Island, 1,165-1,812 m (12) (LACM 76-253, 76-269, 246, 76-264, 76-263); south of San Miguel Island, 249 m (2) (LACM 77-282); San Pedro Bay, 32 m (2) (LACM77-273); off San Diego, 47-81 m (36) (SD Sta. A-2, A-3, A-4, A-5, A-8, A-9, A-10, A-11, A-13, A-14, B-1, B-3, B-5).—Oregon, off Newport, 100-200 m (11) (OSU).—British Columbia, off Bamfield, Vancouver Island, 106-175 m (82).

**Description.** Elongate, slender to somewhat robust, up to 28 mm long (holotype 15.5 mm) (Fig. 2.17A). Neck sometimes swollen with 2 obvious constrictions; anterium often extended (Fig. 2.17C). Anterior trunk shaggy with thick-set spicules, same width as neck at anterior constriction, longer than posterior trunk in specimens >15 mm long, width to 1.3 mm, only somewhat narrower than posterior trunk, up to 1.6 mm. Posterior trunk translucent to opaque. Dorsoterminal sense organ distinct (Fig. 2.17D). Contracted posterior mantle cavity wall flat to rounded, covered by spoke-like spicules (Fig. 2.17E). Oral shield small, usually wider than high, up to 1.68 x 1.58 mm, indistinctly dorsally cleft, dorsal lobes small, close to each other (Fig. 2.17B). Spicules symmetrical, keeled, all but neck spicules with many sharp parallel ridges, flat except at anterior constriction where trunk spicules curve slightly outward; narrowly or broadly arrowhead-shaped on neck, up to 146 μm long, base 14-50 μm, up to 8 μm thick (Fig. 2.17F); most anterior trunk spicules at constriction less than 200 μm long, but up to 215 μm, flared at base or with straight sides, sharply keeled to base, thickest at keel and lateral ridges in three longitudinal bands up to 7.5 μm, or thickest laterally (Fig. 2.17G); spicules between anterior and posterior trunk thinner, with ridges and keel 3.5 μm thick and up to 200 μm long (Fig. 2.17H); posterior trunk spicules up to 215 μm long and 50 μm wide, keeled and ridged, thickest medially, 5 μm or less (Fig. 2.17J). Radula cone length up to 300 μm, wider laterally than frontally, curved in lateral view, denticles 40-45 μm, spring between denticles not cuticularized, triangular plate often lacking (Fig. 2.17 K,L).

**Biology.** *Falcidens longus* was collected from sediments ranging from fine sand to muddy silt with up to 20% clay in both the Santa Maria Basin and Southern California Bight. It occurred at the same stations as *Falcidens macracanthos* north of Pt. Conception, and with *Chaetoderma nanulum*, *C. hancocki*, *C. pacificum*, *C. marinelli*, *Falcidens hartmanae*, *Limifossor fratula*, *Spathoderma californicum*, and a species of *Psilodens* in the Southern California Bight. *Falcidens longus* is one of the more common chaetoderm species, and box cores often contain small juveniles.

**Etymology.** From the Latin for "long," indicating a long, slender species.

**Remarks.** Unusual for a species of *Falcidens*, but similar to *F. macracanthos*, the spring joining the radular denticles of *F. longus* lacks tanning, and the triangular plate, which is very thin, is often missing in large specimens. *Falcidens longus* can be differentiated from *Chaetoderma* species by radula morphology and externally from *F. macracanthos* by its shorter, thinner spicules and by the predominance of triply thickened spicules of the anterior trunk; from *C. pacificum* by more numerous parallel ridges and flared base on anterior trunk spicules and shorter posterior trunk spicules; and from *C. elegans* by a more robust shape and thicker anterior trunk spicules which are flared basally and bear more ridges. Easily confused with *C.marinelli* (q.v. for differences between the two species).

**Distribution.** A continental shelf species from off Vancouver Island, British Columbia, to the Southern California Bight between 32-250 m, except to 1,812 m in the deep basin south of Santa Cruz Island.

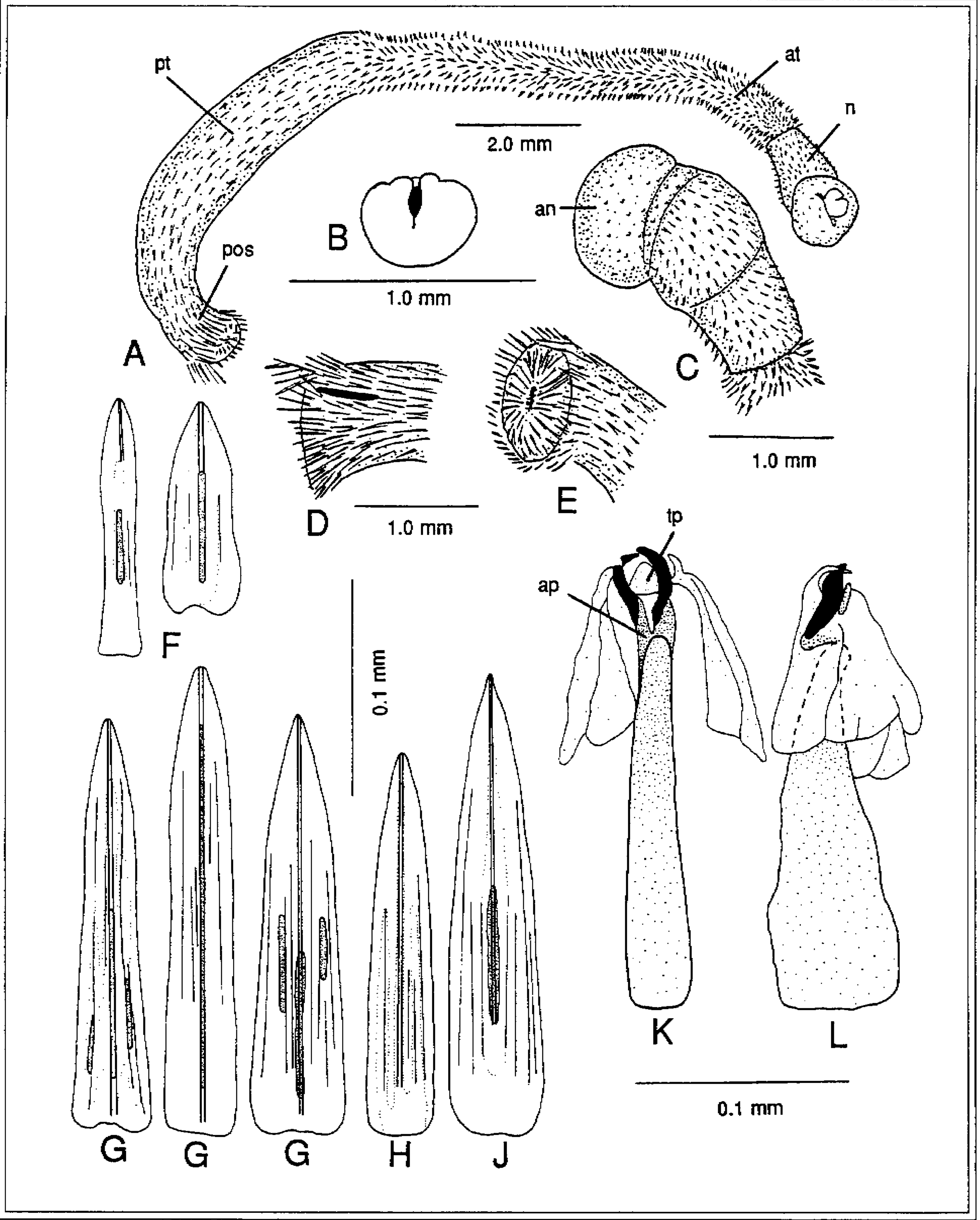

**Figure 2.17.** ***Falcidens longus*** **Scheltema, new species**: A, holotype (USNM 860391); B, oral shield of specimen A; C, neck region of specimen A; D, E, posterium of specimen A; F-J, spicules from neck (F), anterior trunk at constriction (G), mid-anterior trunk (H), and mid-posterior trunk (J), F right, G left from paratype, rest of spicules from holotype; K, frontal view and L, lateral view of radula (paratype, LACM 2749).

## *Falcidens macracanthos* Scheltema, new species

Fig. 2.18

**Material Examined.** California, Santa Barbara Channel, Sta. 85, **paratype** (LACM 2752); Sta. R-4, **paratype** (LACM 2751); Sta. PJ-1, paratype (LACM 2750); Sta. PJ-17, **holotype** (USNM 860392).—San Pedro Basin, depth 82 m (1) (LACM 53-132).

**Description.** A short, thickset species distinguished by long spicules in region of obvious constriction between smooth neck and shaggy anterior trunk and by relatively thick body (Fig. 2.18A). Largest of 4 known individuals 14.0 mm long; holotype 9.9 mm long. Anterior trunk widest at constriction, up to 1.2 mm, narrowing slightly to 1.9 mm posteriorly; posterior trunk somewhat longer than anterior trunk and wider, up to 1.4 mm in diameter, and translucent. Sides of posterium straight, posterior wall of contracted mantle cavity flat, with spoke-like arrangement of spicules (Fig. 2.18A, B). Dorsoterminal sense organ obvious. Oral shield with large lobes, somewhat higher than wide in holotype, 1.40 mm wide x 1.45 mm high (Fig. 2.18C). Spicules from neck and anterior trunk long and thick. Neck spicules flat, with no or faint ridges, arrow-shaped, up to 170 µm long x 38 µm wide x 8 µm thick, thickest basally and either laterally or medially (Fig. 2.18E); anterior trunk spicules thickset, flat, held erect, with several medial ridges but not keeled, grooved abfrontally, thickest either laterally or laterally and medially, base flat and slightly flared, up to 400 x 52 x >10 µm (Fig. 2.18F), shorter in small specimens (Fig. 2.18H); mid-posterior trunk spicules thinner, up to 7 µm, and shorter, less than 300 µm, with many parallel ridges, thickest medially, base either rounded (Fig. 2.18D) or straight. Radula small, cone length up to 223 µm, lateral width up to 100 µm, wider than frontal width, up to 72 µm, not curved in lateral view, denticles up to 50 µm, spring between denticles not cuticularized, triangular plate present or lacking (Fig. 2.18 G, J, K).

**Biology.** *Falcidens macracanthos* has been collected from sandy silts with up to 16% sand, and from silty sands with up to 72% sand; clay particles were 12% or less. It occurred at the same stations as *Chaetoderma argenteum*, *Falcidens longus*, and ?*Genitoconia mariensis* in the Santa Maria Basin and with *C. pacificum* in the San Pedro Basin.

**Remarks.** The spicules and body shape are similar to *Chaetoderma marinelli*, but most anterior trunk spicules at the constriction are much longer, 350-400 µm, whereas in *C. marinelli* they are up to 300 µm long and have more parallel ridges. The radula morphology also distinguishes the two species. Like *F. longus*, the hinge between the denticles in *F. macracanthos* is not tanned, and the triangular plate, present in the small specimen examined, was lacking in the large specimen.

**Etymology.** From the Greek *makros*, meaning large, and *akantha*, a spine.

**Distribution.** A continental shelf species known from the Santa Maria and San Pedro Basins between 82-145 m.

## *Furcillidens* Scheltema, new genus

**Type Species:** *Crystallophrisson incrassatum* Schwabl, 1963.

**Diagnosis.** Denticles lacking, the chitinous dome strengthened by a forked distal process of the cone (Fig. 2.19C).

**Remarks.** The radula is unique among all known species and genera of Chaetodermomorpha. The forked distal process may be homologous with the lateral processes found in the genus *Chaetoderma*.

**Etymology.** From Latin *furcilla*, little fork, and *dens*, tooth; masculine.

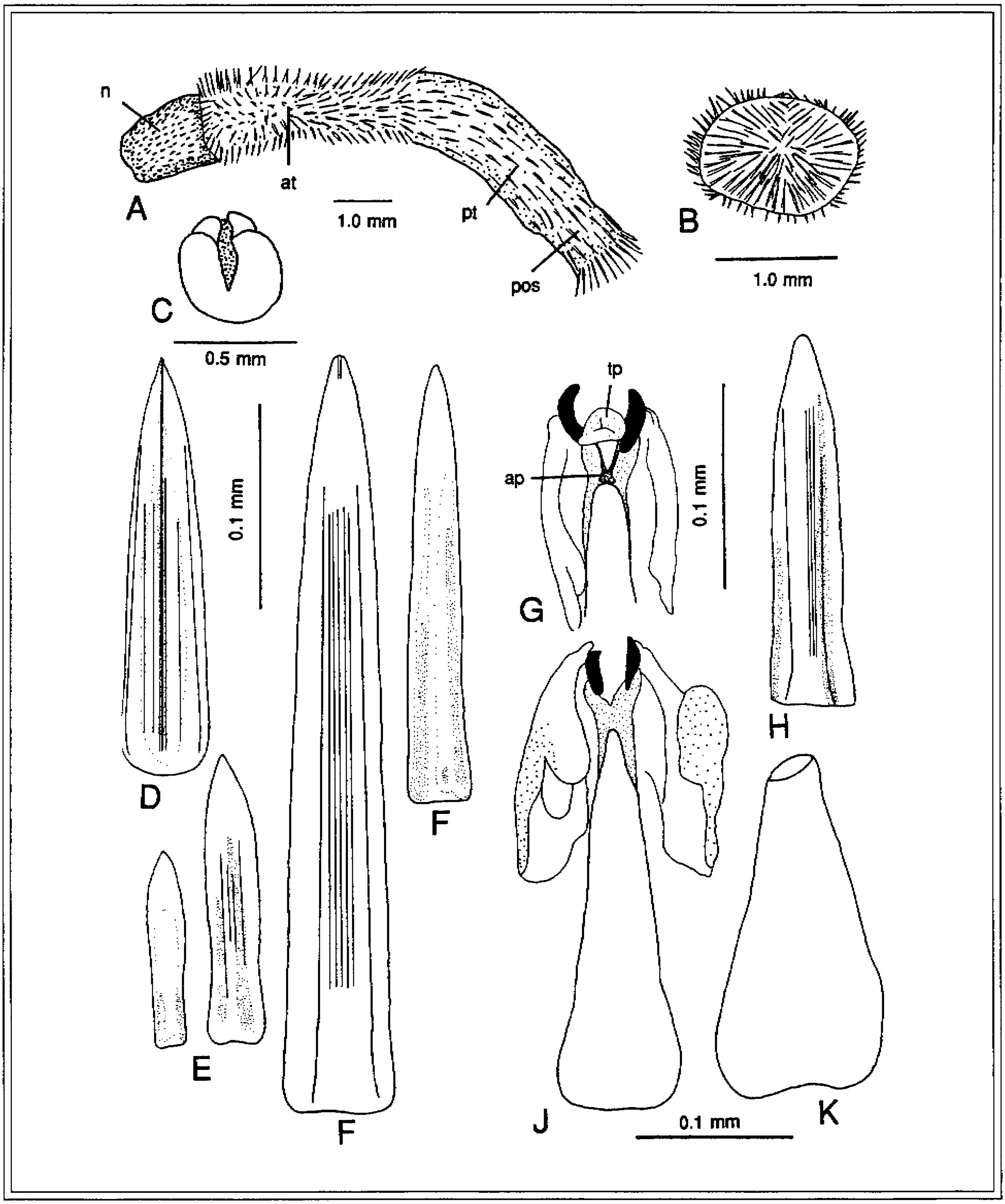

**Figure 2.18.** ***Falcidens macracanthos*** **Scheltema, new species**: A, holotype (USNM 860392; B, C, posterior mantle cavity wall and oral shield, respectively, of specimen A; D-F, spicules of paratype no. 1 (LACM 2750) from neck (E), anterior trunk (F), and mid-posterior trunk (D), spicule F at right same as spicule to left, greatly reduced, showing pattern of thickening; G, abfrontal view of radula of small specimen 5.4 mm long (paratype no. 3, LACM 2752) showing triangular plate; H, spicule of same specimen as G; J, K, frontal and lateral views of radula of paratype no. 2 (LACM 2751) (drawn at smaller scale than G).

## ***Furcillidens incrassatus*** **(Schwabl, 1963), new combination**

Figure 2.19

*Crystallophrisson incrassatum* Schwabl, 1963: 267, fig. 8.

**Material Examined.** Santa Barbara Channel, Sta. 91 (1) (USNM); Sta. 99 (2) (USNM); 504 m (3) (LACM 77-219); 549 m, **lectotype** (LACM 2096).

**Description.** A distinctive species up to nearly 18 mm long, with a greatly expanded neck and anterium, short, narrow anterior trunk, and broad posterior trunk up to nearly 4 mm in diameter and more than twice length of anterior trunk (Fig. 2.19A). Neck and anterium separated by strong sphincter in front of which lie the radula and salivary glands; either neck or anterium or both may be expanded. Posterium set off from posterior trunk by distinct ridge, cone-shaped when contracted and covered by long spicules. Dorsoterminal sense organ distinct, entirely within posterium. Oral shield relatively small with large dorsal lobes, usually not expanded, perhaps pierced by mouth opening, nearly round, 1.6 mm wide by 1.5 mm high (Fig. 2.19B). Spicules long, narrow, thick, without ridges or sharp keel, anterior and posterior spicules similar. Neck spicules somewhat arrowhead- to rod-shaped, curved, usually narrowest at base, thickened asymmetrically, up to 190 μm long × 18 μm wide × >10 μm thick (Fig. 2.19E, F); anterior trunk spicules indented distally just before tip, and often also indented one or more times along length, thickest distally or distally and basally, basally curved, length mostly between 300 and 425 μm long, but up to 550 μm, about 30-40 μm wide, and 10 μm or more thick (Fig. 2.19G, H); mid-posterior trunk spicules with few or no indentations, sometimes with basal keel, many thickened asymmetrically, 400 μm or less long, base to 40 μm wide, and 7.5 to >10 μm thick (Fig. 2.19J). Radula large, total length 850 μm, cone length to fork 500 μm, narrow frontally, 110 μm, and broad laterally, 340 μm; cone weakly and unevenly sclerotized, surrounded by cuticle not sclerotized; cuticle of dome in 2 parts, each surrounding a process of cone above fork and sclerotized laterally, 400 μm long (Fig. 2.19C,D).

**Biology.** Individuals came from soft muddy silts with less than 5% sand and up to 35% clay. The unique body shape and radula morphology of *Furcillidens incrassatus* indicate an unusual environment for an aplacophoran, and no other aplacophoran species was found with it.

**Remarks.** No other species is likely to be confused with *F. incrassatus.*

**Distribution.** An upper continental slope species known only from the Santa Barbara Channel between 504-549 m.

## Family Prochaetodermatidae

**Diagnosis.** Small Chaetodermomorpha usually <5 mm long with 3 body regions: anterium (often retracted), broad trunk, and narrow, tail-like posterium; without dorsoterminal sense organ; with unique pair of large jaws, usually discernible through cuticle (Fig. 2.20A); radula small with about 12 rows of distichous, serrated teeth, a central plate, and a lateral extension of the radular membrane beside each tooth (Scheltema, 1981); oral shield divided; spicule morphology similar throughout body, increasing in length posteriorly, ventral spicules shorter than dorsal spicules.

### Genus *Spathoderma* Scheltema, 1985

*Prochaetoderma* (*partim*). Salvini-Plawen, 1992.

**Type Species:** *Spathoderma clenchi* Scheltema, 1985.

**Diagnosis.** Spicules spatulate, base flat and relatively long, blade narrow and either curved outward from body, or twisted in relation to base, or both.

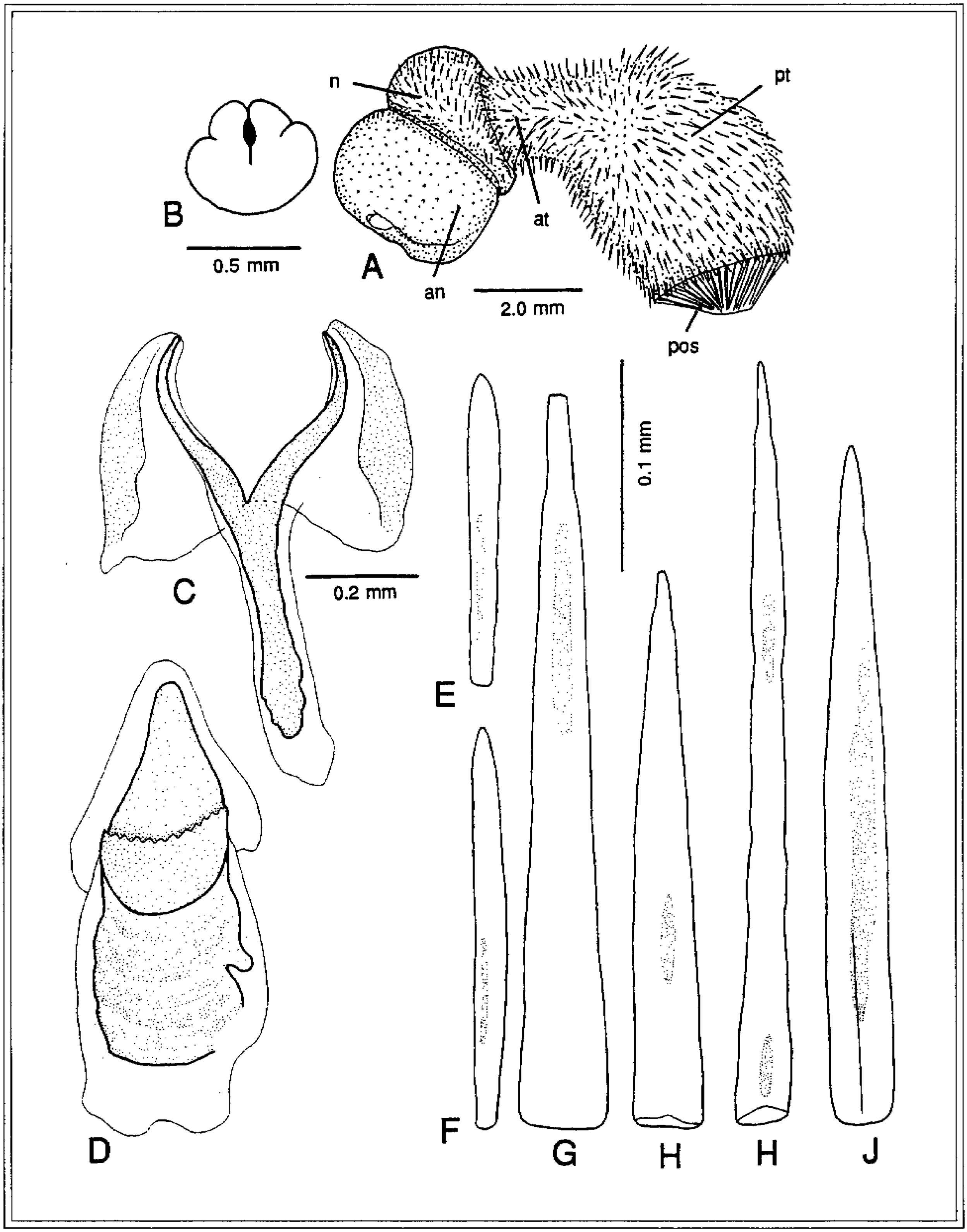

**Figure 2.19.** *Furcillidens incrassatus* (Schwabl): A, specimen from LACM 77-219; B, oral shield, specimen (SMB Ph. I Sta. 99 USNM); C, D, radula, frontal and lateral views, respectively, sclerotized portions stippled (SMB Ph. I Sta. 91, USNM); E, F, neck spicules; G, H, anterior trunk spicules; J, posterior trunk spicule; D, F, H, J, (SMB Sta. 91); E, G, lectotype (LACM).

### *Spathoderma californicum* (Schwabl, 1963)

Figure 2.20

*Prochaetoderma californicum* Schwabl, 1963: 265-267, figs. 4-7.—Salvini-Plawen, 1992: 323.

**Material Examined.** California, Santa Maria Basin, Sta. 5 (8, SBMNH); Sta. 62 (5) (USNM); Sta. R-6 (1) (probably collected dead, USNM).—Southern California Bight, South of Santa Cruz Island, 1,756 m (4) (LACM 76-253); San Pedro Basin, 536-689 m (6) (LACM 77-204, 77-275, 77-202, 77-274, 77-261) and 693 m (5) (**lectotype**, LACM 2091, and 4 **paralectotypes**, LACM 2092).

**Description.** Length 4.0 mm or less, trunk length and width up to 2.5 × 0.7 mm, posterium usually less than 1.0 mm long, width 0.3 mm or less (Fig. 2.20A-C). Oral shield small, each side of pair 0.1 mm high × <0.1 mm wide (Fig. 2.20B). Spicules orientated dorsoposteriorly from ventral midline (Fig. 2.20B), becoming anterior-posterior on posterium; with single row of long spines surrounding mantle cavity (Fig. 2.20B, C). Spicules with long base separated from blade by an indented waist, with blade twisted in relation to base and bent slightly outwards (Fig. 2.20K, L), up to 6 µm thick; from dorso-anterior trunk, up to 100 µm long, base up to 32 µm wide (Fig. 2.20H); from mid-dorsal trunk, up to 170 µm long × 32 µm wide (Fig. 2.20J); from junction of dorsal trunk with posterium, up to 185 µm long and 32 µm wide (Fig. 2.20K); and from midventral trunk, <160 µm long to <30 µm wide (Fig. 2.20M). Jaws to 447 µm long × 348 µm wide × 104 µm thick (Fig. 2.20A, F, G); radula tooth length about 130 µm (Fig. 2.20D); lateral extension of radular membrane 36 µm (not figured); central plate curved and somewhat pointed at each end, 38 µm × 8 µm (Fig. 2.20E).

**Biology**. *Spathoderma californicum* was collected from the Santa Maria Basin in silt and sandy silt with up to 34% sand and <15% clay. Species of Prochaetodermatidae are often one of the numerically dominant forms in the deep sea at 1,500 m or more. This dominance apparently does not occur in the shallower waters off the California coast (Blake, 1993: Vol 1, pp. 39-41). In the Southern California Bight the species occurred at the same stations as *Chaetoderma hancocki*, *C. nanulum*, *C. scabrum*, *Falcidens hartmanae*, *F. longus*, and *Limifossor fratula*.

**Remarks**. *Spathoderma californicum* is distinctive and easily differentiated from the only other "tailed" species in the Santa Maria Basin, *Falcidens hartmanae*, by the lack of an anterior constriction, presence of jaws, and spicules that spiral from ventro-anterior to dorsoposterior. *Spathoderma* is not synonymous with *Prochaetoderma* (Salvini-Plawen, 1992), species of which have flat spicules with base and blade oriented in the same plane.

**Distribution**. An upper continental slope species, perhaps restricted to areas south of Monterey Bay between 500-1,800 m. Closely related species occur off the Farallon Islands and Oregon coast.

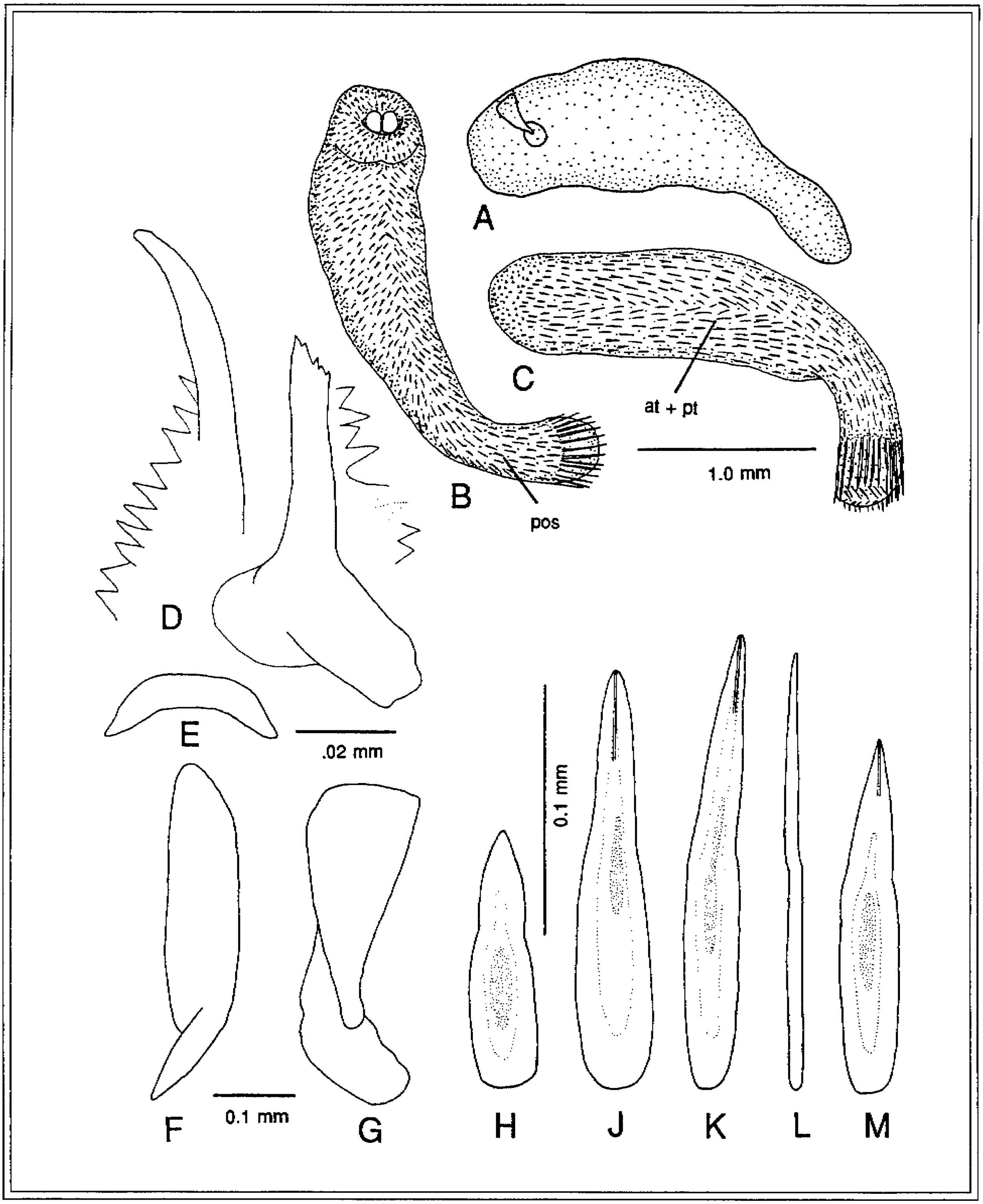

**Figure 2.20.** *Spathoderma californicum* (Schwabl): A, paralectotype (LACM 2092), spicules dissolved, jaws evident through cuticle; B, C, specimen in ventral (B) and dorsal (C) view (SMB Ph. I Sta. 62, USNM); D-G, radula apparatus of paralectotype; D, distal and proximal ends of two teeth; E, central plate; F, G, jaws in side and medial views; H-M, spicules of specimen B, C; H from dorso-anterior, J from mid-dorsal trunk, K, L from region between trunk and posterium, M from midventral trunk.

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# 3. CLASS POLYPLACOPHORA

by

Douglas J. Eernisse [1]

## Introduction

Chitons (Mollusca: Polyplacophora) are an ancient lineage of molluscs recognizable by their distinctive eight overlapping shell plates called valves. All valves articulate to form an oval to elongate dorsal or ventral profile (Figure 1a-e). In their normal attached position, the valves are highest along the chiton's axis of bilateral symmetry, with left and right eaves of the medial (intermediate) valves sloping down laterally, more or less steeply, from either side of this central crest. The middle (fourth and fifth) valves are the widest, with others becoming progressively narrower toward the roughly hemispherical head and tail valves.

When alive, chitons cling tightly to hard substrates with their mucus-covered and muscular foot. The foot and other ventral soft tissues are hidden from view by the chiton's dorsal-plated armor, which itself is embedded in a flexible and muscular tissue known as the girdle. The girdle's distal edge and underside (ventral surface) conform tightly to the substrate, while its dorsal surface can be variously ornamented, for example, with a tunic of scales (Figure 3-1a), elaborately branching bristles, or needle-like to stout spines.

Chitons are muscular animals. Besides their valves' firm mounting in the girdle tissue, each of their eight valves is firmly attached on its inner (ventral) surface by a double-cord pair of muscle groups. Living monoplacophorans have a similar arrangement of eight paired muscle groups (Wingstrand, 1985). Most species will roll themselves into a ball when dislodged or when submerged in fixatives if muscle relaxation is neglected prior to treatment. When preserving chitons as biological specimens, the chiton should first be relaxed in a solution of 7.3% magnesium chloride, and then bound onto a wooden tongue depressor or glass slide by wrapping it longitudinally, such as with thin strips of torn nylon hosiery, before placing it into the fixative.

The valves' outermost (dorsal) layer, the tegmentum, is often brightly colored, and is penetrated by numerous sensory organs dispersed in regular patterns across the valve surface. These organs may be visible on or between minute raised pedestals or ridges that give the valve a granular or sculptured appearance. These sensory organs, the esthetes, arise from an intricate series of diverging nerve channels penetrating the tegmentum, originating as primary nerve bundles around the tegmental margin. In most chiton species, these nerve bundles are routed to the dorsal surface through slits at the valves' distal margins. As can be seen in the disarticulated valves of most chitons (except lepidopleurids), these slits divide the insertion plates (articulamentum) into "teeth."

Chitons are an exclusively marine group, numbering just over a thousand recognized species including about 830 extant species as well as those known only as fossils. Many species have a maximum adult size less than 1 cm length, but lengths of several cm are also common, and a shallow-water inhabitant of northern Pacific shores, *Cryptochiton stelleri*, can reach 33 cm length. Over half of all species live in intertidal to

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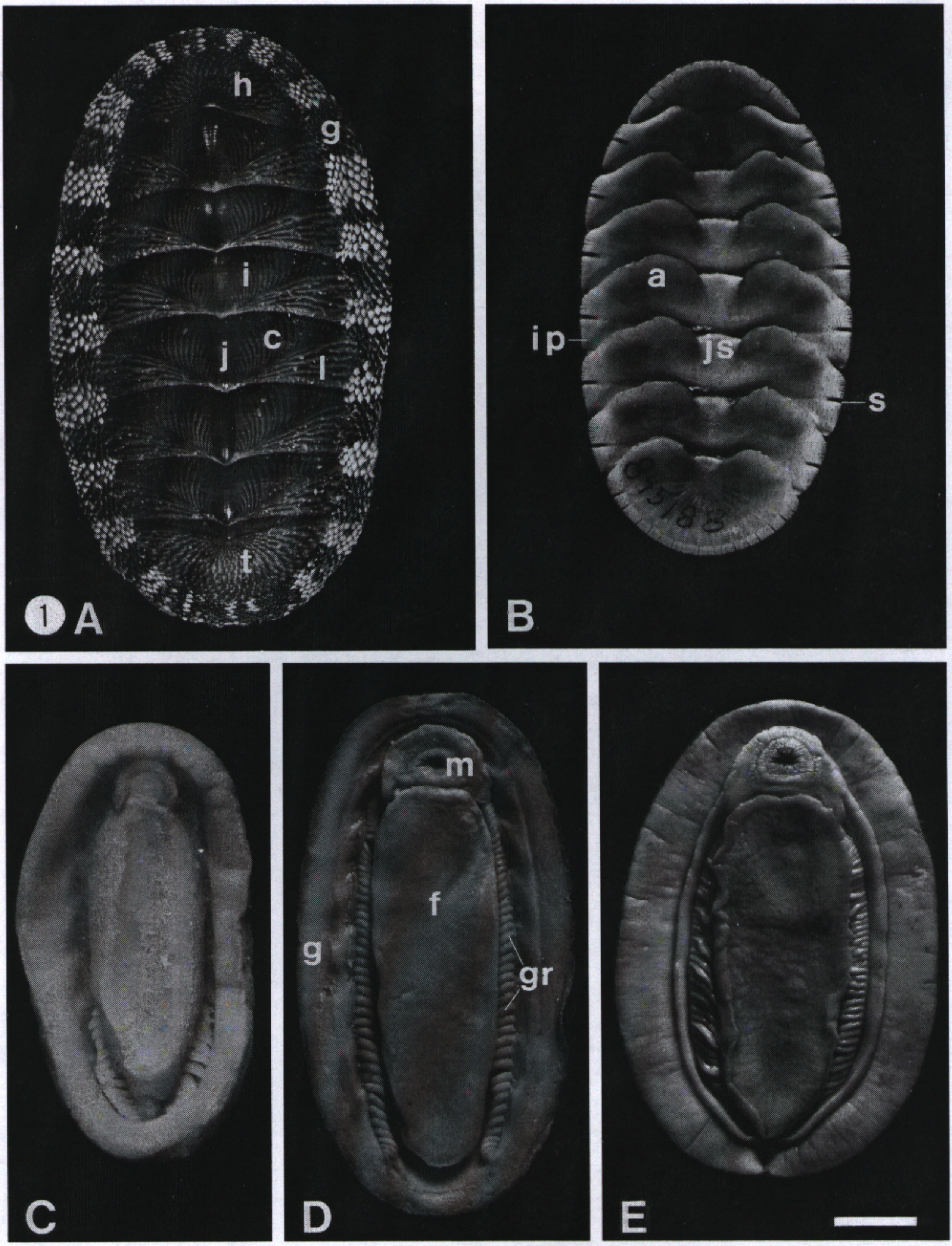
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shallow subtidal habitats, but chitons are also present in deeper habitats wherever suitable hard substrates exist, and some even live in the deepest ocean trenches. Chitons attach and creep over hard substrates using their broad sticky foot. They usually feed by scraping or biting with several pairs of magnetite-reinforced major (second) lateral radular teeth. Their mantle cavity is u-shaped, extending away from their mouth and surrounding either side of the foot until it is joined in the anal region posterior of the foot (Figures 1c-e). There are multiple gills on either side of the foot, with each gill row hanging like a curtain from the mantle cavity roof. In the suborder Lepidopleurina (e.g., *Leptochiton*), the left and right gill rows form a continuous hemispherical arch restricted to the posterior mantle cavity surrounding the anus (Figure 1e). In contrast, the more familiar chitons comprising the suborders Ischnochitonina and Acanthochitonina have laterally placed gill rows with considerable separation between the last gill in each row (Figures 1c-d). Other extant chitons also differ from lepidopleurid chitons in possessing more extensive and "slit" distal extensions of the valves, anchored in the girdle, known as insertion plates. Microscopic distinctions include the greatly reduced acrosome of their sperm, as well as the much more elaborate spine-, cup-, or cone-like extracellular egg "hulls" that cover their eggs.

Chiton anatomy was recently reviewed by Eernisse and Reynolds (1994). Systematic monographs by Pilsbry (1892-94) and Thiele (1909-1910) are being updated in an ongoing series by Kaas and Van Belle (1980, 1985a, 1985b, 1987, 1990, 1994). Kaas and Van Belle have largely followed the classification proposed by Van Belle (1983, 1985) and, with minor exceptions, this classification is also followed here and in a worldwide geographic distribution and nomenclature database (Eernisse, in press).

The current classification includes all living chitons in a single order, Neoloricata. The most familiar and conspicuous chitons belong to the suborders Ischnochitonina (including Ischnochitonidae, Chitonidae, Mopaliidae, Lepidochitonidae, and several other common families) and Acanthochitonina (including Acanthochitonidae and Cryptoplacidae). Members of a third suborder, Lepidopleurina, mostly live in deeper water, have white to tannish tegmental coloration, and differ from the other chitons as discussed above.

Ecological studies of chitons have mostly focused on shallow water species. The diet of chitons varies, depending on the species, with a wide variety of plant and animal species consumed by chitons. In intertidal communities, chitons are mainly herbivorous, feeding on fleshy or crustose algal blades, or films of diatoms, but also detritus and colonial animals. Some intertidal chitons exhibit homing behavior (Thorne, 1968; Mook, 1983; Chelazzi *et al.*, 1987), and some species excavate home depressions in a manner similar to some limpet species, probably by softening the substrate with acidic secretions from their foot, and then excavating the depression further with their radula. Chitons can also have an important role in determining community ecological structure, in some cases benefitting from the presence of other chitons when their feeding activities promote the growth of preferred algal species (Dethier and Duggins, 1984; Duggins and

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**Figure 3.1.** External anatomy of chitons, from Eernisse and Reynolds (1994). Figures oriented with anterior end at the top. A. Dorsal view of *Chiton tuberculatus* (Ischnochitonina: Chitonidae). c, central area (note the anterior portion of tail valve with same sculpturing pattern); g, girdle elements (overlapping scales in this case); h, head valve; j, jugum and jugal area; l, lateral area (note head valve and posterior part of tail valve have similar sculpturing); t, tail valve. B. Ventral view of disarticulated valves of *Chiton squamosus*. a, apophyses; ip, insertion plates; js, jugal sinus; s, slit in insertion plate of articulamentum shell layer. C. Ventral view of *Ferreirella caribbeanensis* (Lepidopleurina: Leptochitonidae). Note posterior placement of gill rows, which are adanal (most posterior gill in each row is not the largest) and without interspace. D. Ventral view of *Chiton bowenii*. Gill rows are adanal with interspace. f, foot; g, ventral side of girdle; gr, left gill row; m, mouth and oral platform. E. Ventral view of *Mopalia hindsii* (Ischnochitonina: Mopaliidae). Gill rows are abanal (most posterior gill in each row is largest) with interspace. Scale bars: A, B = 5.5 mm; C-E = 1 cm.

Dethier, 1985). Compared with the enormous variation known for gastropod radulas, the chiton radula is relatively conserved. Yet subtle variations of the radular tooth orientation have been shown to be important in which types of food a particular chiton species feeds on (Bullock, 1988). The radular tooth shape is also sometimes correlated with diet, for example, chitons that feed on crustose coralline algae have broad shovel-like major (2nd) lateral teeth (e.g., *Tonicella lineata*), and chitons that specialize on deep-water sunken wood (e.g., *Ferreirella* spp.) have expanded fifth lateral teeth. Other examples of dietary specialization include deep-water sponge feeders (e.g., Warén, 1991), but there is little evidence that a preference for a sponge diet has led to a modification of the radula. Members of *Placiphorella* (McLean, 1962), and probably also members of *Loricella*, and *Spongioradsia*, have special notoriety because they feed as ambush predators, entrapping mainly small crustaceans as they pass under an uplifted head flap. This carnivorous behavior has likely had three convergent origins, because each genus exhibits what is best regarded as a derived trait within its particular distinct chiton family.

Chitons have been collected from >7,000 m in some of the deepest oceanic trenches, and have also been found associated with deep sea hydrothermal vents (Saito and Okutani, 1990). Vast expanses of deep sea habitat are composed of soft sediments that would be unsuitable habitat for chitons if it were not for some scant hard substrate scattered across the sea floor. For example, chitons have been collected from manganese nodules, which are among the only hard substrate available in deep oceanic habitats (Mullineaux, 1986). These chitons probably feed on foraminiferans and other small animals also found on the nodules. The ecology of chitons that live in intermediate depths, such as those in the present study (50-250 m), is perhaps even less well known. Chitons from these depths tend to be taken incidentally to other dredged animals, and most recovered chiton specimens are already dead or removed from their natural habitat by the time they are identified. Because basic natural history data is generally lacking, there continues to be great value for any observations that can be recorded, even when specimens must remain unidentified.

## Observing External and Internal Features

The valves and girdle are the most emphasized aspects of chitons because they are the most conspicuous features of the outer (dorsal) surface), and the valves commonly have survived as fossils. The approximately bilaterally symmetrical body of a chiton and the tendency for body parts to be repeated along this axis makes references to anatomical features relatively straightforward. The terminal "head" and "tail" valves correspond to the ventral mouth and anus, respectively, with "right" and "left" sides normally referring to the body as viewed dorsally with the head (anterior) valve uppermost. The right versus left distinction is not emphasized, however, because right and left sides are approximately mirror images. Figure 3.1 illustrates the most important distinctions of relevance to the identification of chitons. It should be emphasized that although every effort has been made to avoid reference to features of valves, girdle, and radula that require their disarticulation (separation) to observe, it is not always possible or efficient to identify chitons from outer appearances alone. After first noting salient external features of the intact chiton (especially gills, dorsal coloration, and measurements), the disarticulation of chitons can be accomplished by bringing a specimen to near boiling in clean freshwater to which several potassium hydroxide pellets have been added. The disarticulated valves are pulled apart with fine forceps before the specimen has fallen apart by itself, and then each valve is well rinsed in distilled water. Valves should be stored dry in separate marked vials. Girdle fragments and the radula are pulled gently from the remaining tissue and, after careful rinsing, are either mounted for light or scanning electron microscopy or stored in ethanol for later observation. These procedures will permit a much more careful examination of chiton morphology.

# Systematic Treatment for Polyplacophora Most Likely to Occur in the Santa Maria Basin Area (Following Van Belle, 1983)

- Class Polyplacophora Gray, 1821
  - Order Neoloricata Bergenhayn, 1955
    - Suborder Lepidopleurina Thiele, 1910
      - Family Leptochitonidae Dall, 1889
        - *Leptochiton* Gray, 1847
        - *Oldroydia* Dall, 1894
        - *Hanleyella* Sirenko, 1973
    - Suborder Ischnochitonina Bergenhayn, 1930
      - Family Ischnochitonidae Dall, 1889
        - Subfamily Chaetopleurinae Plate, 1899
          - *Chaetopleura* Shuttleworth, 1853 (*Pallochiton*) Dall, 1879
        - Subfamily Ischnochitoninae Dall, 1889
          - *Lepidozona* Pilsbry, 1892
          - *Ischnochiton* Gray, 1847 (*Stenosemus*) Middendorff, 1847
        - Subfamily Callistoplacinae Pilsbry, 1893
          - *Callistochiton* Carpenter MS, Dall, 1879
      - Family Mopaliidae Dall, 1889
        - *Mopalia* Gray, 1847
        - *Placiphorella* (Carpenter MS) Dall, 1879

# Glossary

**Abanal.** Condition when the largest gill is the most posterior gill of each gill row, located beneath valve 7 or 6 on each side of the foot.

**Adanal.** Condition when the largest gill of each gill row is intermediate, located beneath valve 7 or 6 on each side of the foot, with progressively smaller gills tapering to the posterior and anterior.

**Apophyses** (or **sutural laminae**). Paired anterior projections of the articulamentum layer of valves 2-8 articulating beneath the next valve in series on either side of the midline.

**Apex.** Highest point of each valve coinciding with the midline.

**Articulamentum.** The inner, white to colored and semi-porcelaneous shell layer, generally projecting past the tegmentum on the sides and front of the valves to form the insertion plates and apophyses, respectively.

**Beak.** Central posterior projection when present of the posterior margin of an intermediate valve.

**Central area.** Upper surface of an intermediate valve, lying centrally and sometimes differing in sculpture from each valve's lateral areas.

**Cleft.** Posterior split in the girdle corresponding to a posterior sinus in the tail valve.

**Ctenidium.** Primary molluscan gill as the chiton gill is commonly regarded (excludes the secondary gill lappets found in some molluscs but not chitons).

**Esthete.** Numerous tiny sensory/secretory organs found in the upper exposed tegmental shell layer of all chitons.

**Gill** Multiple feather-like respiratory structures hanging in paired rows from the roof of the pallial groove on either side of the foot, with each gill made up of a main axis bearing alternating series of oval, thin, ciliated laminae, tapering in size towards the proximal tip of the gill.

**Girdle.** Flexible, leathery, muscular integument holding the valves in place, often ornamented with scales, spicules, or hairy processes.

**Granules.** Grain-like elevations of the valve or girdle.

**Hairs.** Lengthy string-like corneous processes of the girdle.

**Head flap.** A greatly expanded anterior girdle margin used for trapping passing prey by some chitons (e.g., *Placiphorella*).

**Head valve.** (or valve 1) The most anterior valve, which generally has a semicircular shape insertion plate. Distal projections of the articulamentum layer of valves 1-8 of most chitons, and which anchor the valves by imbedding into the girdle tissue.

**Insertion plate slit.** Slit-like divisions of the insertion plates, corresponding to the placement of the nerve bundles that innervate the esthetes.

**Insertion teeth.** Unslit parts of the insertion plates.

**Intermediate valves.** Valves 2 to 7, which generally have a similar shape in contrast to the head and tail valves.

**Interspace.** Condition when the left and right gill rows are separated, that is, restricted to the lateral portions of the pallial groove, with the last gill in each row at some distance from the anus. Opposite is no interspace, when each gill row extends to near the anus.

**Jugal area**(or **jugum**). Longitudinal ridge along the midline in the central areas of the intermediate valves, generally referred to only when it has sculpturing distinct from the rest of the central area, as in Acanthochitonidae.

**Jugal lamina** Extension of the articulamentum in the jugal sinus which connects the apophyses.

**Jugal sinus.** Depression between the apophyses.

**Lateral areas.** Paired triangular-shaped regions of the upper valve surface of an intermediate valve that are more or less distinguished from the central area by their often diagonal sculpturing.

**Major laterals.** Second of (normally) eight lateral "tooth" pairs of each of about 30 to 200 rows of the chiton radula; the main functional feeding structures of the radula, conspicuous because of their black, magnetite-capped, cusps.

**Mucro.** Generally used to indicate a small pointed process ending in a sharp rigid point, but normally used in chitons in reference to the "beak" of the tail valve, which is mostly near center or just slightly anterior (subcentral) along the midpoint of the tegmentum's midline, but can also be somewhat posterior or even terminal.

**Pallial groove.** The u-shaped cavity on the lateral and posterior sides of the foot posterior to the oral platform, bounded by the ventral girdle surface, so named because of the presence of paired gill rows in this cavity.

**Plate.** See valve.

**Pleural areas.** Side slopes of the central areas of an intermediate valve (not including the jugal region).

**Post-mucronal slope.** Slope of the midline of the tail valve between the mucro and the girdle, best viewed from a lateral orientation.

**Quincunx.** Arrangement of five entities in a square, having one in each corner and one in the center.

**Radial.** Extending as rays from the center.

**Radula.** Rasp-like ribbon armed with rows of teeth and plates; the characteristic feeding organ of most molluscan groups including all chitons, which normally have 17 teeth (or plates) per row.

**Rib.** Raised bands of sculpturing, commonly in reference to the sculpturing or valves or girdle elements.

**Riblet.** Fine ribs.

**Scales.** Flattened calcareous girdle elements, often superimposed and imbricating as in a coat of armor.

**Slit formula.** The observed number or range of numbers of insertion plate slits, standardly recorded for head/(one side of) intermediate/ tail valves (e.g., 8-10/1/12-14 where 8-10 slits were observed in the head valve, 1 on each side of each intermediate valve, and 12-14 on the tail valve).

**Spicule.** Sharp-pointed, blunt to needle-like, calcareous element of the girdle, small enough to require microscopic examination.

**Spine.** Sharp-pointed calcareous element of the girdle, large enough to be conspicuous to the eye.

**Sutural hair.** Hairs occurring characteristically at the valve sutures.

**Sutural spines.** Clusters of spines occurring characteristically at the valve sutures (e.g., *Acanthochitona*).

**Sutural laminae.** See apophyses.

**Tail valve (or valve 8).** The most posterior valve.

**Tegmentum.** The often brightly colored upper (dorsal) exposed shell layer of chitons, that is partly organic and partly inorganic and can be sculptured with granules, pustules, riblets, or ribs.

**Tubercles** (or **nodules**). Small, nob-like projections.

**Valve.** One of eight shell plates characteristic of chitons.

# Taxa Treated in This Atlas

Species Examined from the MMS Santa Maria Basin Collections:

- *Leptochiton rugatus* (Carpenter *in* Pilsbry, 1892)
- *Hanleyella oldroydi* (Bartsch MS, Dall, 1919)
- *Lepidozona scabricostata* (Carpenter, 1864)
- *Lepidozona retiporosa* (Carpenter, 1864)
- *Callistochiton palmulatus* Carpenter MS, Dall, 1879
- *Mopalia phorminx* Berry, 1919

Additional Species Likely to be Encountered in the Study Area:

- *Leptochiton nexus* Carpenter, 1864
- *Oldroydia percrassa* (Dall, 1894)
- *Chaetopleura* (*Pallochiton*) *gemma* Carpenter MS, Dall, 1879
- *Lepidozona mertensii* (Middendorff, 1847)
- *Lepidozona interstincta* (Gould, 1852)
- *Lepidozona sinudentata* (Carpenter *in* Pilsbry, 1892)
- *Lepidozona willetti* (Berry, 1917)
- *Ischnochiton* (*Stenosemus*) *albus* (Linnaeus, 1767)
- *Callistochiton crassicostatus* Pilsbry, 1893
- *Callistochiton decoratus* Carpenter MS, Pilsbry, 1893
- *Mopalia imporcata* Carpenter, 1865
- *Placiphorella pacifica* Berry, 1919

Does not include species restricted to shallow depths (< 30 m).

# Key to the Polyplacophorans of the Santa Maria Basin

This key should be generally useful for chitons collected from deep water (> 30 m) off the California coast, and may also suffice for those collected further to the north, at least along the coast of Oregon and outer coast of Washington. No key of similar emphasis has been previously published. As for the preceding listing of chiton species likely to be encountered in the study area, the following key does not treat the considerable number of west coast chiton species that are known only from depths of less than about 30 m. There is no up-to-date key available for intertidal and shallow subtidal chitons of southern California, but there are a number of valuable sources (e.g., McLean, 1969; Burghardt and Burghardt, 1969; Smith, 1975; Haderlie and Abbott, 1980; Putman, 1982; Kaas and Van Belle, 1985a, 1985b, 1987, 1990; Kozloff and Price, 1987). There is a small amount of overlap in species that are common along the Baja California coastline, but relatively little with species in the Panamic province further south (Skoglund, 1989). Several reviews of the temperate eastern Pacific members of particular genera have been presented (e.g., Ferreira, 1978, 1979a, 1979b, 1982; Eernisse, 1986; Waters, 1992), but these have tended to emphasize shallow-water species that are largely unrepresented in the present survey.

1A. Girdle much wider in the anterior (head) region than in the posterior (tail) region; oral region with conspicuous cephalic lappets extending anteriorly; tegmentum of intermediate valves at least four times wider than long, and depressed in lateral regions; girdle bristles with many calcareous spicules projecting along their length (not taken in survey material) ........................ *Placiphorella pacifica*

1B. Girdle equally wide in head and tail region; oral region with a simple platform surrounding the mouth; tegmentum of intermediate valves less than four times as wide as long, with straight or convex lateral slopes; girdle bristles, if present, without conspicuous calcareous spicules along their length .................................................................................................................. 2

2A. Conspicuous flexible, golden to dark brown hairs on girdle ........................................................ 3

2B. Girdle with short pointed spicules, small glassy strap-like bristles, slender spines, or scales, but no conspicuous and flexible hairs ........................................................................................ 4

3A. Girdle bristles wispy, many as long as the girdle is wide, each with sparse lateral branches; head valve with about 8-10 heavy radiating ribs, interspersed by one or more radiating rows of shorter but distinct pustules; intermediate valves with the two heaviest ribs defining the extent of each lateral region, again interspersed by one or more radiating rows of shorter but distinct pustules; central areas with distinct longitudinal ribbing, between which is a dense lattice of somewhat irregular and much finer lateral subribs; mucro subcentral; tegmentum usually white (see Figures 3.6 A-D) ............................................................................................................ *Mopalia phorminx*

3B. Girdle bristles stout, mostly shorter than the girdle width, with dense branching along their length giving them a bushy appearance; head valve with about 10 heavy radiating ribs, and intermediate valves with the two heaviest ribs defining the extent of each lateral region, but pustules between these ribs are not set off in well spaced, strictly radial, rows; central areas with distinct longitudinal ribbing, between which is a quite regular lattice of much finer lateral subribs; mucro nearly terminal; tegmentum usually golden (see Figures 3.6 E-H) ................................................ *Mopalia imporcata*

4A. Gill rows without an interspace, with left and right rows forming a nearly continuous curtain in the posterior part of the pallial groove near the anus; tegmentum whitish, tan, or drab grey, but not brightly colored; disarticulated valves without insertion plates ..................................................... 5

4B. Gill rows with an interspace, with left and right rows on either side of the foot and well separated, not extending to near the anus; tegmentum coloration bright or drab; disarticulated valves with insertion plates extending laterally in the intermediate valves, anterior in the head valve, or posterior in the tail valve ..................................................................................................................... 8

5A. Jugal region of each intermediate valve conspicuously raised with its broad anterior end (away from apex) characteristically projecting forward for almost half the length of the next valve's central region; jugum of posterior (tail) valve likewise conspicuously raised and coming to a point at the mucro; valves heavy with coarse, somewhat irregular, patterns of sculpturing; body often much longer than 15 mm, up to a maximum of about 28 mm; girdle encroaching between valves (not taken in survey material) ........................................................................... *Oldroydia percrassa*

5B. Jugal region of the intermediate and tail valves not conspicuously raised relative to the central regions; valves delicate with fine patterns of mostly regular sculpturing; body seldom (if ever) as long as 15 mm, usually less than 10 mm; girdle not encroaching between valves ........................ 6

6A. Lateral regions of intermediate valves and head and tail valves with randomly arranged, rather prominent, pustules, especially at the extreme margins; lateral regions not raised but with sculpturing distinct from the central regions, which have regularly arranged longitudinal rows of much smaller pustules; dorsal side of girdle with many long, smooth, calcareous needles up to 400 µm scattered in tufts among much shorter spicules (see Figure 3.3) .................................... *Hanleyella oldroydi*

6B. Lateral regions of intermediate valves and head and tail valves with uniformly fine granules over entire tegmentum, arranged in regular rows, radiating in lateral areas and longitudinal in central areas, which otherwise are not distinguishable; dorsal side of girdle with small elongate spicules generally less than 70 µm length, longer spines up to 400 µm, if present, not generally occurring in tufts .................................................................................................................................... 7

7A. Postmucronal slope straight; dorsal girdle elements mostly rectangular scales with 13-16 riblets and not longer than about 60 µm, although some ribbed spicules occur, especially in valve junctions; foot may be reddish in living specimens; black caps of major lateral radular teeth unicuspid and quite elongate (see Figure 3.2) ...................................................................... *Leptochiton rugatus*

7B. Postmucronal slope concave; dorsal girdle elements primarily smooth spicules, mostly shorter than 70 µm, with scattered needlelike spines up to at least 400 µm; foot not known to be reddish in living specimens; black caps of major lateral radular teeth bicuspid and only moderately elongate (not taken in survey material) ............................................................................... *Leptochiton nexus*

8A. Head and tail valves with very prominent ribs ........................................................................ 9

8B. Head and tail valves without prominent ribs, although there may be distinct radiating rows of globular tubercles ....................................................................................................................... 11

9A. Tail valve prominently bulging well above the other valves, shaped like a fist; rounded mucro near valve VII and not raised relative to the highly convex postmucronal slope .............. *Callistochiton palmulatus*

9B. Tail valve not prominently bulging, mucro subcentral to terminal, above the postmucronal slope. ......................................................................................................................................... 10

10A. Mucro high and terminal, postmucronal slope nearly vertical; head valve with about seven stout ribs, each with several pustular subribs (not taken in survey material) .......................................... ................................................................................................ *Callistochiton crassicostatus*

10B. Mucro intermediate height and subcentral, postmucronal slope straight to slightly convex; head valve with about eleven scalloped ribs without subribs (not taken in survey material) .................. ........................................................................................................ *Callistochiton decoratus*

11A. Lateral areas of intermediate valves and head and tail valves with weak sculpturing, similar to that of central areas; body length shorter than 20mm ........................................................................ 12

11B. Lateral areas of intermediate valves with rows of prominent round tubercles; head valve and posterior part of tail valve sculptured as in lateral areas; body length sometimes longer than 20mm ........ 13

12A. Girdle scales overlapping but conical and slightly bent, not flattened rectangular, and much longer than wide (170 x 100μm); apophyses not connected by a jugal lamina (requires disarticulation); tegmental coloration white, often smeared with dark deposits, especially along the posterior margins of the valves (not taken in survey material) .................................*Ischnochiton* (*Stenosemus*) *albus*

12B. Girdle scales overlapping and approximately rectangular, wider than tall (170 x 270 μm); apophyses connected by a jugal lamina that is notched where it connects on each side; only occasional specimens are pure white, with other specimens of variable colors including cream, yellow, orange, brown, or olive (not taken in survey material) ........................................................ *Lepidozona interstincta*

13A. Girdle with sparsely scattered small, strap-like glassy bristles (requiring microscopic examination), without imbricating scales; apophyses not connected by a jugal lamina (requires disarticulation); tegmental color orange or, more rarely, green, except for a black, spotted with white, tail valve; typically with tiny black pigment spots scattered across tegmentum (not taken in survey material) ........................................................................................... *Chaetopleura* (*Pallochiton*) *gemma*

13B. Girdle with prominent overlapping scales; apophyses connected by a jugal lamina that is usually notched where it connects on each side; tegmental color varies but tail valve not characteristically black and spotted with white; without tiny black pigment spots in the tegmentum .................... 14

14A. Central areas of intermediate valves with longitudinal to arching diagonal rows of conspicuous but shallow pits, without conspicuous intervening longitudinal ridges; girdle scales small (less than 150 μm), nearly as tall as wide, with faint transverse ridges and not capped by nipples; color of tegmentum usually uniform, and brown but occasionally tan or apricot, or a broadly banded combination of the two (note: tubercles and even central area pitting may be difficult to observe in some specimens; see Figure 3.5) ........................................................................................ *Lepidozona retiporosa*

14B. Central areas of intermediate valves with distinct longitudinal ridges, sometimes with shallow pits in between; girdle scales small (100 μm) to large (450 μm), usually wider than tall, with or without ribbing and with or without nipples at the top ...................................................................... 15

15A. Ridges prominent in all or much of the central areas of intermediate valves, forming a heavy lattice extending across the apex ................................................................................................. 16

15B. Ridges generally indistinct in central part of central areas, not latticed, although lateral portions are latticed ....................................................................................................................... 17

16A. Sculpturing of lateral areas, head valve, and posterior portion of tail valve dominated by regular rows of globular pustules; girdle scales strongly convex, smooth or only weakly striated, crowned with a nipple that is not strongly set apart from the rest of the scale at its base; body length to as large as 50 mm (not taken in survey material) .............................................*Lepidozona mertensii*

16B. Sculpturing of lateral areas, head valve, and posterior portion of tail valve highly variable, from granular irregular to nearly smooth, but usually without regular rows of globular pustules; girdle scales rectangular and only slightly convex with about 10-13 longitudinal striations, not capped by a nipple; body length not usually exceeding 20 mm (not taken in survey material) ....................... ............................................................................................................ *Lepidozona sinudentata*

17A. Head valve with 20-40 ribs; intermediate valves not beaked; girdle scales strongly convex, crowned with a strongly ribbed nipple that rises distinctly from its base (in those scales where it has not been broken off); tegmental color usually uniform reddish brown (not taken in survey material) .......... ........................................................................................................................ *Lepidozona willetti*

17B. Head valve with 32-50 ribs; intermediate valves with small but distinct beak; girdle scales only moderately convex, without a nipple but ornamented with about 15 longitudinal ribs; tegmental color uniform orange brown to creamy white (see Figure 3.4)................ *Lepidozona scabricostata*

# Descriptions of Species

## Family Leptochitonidae Dall, 1889

### Genus *Leptochiton* Gray, 1847

### Subgenus *Leptochiton sensu stricto*

**Type Species:** *Chiton cinereus* Montagu, 1803, not Linnaeus, 1767 (=*Chiton asellus* Gmelin, 1791), by subsequent designation, Gray, 1847.

**Diagnosis.** Small oval to elongate oval bodies, valves rounded and thin, lateral areas hardly elevated, tegmentum finely granulose, with granules in lines or quincunx. Mucro submedian, girdle clothed with small scales, sometimes interspersed with spicules, or wholly spiculose, no insertion plates as in other members of the family, gill rows adanal without interspace, as for other members of the suborder (based on Ferreira, 1979; Van Belle, 1983). [At present, there is no evidence for the monophyly of this assemblage. The approximately 70 members of the subgenus are grouped because they lack the distinctive, much larger, tail valve of subgenus *Parachiton* Thiele, 1909, or the scattered silky hairs that extend between the valves in the monotypic subgenus *Pilsbryella* Nierstrasz, 1905, or the distinctive characteristics of other genera in this family, including *Lepidopleurus* (Leach MS) Risso, 1826, *Oldroydia* Dall, 1894, and *Hanleyella* (see below).]

### *Leptochiton rugatus* (Carpenter *in* Pilsbry, 1892)

Figure 3.2

*Leptochiton rugatus* (Carpenter MS) Dall, 1879 (*nomen nudum*).

*Lepidopleurus internexus* Carpenter in Pilsbry, 1892.

*Lepidopleurus alascensis* Thiele, 1909.

See Ferreira (1979) and Kaas and Van Belle (1985a; 1994) for extensive synonymies.

**Material Examined.** The syntype specimens, and many lots from CAS and personal collections. California: Santa Maria Basin, Phase I Hard-Substrate Station BRA 16 (2 specimens, 91.5-123 m) and Station BRA 20 (2 specimens, 90-130.5 m).

**Description.** Animal to about 16 mm maximum length, with oval to elongate profile; dorsal elevation moderate, with intermediate valve profile well rounded, without central ridge, without beak; tegmental coloration white to cream, occasionally colored brown, black, or orange by environmental deposits; tegmentum sculptured with fine granules, forming fine longitudinal ribs in central areas, and fine radial ribs in somewhat raised lateral areas; articulamentum white, apophyses small, triangular (or truncated in tail valve), and well separated; no insertion plates (as for family); girdle narrow, dorsal surface with rough granular appearance, covered with scales of varying shape, from nearly rectangular (about 60μm long) to elongate blunt curved or straight spicules, with bunches of spicules (about 140 μm long) especially pronounced at valve sutures (these require magnification to observe); radula with unusually large number of closely spaced tooth rows; girdle scales mostly with longitudinal ribbing; gills adanal without interspace (as for suborder), rarely more than 10 per gill row; foot and gills can be dark magenta red color from tissue hemoglobins (at least in shallow-water specimens); major lateral teeth of radula are unicuspid, elongate, and sharply pointed.

**Remarks.** *Leptochiton rugatus* differs from most other chitons, including other typical members of *Leptochiton* (e.g., the European *L. asellus*), in having numerous, closely packed, rows of teeth in its radula. The major lateral teeth are nearly touching and are hook-like, not broad as in most chitons (c.f. the tricuspid major laterals of *L. asellus* and many west coast intertidal chitons). The functional significance and taxonomic distribution of this distinctive radular morphology is mostly unexplored.

Eernisse *et al.* (1988) have documented another interesting attribute of the biology of *L. rugatus*. It had often been observed that *L. rugatus* collected intertidally, typically from the undersides of large boulders buried in anoxic mud, have a reddish- to magenta-colored foot. Eernisse *et al.* demonstrated that this was due to the presence of tissue hemoglobins, which is the first time hemoglobins have been found in chiton tissues apart from their normal presence in the buccal mass (where the radula is produced). They were also observed in the gills. However, red-footed *L. rugatus* have never been reported from subtidal depths. This may be because most subtidal collections are preserved before being examined, which results in loss of the red coloration, but it may also be an indication that the intertidal *L. rugatus* differ in this attribute. If so, this difference could conceivably reflect the habitat difference, or could also indicate that intertidal *L. rugatus* are not the same species as the subtidal ones. There is not much about the valve or girdle morphology that is distinctive, so cryptic species are at least plausible. An obstacle to answering these questions is the generally sporadic occurence of *L. rugatus*. Those interested in pursuing the systematics of *L. rugatus* might also consider intertidally occurring Southern Hemisphere species of *Leptochiton*, also reported to have a red foot (Eernisse *et al.*, 1988). Similar to its wide depth distribution, *L. rugatus* also is reported to have one of the widest geographic distributions known for chitons, with a mostly continuous range extending from the Gulf of California, up the west coast, across the Aleutian Islands, and down to South Korea. Contrary to their earlier (1985a) view, Kaas and Van Belle (1994) have recently concluded that some of the far western Pacific specimens formerly considered by Ferreira (1979b) as *L. rugatus* are instead *L. assimilis* Thiele, 1909. Sirenko and Scarlato (1983) had earlier reached this same conclusion. However, Kaas and Van Belle do not appear to extend this change of view to the South Korean record (Dell'Angelo *et al.*, 1990).

**Figure 3.2.** *Leptochiton rugatus* (Carpenter *in* Pilsbry, 1892). Dorsal view of specimen, 6 mm length, from Bah'a San Luis Gonzaga, Baja California, Mexico.

Chitons all have nonfeeding larvae whose pelagic existence is relatively brief (Eernisse, 1988), and thus do not tend to have as wide of a distribution as marine animals with longer pelagic larval stages (Eernisse, in press). If the reported distribution is accurate, then *L. rugatus* is perhaps the most widely distributed of the rich fauna of chiton species present in the northern Pacific. It would be extremely interesting, albeit difficult to achieve, to apply molecular-based methods of comparison to individuals throughout the range of *L. rugatus*. This would enable an assessment of the degree of genetic continuity between populations living at the extremes of their distribution and at very different depths.

**Type Locality and Type Specimens.** Originally, "Monterey, California, to Todos Santos Bay, Lower California" but restricted to "near S. Tomas River, Lower California," Mexico [31°32'N; 116°26'W], as indicated on a label with the syntypes (Ferreira, 1979). Three syntypes, including 2 intact and one disarticulated (ANSP 35586).

**Habitat.** From the intertidal, sometimes under large boulders submerged in anoxic mud, e.g., San Juan Is., Washington (Eernisse *et al.*, 1988), or with *Stenoplax conspicua* [(Carpenter MS) Pilsbry, 1892] under rocks at Bird Rock, San Diego Co., California (Eernisse, pers. obs.), to at least 453 m (Kaas and Van Belle, 1985a). Present material includes two specimens from 91.5-123 m (Station BRA 16, 34°46.5'N 120°50.2'W) and two specimens from 90-130.5 m (Station BRA 20, 34°46'N 120°50'W).

**Distribution.** In the eastern Pacific, from Magdalena Bay, and most of the Gulf of California, Mexico to Cohen Id., Alaska, and the Aleutian Islands. In the western Pacific, from South Korea, and possibly parts of the Sea of Japan, the Okhotsk Sea, and the Bering Sea (but see Comments below) (Smith, 1947: 6; Jakovleva, 1965: 28; Ferreira, 1979; Putman, 1982: 365; Sirenko and Scarlato, 1983; Kaas and Van Belle, 1985a: 211, but cf. Kaas and Van Belle, 1994: 17; Eernisse *et al.*, 1988; Dell'Angelo *et al.*, 1990: 32; Vermeij, 1990: 349).

## *Hanleyella* Sirenko, 1973

**Type Species:** *Hanleyella asiatica* Sirenko, 1973, by original designation.

**Diagnosis.** Small ovate bodies, valves thin, lateral areas not elevated, tegmentum granulose, granules becoming larger towards outer margins, flat granules in central areas separated from each other by spaces larger than their diameters, apophyses rather large for family, sloping gently towards jugal sinus (front border of valve), girdle clothed with minute spicules and many large hyaline (noncalcareous) spines, no insertion plates as in other members of family, radula with tricuspid major lateral teeth as in many other chiton genera, gill rows adanal without interspace, as with other members of suborder (based on Ferreira, 1979; Van Belle, 1983).

## ***Hanleyella oldroydi* (Bartsch MS, Dall, 1919)**

Figure 3.3

*Lepidopleurus (Leptochiton) oldroydi* Bartsch MS, Dall, 1919: 500.

*Leptochiton oldroydi*; Smith, 1947: 6.

*Hanleyella oldroydi*; Ferreira, 1979: 158; Kaas and Van Belle, 1985a: 190.

**Material Examined.** The holotype specimen; also many lots at CAS. California: Santa Maria Basin, Phase I Hard-Substrate Station BRA 6 (> 10 specimens, 54-63 m) and Station BRA 17 (1 specimen, 160.5-168 m).

**Description.** Very small species, up to 8.2 mm length and 4.3 mm wide, whitish with strong sculpturing; randomly arranged, rather prominent, pustules in lateral regions of intermediate valves, lateral areas otherwise not raised; central regions with much smaller pustules in regularly arranged longitudinal rows; distal extremities of head and tail valves with sculpturing similar to extreme margins of lateral regions of intermediate valves; mucro subcentral, postmucronal slope straight; apophyses small and triangular, except rounded in tail valve; dorsal girdle with many long, smooth, calcareous needles up to 400 µm in small bunches at valve junctions and similar tufts scattered among much shorter (40 to 70 µm) and stouter spicules; ventral side of girdle covered with ribbed, somewhat smaller, scales; radula with up to about 45 mature rows of teeth; major lateral teeth tricuspid, with outer cusps relatively small; about 7 gills per side, with gill rows extending only to about anterior extent of seventh valve.

**Remarks.** This poorly-known species is of small body size but is easy to recognize, due to its characteristic valve sculpturing. It is among the most abundant of the chitons within the study area, as suggested by its numerical dominance in the examined collections. The only other member of the genus, *Hanleyella asiatica*, is mostly a northwestern Pacific species, although Clark (1991) has recently extended its known range to include the Aleutian Islands and southeastern Alaska, about 4,000 km east of its previously known range limit. *H. asiatica* is known to brood its embryos, but nothing is known about the reproductive biology of *H. oldroydi*.

**Type Locality and Type Specimens.** Monterey, California, USA. Holotype (USNM 218767).

**Habitat.** Recorded from 18 m (Ferreira, 1979) to maximum depths of about 200 m (Smith, 1947; Ferreira, 1979). The present material included many tiny specimens from 54-63 m (Station BRA 6, 34°30'N 120°36'W) and a single 6 mm specimen from 160.5-168 m (Station BRA 17, 34°50'N 120°51'W). These records correspond well with the previously reported median depth of about 100 m.

**Distribution.** Cabo San Quint'n, Baja California, Mexico [30°17.7'N; 115°54.7'W] to Kosciusko Island, Alaska [55°57'N; 133°40'W] (Smith, 1947: 6; Ferreira, 1979: 159; Baxter, 1983: 68; Kaas and Van Belle, 1985a: 220).

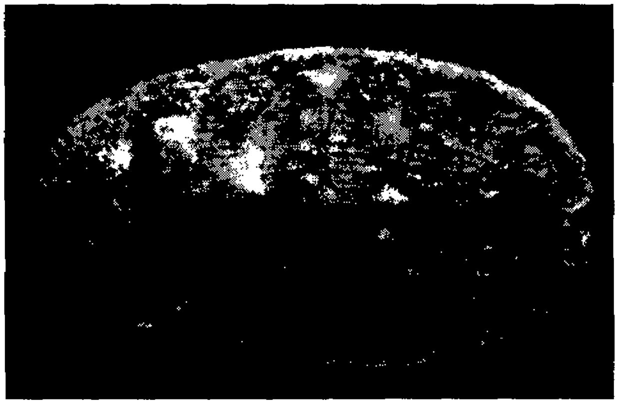

**Figure 3.3.** *Hanleyella oldroydi* (Bartsch MS, Dall, 1919). Dorsal view of specimen, 4 mm length, dredged off Ensenada, Baja California, Mexico.

## Suborder Ischnochitonina Bergenhayn, 1930

### Family Ischnochitonidae Dall, 1889

### Subfamily Ischnochitoninae Dall, 1889

### Genus *Lepidozona* Pilsbry, 1892

**Type Species:** *Chiton mertensii* Middendorff, 1847, by original designation.

**Diagnosis.** Of small to large size, tegmentum usually sculptured with radial rows of pustules or graniferous ribs on end valves and lateral areas of intermediate valves, with longitudinal riblets and often latticed interstices on central areas; slit formula: many/1 or more/many, teeth sharp, somewhat rugose; valves II to VIII with delicately denticulate jugal plate across sinus, separated from apophyses by small notch on each side; girdle scales strongly convex, smooth or striated, in some species with nipple-like prolongation near the top; gill rows adanal with interspace as in subfamily; major lateral teeth of radula with uni- or bicuspid caps as found in some other chiton genera, often with accessory "appendix" tooth near base of mineralized cusp.

### Subgenus *Lepidozona sensu stricto*

**Diagnosis.** Members of subgenus with single-slitted insertion plates of intermediate valves (unlike multi-slitted ones of subgenus *Tripoplax* Berry, 1919) (genus and subgenus diagnoses based on Van Belle, 1983; Kaas and Van Belle, 1987).

### *Lepidozona scabricostata* (Carpenter, 1864)

Figure 3.4

*Ischnochiton subexpressus* (Carpenter MS) Palmer, 1945 (*nomen nudum*).

*Ischnochiton* (*Lepidozona*) *golischi* Berry, 1919.

*Lepidozona inefficax* Berry, 1963.

See Ferreira (1978) and Kaas and Van Belle (1987) for more extensive synonymies.

**Material Examined.** The holotype specimen. California: Santa Maria Basin, Phase I Hard-Substrate Station BRA 2 (2 juvenile specimens, 120-123 m) and Station BRA 21 (1 specimen, 75-90 m).

**Description.** Animal maximumally about 24 mm long, but most specimens much smaller; body profile elongate oval; valves quite elevated; valves unlike most other members of genus in having a small, but distinct, beak; tegmental coloration uniform cream to orange or brown; tegmentum with tiny granules in quincunx arrangement; radiating rows of pustules number 32-50 on head valve, 3-7 in the raised lateral areas of intermediate valves, and about 25 to 40 in the postmucronal region of tail valve; pleural areas with many (10-24) fine longitudinal riblets, often ornamented with transversely oval nodules and not conspicuously latticed in between; jugal region nearly smooth; mucro of tail valve slightly anterior, with slightly concave postmucronal slope; valve slit formula 10-13/1/11-14; insertion plate teeth sharp, separated by distinct slits; eaves solid; articulamentum white; apophyses and jugal laminae quite short in relation to valves; girdle thin with dorsal side colored like tegmentum and covered with small (100 to 220 μm wide) closely overlapping scales; most scales wider than tall, each with about 15 longitudinal ribs; scales not capped with nipple; gills adanal with interspace (as in family) and holobranchial, with about 30 gills per side; major lateral teeth of radula unicuspid with sharp points and no accessory blades.

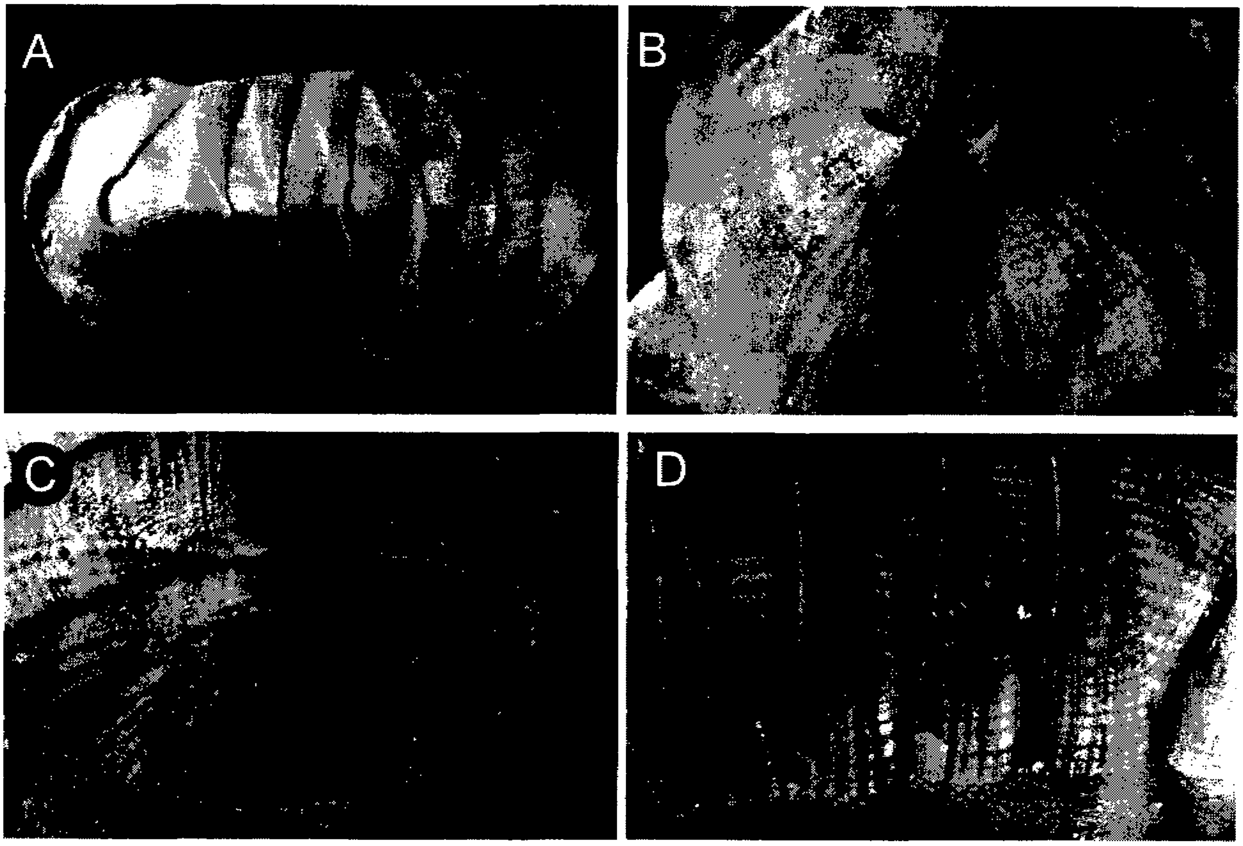

**Figure 3.4.** *Lepidozona scabricostata*, specimen (18 mm length) dredged by fishermen from 340 m on coral, off Carlsbad, California: A, dorsal view; B, head valve region; C, tail valve region; D, lateral areas of intermediate valves and girdle.

**Remarks.** Berry (1925) gave a relatively detailed description of a photographed specimen referred to as *Ischnochiton (Lepidozona) golischi* Berry, 1919 [= *Lepidozona scabricostata* (Carpenter, 1864)]. The holotype and paratype specimens of *I. golischi* were from separate collections at about 600 m off Santa Monica, California. In both these cases, the chitons were living on the stems of coral, and a specimen figured here is from a similar habitat (Figure 3.4, see also Figure 3.5), but there is little indication that *L. scabricostata* is restricted to a coral habitat. Collections of coral from the study area, if they exist, have not been searched specifically for *L. scabricostata*.

**Type Locality and Type Specimens.** Catalina Island, California, United States, 18-36 m. Holotype (USNM 16268)

**Habitat.** Reported rarely from intertidal collections. More common from deeper collections down to 1460 m. Present material includes an adult from 120-123 m (Station BRA 2, 34°11'N 120°28'W), and two tiny juveniles from 75-90 m (Station BRA 21, 34°47'N 120°46'W).

**Distribution.** *Lepidozona scabricostata* is known from collections as far north as the Gulf of Alaska, SW of Lituya Bay (57°50.12'N, 136°48.71'W, 119 m), and from as far south as Sebastian Viscaino Bay, Baja California Norte (Ferreira, 1978: 32; Baxter, 1983: 65; Kaas and Van Belle, 1987: 292; Clark, 1991: 93), but most previous reports are from relatively deep-water collections off southern California. North of Point Conception, it has only been reported from Cape Flattery, Washington, Sitka Sound, Alaska, and the above-mentioned northernmost locality.

## *Lepidozona retiporosa* (Carpenter, 1864)

Figure 3.5

*Leptochiton punctatus* Whiteaves, 1887.
*Ischnochiton aureotinctus* Carpenter in Pilsbry, 1892.
*Ischnochiton venezius* Dall, 1919.
See Ferreira (1978) and Kaas and Van Belle (1987) for more extensive synonymies.

**Material Examined.** The holotype specimen; also many specimens personally collected. California: Santa Maria Basin, Phase I Hard-Substrate Station BRA 25 (2 specimens, 64.5-72 m), and Phase I Soft-Substrate Station BSS 6 (4 specimens, 109 m).

**Description.** Animal small, not exceeding 17 mm long, but most specimens much smaller; body profile oval; valves only moderately elevated, not beaked; uniform tegmental coloration usually cream but sometimes tan or apricot, or broad transverse bands of the latter 2 colors; tegmentum with granules of uniform size in quincunx arrangement on head valve, lateral areas of intermediate valves, and postmucronal region of tail valve; faint ribs 20-30 on head valve, 3-6 on each lateral area, and 10-15 (very faint) on tail valve; lateral areas distinctly raised even though ribs rather weak; all these ribs bear rows of very sparse, small rounded tubercles, sometimes broken off and generally requiring magnification to observe; central areas with longitudinal or diagonally arching rows of shallow pits, separated by slightly higher areas not forming definite ridges; jugal region occasionally eroded, appearing nearly smooth; mucro of tail valve subcentral, postmucronal slope somewhat concave; valve slit formula 8-13/1/8-12; regularly spaced insertion plate teeth indistinctly slit; eaves solid; articulamentum white; apophyses and jugal laminae short, moderately wide; girdle thin with dorsal side colored like tegmentum and covered with small (about 145 µm wide) closely overlapping rectangular scales, each with about 9 longitudinal ribs; scales not capped with nipple; gills adanal with interspace (as in the family) and holobranchial; major lateral teeth of radula bicuspid with outer cusp much longer than inner one and without accessory blade.

**Remarks.** This species is most readily recognized by the pitted appearance of its central areas, and can be mistaken for a member of *Ischnochiton* due to the subtleness of its round tubercles. Ferreira (1978) observed that *L. retiporosa* can sometimes be collected on the same rocks as *L. scabricostata* and *L. willetti*, with all three species colored nearly identically (see also Figs 4-10). Little is known about the biology of this mostly deeper water chiton.

**Type Locality and Type Specimens.** Puget Sound, Washington, United States. Holotype (USNM 4499).

**Habitat.** 0-1463 m. Present material consists of two specimens from 64.5-72 m (Station BRA 25, 35°06'N 120°48'W) and four specimens from 109 m (Soft Substrate Station BSS 6, 35°21'N 121°00'W).

**Distribution.** This species is commonly dredged in Puget Sound (the type locality) and vicinity (Eernisse, pers. obs.) and is known to range as far north as Kenai Peninsula, Kachemak Bay, Alaska (R. N. Clark, pers. comm.), and as far south as the tip of Baja California, Mexico (from Kues, 1974; Ferreira, 1978; Baxter, 1983; Kaas and Van Belle, 1987).

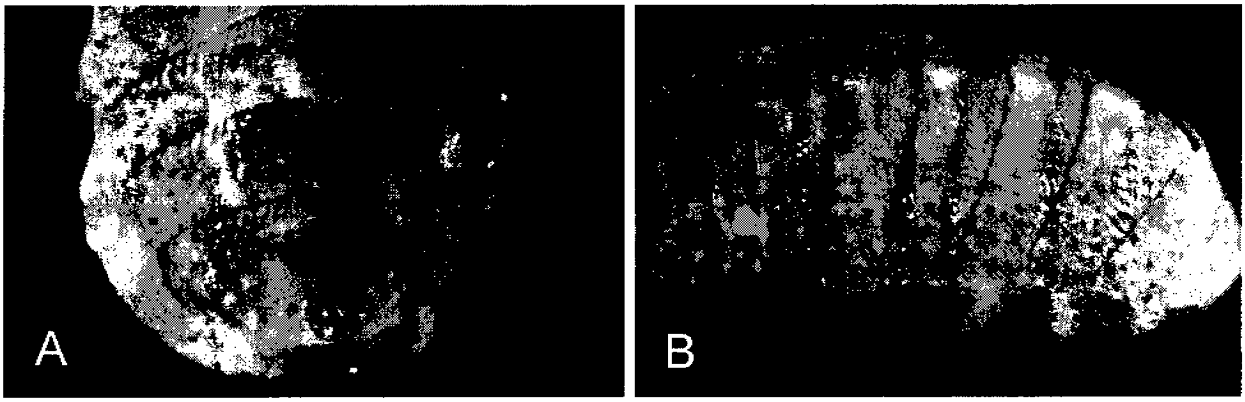

**Figure 3.5.** *Lepidozona retiporosa,* specimen (8 mm length) dredged by fishermen from 340 m on coral, off Carlsbad, California: A, tail valve region; B, lateral dorsal view.

## Subfamily Callistoplacinae Pilsbry, 1893

### *Callistochiton* Carpenter MS, Dall, 1879

**Type Species:** *Callistochiton palmulatus* Carpenter MS, Dall, 1879, by monotypy.

**Diagnosis.** Small to medium length, elongate-oval to elongate; tegmentum strongly sculptured with heavy radial ribs on end valves and lateral areas of intermediate valves; slit formula: many/1/many; incisions of insertion plates generally correspond in number and position to radial ribs; teeth sharp, usually thickened at edges of slits, sometimes peculiarly scalloped; eaves solid; apophyses separated; shell eyes absent; girdle rather narrow; differs from only other genus in subfamily, *Ceratozona* Dall, 1882, by it's girdle, generally clothed with scales, sometimes interspersed with spines and spicules, or nude with series of bristle-bearing pores; without peculiar corneous spines found in *Ceratozona*; gill rows adanal with interspace as for other members of this and several other families (based on Van Belle, 1983).

### ***Callistochiton palmulatus*** **Carpenter MS, Dall, 1879**

*Callistochiton palmulatus* Carpenter *in* Pilsbry, 1893 var. *mirabilis* Pilsbry, 1893.
*Callistochiton acinatus* Dall, 1919.
*Callistochiton celetus* Dall, 1919.
*Callistochiton connellyi* Willett, 1937.
See Ferreira (1979a) and Kaas and Van Belle (1994) for more complete synonymies.

**Material Examined.** Specimens from the private collection of G. A. Hanselman. California: Santa Maria Basin, Phase I Hard-Substrate Station BRA 6 (3 specimens, 54-63 m).

**Description.** Small, up to 16 mm long; oval to elongate oval in shape, becoming increasingly elongate, high spired with increasing size; intermediate valve slopes with convex, rounded profile; not beaked; tegmental color greyish tan to rusty brown; most easily distinguished from other members of *Callistochiton* by distinctive fist-shaped bulging tail valve, with anterior mucro and extremely convex postmucronal slope (premucronal slope is actually concave); tail valve is considerably elevated relative to other valves, but less so in smaller specimens; head valve somewhat more than semicircular with a strongly convex front slope; valves heavily sculptured, particularly in larger specimens; ribs typically with 9 on head valve, 2 on each lateral area of intermediate valves, and about 5 or 6 on tail valve; these ribs extremely pronounced, pustulose; central areas with about 15 longitudinal latticed riblets per side; riblets in jugal region diverge toward anterior margin, forming V-shaped pattern; articulamentum white to light grey; apophyses about one quarter length of tegmentum, connected by an unnotched jugal lamina; valve slit formula 9-11/1/more than 20; slits correspond to ribs on head, but not tail, valve; valve insertion plate teeth thick, short, and quite rounded on tail valve; girdle very thin, with dorsal surface colored somewhat more deeply than drab valves; dorsal girdle elements small, oval to rectangular, overlapping scales, nearly twice as wide as high, about 130 µm wide, with about 11 longitudinal riblets; gills holobranchial (the distinction between adanal and abanal difficult to discern in *Callistochiton*); major lateral teeth of radula bicuspid, with longer outer cusp than inner one.

**Type Locality and Type Specimens.** Santa Barbara, California, United States. Ferreira (1979a), designated a neotype, PRM 48. The specimen has been figured by Palmer (1958: fig. 1).

**Habitat.** Occurring intertidally to approximately 100 m. Present material consists of three specimens from 54-63 m (Station BRA 6, 34°30'N 120°36'W).

**Distribution.** Continuously distributed between Buckhorn Creek, Mendocino Co., California (27° N) and San Pablo Point, Baja California (39°N) (from Oldroyd, 1927: 894; Abbott, 1974: 399; Ferreira, 1979a; Putman, 1982: 365; Kaas and Van Belle, 1994: 170).

## Family Mopaliidae Dall, 1889

### *Mopalia* Gray, 1847

**Type Species:** *Chiton hindsii* Sowerby in Reeve, 1847, by subsequent designation, Gray, 1847.

**Diagnosis.** Small to large size, valves normal in proportion, slit formula: ± 8/1/sinus + 2, girdle slightly dilated at the sides, covered with diverse chitinous productions but lacking scales, gill rows abanal with interspace as for other genera in this and certain other families.

### ***Mopalia phorminx* Berry, 1919**

Figure 3.6 A-D

**Material Examined.** The holotype specimen and other lots at SBMNH. California: Santa Maria Basin, Phase I Hard-Substrate Station BRA 4 (1 specimen, 168-237 m) and Station BRA 21 (1 juvenile specimen, 75-90 m).

**Description.** Animal up to 20 mm long, usually smaller; body profile elongate oval; dorsal elevation moderate; side slopes straight; valves not beaked; tegmentum whitish tan overall, but mottled with yellow and brown; tegmental sculpture quite pronounced, with about 8-10 pustular ribs on head valve, interspersed by 1 or more radiating rows of shorter but distinct pustules; unraised lateral areas of intermediate valves have 2 ribs similar to those of head valve, again interspersed with 1 or more rows of smaller pustules;

relatively small tail valve with one similar, laterally directed rib per side; central areas of intermediate valves with many well distinguished longitudinal latticed ribs; mucro of tail valve somewhat posterior of the midpoint, with more or less straight postmucronal slope; girdle with long wispy bristles, longer than girdle width, each with sparse lateral branches; dorsal surface of girdle also covered with small calcareous blunt spicules, up to 100 μm long; gills abanal with interspace (as for family), gill rows extending about two-thirds of length of foot, about 14 gills per side (holotype); major lateral teeth of radula tricuspid with middle cusp longest.

**Remarks.** Scott *et al.* (1990) designated the specimen at SBMNH as lectotype, but there appears little reason to doubt that the specimen in question is the holotype (Kaas and Van Belle, 1994). This is an uncommon species about which little is known. Specimens from Alaska closely resemble the present material. *Mopalia phorminx* (Figures 3.6 A-D) is superficially similar in morphology to *M. imporcata* (Figures 3.6 E-H), with which it cooccurs.

**Type Locality and Type Specimens.** Monterey Bay, California, United States, 62 m. Holotype (SBMNH 34388).

**Habitat.** 18 to 183 m. Present material consists of an adult specimen from 168-237 m (Station BRA 4, 34°28'N 120°40'W) and a juvenile from 75-90 m (Station BRA 21, 34°47'N 120°46'W).

**Distribution.** There have been sporadic collections of *Mopalia phorminx* as far north as Naked Island, Prince William Sound, Alaska, and as far south as San Pedro, California (from Abbott, 1974: 403; Baxter, 1983: 67; Clark, 1991: 94; Kaas and Van Belle, 1994: 259).

## Acknowledgements

George Hanselman generously provided photographs, including all those used herein not otherwise credited, as well as many others that were useful in making identifications and key distinctions; Roger Clark provided much valuable consultation. The following curators provided access to collections that were useful to this study: George Davis, ANSP; James McLean, LACMNH; Terry Gosliner, CAS; Bob Hershler and M. G. Harasewych, USNM; and Henry Chaney and Paul Scott, SBMNH. Part of this study was completed while the author was Visiting Scientist at the Smithsonian Institution, Laboratory of Molecular Systematics.

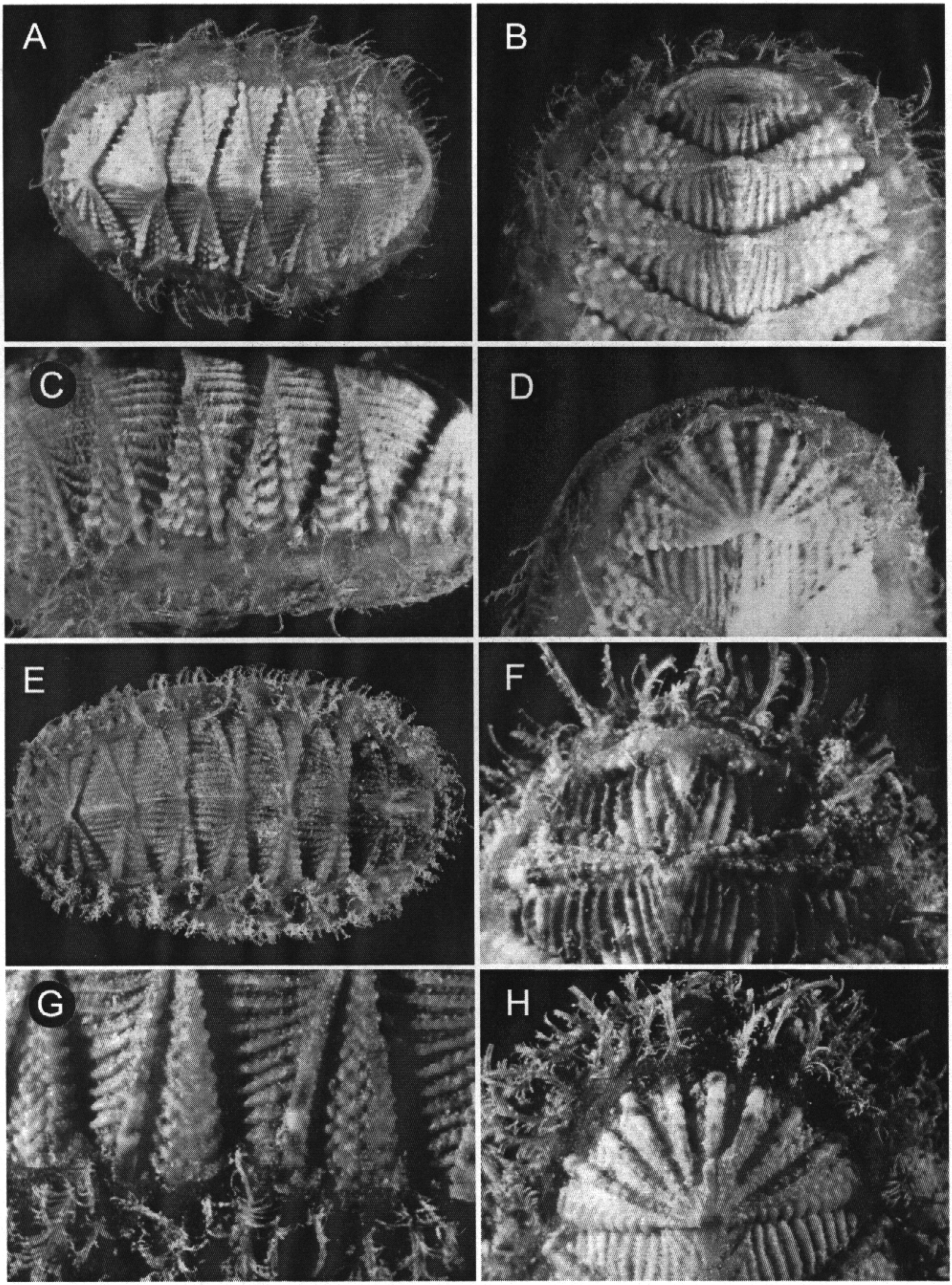
A
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**Figure 3.6.** *Mopalia phorminx*, specimen from Gulf of Alaska, 10 mm length: A, dorsal view of specimen; B, close-up of tail valve region; C, lateral areas of intermediate valves; D, head valve region. *Mopalia imporcata*, specimens from Port Gamble, Washington: E, dorsal view of specimen of 11 mm length; F, close-up of tail valve region of 17 mm long specimen; G, lateral areas of intermediate valves of same specimen as F; H, head valve region of same specimen as F.

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# 4. CLASS SCAPHOPODA

by

Ronald L. Shimek[1]

## Introduction

Scaphopods are bilaterally symmetrical mollusks that are enclosed in a tubular curved shell with openings at both ends. The shell is secreted by the mantle, which surrounds the entire animal enclosing the mantle cavity. Although the derived anatomical orientation is different, functionally the large aperture and the foot are anterior, the narrow apex posterior, the concave side dorsal, and the convex side ventral. These functional orientations are used in the text.

Within the mantle cavity, the feeding tentacles or captacula originate from folds lateral to the base of the proboscis or buccal pouch on the reduced head. The foot extends from the anterior aperture for burrowing (Lacaze-Duthiers, 1856-57; Morton, 1959; Fisher-Piette and Franc, 1968) and the captacula emerge from the same aperture during feeding (Morton 1959, Dinamani 1964a, 1964b; Poon, 1987; Shimek, 1988) (Figure 4.1).

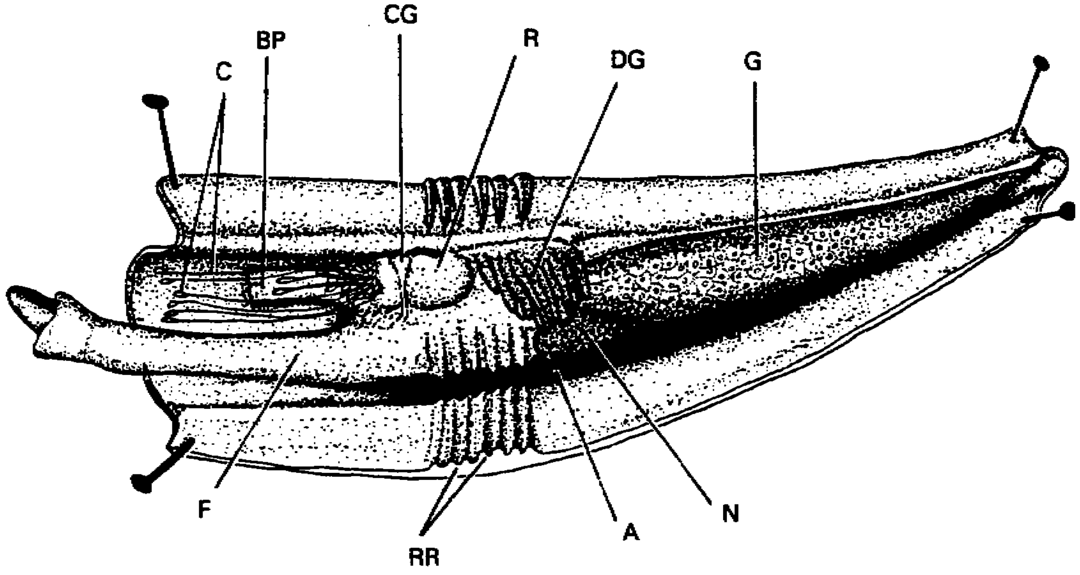

**Figure 4.1.** Semi-diagrammatic illustration of a dentaliid scaphopod with the shell removed, and the mantle reflected as if cut with a scalpel. Major organs and structures are labelled. A = Anus; BP = Buccal Pouch; C = Captacula; CG = Cerebral Ganglia; DG = Digestive Gland; F = Foot; G = Gonad; N = Nephridium; R = Radula; RR = Respiratory Ridges.

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The visceral mass extends to the shell apex and is not coiled or folded. The radula is relatively massive and heavily mineralized (Morton, 1959; Vouvelle and Grasset, 1983; Shimek, 1990). The mouth is located terminally on a short buccal pouch, or proboscis, inside the mantle cavity. The short esophagus extends to a relatively large stomach opening into one or two digestive glands. The coiled intestine leads to the anus near the middle of the body (Lacaze-Duthiers, 1856-57; Morton, 1959; Taib, 1981a).

No eyes, osphradia, or ctenidia are found. The mantle has numerous sensory cells and some discrete sense organs (Steiner, 1990). The nervous system resembles that of bivalves, but is more elaborate. While the open circulatory system is relatively large, the heart consists of only a single ventricle (Steiner, 1990). Excretory organs are present, but the renopericardial connection to them is unclear (Reynolds, 1990). The sexes are separate (Wada, 1968).

One or two pairs of dorsal retractor muscles attach subapically to the shell and give rise to the pallial and pedal musculature. The pedal and retractor musculature and the relative hemocoelic volumes are different in the two orders, and the action of the foot is correspondingly different. In the Order Dentaliida, the foot is extendable and functions as a muscular hydrostat, while in the Order Gadilida the foot is introvertable and hydraulic (Figure 4.2 A-B).

The gross anatomy of scaphopods is relatively well known. The early investigations of Lacaze-Duthiers (1856-57) on the anatomy and embryology of *Antalis* (= *Dentalium*) *dentalis* are the basis for all subsequent work. A substantial body of work from the late nineteenth century elaborated on the work of Lacaze-Duthiers and lead to the basic understanding of scaphopod morphology (Fol, 1889; Pelseneer, 1891; Plate, 1892; Leon, 1894; Boissevain, 1904). Simroth (1894a, b), erected the Class Scaphopoda.

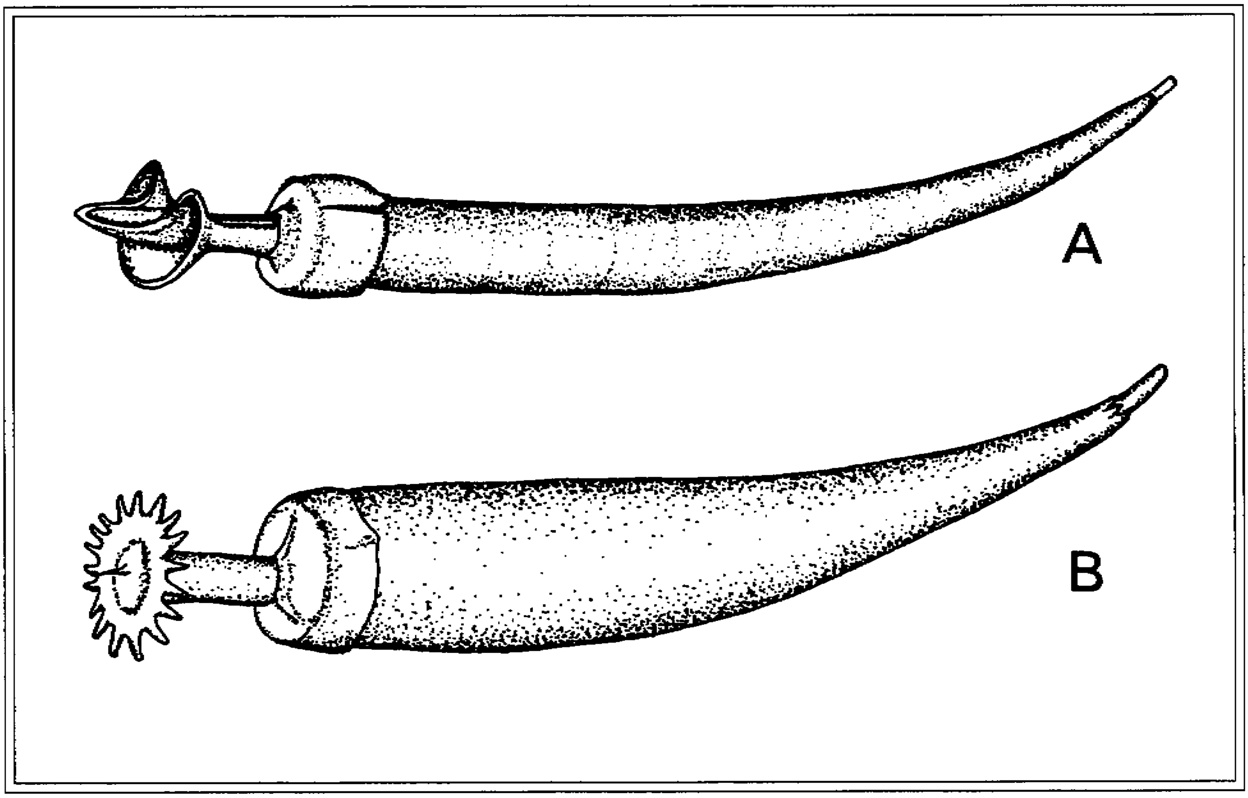

**Figure 4.2.** Generalized Scaphopods. A. Dentaliid scaphopod with the foot extended and the epipodial lobes extended; B. Gadilid scaphopod with the foot extended, note the foot's terminal disc.

More recent investigations have focused on the cellular and fine structure of individual tissues, organs, and organ-systems within individual taxa (Gabe, 1949; Gabe and Prenant, 1950a, b; Arvy and Gabe, 1951; Sahlmann, 1973; Taib, 1976, 1981a, b; Reynolds, 1988, 1990; Steiner, 1990, 1992; Shimek and Steiner, in preparation). Recently, Steiner (1990) has completed comparative ultrastructural and morphological investigations across the entire Class Scaphopoda. This work will undoubtedly lead to a more thorough understanding of scaphopod functional morphology (Shimek and Steiner, in press) and will likely result in a systematic revision of the Class.

Scaphopod gametes have been extensively used in developmental research since the early part of the twentieth century, (Wilson, 1904; Van Dongen and Geilenkirchen, 1974a, 1974b, 1974c, 1975; Dufresne-Dube *et al.* (1983). However, except for one or two species of dentalids, little is known about the larval development of scaphopods.

Scaphopods are entirely marine, and live in unconsolidated sediments. About 300 extant species have been described, of which, about 25 have been described from the west coast of North America. Scaphopods are found from the low intertidal to abyssal depths (Knudsen, 1964) and, while very common in some shallow water communities, (Shimek, 1989, 1990), they are more diverse in deeper waters (≤500 m) (Scarabino, 1979).

Although dentaliid scaphopods have been known to eat foraminiferans and other small shelled prey (Morton, 1959; Dinamani, 1964a, b), quantitative data on feeding has only recently been obtained (Gainey, 1972; Bilyard, 1974). The first account of the feeding behavior of any gadilid was published by Poon (1987). Shimek (1988) provided additional quantitative data on gadilid and dentaliid feeding. Shimek's (1990) detailed analysis of comparative dietary and habitat resource utilization of several sympatric scaphopod species provided the first evidence of the ecological role of these predators.

Scaphopod systematics is in a state of flux. The comprehensive conchological and systematic treatments by Pilsbry and Sharp (1897-98) and Henderson (1920) have been the basis for all subsequent work. In a series of papers, Emerson (1951, 1952, 1962) revised and clarified basic scaphopod systematics. Starobogatov (1974) and Palmer (1974) separately elevated the families Dentaliidae and Siphonodentaliidae (now Gadilida) to ordinal rank. Kraeuter (1971), Chistikov (1975), Emerson (1978), and Scarabino (1979) are other important contributors to scaphopod classification on the generic and family level. Steiner (1990, 1992) has clarified many of the differences between the two orders, and further substantial revisions to the class will likely result.

## Glossary

**Apertural tube**. A thin cylindrical tube produced as a secondary shell by the mantle of the dorsal or apical aperature in scaphopods.

**Buccal pouch**. Lateral pouches or extensions of the buccal tube or proboscis in scaphopods; used to store captured prey prior to maceration.

**Captaculum** (plural = **captacula**). Scaphopod sensory and food capturing tentacles consisting of a slender stalk and a terminal bulb with a central pit or alveolus. Captacula adhere to a food item and pull it into the mantle cavity.

**Digestive or midgut glands (=glandular pouches** from the molluscan stomach). Site of most digestion. In the scaphopod order Dentaliida there are two glands (one on each side) in the order Gadilida, only one gland, on the left side, is found.

**Mantle**. Specialized epithelial and epidermal layer in the Mollusca that secretes the shell.

**Mantle cavity**. In molluscs, this cavity is formed internal to the mantle and contains the mouth, excretory aperatures, gonadal aperatures, as well as the respiratory structures. In scaphopods, the mantle cavity is tubular and open at both ends.

**Obsolete**. A term used to describe shell sculpture in molluscs, meaning that the sculpture becomes indistinguishable form the background ornamentation.

**Osphradia**. Molluscan chemosensory organ; lacking in scaphopods.

**Pallial musculature**. Musculature of the mantle in molluscs.

**Pedal musculature**. Musculature of the foot in molluscs. In the scaphopod Order Dentaliida, this musculature is continued into the body wall musculature, while in the Order Gadilida, this musculature continues as the dorsal retractor muscles.

**Proboscis**. In scaphopods, the cylindrical tube formed from the tissue posterior to the lips to the bulbous region of the radula; also known as the **buccal tube**, it generally contains the buccal pouches used to store prey.

**Radula**. The molluscan trituration or rasping structure. Formed in a ventral diverticulum of the foregut, it consists of secreted teeth on a basal ribbon. In scaphopods, it is relatively large and highly mineralized with calcium and iron salts.

**Renopericardial connection**. The typical molluscan connection between the exretory tissue and the pericardium.

**Retractor musculature**. In molluscs, the musculature connecting the foot to the shell. Contraction of this musculature pulls the foot into the shell.

## Systematic Treatment for the Santa Maria Basin Area

(Following Steiner, 1990)

Class Scaphopoda Bronn, 1862

Order Dentaliida DaCosta, 1776
- Family Dentaliidae Gray, 1834
  - *Antalis* H. and A. Adams, 1854
  - *Dentalium* Linnaeus, 1758
  - *Fissidentalium* Fischer, 1885
- Family Rhabdidae Chistikov, 1975
  - *Rhabdus* Pilsbry and Sharp, 1897

Order Gadilida Starobogatov, 1977
- Family Gadilidae Stoliczka, 1868
  - *Gadila* Gray, 1847
  - *Siphonodentalium* M. Sars, 1859
  - *Cadulus* Philippi, 1844
- Family Pulsellidae Scarabino, 1982
  - *Pulsellum* Stoliczka, 1868

# Taxa Treated in This Atlas

**Species Examined from the MMS Santa Maria Collections**

*Dentalium vallicolens* Raymond, 1904
*Rhabdus rectius* (Carpenter 1864)
*Cadulus tolmiei* Dall, 1897
*Gadila aberrans* (Whiteaves 1887)
*Siphonodentalium quadrifissatum* (Pilsbry and Sharp 1898).

**Additional Species Likely to be Encountered in the Study Area**

*Antalis pretiosum* (Sowerby 1860)
*Dentalium neohexogonum* (Pilsbry and Sharp 1897)
*Fissidentalium megathyris* (Dall, 1890)
*Fissidentalium erosum* Shimek and Morens, 1996
*Cadulus californicus* (Pilsbry and Sharp 1898)
*Gadila perpusillus* (Sowerby, 1832)
*Pulsellum salishorum* Marshall, 1980

# Key to the Scaphopods of the Santa Maria Basin

1A. Shell length commonly exceeding 2 cm; median radular tooth twice as wide as long; foot extendable with more-or-less conical tip ........ 2

1B. Shell length commonly less than 2 cm; median tooth of radula nearly as long as wide, may be very small compared to other teeth; foot an introvert with expandable disklike tip ........ 8

2A. Shell without longitudinal or linear sculpture; annular sculpturing or lines may be present ........ 3

2B. Shell has longitudinal or linear sculpture, at least near narrow, apical, end of shell; surface of shell sometimes severly eroded, but sculpture found in uneroded areas ........ 5

3A. Shell robust, thick, white, without longitudinal or linear sculpture, but with obvious annular markings; if apical end intact, narrow slit may be present ........ *Antalis pretiosum*

3B. Shell thin, often fragile, white to tan, often showing healed fractures or evidence of surface erosion . 4

4A. Shell nearly straight, white; very fragile, uneroded shell smooth, not glossy; juvenile shell smooth without sculpture ........ *Rhabdus rectius*

4B. Shell nearly straight, beige to tan; uneroded shell glossy; if juvenile shell present, with longitudinal striations or ridges ........ *Dentalium vallicolens*

5A. Longitudinal shell sculpture with 6 major ribs or ridges, and often many smaller secondary ribs continuing to anterior aperture; although ribs may appear rounded or blunt at aperture; shell white ........ *Dentalium neohexogonum*

5B. Longitudinal shell sculpture consists of 7 or more major ribs ........ 6

6A. Longitudinal shell sculpture with 7 or more major ribs or ridges starting at apical end and continuing anteriorly only short distance; anteriorly ribs become less distinct and fine striae or lines appear between them; fine striae may continue to anterior aperture but may require magnification to be observed; shell long and narrow, somewhat fragile; shell nearly straight, beige to tan; uneroded shell glossy ........ *Dentalium vallicolens*

6B. Longitudinal shell sculpture with numerous incised ribs running length of shell; shell robust and large, often more than 6 cm long; ventral aperture 1 cm in diameter. Found in deep water, generally in excess of 500 m. ........ 7

7a Total length of preserved, unrelaxed soft parts more than one-half total shell length; surface of shell with little erosion, ventral aperture round, shell white, but may have brownish adherent periostracum or organic layer ........ *Fissidentalium megathyris*

7b Total length of preserved, unrelaxed soft parts less than one-half total shell length; surface of shell with considerable erosion, particularly near posterior (apical end), ventral aperture wider than high, shell white, but may have blackish adherent periostracum or organic layer ........ *Fissidentalium erosum*

8A. Shell widest at aperture ........ 9

8B. Shell widest posterior to aperture ........ 12

9A. Apex of shell with 4 small slits and lobes; shell white although ovary may be pink in mature animals ........ *Siphonodentalium quadrifissatum*

9B. Apex of shell without 4 small slits and lobes ........ 10

10A. Shell smooth or eroded, but not polished or glossy ........ *Pulsellum salishorum*

10B. Shell glossy, highly polished ........ 11

11A. Shell obviously wider (more than 1.75 times as wide) at aperture than in middle third of shell ........ Juvenile *Cadulus* spp.

11B. Shell only slightly (less than 1.5 times as wide) wider at aperture than in middle of shell ........ Juvenile *Gadila* spp.

12A. Widest point in middle third of shell; shell either decidedly swollen or not noticeably enlarged ........ 13

12B. Widest point in anterior third of shell; shell only slightly wider posterior to aperture than at aperture, not noticeably swollen, maximum width generally about one sixth or less total length; length generally less than 1 cm ........ 15

13A. Shell swollen, widest part of shell very evident, maximum width about one fifth or more of total length; apex of shell may have lobes; ovary brown; length often more than 1 cm ...................... 14

13B. Shell slender, widest part only slightly wider than aperture; maximum width less than one fifth total shell length; apex of shell with 4 small slits and lobes, shell white although ovary may be pink in mature animals ....................................................................... *Siphonodentalium quadrifissatum*

14A. Shell robust, white, opaque; without lobes around apical aperture ................................................. ............................................................................................................... *Cadulus californicus*

14B. Shell thin, hyaline, transparent or translucent in living animals; with 0-7 lobes around apical aperture ...................................................................................................................... *Cadulus tolmiei*

15A. Shell narrows sharply to aperture; aperature can appear constricted ............................................... ............................................................................................................... *Gadila perpusillus*

15B. Shell narrows gradually to aperture and only slightly narrower than widest point of shell ............ ................................................................................................................. *Gadila aberrans*

## Descriptions of Species

For the descriptions, a typological descriptive approach was used and supplemented by a quantitative shell morphometric analyses that was based on the mathematical properties of shell shape (Raup 1964). The morphometric analyses ideally require "perfect" undamaged shells. Such shells are rare, and to increase statistical reliability, it was necessary to examine and measure shells with minor fractures, apertural lip breaks, and apical fractures. I tried to be as conservative in the use of these shells as possible, but their use undoubtedly increases variance into the analyses. In each description, the heading "Material Examined" refers only to those shells actually measured. For each species, numerous other individuals were actually examined. Three morphometric indices were used for the majority of the descriptions, for detailed derivations of the indices and measurements, see Shimek (1989).

The three principal morphometric indices are:

Whorl Expansion Rate: $$Ws = \frac{LTot^{\frac{1}{a\tan\left(\frac{(arc)}{LTot-Larc}\right)}}}{\sqrt{(LTot-Larc)^2+(arc)^2}}$$

Width Index: $$WI = \frac{\ln(ApW + 1)}{\ln(W\max + 1)}$$

Length Index: $$LI = \frac{\ln(LW\max + 1)}{\ln(LTot)}$$

Where: Ltot = Total Length

LWmax = Length from anterior aperture to the maximum shell width

Wmax = Maximum shell width

ApW = Aperture width

arc = Maximum perpendicular distance from the chord connecting the dorsal margin of the posterior aperture to the dorsal margin of the ventral aperture.

Larc = Distance from the apex to the point were "arc" is measured.

The mean and standard deviations of the indices or measurements were computed, with the exception of Ws, the whorl expansion rate. The whorl expansion rate is a logarithmic function and calculations of this index are sensitive to small changes of shape. I used the mean of the natural logarithm of this index for comparative purposes. The mean of a logarithmically transformed numerical array is the median of the untransformed array. The median is a better indicator of the central tendency of that array than is the mean as it is less sensitive to extreme values (Sokal and Rohlf, 1981). The mean Ws is also given for comparative purposes. The morphometric indices were compared between and within populations to assess variance, by the use of standard statistical graphics software (STSC, 1986-91). Any significant differences were noted in the discussions.

## Order Dentaliida DaCosta, 1834

### Family Rhabdidae Chistikov, 1975

### Genus *Rhabdus* Pilbury and Sharp, 1897

**Type Species**: *Dentalium rectius* Carpenter, 1864.

**Diagnosis**. Shell almost perfectly straight, very slender, regularly tapering toward apex, thin, and very fragile, translucent and almost colorless except where heightened by erosion. Sculpture none, with growth-striae being nearly or quite invisible except where slight surface erosion has traced them. Aperature hardly oblique, circular. Anal orifice circular, but apparently without true slit or notch.

### ***Rhabdus rectius* (Carpenter, 1864)**

Figure 4.3

*Dentalium rectius* Carpenter, 1864:603, 648.—Pilsbry and Sharp, 1897:113-114.—Grant and Gale, 1931:437.

*Dentalium dalli* Pilsbry and Sharp 1897:114-115.

*Dentalium watsoni* Pilsbry and Sharp 1897:113.

**Material Examined**. California, Santa Maria Basin, Sta. 61 (5); Sta. R-2 (4); Sta. PJ-9 (2).—British Columbia, Barkley Sound, Vancouver Island, specimens from 4 localities: Mayne Bay, 35-40 m, Imperial Channel, 75-80 m, Trevor Channel, 30-110 m, Sarita Bay, 150-350 m (483) (Shimek, 1989).

**Description**. Shell slender, tapering, fragile, slightly curved; but adult shells appearing straight; shell translucent to transparent in juveniles, relatively opaque in adults (shell length 30 mm). Shell chalky, not polished; ventral (= oral or anterior) aperture round, perpendicular to longitudinal axis of shell; annular growth lines prominent; dorsal aperture often showing signs of healed fractures and decollation (Reynolds, 1992), and sometimes with secondary apertural tube. Adult size indeterminate; specimens with total length over 75 mm uncommon, specimens over 130 mm rare (Figure 4.3).

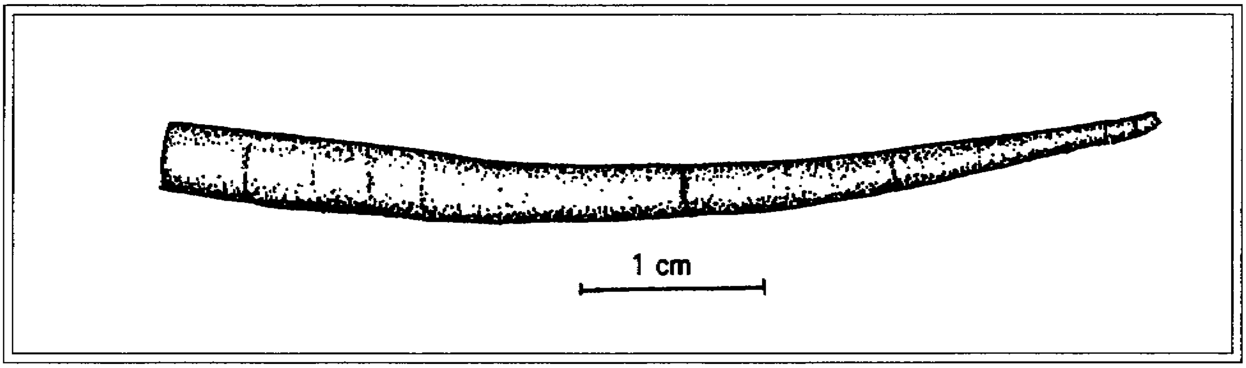

**Figure 4.3.** *Rhabdus rectius* (Carpenter, 1864).

*Shell Morphometric Indices* (Shimek, 1989). Shell maximum width/length to shell ratio = 0.072 ±0.39, ln(Ws) = 14.86 ± 7.00 (Ws = $2.8 \times 10^6$); WI = 1, and LI = 0, as aperture is widest portion of shell. Santa Maria Basin Specimens: Shell maximum width/length to shell ratio = 0.070 ± 0.07, ln(Ws) = 17.10 ± 11.09 (Ws = whorl expansion rate = $1.6 \times 10^{20}$); WI = 1, and LI = 0, as aperture widest portion of shell.

*Externally Visible Soft-part Morphology.* Mantle dull milky-white; radula dark; digestive gland functionally dorsal. Mantle a circular opening when extended from ventral aperture. Mantle often forming dorsolateral folds, with foot extending through opening. Mantle sometimes protruding several millimeters beyond dorsal aperture in adult (shell length > 10 mm). No consistent sexual differences in shape of "pavillon," or tube formed from the dorsal mantle edge, visible in living animals. Foot extendable for about 5-10 mm in adults, dentaliform, with central projection and epipodial lobes; lateral margins of epipodial lobes smooth. Captacula numerous, several hundred in adults, extendable to 5+ mm; terminal bulb densely ciliated, stalk arranged in linear band (visible with magnification) (Shimek, 1988).

*Visible Internal Morphology.* In juveniles with thin shells, radula visible through shell, brownish to black, highly mineralized. Cerebral ganglia visible through shell ventral (= anterior) to radular mass, pinkish. In adult animals with thicker shells, above features may not be visible, but following features generally apparent: digestive gland dark brown to black, prominent, visible through the shell; gonads visible through adult shells, brilliant white in males, yellow (ova) in females (Hebert, 1986).

*Internal Morphological Characters.* Radula large for size of animal; radular formula 1-1-1-1-1; marginal teeth large, platelike; lateral teeth rounded, with cusps, central tooth large; all teeth mineralized with iron and calcium salts.

**Biology**. *Rhabdus rectius* eats a wide variety of food items including sediment, fecal pellets, kinorhynchs, and various invertebrate eggs, however, foraminiferans are the most numerous prey. *Rhabdus rectius* is a sediment generalist, however, it is most abundant in silty areas with more than about 5% organic material by weight. In British Columbia, the species ranged in abundance from about 5 animals per $m^2$ in clean sand, to about 66 animals per $m^2$ in silt. Foraminiferans were rare where it was most abundant.

**Type Locality and Type Specimens.** Holotype USNM (5283); Puget Sound, Washington.

**Distribution**. Peru to Alaska; Cook Inlet (Pilsbry and Sharp 1897-98; Keen 1971; Baxter 1987).

## Family Dentaliidae Gray, 1834

### Genus *Antalis* H. and A. Adams, 1854

**Type Species**: *Dentalium entalis* Linnaeus, 1758.

**Diagnosis**. Shell circular or polygonal in section, with longitudinal ribs or striae at least in juveniles, although these sometimes lacking in adults, or found only near the apex; apex generally with V-shaped notch at or near convex side, sometimes with solid plug and central short tube or orifice. Foot with epipodial sheath. Shell greatest in diameter at anterior (= ventral) aperature.

**Remarks**. No species of *Antalis* were encountered in the Santa Maria Basin collections. However, it is likely that *A. pretiosum* is present. See the key for differential characters.

### Genus *Dentalium* Linnaeus, 1758

**Type Species**: *Dentalium elephaninum* Linnaeus, 1758.

**Diagnosis**. Shell prismatic, generally with distinct ribs; ribs often strongly developed toward apex, with 4-14, sometimes as many as 20. Apex with no notch or slit, or short one. Foot with epipodial sheath. Shell greatest in diameter at anterior aperature.

### ***Dentalium vallicolens* Raymond, 1904**

Figure 4.4

*Dentalium vallicolens* Raymond, 1904:123-124.—Keen, 1971:883.—Abbot 1974:386.

**Material Examined**. California, Santa Maria Basin, Sta. 61 (2); Sta. 86 (1); Sta. R-6 (2); **syntype** collection from off Santa Monica Bay, 290 m, off Point Fermin, 200 m, and La Jolla Canyon, off San Diego, 128 m: (CAS, 064383) (1); (CAS, 064385) (1): (CAS, 066519) (4); off Los Angeles and Orange County, 128-164 m, (LACMNH, 41-7.1) (2), 62-150 m, (LACMNH, 40-116.3) (1), 128-164 m, (LACMNH, 39-100.3) (2), off San Diego, 124 m, CAS (075694) (1); 198-430 m, (CAS, 075698) (1); 164-184 m, (CAS, 075699) (1); (CAS, 075700), (1).—Mexico, off Guadelupe Island, Melpomene Cove, 20-36 m, Baja California, Cabo San Lucas, 24 m, (CAS, 075695) (3); Mexico, 117-119 m, (LACMNH 41-33.2) (7).

**Description.** Undamaged adult shell smooth, relatively polished, sometimes with many healed fractures; most shells chalky due to erosion; shells white in juveniles, tending to tan or beige in adults. As typical for dentaliids, younger specimens proportionally more slender and strongly curved than adults; shell laid down after sculpture becomes obsolete almost straight. Dorsal (apical) aperture of juvenile specimens surrounded by 6-17 strong ribs; these becoming obsolete as animal grows; first, finer riblets occurring between them, after which they decrease in height. Finally at about 20-30 mm total shell length, or at about an aperture width of 3 mm, shell appearing smooth without magnification; fine longitudinal lines or striae visible with magnification. Annular sculpturing variable, from weak to absent: generally as fine lines visible under 10x magnification; complete growth rings rare; aperture circular (Figre 4. 4).

*Shell Morphometric Indices.* For all specimens, shell maximum width/length to shell ratio = 0.116 ± 0.073, ln(Ws) = 6.05 ± 2.84 (Ws = 6.12 × $10^4$); WI = 1 and LI = 0 as aperture widest portion of shell). Adults defined as those animals with aperture width of 3 mm or greater; these animals exhibiting relatively smooth shell form of the adult. Specimens with adult morphology varying in total length from 14.2 to 65.0 mm; aperture = maximum width 3.0 to 7.0 mm; smaller specimens more strongly curved; whorl expansion rates range from about 10 for smaller individuals to about 1.5 × $10^6$ for largest; adult shell maximum width/length to shell ratio = 0.12 ± 0.09, ln(Ws) = 6.60 ± 2.99 (Ws = 9.06 × $10^4$).

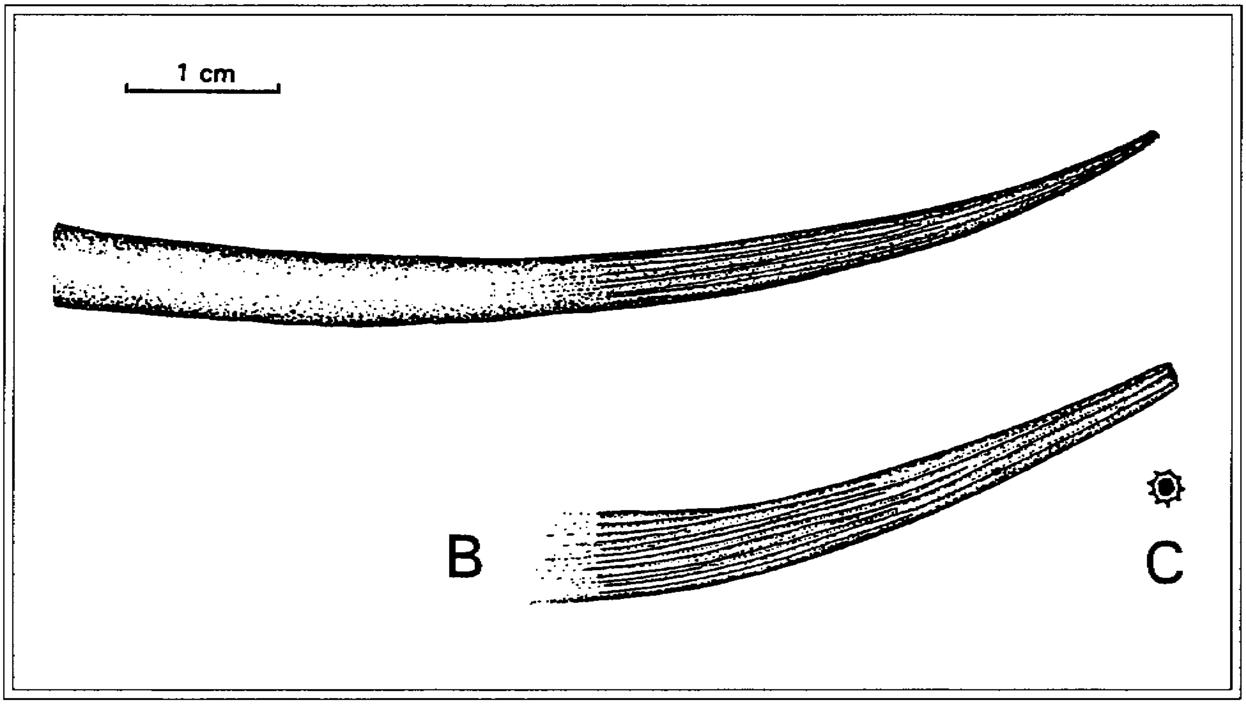

**Figure 4.4.** *Dentalium vallicolens* Raymond 1904. A. Entire shell. B. Dorsal shell apex showing longitudinal ribs. C. Dorsal shell apex, apical view showing longitudinal ribs.

Internal morphology not known.

**Biology**. In the Santa Maria Basin, *Dentalium vallicolens* occurred in sediments having high silt inventories. Several of the museum specimens exhibited evidence of drilling by naticids. Many specimens show healed fractures indicating decollation or unsuccessful attempted predation, possibly by crabs or fish. The ratfish, *Hydrolagus colliei*, preys on *Rhabdus rectius* in British Columbia, perhaps similar predation occurs here (Shimek, 1990).

**Type Locality and Type Specimens** California: Santa Monica Bay, 290 m, off Point Fermin, 200 m, from La Jolla Canyon off San Diego, 128 m.

**Distribution**. Straits of Juan de Fuca to Gulf of California (Keen 1971), but the published northern limit of this species is doubtful and in need of verification.

### Genus *Fissidentalium* Fischer, 1885

**Type Species**: *Dentalium ergasticum* Fischer, 1885.

**Diagnosis**. Shell large and solid, sculptured with many longitudinal riblets; apex typically with long slit, but often simple, sometimes with slit divided by series of fissures. Foot with epipodial sheath. Shell with greatest diameter at anterior aperature.

**Remarks**. No specimens of *Fissidentalium* were encountered in the Santa Maria Basin collections. However, it is likely that *F. megathyris* and *F. erosum* might be eventually encountered. See the key for differential characters.

## Order Gadilida Starobogatov, 1977

### Family Gadilidae Stoliczka, 1868

### Genus *Cadulus* Philippi, 1844

**Type Species:** *Dentalium ovulum* Phillipi, 1844.

**Diagnosis.** Tubular, circular or oval in section; somewhat arcuate; more-or-less bulging or swollen near middle, constricted toward anterior aperature. Shell smooth or delicately striated. Anterior aperature constricted, widest portion of shell posterior to aperature. Foot expanded into terminal disk with fringing tentacles.

### *Cadulus tolmiei* Dall, 1897

Figure 4.5

*Cadulus tolmiei* Dall, 1897:13, pl 1.—Pilsbry and Sharp, 1898:181-182.

**Material Examined.** California, Santa Maria Basin, Sta. 50 (2); Sta. R91 (2).—British Columbia, W. coast Vancouver Island, Barkley Sound, Sarita Bay, 150-350 m, (16) (Shimek 1989).—Types: *Cadulus tolmiei* USNM (107613); *Cadulus californicus* Pilsbry and Sharp, 1897, USNM (107698).

**Description.** Adult shell thin, translucent, polished, slightly bluish-white, internal organs easily visible through shell. Shell widest in anterior third, decidedly curved (Figure 4.5). Ventral or anterior aperture oblique, circular. Apical (dorsal) aperture typically surrounded by lobes, but these variable in number from 2 to 7, and fissures between them varying in prominence (Shimek 1989). Juveniles easily distinguished from adults, with widest part of shell at aperture. Growth probably determinate, with little growth occurring after aperture narrows.

*Shell Morphometric Indices.* Shell maximum width/shell length = 0.22 ± 0.02, ln(Ws) = 5.49 ±1.00 (Ws = 376); WI = 0.71 ± 0.19, and LI = 0.56 ± 0.06. Mean adult total shell length 9.98 ±1.03 mm, range from 7.40 to 12.15 mm. Mean maximum shell width was 2.17 ± 0.17 mm.

*Externally Visible Soft-part Morphology.* Mantle generally dull white. Mantle with triradiate fold, when extended from ventral aperture; foot extending through center of this triradiate area. Mantle may protrude about 1 mm beyond dorsal aperture in an adult (shell length > 10 mm). Foot extendable to length of shell, caduliform, with terminal disk, papillate laterally. Captacula numerous, over 200 in adults, extendable to 2-3 mm; terminal bulb densely ciliated, stalk cilia limited to tufts arranged linearly (visible with magnification) (Poon, 1987; Shimek, 1988).

*Visible Internal Morphology.* Radula visible through shell, brownish, highly mineralized; most highly mineralized areas appearing black. Cerebral ganglia visible through shell ventral (= anterior) to radular mass, pinkish. Digestive gland dark brown or black to violet, prominent, visible through shell. Gonads visible through adult shells, brilliant white in males, brown (ova) in females.

*Internal Morphological Characters.* Radula large for size of animal; radular formula 1-1-1-1-1; marginal teeth large, platelike; lateral teeth hooked, central tooth small; all teeth mineralized with iron and calcium salts.

**Biology.** Santa Maria Basin specimens of *Cadulus tolmiei* occur in sediments with high sand and sand/silt. British Columbia specimens are found in silty sand; foraminiferans are common in this habitat; depth distribution 50-400 m. This species is a predator on small foraminiferans, particularly *Uvigerina* spp. Prey are maintained in the buccal pouch (= proboscis) prior to trituration (Poon, 1987).

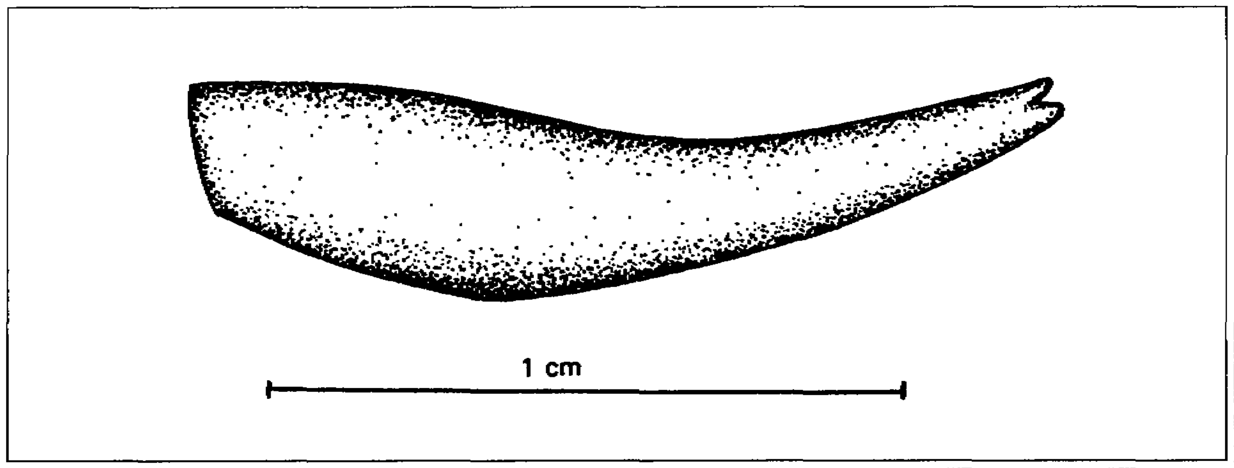

**Figure 4.5.** *Cadulus tolmiei* Dall, 1897.

**Remarks**. *Cadulus tolmiei* is distinguished from *C. californicus* by the possession of a thinner, more translucent, shell, and the relatively less inflated region around the widest portion of the shell (Pilsbry and Sharp 1897-1898).

**Type Locality and Type Specimens**. Near Vancouver Island, (USNM, 107613).

**Distribution**. *Cadulus tolmiei* ranges from Baja California through the Eastern Bering Sea (Abbott 1974; Baxter 1987).

### Genus *Gadila* Gray, 1847

**Type Species**: *Dentalium gadus* Montagu, 1829.

**Diagnosis**. Shell decidedly curved, with general contour anteriorly convex, but concave dorsally; slightly swollen near middle or toward aperature, tapering toward apex; apical orifice not constricted by callus ring, or with callus far within and weak; edges not slit. Anterior aperature constricted in adults, with widest portion of shell posterior to aperature; aperature either not constricted in juveniles or only slightly constricted. Foot expands into terminal disk with fringing tentacles; may have one or more central filaments or tentacles.

### *Gadila aberrans* (Whiteaves, 1887)

Figure 4.6

*Cadulus aberrans* Whiteaves, 1887:124, fig. 2.—Shimek, 1989 (synonymy).

*Cadulus hepburni* Dall, 1897:12, pl. 1, fig 13.

*Cadulus fusiformis* Pilsbry and Sharp, 1898:193, pl. 35, fig. 14.—Grant and Gale, 1931:493. (synonymy).

*Cadulus nitentior* Arnold, 1903:187, pl. 8, fig. 13.

**Material Examined.** California, Santa Maria Basin, Sta. 21 (6); Sta. R-8 (2).—Off Central California, 36 m, (LACMNH, 60-23), (81); Off Los Angeles, 82 m, (LACMNH, 70-115) (2); 14 m, LACMNH (65-1) (6); Off San Diego, 25 m, LACMNH (122873) (6); Mexico, 31-46 m, LACMNH (71-158) (39); Off British Columbia, 274 m, (LACMNH, 72-140) (9).—Additional 61 specimens from the Institute of Ocean Sciences, Canada (listed in Shimek, 1989).—Vancouver Island, Barkley Sound (233) (R. Shimek research specimens, listed in Shimek, 1989).

**Description.** Shell slender, slightly curved, highly polished, lustrous, translucent white; minute growth lines present (visible with magnification only); ventral (= oral or anterior) aperture oblique, round; dorsal (= anal, or posterior) aperture rounded, not lobed. No dorsal secondary apertural tube (such as found in *Rhabdus rectius*). Shell lip thin and sharp. Juvenile specimens, to about 10 mm in total length, without constriction of ventral aperture; adult size determinate, total length to about 13 mm; with slightly constricted aperture (Figure . 6).

*Shell Morphometric Indices.* All adult specimens (Shimek, 1989, and the Santa Maria Basin specimens): Shell maximum width/shell length = 0.13 ± 0.02, ln(Ws) = 6.07 ± 1.23; (Ws = 1335); WI = 0.85 ± 0.06, and LI = 0.51 ± 0.07. Santa Maria Basin adult specimens: shell maximum width/shell length = 0.14 ± 0.01, ln(Ws) = 6.67 ± 1.33 (Ws = 2316); WI = 0.83 ± 0.06, LI = 0.38 ± 0.04.

*Externally Visible Soft-part Morphology.* Mantle generally dull white, except for golden ring at area of outer mantle fold; when extended from ventral aperture, mantle with triradiate fold. Foot extending through center of triradiate area. Mantle sometimes protruding about 1 mm beyond dorsal aperture in adult (shell length > 10 mm). No consistent sexual differences in shape of the "pavillon," or tube formed from dorsal mantle edge in living animals (Scarabino, 1979; McFadien-Carter, 1983). Foot extendable to length of shell, caduliform, with terminal disk, papillate laterally, sometimes with 1 or 2 small papillae visible on distal face of terminal disk. Captacula numerous, over 100 in adults, extendable to 2 to 3 mm; terminal bulb densely ciliated, stalk cilia limited to tufts arranged linearly (visible with magnification) (Shimek, 1988).

*Visible Internal Morphology.* Radula visible through shell, brownish, highly mineralized, most highly mineralized areas black; cerebral ganglia visible through shell ventral (= anterior) to radular mass, pinkish. Digestive gland dark brown to black, prominent, visible through shell. Gonads visible through adult shells; males, brilliant white; females with ova brown, occasionally pink (Hebert, 1986).

*Internal Morphological Characters.* Radula large for size of animal; radular formula 1-1-1-1-1; marginal teeth large, platelike; lateral teeth hooked, with 2 cusps, central tooth small; teeth mineralized with iron and calcium salts.

**Biology.** In British Columbia, *Gadilia aberrans* is found in clean, well-sorted sand with about 5% organic material by weight; in the Santa Maria Basin, the sediments consist of mixed sand/silt. Foraminiferans are common in this habitat; depth distribution 20-100 m. Population densities are about 10 animals per m$^2$. Predator on small living foraminiferans (maximal dimension generally < 0.3 mm); prefers *Cribrononion lene* (Cushman and McCulloch, 1940) and *Rosalina* cf. *columbiana* (Cushman, 1925), eats *Elphidiella hannai* (Cushman and Grant, 1927) as encountered, and rejects or eats fewer than would be expected of *Florilus basispinatus* (Cushman and Moyer, 1930) and *Buliminella* species. The most abundant minor prey

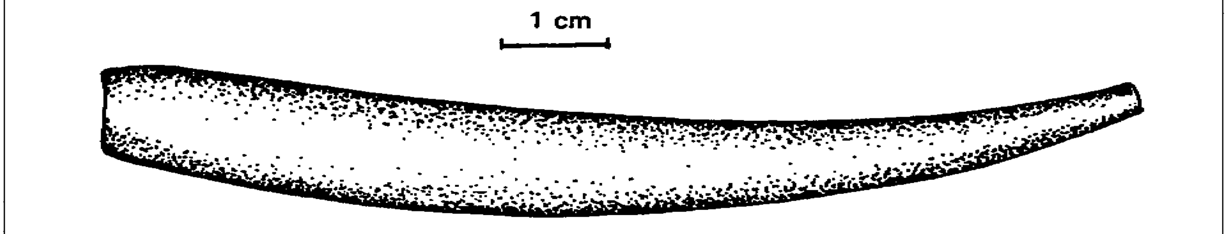

**Figure 4.6.** *Gadila aberrans* (Whiteaves, 1887).

species are *Buliminella elegantissima* (d'Orbigny, 1839) and *B. exilis* (H. B. Brady, 1884); other foraminiferan species are also taken. Prey is maintained in a buccal pouch (= proboscis) prior to trituration; and there may be more than 125 foraminiferans in the pouch. *Gadila aberrans* is a major infaunal predator where it is found and may be important in determining the abundances of other infauna by its predatory activities (Shimek, 1990).

**Remarks**. *Gadilia (= Cadulus) aberrans* is the same as *C. hepburni* Dall, 1897, *C. fusiformis* Pilsbry and Sharp, 1898, and *C. nitentior* Arnold, 1903. Shimek (1989) examined variation in shell morphometrics from populations of Gadilid scaphopods ranging from Vancouver Island to Southern California and concluded that the northern *Gadila aberrans* was indistinguishable from the northern *C. hepburni* and the southern species, *C. fusiformis* and *C. nitentior*.

**Type Locality and Type Specimens.** Quatsino Sound, Vancouver Island, British Columbia, in 60-100 m. NMC (555). The following lectotypes were designated by Shimek (1988): *C. hepburni*, Dall, 1897, (USNM 107612); from Near Victoria, Vancouver Island, British Columbia, in 120 m; *C. fusiformis*, Pilsbry and Sharp, 1898, (USNM 133809); from San Pedro, California, at 50 m; *C. nitentior*, Arnold, 1903, (USNM, 23729); from Pleistocene, Deadman Island, San Pedro bluffs, California.

**Distribution.** Southern California through Prince William Sound, Alaska (Shimek, 1989)

### Genus *Siphonodentalium* M. Sars, 1859

**Type Species**: *Siphonodentalium vitreum* M. Sars, 1859.

**Diagnosis**. Shell cylindrical, very smooth and glossy, thin, pellucid, glassy; arcuate; apex relatively large, with edges cut into lobes or teeth, slowly tapering from aperature to apex. Aperature cicular, oblique. Anterior aperature constricted, widest portion of shell posterior to aperature. Foot expanded into terminal disk.

## *Siphonodentalium* quadrifissatum (Pilsbry and Sharp, 1898)

Figure 4.7

*Cadulus quadrifissatus* Pilsbry and Sharp, 1898:150-151, pl. 29.—Keen, 1971:889.

**Material Examined.** California, Santa Maria Basin, Sta. 58 (3); Sta. PJ-22 (4); Sta. R-6 (4); Sta. R-2 (3).—Off Los Angeles, (CAS, 075696) (82); Orange County, Newport Bay, (CAS, 075702) (4); off San Diego, 20 m, (CAS, 075701) (6); off Santa Cruz Island, NW of Pelican Bay, 64-71 m, (LACMNH, 41-81.2) (2); NE of San Miguel Island, 64-71 m, (LACMNH, 41-58.3) (5).—Mexico, Guadelupe Island, 10-18 m, (CAS, 075697) (4); off Guadelupe Island, 15-37 m, (LACMNH, 65-42.4) (34); off Mexico, 18-36m, (LACMNH, 65-43) (5); 9 m, (LACMNH, 71-22) (27).

**Description.** Shell slender, slightly tapering; middle third of shell slightly but perceptibly swollen; subtransparent, bluish, often with milky white bands parallel to anterior aperture found near larger end; smooth and rather glossy, growth lines hardly visible; posterior third slowly tapering, tube then nearly cylindrical almost to aperture. Aperture oblique, circular to transversely oval. Dorsal apex cut into 4 conical lobes by short slits; relative length and prominence of these teeth varying substantially, probably related to remodeling cycle of shell by animal; edges of lobes somewhat bevelled distally (Figure 4.7).

*Shell Morphometric Indices.* Derived from examination of 193 adult specimens. Shell maximum width/shell length = 0.16 ± 0.02; ln(Ws) = 5.49 ± 1.25, (Ws = 634); WI = 0.85 ± 0.06, LI = 0.47 ± 0.10. Adult total shell length = 4.5 to 11.9 mm, mean = 7.25 ± 1.37 mm, maximum width = 0.8 to 2.35 mm, mean = 1.11 ± 0.20 mm.

*Visible Internal Morphology.* Gonads visible through adult shells; white in males, pink, in females; ova brown or pink (Hebert, 1986; Levitt, personal communication).

**Biology**. In the Santa Maria Basin, *Siphonodentalium quadrifissatum* occurred in sediments having high percentages of silts.

**Remarks**. The examined specimens appear to have a wide range of morphometric parameters. The Santa Maria basin material has lower length index values, LI ≤ 0.45, than do most of the examined specimens, but statistically they are not significantly different from the total array of specimens, however; they may represent either an ecotopic or populational variant. Other morphological differences became apparent with the examination of the distributional material. These differences included decidedly different shell thicknesses, whorl expansion rates, and maximum widths. Unfortunately, there were no clear correlations between any of these morphological characteristics and either habitats or localities. Habitat or locality data given with

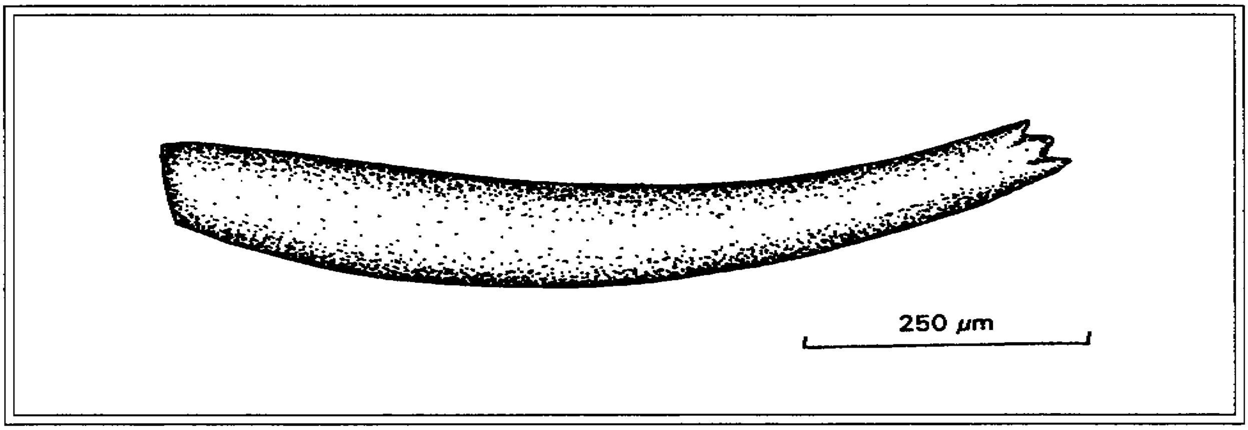

**Figure 4.7.** *Siphonodentalium quadrifissatum* (Whiteaves, 1887).

the specimens, however, were often quite limited. *Siphonodentalium quadrifissatum* in the central California region may be a single variable species. Alternatively, there may be several, perhaps three or more, species with the same general characteristics, i.e., slender gadilids with four fissures and apical lobes, living sympatrically in the area. I believe this latter hypothesis to be correct, but to separate these taxa statistically using only shell morphometric characteristics may be impossible. Examination of living animals is required with reference to their ecological requirements; particularly habitat and dietary preferences.

**Type Locality and Type Specimens.** San Diego, California, 10 m; CAS.

**Distribution.** Monterey Bay to Baja California (Keen 1971).

### Family Pulsellidae Scarabino, 1982

### Genus *Pulsellum* Stoliczka, 1868

**Type Species**: *Siphonodentalium lofotense* M. Sars, 1864.

**Diagnosis**. Shell cylindrical, smooth, may be glossy, thin, arcuate; slowly tapering from aperature to apex; apex lacking lobe and teeth. Aperature circular, oblique. Adult anterior aperature either not constricted, or only slightly constricted; widest portion of shell posterior to aperature. Foot expands into terminal disk with single terminal filament.

**Remarks**. No specimens of *Pulsellum* have been observed from the Santa Maria Basin collections, however it is likely that *P. salishorum* might be encountered. See the key for differential characters.

## Acknowledgements

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# 5. CLASS BIVALVIA

by

Paul H. Scott[1]

## Introduction

The bivalves comprise a major class of invertebrates, with about 8,000 living species (Boss, 1982). The class is exclusively aquatic, though some intertidal species can survive many days out of water, and inhabitants of ephemeral lakes can aestivate in moist sediments for several months. Bivalves are found in all aquatic habitats, from lakes at high elevations and temporary rain ponds to the deepest reaches of the oceans. They range in size from adults that attain less than one millimeter in length to tropical species with shells nearly 2 meters long.

Bivalve shells were among the first biological samples returned by early exploring expeditions and were frequently collected washed up on beaches, skeletons divorced from the soft parts that secreted them. Much early work was done excusively with shells, leading to many misconceptions. While identifications of most taxa may be based entirely on shell characters, an understanding of the function of the shell requires some knowledge of anatomy. Further, although assignment to higher taxa can be largely based on shell characters, including microstructure, the study of anatomy assists in the identification of relationships and establishes evolutionary trends.

Most bivalves feed on small particles, and even carnivorous forms, lacking jaws or a radula, are not able to chew or break up food and have poor muscular equipment to manipulate food into the mouth. The only exception is the Teredinidae, which mechanically rasps burrows in wood with the serrated ends of its valves. The raspings have secondarily become food for the shipworms. The microphagous behavior has limited the type of food available. In spite of the severe constraints imposed by enclosure in a rigid shell, an inability to protrude the mouth, and nutrition limited to the uptake of small particles, bivalves reveal a remarkable diversity of life styles and habitats. The epifaunal situation is probably primitive and is prevalent in many unrelated lineages. In addition, some lineages that have become infaunal have then given rise to groups that have returned to explore the epifaunal habit. The infaunal situation generally correlates with the development of siphons, and a progression is apparent from the colonization of friable and soft sediments to progressively harder and more refractory substrata. The boring habit has been developed in eight superfamilies. Primitively, boring was solely by mechanical means, but in *Lithophaga* and some other modern borers penetration is achieved by chemical means.

A small number of bivalves are commensal, chiefly belonging to the Galeommatoidea. The only parasitic bivalves are the rare dwarf males that live in a much larger female, the glochidial larvae of some freshwater bivalves, and a few that occur in the buccal pouches of holothurians. A number possess symbiotic algae within their pallial tissues, e.g., the giant clams (Tridacnidae) and in at least some of the closely allied Cardiidae.

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A symbiosis with chemoautotrophic bacteria has been demonstrated for a number of unrelated groups that inhabit sulfur-rich environments. The first discovered was the fascinating fauna around the deep-sea hydrothermal vents and sulfide seeps. Then, similar communities were discovered in sulfide and petrochemical seeps in shallower water, followed by the discovery that some very shallow-water lucinoids possess chemoautotrophic bacteria in their ctenidia.

## Glossary

**Accessory muscle.** A muscle attached to the interior of the shell, other than the adductor or pallial muscles.

**Accessory scar.** Small attachment impressions on the shell interior made by other than the adductor and pallial muscles.

**Adductor muscles.** Transverse muscle bundles that bridge the valves and draw them together. Usually one or two are present, rarely a third accessory adductor muscle may be present.

**Adductor scar.** Impression on inside of shell where adductor muscles were attached.

**Alate.** With wing-like projections.

**Alivincular.** A ligament usually centrally placed with lamellar layers both anterior and posterior to fibrous layer (e.g. *Ostrea*).

**Amphidetic.** A ligament extending on both sides of the umbo (e.g. *Glycymeris*).

**Auricle.** Ear-like projections of the hinge line (e.g. *Chlamys*).

**Auricular crura.** Tubercles and ridges on the hinge plate of some Pectinidae (singular: crus).

**Aragonite.** Orthorhombic form of calcium carbonate.

**Beak.** Projecting regions marking the early growth of the the bivalve shell. Equivalent to umbo.

**Bifid.** Divided by a groove. Usually applied to teeth.

**Bifurcate.** Divide into two. Usually applied to sculpture.

**Buttress.** Internal wall or projection supporting hinge plate structures.

**Byssal gape.** Opening between shell commisure for passage of the byssus.

**Byssal notch.** Furrow in the right valve of some Pectinidae for passage of the byssus.

**Byssal sinus.** Embayment in the right valve of some Pectinidae corresponding to the byssal notch.

**Byssate.** With a byssus. Equivalent to byssiferous.

**Byssus.** Fibres secreted by glands associated with the foot used to anchore the bivalve to the substrate, or to construct "nests" and brood pouches.

**Byssiferous**. With a functional byssus.

**Calcite.** Crystalline form of calcium carbonate.

**Cancellate.** Sculpture of intersecting radial and commarginal raised structures.

**Cardinal teeth.** Teeth below the umbo, correctly only applied to the Heterodonta.

**Cardinal crura.** Narrow plate-like teeth radiating from the resilifer in some Pectinidae.

**Carina.** Keel-like radial ridge on the outside of the shell.

**Cementation.** Fixation to the substrate by shell secretion.

**Chondrophore.** Elongate spoon-like process projecting from the hinge plate and containing the resilium.

**Clavicle.** A narrow delicate buttress supporting the hinge plate.

**Commarginal.** Parallel to the ventral shell margin and marking the direction of accretionary growth. Usually applied to sculpture. Also called **concentric**.

**Commissure.** Contacting margins of the two valves of the shell.

**Conchiolin.** Protein material forming shell matrix.

**Costa.** Raised rounded portion of the shell surface.

**Crenate.** With even notches or regularly corrugated.

**Cruciform muscle.** Intersecting muscle bundles associated with the siphons in some Tellinacea.

**Crura**. a peduncle or tooth-like projection on the hinge plate of some bivalves.

**Crus**. single limb of a crura.

**Ctenolium.** A row of small teeth on the edge of the byssal notch of some Pectinidae.

**Dehiscent.** Sloughing off, applied to periostracum.

**Demibranch.** One of two plate of filaments making up the gill on one side.

**Denticle.** Tooth-like process.

**Dentition.** Collective term for hinge plate teeth and associated sockets.

**Digestive diverticulum.** Paired arborecent mass of tubules attached to the stomach.

**Dimyarian.** With two adductor muscles.

**Disc.** The central part of the external surface of the valve, not including developments such as the auricles and rostrum.

**Dissoconch.** The post-larval shell, sometimes retained on the apex of the umbo.

**Divaricate.** Branching, usually bifid and frequently, bifid, sculpture.

**Duplivincular.** Ligament with the lamellar component separated into a series (e.g. *Arca*).

**Dysodont.** With small denticles near the umbo.

**Edentate.** Hinge plate lacking dentition.

**Ear.** Lateral projecting of the hinge line in the Pectinacea.

**Edentulous.** see edentate.

**Entire**. Pallial line lacking a pallial sinus.

**Equilateral.** With the umbo central and the anterior and posterior parts of the shell nearly equal in size.

**Equivalve.** With the valves equal in size and shape.

**Escutcheon.** Area of hinge line posterior to the umbo and usually marginal to the ligament and differentiated by sculpture. Frequently demarcated by a margical stria.

**Eulamellibranch.** Complex gill with permanently attached filaments, transverse plates of tissue and vertical strenghening rods.

**Euthetic.** Oriented perpendicular to the substrate (e.g. *Mytilus*).

**Evanescent.** Ephemeral structures, overgrown and lost in adult individuals. Usually applied to dentition (e.g. *Serripes*).

**Fascicle.** A bunch of radial ribs, present in some *Chlamys*.

**Fibrous ligament.** Portion of the ligament impreganated with calcium carbonate, elastic to compressional stress.

**Filibranch.** Gill with free or temporarily attached filaments.

**Fossette.** Obsolete term for the resilifer.

**Gape.** Opening between valve commissure after closure of the shell.

**Gill.** Respiratory, water transporting, and particle retaining organ of the majority of bivalves. Equivalent to ctenidium.

**Growth check.** Strong concentric line on surface of the valve marking cessation of seasonal growth.

**Growth striae.** Fine concentric lines on the surface of the valve marking intervals in growth.

**Hetermyarian.** Having unequally sized adductor muscles.

**Heterorhabdic.** Gill with filaments differentiated.

**Hinge.** Collective term for structures on the dorsal commissure of the shell.

**Hinge line.** Long axis of the hinge plate.

**Hinge plate.** Shell platfrom bearing structures associated with the articulation of the valves of the shell.

**Hirsute.** Unevenly hairy, usually applied to periostracum. (e.g. *Modiolus*).

**Homorhabdic.** Gill with all filaments alike.

**Hypobranchial gland.** A glandular region associated with the gill and mantle in protobranchs and may help consolidate rejecta.

**Hypoplax.** An accessory plate covering the posterior ventral gape of some Pholadidae.

**Imbricate.** Overlapping like roof shingles, applied to sculpture.

**Inequilateral.** Umbo not central and anterior and posterior parts of the shell different in size.

**Inequivalve.** Shell valves unlike in size or shape.

**Internal ligament.** Alternative term for resilium.

**Integripalliate.** Obsolete term for pallial line without a pallial sinus. (see entire).

**Interspace.** Region between adjacent ribs.

**Isomyarian.** With equal sized adductor muscles.

**Lamella.** A plate-like extension of the external sculpture.

**Lamina.** A thin plate of shell on the hinge plate.

**Lanceolate.** A long tapering form, usually applied to the lunule and escutcheon.

**Ligament.** Elastic proteinaceous structure linking the shell valves.

**Ligament groove.** Narrow depression accomodating the ligament.

**Ligament pit.** Broad subumbonal depression accomodating the ligament.

**Lira.** A minute raised area, usually between two furrows. (plural: lirae).

**Lithodesma.** An accessory tooth-like plate supporting the resilium, usually limited to the Anomalodesmata.

**Lunule.** Subcircular to heart-shaped depression in front of the umbo, usually with different sculpture and set off by marginal striae.

**Mantle.** Tissue plate investing the bivalve body and sometimes prolonged into siphons.

**Monomyarian.** With a single adductor muscle.

**Mosaicostracum.** Thin boundary layer joining the periostracum to the shell.

**Multivincular.** Ligament type with serially repeated alivincular elements.

**Myostracum.** Attachment layer deposited on muscle attachments.

**Nacreous.** Shell microstructure of thin aragonitic layers, characterized by iridescence.

**Nodose.** Sculpture with tubercles or nodes.

**Nymph.** Elongate platform on the hinge plate for mechanical attachment of the external ligament.

**Opisthodetic.** Term applied to ligament located entirely posterior to umbo.

**Organ of Bojanus.** The kidney of bivalves, two contorted tubules close to the heart.

**Orthocline.** Perpendicular to hinge axis, usually with reference to dentition.

**Opisthogyrate.** With umbo pointing posteriorly.

**Orthogyrate.** With umbones pointing towards each other.

**Ostium.** Aperture between gill filaments for passage of water (Plural. ostia).

**Pallial.** Pertaining to the mantle.

**Pallial line.** Scar left on valve interior from attachment of marginal pallial muscles.

**Pallial sinus.** Posterior embayment formed in pallial line to accomodate the siphonal retractor muscles.

**Palp proboscides.** Two long protrusible organs used to convey detritus particles to the mouth, limited to the paleataxodonts.

**Parivincular.** Elongated external ligament situated posterior to umbo.

**Pedal gape.** Opening in shell commissure to accomodate the foot.

**Pedal muscles.** Muscles attached to interior of the valve used to control the foot.

**Periostracum.** Outer proteinaceous layer of the shell. Equivalent to epidermis.

**Pericardial gland.** Tissue mass associated with the pericardium and extending into the mantle. Equivalent to the Organ of Keber.

**Pilose.** Evenly and finely hairy, usually applied to periostracum.

**Pericalymna larva.** Larval type of the protobranch bivalves.

**Pleurothetic.** Lying on one valve in the sagittal plane (e.g. Pectinidae).

**Porcelaneous.** Calcium carbonate with white, translucent texture, usually forming interior layer of the shell.

**Posterior slope.** Segment of shell exterior posterior and ventral of the umbo.

**Primary ligament.** Exterior part of ligament representing the primitive condition of periostracal and fibrous layers.

**Prismatic.** Shell microstructure consisting of calcitic or aragonitic prisms.

**Prodissoconch.** Larval shell, frequently retained on the tip of the umbo.

**Prosodetic.** Located anterior to the umbo, usually applied to the ligament.

**Prosogyrate.** Umbo pointing anteriorly.

**Protoplax.** Elongate accessory plate, sometimes divided longitudinally, covering anterior dorsal margin of some Pholadidae.

**Provinculum.** The hinge plate of the prodissoconch, bearing larval teeth.

**Pseudocardinal.** Subumbonal teeth with a different origin than those of the Veneridae.

**Pseudolamellibranch.** Complex gill with filaments permanently fused.

**Punctate.** Surface with numerous small pits. (Singular punctum, plural puncta).

**Radial.** Direction of growth away from the umbo. Usually used to describe sculpture.

**Resilifer.** Recess in the hinge plate to receive the resilium.

**Resilia.** Linear series of ligamental islets in some alivincular ligaments.

**Resilium.** Internal portion of the ligament. Equivalnet to cartilage.

**Reticulate.** Sculture of a network of intersecting elements, frequently oblique.

**Recurved.** Bent.

**Rib.** Prominent elevation forming sculpture, shorter and more compact than a costa.

**Riblet.** Small elevation forming sculpture.

**Rostrate.** Pointed or beaked.

**Rostrum.** Elongation of shell forming a tube protecting the siphons.

**Sagittal plane.** Anterior-posterior plane of symetry of the shell or soft parts.

**Sculpture.** Relief pattern on the shell exterior.

**Siphon.** Tube extensions of the fused mantle.

**Siphonal retractors.** Muscle used to withdraw the siphons and attached to the pallial sinus.

**Spine.** Long calcareous projecting sculpture.

**Squamate.** Sculpture with small scales.

**Stria.** Minute incised line sculpture. (Plural: striae).

**Sulcus.** Radial depression of the valve, usually carried to the interior of the valve.

**Thread.** Narrow elevation in sculpture, more robust that a lira.

**Trochophore larva.** Earliest larval form of all bivalves, not directly referable to the annelid trochophora.

**Truncate.** Valve marginal curvature interupted by abrupt segment.

**Tumid.** Inflated and prominent, usually applied to umbones.

**Umbo.** Projecting region of the valve marking the earliest shell. Equivalent to beak. (Plural. umbones).

**Umbonal cavity.** Dorsal chamber under the hinge plate.

**Valve.** One of the lateral calcareous plates that make up the shell.

**Veliger.** Larval stage of the majority of bivalves.

**Vinculum.** Secondary deposite of shell on the hinge plate submerging the dentition.

**Xenomorphic.** Assumption in form and sculpture of the substrate in some cemented bivalves (e.g. *Anomia*).

## Key to the Superfamilies

1A. Hinge with taxodont dentition (reduced to a few teeth in some) .......... 2
1B. Hinge edentate or with other than taxodont dentition .......... 5

2A. Ligament internal .......... 3
2B. Ligament mostly or entirely external .......... Nuculanoidea (in part)

3A. Hinge teeth few in number, entirely or mostly on one side of beaks .......... Manzanelloidea
3B. Hinge teeth more than 8 and on both sides of beaks .......... 4

4A. Shell very iridescent internally .......... Nuculoidea
4B. Shell porcellaneous (or slightly iridescent) .......... Nuculanoidea (in part)

5A. Dorsal margin produced anteriorly and posteriorly into triangular ears, or ligament in series of pits .......... 6
5B. Dorsal margin not produced into ears; ligament not divided into series of pits .......... 7

6A. Shell much higher than long; ears small .......... Limoidea
6B. Shell height and length more or less similar; ears large .......... Pectinoidea

7A. Hinge simple, without conspicuous interlocking cardinal teeth, projecting chondrophores, or myophores (may have inconspicuous denticles or a resilifer on hinge plate, or left valve may fit into lateral grooves in right valve) ........ 8
7B. Hinge complex, with 2 or more interlocking cardinal teeth in at least one valve (may also have a chondrophore) ........ 19

8A. Adductor muscle scars very unequal in size; anterior scar smaller, near beaks; beaks anterior in most ........ Mytiloidea
8B. Adductor muscle scars of approximately same size; beaks not anterior ........ 9

9A. Periostracum produced well beyond shell margin ........ Solemyoidea
9B. Periostracum, if conspicuous, not produced well beyond shell margin ........ 10

10A. Shell porcelaneous within ........ 11
10B. Shell nacreous within ........ 17

11A. Shell rudimentary, without true hinge ........ Galeommatoidea (some)
11B. Shell normal; valves connected by hinge ........ 12

12A. Valves closing tightly ........ 13
12B. Shell gaping ventrally or anteriorly ........ Hiatelloidea

13A. With a conspicuous pallial sinus ........ Thracioidea
13B. Without a pallial sinus ........ 14

14A. With conspicuous radial ribs, mostly on posterior end ........ Cuspidarioidea (part)
14B. Radial ribs absent or feeble ........ 15

15A. Ligament sunken onto hinge plate, not under beaks ........ Lucinioidea (Thyasiridae)
15B. Ligament internal under beaks ........ 16

16A. Sculpture of conspicuous commarginal ribs ........ Myoidea (Spheniopsidae)
16B. Surface smooth ........ Cuspidarioidea (part)

17A. Internal dorsal surface with crurae ........ Pandoroidea (Pandoridae)
17B. Without crurae ........ 18

18A. Shell ovoid ........ Verticordioidea
18B Shell elongate, subquadrate ........ Pandoroidea (*Lyonsia*)

19A. Shell cemented to substratum by 1 valve ........................................ Chamoidea
19B. Shell not cemented ........................................ 20

20A. Shell with radial ribs over most of surface, showing as crenulations within (reduced in some to internal crenulations only) ........................................ 21
20B. Sculpture absent, commarginal, cancellate, or only weakly radial ........................................ 22

21A. Shell with anterior and posterior lateral teeth ........................................ Lucinoidea (*Parvilucina*)
21B. Shell without lateral teeth, or with only an anterior lateral ........................................ Carditoidea

22A. Shell with an entirely internal ligament, or with partially internal ligament ...... Galeommatoidea(part)
22B. Shell with an entirely external ligament ........................................ 23

23A. Shell with a conspicuous pallial sinus ........................................ 24
23B. Shell pallial sinus absent or very shallow ........................................ Lucinoidea

24A. Hinge with 3 cardinal teeth in 1 or both valves ........................................ Veneroidea
24B. Hinge with 2 teeth in each valve ........................................ Tellinoidea (most)

# Subclass Palaeotaxodonta Korobkov, 1954

**Diagnosis.** Shell cross-lamellar, porcellaneous or nacreous, equilateral to strongly inequilateral, rounded to elongate, usually equivalve. Periostracum thin, adherent, varnished or dull. Sculpture weak to very strong. Hinge plate strong, with replicated taxodont teeth or with a few horizontal teeth, edentate in some solemyoids. Ligament usually amphidetic (opisthodetic in a few), external or internal. Gills protobranch, usually large. Labial palps variable, palp proboscides usually present. Pallial line entire. Two subequal adductor muscle scars, with other associated scars. Mantle lobes largely free. Foot with papillated planar sole. Siphons present or absent. Larva a pericalymma.

**Biology.** The majority of species are deposit feeders and shallow infaunal dwellers. Palaeotaxodonts are a highly adaptable group in soft sediments with a very wide distribution and are frequently the dominant bivalves in the deep ocean and abyssal regions.

The characteristic features of the subclass are the protobranch gill, the palp proboscides (except in the solemyoids), and the series of identical or similar vertical teeth, set in a row on the anterior and posterior hinge plate. In some lineages, one limb of the chevron-shaped tooth becomes elongated, resulting in horizontal lamellar teeth. In the Order Solemyoida, dentition is absent or reduced to a few vertical and horizontal elements.

## Order Nuculoida Dall, 1889

**Diagnosis.** Shell aragonitic and inequilateral. Periostracum thick to thin, usually adherent and varnished. Umbones prominent, prodissoconch large in many species. Sculpture absent or weak. Hinge plate prominent with replicated taxodont teeth, usually vertical, rarely consisting of few horizontal teeth. Ligament amphidetic or opisthodetic, usually internal. Adductor muscle scars nearly equal. Gills protobranch, small and situated posteriorly. Labial palps and palp proboscides large. Foot with byssal groove, sole flattened with papillated margin.

## Superfamily Nuculoidea J. E. Gray, 1824

**Diagnosis.** Shell aragonitic, usually less then 1 cm and inequilateral; interior nacreous. Inflated and equivalve, with a truncate posterior end. Periostracum adherent, usually dark colored. Hinge plate strong, with series of V-shaped teeth separated by a resilifer. Ligament internal, amphidetic. Dimyarian; pallial line weak; pallial sinus absent. Gill small, oblique to horizontal. Labial palps and palp proboscides large. Hypobranchial gland present.

### Family Nuculidae J. E. Gray, 1824

**Diagnosis.** Outline triangular to ovate, inequilateral and equivalve. Umbones posterior, opisthogyrate. Sculpture absent or of various combinations of radial and commarginal riblets or striae. Periostracum thick, polished in many, dull in others, yellow to dark brown. Lunule strong to weak or absent; escutcheon wide and frequently long. Hinge plate strong, with anterior and posterior series of V-shaped teeth separated by a deep resilifer. Adductor muscle scars subequal. Pallial line entire. Mantle lobes free. Foot large, with planar sole and byssal groove, but adult not byssiferous. Alimentary canal with type 1 stomach, strongly chitinised, with two ducts leading to the digestive diverticula; style-sac and mid-gut conjoined; intestine long, convoluted, usually on the right side of stomach, passing through ventricle of heart.

## Genus *Nucula* Lamarck, 1799

*Nucula* Lamarck, 1799. **Type species** (M): *Arca nucleus* Linnaeus, 1758. Recent, North Atlantic.

**Diagnosis.** Shell ovate to subtrigonal, inequilateral, inflated. Periostracum thin, adherent, polished. Sculpture absent or commarginal riblets and/or radial striae. Lunule and escutcheon usually present. Hinge plate wide; taxodont teeth in two series separated by a short, oblique to subvertical resilifer. Ligament amphidetic, internal. Ventral shell margin crenulate.

### ***Nucula carlottensis*** **Dall, 1897**

Figure 5.1

*Nucula carlottensis* Dall, 1897: 6.
*Nucula charlottensis* Dall, in Oldroyd, 1924: 5, *nomen vanum*
*Nucula (L.) keenae* F. R. Bernard, 1983: 253.
*Nucula (L.) takashii* F. R. Bernard, 1983: 255.

**Material Examined.** California, Santa Maria Basin, Phase I, Sta. BSS-16 (591 m); Phase II, Sta. PJ-1 (145 m), PJ-8 (145 m), PJ-9 (169 m).

**Description.** Shell small, trigonal, very inflated. Sculpture of commarginal striae overlain by radial striae. Periostracum yellow to dark brown, silky. Length to 10 mm.

**Type Locality and Type Specimens.** Off Queen Charlotte Islands, British Columbia, Canada; types not found.

**Distribution.** Queen Charlotte Islands, British Columbia (51.4° N) [USNM], to Acapulco, Guerrero, Mexico (16.9° N) [USNM], in 104 - 2,000 m.

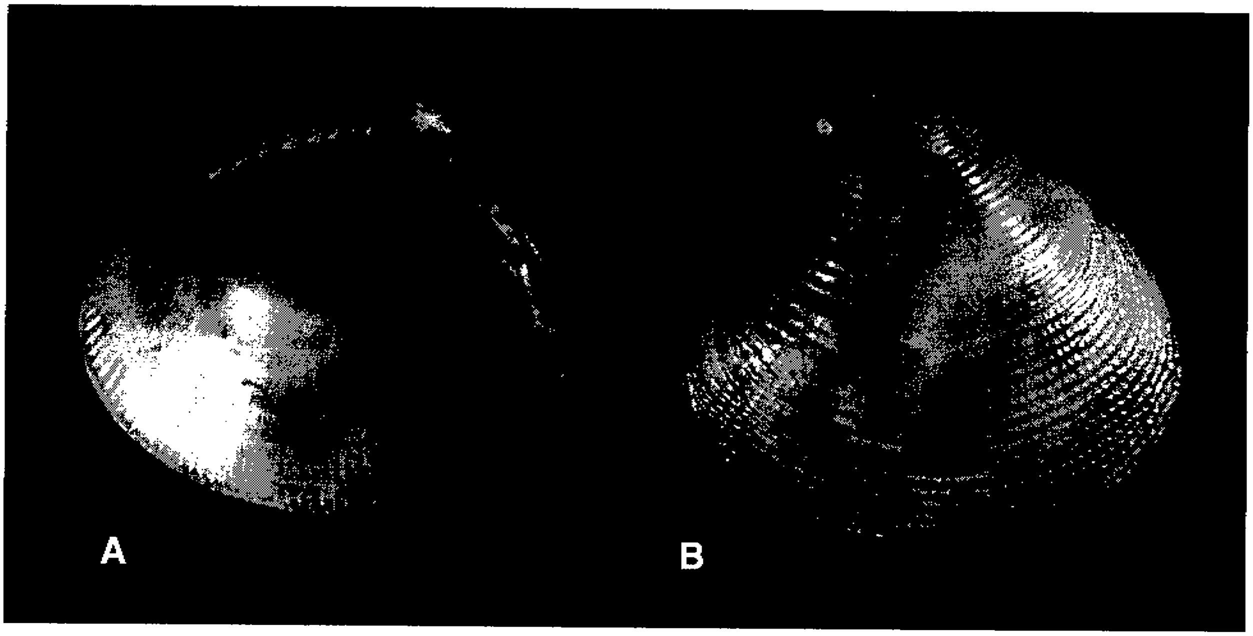

**Figure 5.1.** *Nucula carlottensis*: A, interior of left valve; B, exterior of left valve.

## Genus *Ennucula* Iredale, 1931

*Ennucula* Iredale, 1931. **Type species** (OD): *Nucula obliqua* Lamarck, 1819. Recent, Australia.

**Diagnosis.** Oval; shell surface smooth; inner ventral margin without crenulations.

### *Eunnucula tenuis* (Montagu, 1808)

Figure 5.2

*Arca tenuis* Montagu, 1808: 56.
*Nucula inflata* Hancock, 1846: 333, *non* J. Sowerby, 1827, *non* Wissman and Münster, 1841.
*Nucula expansa* Reeve, 1855: 397, *non* Bronn, 1848.
*Nucula bellotii* A. Adams, 1856: 51.
*Nucula tenuis "typica"* G. O. Sars, 1878: 34.
*Nucula tenuis lucida* Whiteaves, 1887: 120.
*Nucula quirica* Dall, 1916: 9, *nom. nud.*; Dall, 1916: 394.
*Nucula (Ennucula) balboana* Hertlein and Grant, 1972: 145.
*Nucula (Leionucula) leptodonta* F. R. Bernard, 1983: 255.

**Material Examined.** California, Santa Maria Basin, Phase I, Sta. BSS-50 (591 m), Sta. BSS-55 (590 m), Sta. BSS-69 (927 m); Phase II, Sta. R-3 (409 m), PJ-8 (142 m), PJ-9 (142 m).—30 lots from southern California (SBMNH).

**Description.** Shell ovate-trigonal, moderately inflated, smooth or with faint commarginal straie. Beaks near the posterior margin. Ventral margin smooth. Periostracum light olive to dark brown, usually irridescient. Resilifer projecting, oblique, deep. Length to 17 mm.

**Type Locality and Type Specimens.** Near Dunbar, about 30 mi east of Edinburg, Scotland, south side of the Firth of Forth, 56° N, 02.5° E; type material not found, presumably lost.

**Distribution.** Circumboreal and Arctic Ocean (71° N), thoughout the Bering Sea and the Gulf of Alaska (60° N), to San Diego, California (32.7° N), in 10 to 927 m.

**Literature.** Hertlein and Strong (1940: 382), Petersen (1978: 100-101).

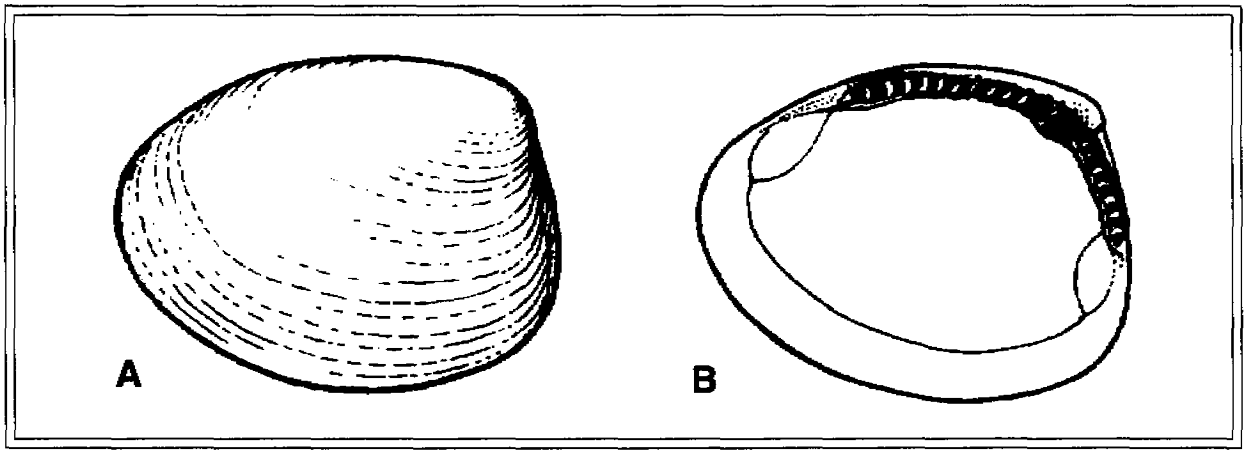

**Figure 5.2.** *Ennucula tenuis*: A, exterior of right valve; B, interior of left valve.

### *Eunnucula cardara* (Dall, 1916)

Figure 5.3

*Nucula cardara* Dall, 1916: 9, *nom. nud.*; Dall, 1916b: 394.
*Leda phenaxia* Dall, 1916: 11, *nom. nud.*; Dall, 1916b: 397.

**Material Examined.** California, Santa Maria Basin, Phase I Sta. 55 (590 m).—Holotype (see below).

**Description.** Shell ovate-elongate, moderately inflated, smooth. Beaks prominent, placed well back of the posterior margin. Periostracum olive to dark brown. Prodissoconch prominent. Resilifer projecting, vertical, deep. Length to 12 mm.

**Type Locality and Type Specimens.** Off San Diego, California; Holotype, USNM 265905.

**Distribution.** Cape Flattery, Washington (48° N), to Cabo San Lucas, Baja California Sur (23° N), in 590 - 2,600 m.

**Literature.** Hertlein and Strong (1940: 383).

## Genus *Acila* H. Adams and A. Adams, 1858

*Acila* H. Adams and A. Adams, 1858. **Type species** (S.D. Stoliczka, 1871): *Nucula divaricata* Hinds, 1843. Recent, China.

**Diagnosis.** Shell inequilateral, much longer anteriorly, ovate to subquadrate, eqivalve. Sculpture of divaricate radial riblets. Periostracum thick, dark brown to yellow. Umbones opisthogyrate. Ventral shell margin crenulated. Interior nacreous. Hinge plate with narrow, oblique resilifer.

**Literature.** Schenck (1932, 1935, 1936), Slodkevich (1967).

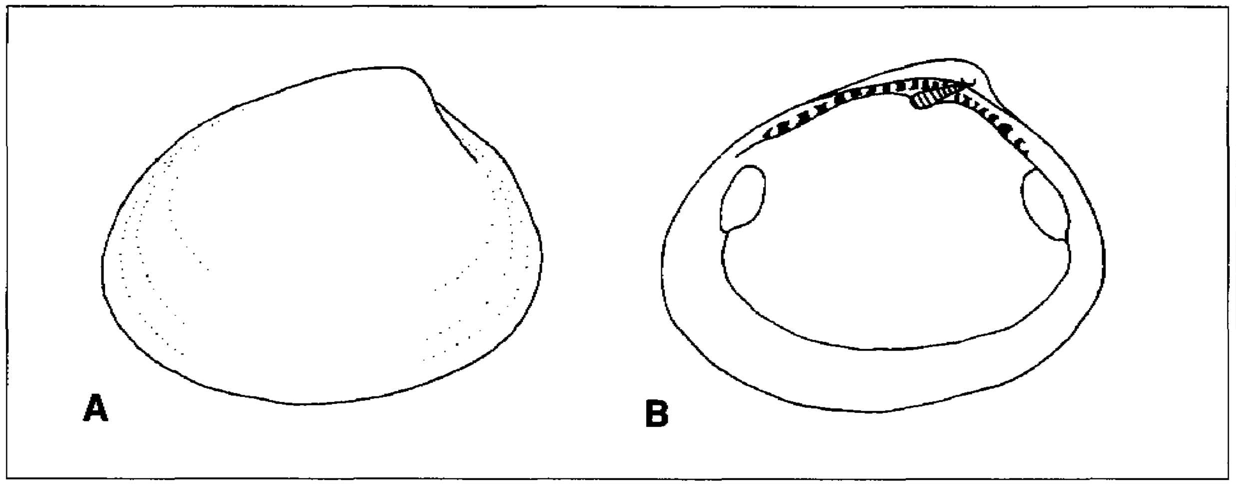

**Figure 5.3.** *Ennucula cardara*: A, exterior of right valve; B, interior of left valve.

## *Acila castrensis* (Hinds, 1843)

Figure 5.4

*Nucula castrensis* Hinds, 1843: 98.

*Nucula divaricata* Conrad, 1848: 432, *non* Hinds, 1843, *non* Valenciennes, 1846.

*Nucula lyalli* W. Baird, 1863: 71.

*Acila empirensis* Howe, 1922: 96.

*Acila (Truncacila) beringiana* Slodkevisch, 1967: 56.

**Material Examined.** California, Santa Maria Basin, Sta. 7; Sta. 103; plus 25 lots from southern California (SBMNH).

**Description.** Shell ovate-subquadrate, inflated. Sculpture of divaricate ribs. Periostracum light olive to dark brown, frequently with adhering sediment and parasitic hydroids. Length to 20 mm.

**Type Locality and Type Specimens.** Sitka, Alaska; type not located.

**Distribution.** Kamchatka; Craig, Alaska (55.5° N), to Las Cruces, Baja California Sur (24.2° N), in 5 - 400 m. Also reported as early as the Miocene in western North America.

**Literature.** Frizzell (1930), Hertlein and Strong (1940: 388-389), Kuznetsov (1961: 94-95), Morse and Meyhéfer (1990), Stasek (1961, 1963: 92), Strathmann (1987: 320).

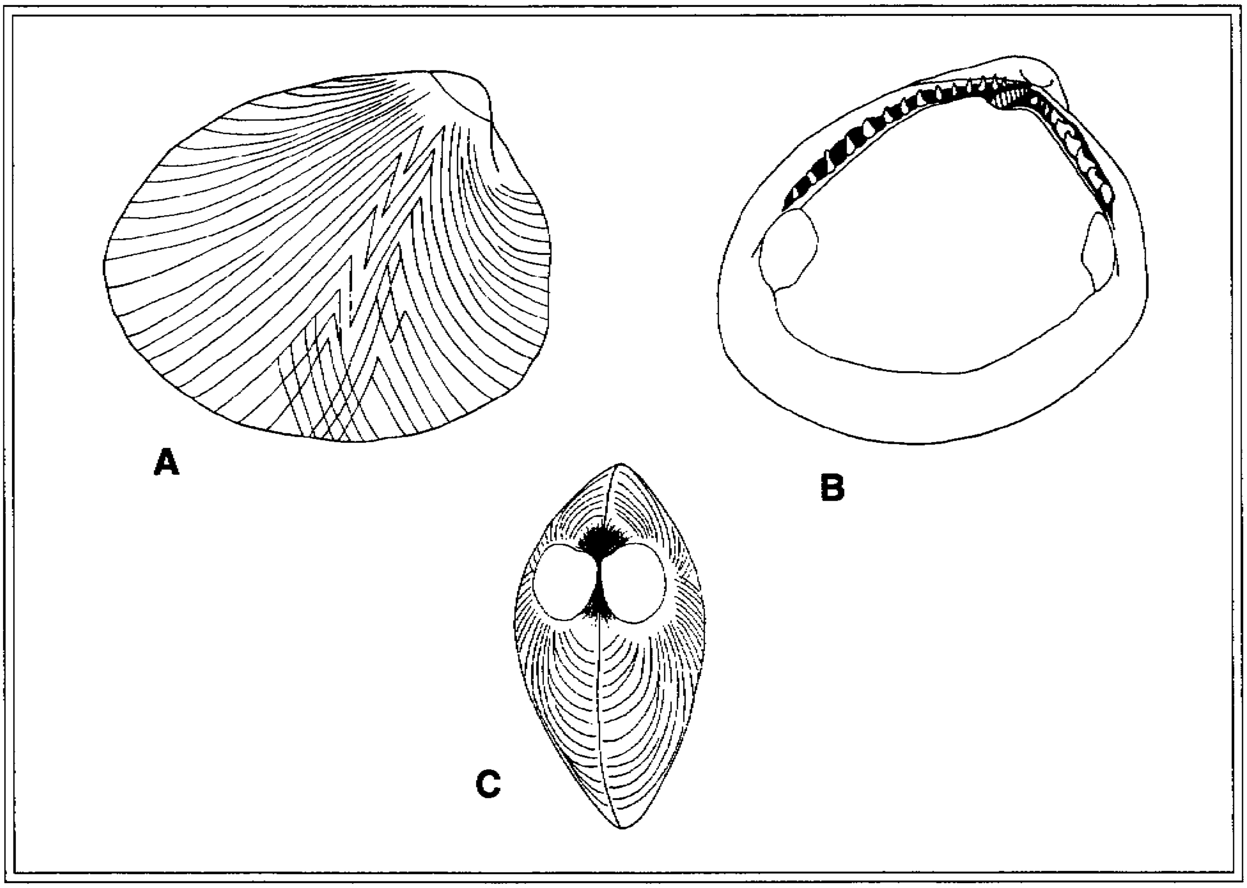

**Figure 5.4.** *Acila castreneis*: A, exterior of right valve; B, interior of left valve; C, dordal view of both valves.

## Order Solemyida Dall, 1889

**Diagnosis.** Shell only weakly calcified, inequilateral, rounded to elongate, equivalve. Periostracum thick and varnished, usually dark brown to black. Sculpture absent, except for incremental lirae, or weak radial ribs and furrows. Interior porcellaneous. Hinge plate edentate, or with several vertical teeth, or obscure tubercles. Dimyarian or monomyarian. Gills protobranch, large. Siphons absent. Labial palps and palp proboscides reduced or absent. Foot with flattened sole.

## Superfamily Solemyoidea J. E. Gray, 1840

**Diagnosis.** Shell strongly inequilateral, anterior elongate, equivalve. Periostracum thick, varnished. Dimyarian.

**Remarks.** One living family that is very widely distributed but absent in the frigid polar seas. The family is adapted for survival in regions of high organic content and low oxygen tension. Most species have symbiotic chemoautotrophic bacteria in their tissues, on which they depend at least to some degree for nutrition. In all species, the alimentary canal is reduced, and may be completly absent.

### Family Solemyidae J. E. Gray, 1840

**Diagnosis.** Shell aragonitic, with outer prismatic and inner homogenous layers. Inequilateral, anteriorly elongated, the shell is weakly calcified and dominated by the thick, varnished periostracum, which extends beyond the shell margins. Sculpture absent, or limited to low wide radial ribs or furrows. Umbones small. Lunule absent; escutcheon weak or absent. Hinge plate weak, edentate, tubercles and thickened props usually present. Ligament parivincular, opisthodetic, sunk in a groove posterior to the umbones and attached to nymph. Adductor muscle scars paired, subequal. Pedal muscle scars prominent. Pallial line obscure, entire. Mantle lobes with hypertrophied margins extensively fused, leaving large antero-ventral and small posterior openings. Hypobranchial gland developed. Foot elongate with discoid sole. Gills protobranch, large; filaments thickened and dark coloured. Labial palps minute. Alimentary canal reduced to simple tube with 2 ducts to the small digestive diverticula and a narrow intestine passing through the ventricle of the heart. In some representatives, the entire alimentary system is absent. Larva a pericalymma.

**Remarks.** This family is represented by shallow infaunal burrowers in soft substrates. The vernacular name, "awning clams," refers to the periostracal fringe projecting beyond the shell margins and usually dissected into triangular sections covering the wide, muscular, fused mantle margins. The calcareous portion of the shell is weak and contains a large amount of organic matrix. The result is that the soft parts are enveloped in a largely periostracal flexible tube, stiffened along the dorsal margins by the shell valves. The high solubility of calcium carbonate in the deep ocean means that even recently dead specimens are represented by the periostracum only, and the ventral margins become separated and result in the characteristic awning shape.

**Biology.** A complex Y-shaped burrow, with no direct communication with the surface may be constructed by smaller species, but large individuals appear to lie at an oblique angle just below the sediment surface, usually in a small depression in the sediment. All species observed appear to be active animals, vigorously burrowing through the substrate, and even capable of undirected swimming by adduction, although this has been observed only in specimens artificially displaced from their burrows. The powerful pumping action is probably associated with clearing the burrow. The family appears to favor regions of reduced oxygen, usually with high organic content.

While the majority of species have a normal functioning alimentary canal, an outstanding feature is the reduction of the gut to a simple tube with barely distinguishable stomach, or its entire loss in some species. It has recently been shown that nutrition is obtained from chemoautrophic bacteria mostly housed in the thick gill filaments. The bacteria utilize hydrogen sulphide to fuel the production of carbohydrates and are able to exist in oxygen-poor environments. The clams live symbiotically with the bacteria and are able to colonize enviroments with decomposing organic remains, high in hydrogen sulfide and poor in oxygen.

The typical location for awning clams in the northeastern Pacific is in basins on the continental shelf and nearshore where there is an accumulation of plant debris. One species is opportunistic and is able to colonize the shallow water around sewage and debris from log storage areas. Those species with stomachs have a less restricted habitat and are generally absent from such polluted habitats. The question whether loss of the gut is a secondary adaptation to exploit available habitats, or a carry-over of an ancient life-style, has been opened by the recent discovery of several organisms, including bivalves, part of a food-chain entirely dependent on inorganic chemicals derived from volcanic activity of deep-ocean rifts.

## Genus *Solemya* Lamarck, 1818

*Solemya* Lamarck, 1818. **Type species** (S.D. Children, 1823): *S. mediterranea* Lamarck, 1818, = *Tellina togata* Poli, 1795. Recent, Mediterranean. *Solenimya, Solenomya,* of authors, *nomen vanum.*

**Diagnosis.** Shell inequilateral, elongate, inflated to compressed, usually equivalve. Shell weak without external sculpture except for weak radial ribs or furrows. Periostracum dominating shell, thick and varnished, extending beyond shell. Umbones not prominent, near posterior end. Hinge plate weak, edentate, with oblique resilifer with or without supporting buttresses. Ligament opisthodetic, internal. Posterior adductor scar small; anterior scar large, continuous with oblique pedal retractor scar.

### *Solemya reidi* F. R. Bernard, 1980

Figure 5.5

*Solemya (Solemya) reidi* F. R. Bernard, 1980: 19.

**Material Examined.** 5 lots from southern California (SBMNH)

**Description.** A medium-size, dark brown species, characterized by a thick periostracum. Posterior ribs low, broad, and widely spaced. With an internal radial strengthening rib. Lacking an alimentary canal. Length to 60 mm.

**Type Locality and Type Specimens.** Texada Island, northern Straight of Georgia, British Columbia, Canada; Holotype, NMC 86074.

**Distribution.** Southeast Alaska (55.3° N) to Santa Monica, California (34° N) forming dense colonies from 40-600 m, usually in areas of high organic content and low oxygen levels; often present near effluent outfalls and log storage areas.

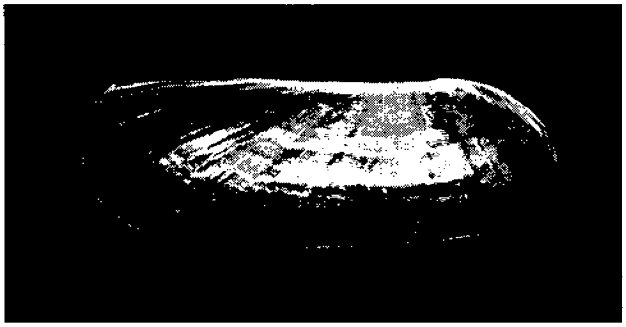

**Figure 5.5.** *Solemya reidi*: exterior of right valve.

**Remarks.** The reduction of the alimentary canal has long been known in the genus, but this was the first species recorded with no gut in the adult. The larva has a complete alimentary system, which is lost at metamophosis. This species was long confused with *S. panamensis* Dall, 1908, which does not occur north of Oaxaca, Mexico (16° N), and differs in being more elongate and in having finer posterior ribs. It is not known whether the latter also lacks a gut. Both merit comparison with *Solemya atacama* Kuznetzov and Shileiko, 1984, described from Peru.

**Literature.** Felbeck (1983), Felbeck *et al.* (1981), C. R. Fisher and Childress (1984), R. G. Gustafson and R. G. B. Reid (1986, 1988a, b), R. G. Gustafson *et al.* (1987), McMahon and R. G. B. Reid (1984), Powell and Somero (1985, 1986), R. G. B. Reid (1980), R. G. B. Reid and F. R. Bernard (1980), Strathmann (1987: 320).

## Superfamily Manzanelloidea Chronic, 1952

= Nucinelloidea Vokes, 1956

**Diagnosis.** Shell subequilateral, small, nuculoid and equivalve. Umbones subcentral. Periostracum thin, polished. Ligament external and opisthodetic, sometimes sunken in marginal grove. Hinge plate strong and short, with few vertical teeth; lateral dentition present in some. Dimyarian or monomyarian. Gill protobranch.

**Remarks.** One living family with cosmopolitan distribution in warm and temperate regions, but penetrating into the deep sea, is recognized.

The placement of this superfamily is not certain. It has been questionably included with the limopsids, but the anatomical structure shows it to be close to *Solemya*, and the shell structure is closer to *Nuculana*. There is little evidence to support the contention that it represents an actinodont lineage. The bipinnate protobranch gill, present in all representatives of the superfamily, is strong evidence of affinity with the paleotaxodonts, as it is not unlikely to have developed independently in unrelated groups. This superfamily is sparsely cosmopolitan and known from the Permian.

### Family Manzanellidae Chronic, 1952

= Nucinellidae Vokes, 1956; Huxleyidae Scarlato and Starobogatov, in Nevesskaia *et al.*, 1971

**Diagnosis.** Shell aragonitic, 2-layered, inequilateral, usually higher than long, equivalve. Periostracum thin and varnished. Sculpture absent, or of incremental striae. Umbones prominent. Interior porcelaneous; ventral margins smooth. Ligament opisthodetic, external, but may be sunken into a fossette. Anterior adductor scar large, posterior scar small or absent. Pallial line entire, sinus absent. Mantle lobes widely open. Gills large, protobranch. Labial palps minute, palp proboscides absent. Alimentary canal absent or reduced, stomach with chitinous lining; style sac and mid-gut conjoined. Intestine traversing ventricle of the heart. Foot developed; flattened sole longitudinally divided and fringed with papillae.

**Remarks.** This family, originating in the early Jurassic, is probably derived from the Permian Manzanellidae. *Manzanella* has approximately equal adductor muscles, and its ligament was probably external.

One species, *Nucinella maxima* Thiele and Jaeckel, 1931, lacks an alimentary system and is similar to the solemyids. J. A. Allen and Sanders (1969) considered *Nucinella* a monomyarian solemyid. Two living genera are known and include 12 species widely distributed in the lower latitudes in shallow to deep water. *Nucinella* has an external ligament and only one adductor muscle. It seems premature to divide this family into two separate families, as has recently been done.

## Genus *Huxleyia* A. Adams, 1860

*Huxleyia* A. Adams, 1860 (April) [not preoccupied by *Huxleya* Dyster, 1858]. **Type species** (M): *H. sulcata* A. Adams, 1860. Recent, Korea.

*Cyrilla* A. Adams, 1860 (June), unnecessary replacement name for *Huxleyia* A. Adams, 1860.

**Diagnosis.** Shell minute, inflated, inequilateral, ovate, usually oblique and equivalve. Periostracum thin and varnished. External sculpture absent. Umbones prominent, posterior. Hinge plate wide, with several vertical teeth and a short lateral tooth. Ligament opisthodetic, chiefly internal in subumbonal fossette. Dimyarian. Pallial line entire.

**Remarks.** Eight species are included in this genus, distributed in the Indo-Pacific to east Africa and Japan, and are known from the Pliocene to Recent. The name is in honor of the British naturalist T. H. Huxley. The gender of the genus, not the naturalist, is feminine.

### *Huxleyia munita* (Dall, 1898)

Figure 5.6

*Cyrilla munita* Dall, 1898: 602, *ex* Carpenter MS.

*Nucula petriola* Dall, 1916: 9, *nom. nud.*; Dall, 1916b: 395.

**Material Examined.** California, Santa Maria Basin, Phase I, Sta. 36 (492 m); Phase II Sta. R-7 (565 m).

**Description.** Shell minute, inflated, with varnished, dark brown periostracum and wide hinge plate bearing 6 or fewer vertical teeth posterior to a deep subumbonal fossette. Strong lateral tooth present in right valve fitting into deep groove in left valve. Length to 3 mm.

**Remarks.** This species cannot be confused with *Nucinella subdola* (A. M. Strong and Hertlein, 1937), a Panamic species with a much smaller fossette and only one adductor muscle. *Huxleyia pentadonta* Scarlato, 1981, which is endemic to the Sea of Okhotsk, differs in being more quadrate.

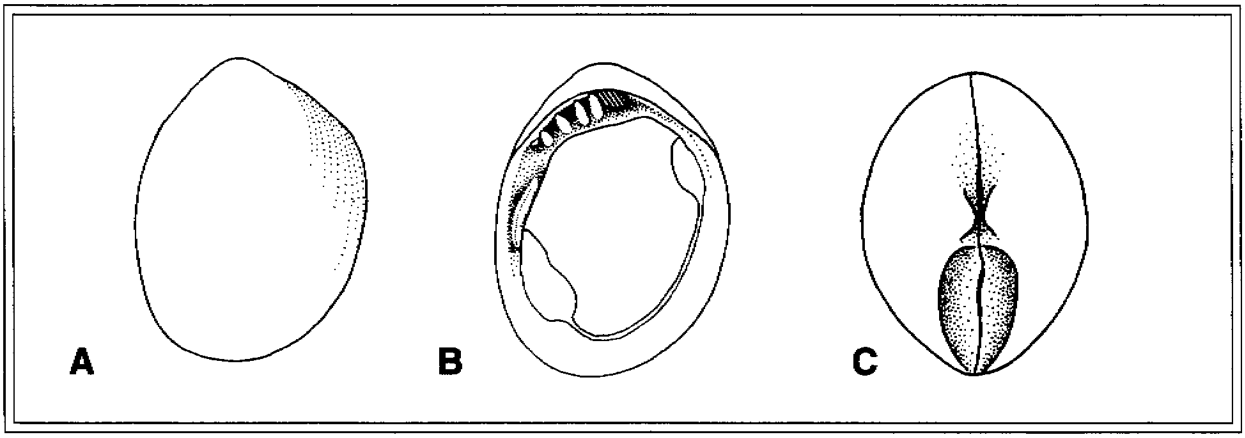

**Figure 5.6.** *Huxleyia munita*: A, exterior of right valve; B, interior of left valve; C, dorsal view of both valves.

**Distribution.** Off Cape Alava, Washington (48.1° N) [SBMNH], to Punta San Pablo, Baja California [Norte] (27.2° N) [LACM], in 70 - 750 m, in soft substrata and course sand. Also in the Pliocene or Pleistocene of southern California.

**Literature.** Hertlein and Strong (1940: 419), A. D. Howard (1953: 235-237), E. J. Moore (1983: 59).

## Superfamily Nuclanoidea H. Adams and A. Adams, 1858

**Diagnosis.** Shell aragonitic, longer posteriorly, usually elongate and equivalve. Periostracum smooth to varnished, olive to dark brown. Surface smooth, or with strong commarginal sculpture. Lunule and escutcheon present or absent. Hinge plate strong, with regular vertical taxodont dentition. Ligament amphidetic, internal or external; resilifer present or absent. Adductor muscle scars subequal. Mantle lobes fused posteriorly, sometimes siphonate. Gills protobranch. Palp proboscides present.

**Remarks.** The superfamily is distinguished from the Nuculoidea by the more elongate shell with a porcellaneous interior. The inhalant current is posterior, and siphons are usually present.

### Family Nuculanidae H. Adams and A. Adams, 1858

**Diagnosis.** Shell aragonitic, homogeneous. Inequilateral, elongate, posterior usually rostrate. Umbones anterior. Sculpture absent, or with weak commarginal lirae, rarely scissulate. Periostracum thin and varnished, usually yellow to dark brown. Hinge plate strong, arched, with 2 series of chevron-shaped teeth separated by resilifer or chondrophore. Ligament amphidetic, partially internal. Adductor muscle scars subequal, or with anterior larger. Pallial line weakly impressed; sinus small to large. Mantle lobes not fused ventrally, posteriorly forming siphonal openings. Gills protobranch usually large. Hypobranchial glands absent. Labial palps long and narrow. Palp proboscides large. Foot with papillated plantar sole. Adult not byssiferous. Alimentary canal with type I stomach and a long, convoluted intestine; style-sac not joined to mid-gut; three ducts from stomach to digestive diverticula; rectum passing through ventricle of heart.

### Genus *Nuculana* Link, 1807

*Nuculana* Link, 1807. **Type species** (OD): *Arca rostrata* Bruguière, 1789, *ex* Chemnitz MS, = *Mya pernula* Müller, 1779. Recent, North Atlantic.

*Leda* Schumacher, 1817. **Type species** (OD): *Arca rostrata* Bruguière, 1789, *ex* Chemnitz MS, = *Mya pernula* MÏller, 1779.

**Diagnosis.** Shell equivalve, usually rather thick. Posterior end strongly rostrate. Sculpture commarginal. Umbones small and opisthogyrate. Escutcheon well developed. Ligament short, in small, oblique resilifer.

## *Nuculana leonina* (Dall, 1896)

Figure 5.7

*Leda leonina* Dall, 1896: 2.

*N. amiata* Dall, 1916: 10, *nom. nud.* Dall, 1916b: 395.

*L. liogona* Dall, 1916: 10, *nom. nud.*; Dall, 1916b: 396.

**Material Examined.** California, Santa Maria Basin, Phase I, Sta.BSS-69 (927 m).

**Description.** Shell elongate. Rostrum long, broad (short in small specimens). Sculpture of strong, widely spaced commarginal ribs, frequently eroded in large specimens. Prodissoconch large, smooth, but eroded in large specimens. Escutcheon narrow, well demarcated. Periostracum very dehiscent, dark in large specimens. Length to 25 mm.

**Type Locality and Type Specimens.** Sea Lion Rock, Washington, 477 - 559 fathoms; Syntypes, USNM 107425, ANSP 68138.

**Distribution.** Southeast Bering Sea (55° N), to San Diego, California (33° N) and to Kamchatka in the western Pacific; in 350 - 2,500 m.

**Literature.** Scarlato (1981: 182-183).

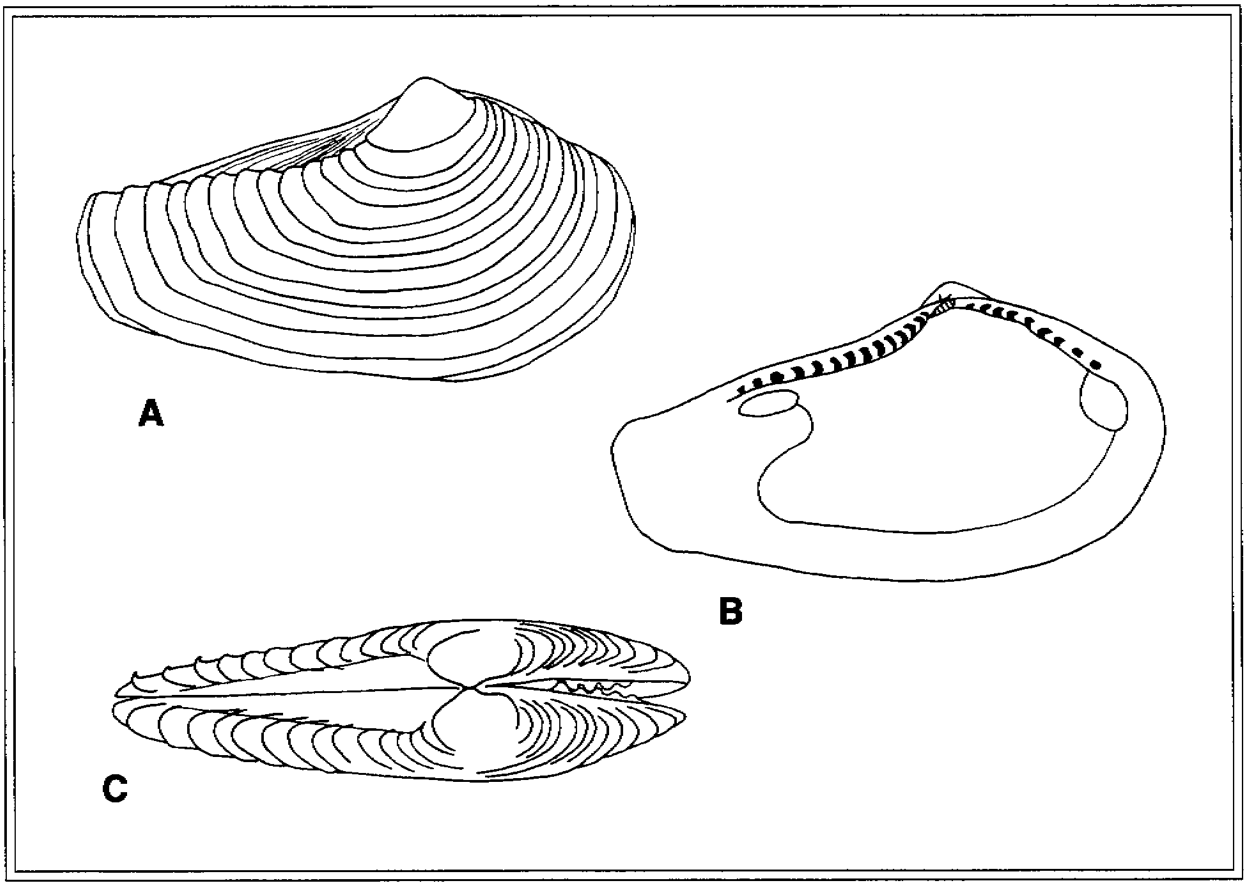

**Figure 5.7.** *Nuculana leonina*: A, exterior of right valve; B, interior of left valve; C, dorsal view of both valves.

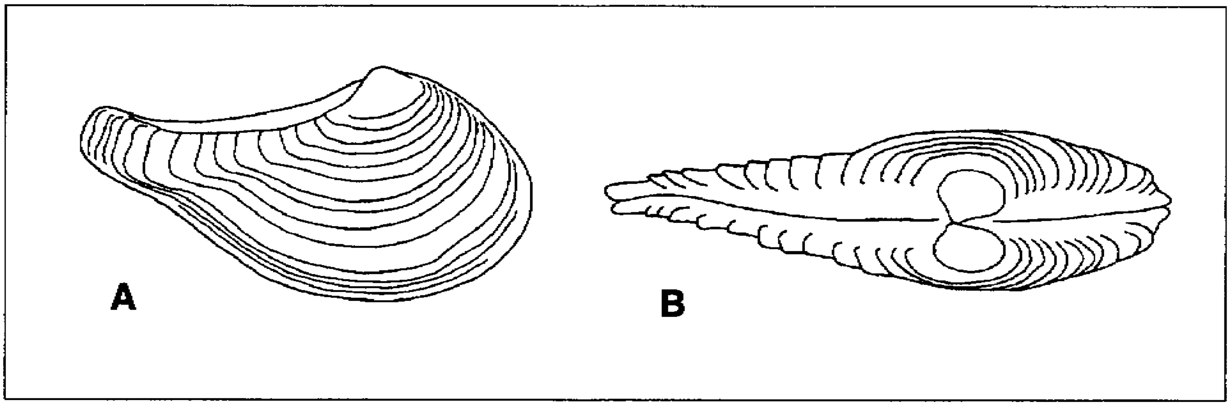

**Figure 5.8.** *Nuculana hamata*: A, exterior of right valve; B, dorsal view of both valves.

### *Nuculana hamata* (Carpenter, 1864)

Figure 5.8

*Leda hamata* Carpenter, 1864b: 644; 1866: 210.

*Leda hamata limata* Dall, 1916: 10, *nom. nud.*; Dall, 1916b: 397.

**Material Examined.** California, Santa Maria Basin, Phase II, Sta.R-4 (92 m), PJ-17 (126 m).—Lectotype (see below).

**Description.** Shell elongate, with sharp, widely spaced commarginal ribs in some; others almost smooth. Rostrum very long and narrow, strongly recurved. Periostracum dull to silky. Escutcheon prominent. Length to 12 mm.

**Type Locality and Type Specimens.** Catalina Island, California, 20 - 60 fathoms; Lectotype, USNM 107420.

**Distribution.** Forrester Island, Alaska (55° N) [SBMNH], to Isla Cedros, Baja California [Norte] (27° 55'N), but possibly as far south as Panama [USNM], in 30 - 550 m. Also reported as early as the Pliocene in western North American.

**Literature.** E. J. Moore (1983: 22).

### *Nuculana conceptionis* (Dall, 1896)

Figure 5.9

*Leda conceptionis* Dall, 1896: 2.

*Leda gomphoidea* Dall, 1916: 11, *nom. nud.*; Dall, 1916: 396.

**Material Examined.** California, Santa Maria Basin, Phase I, Sta.BSS-63 (930 m), BSS-77 (578 m); Phase II, Sta. R-3 (409 m), PJ-20 (148 m).—Syntypes, USNM 107426 (see below).

**Description.** Shell very elongate, thin, compressed, smooth, with a highly varnished, iridescent periostracum. Rostrum narrow. Escutcheon narrow, poorly defined. Length to 30 mm.

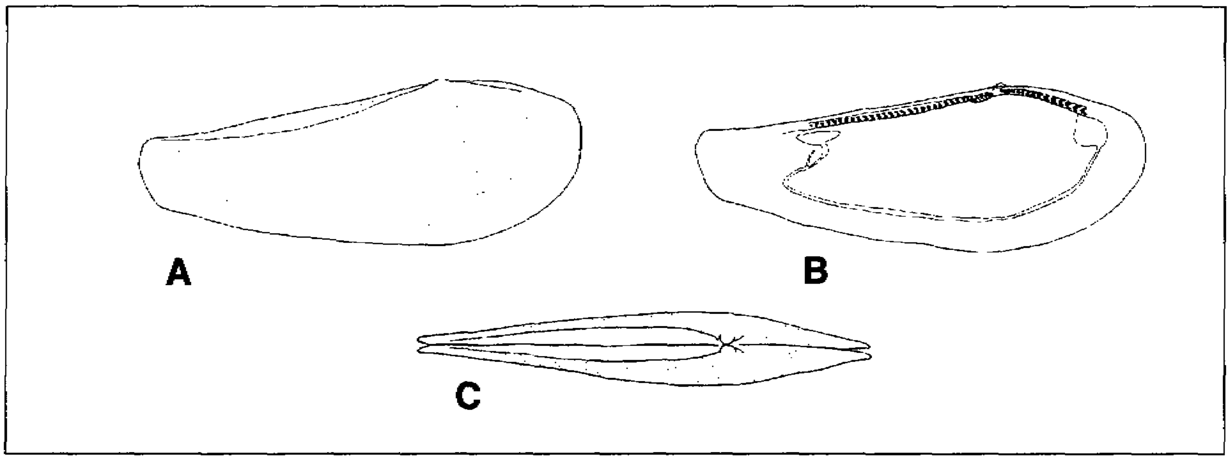

**Figure 5.9.** *Nuculana conceptionis*: A, exterior of right valve; B, interior of left valve; C, dorsal view of both valves.

**Type Locality and Type Specimens.** Pt. Conception, California; Syntypes, USNM 107426, ANSP 68137.

**Distribution.** Pribiloff Islands, Bering Sea (57° N) to off Newport Bay, California (33° 30'N) in 148 - 2,300 m.

### ***Nuculana taphria*** **(Dall, 1896)**

Figure 5.10

*Leda taphria* Dall, 1896: 70, *nom. nov. pro Nucula caelata* Hinds, 1843: 99, *non Nucula coelata* Conrad, 1833 [see ICZN Code Art. 58].

**Material Examined.** California, Santa Maria Basin, Phase I, Sta.BSS-21 (49 m); Phase II, R-8 (308 m).

**Description.** Shell short, inflated. Sculpture of sharp, heavy commarginal ribs that become obsolete on posterior slope. Rostrum sharply pointed. Periostracum shiny, iridescent. Escutcheon wide, less clearly demarcated by radial ridges than in *Nuculana penderi* (Figure 5.10). Length to 20 mm. Shell subequilateral, inflated, elongate to ovate. Sculpture of strong commarginal ribs or corrugations. Posterior end with a pointed rostrum, set off by shallow radial sulcus. Anterior and posterior set of teeth subequal. Pallial sinus deep.

**Type Locality and Type Specimens.** Unknown, possibly at BMNH.

**Distribution.** Fort Bragg, California (39.5° N) to Isla Cedros, Baja California [Norte] (28° N) in 10 - 100 m. Reported as early as the Oligocene in northwest America.

**Literature.** E. J. Moore (1983: 19-20).

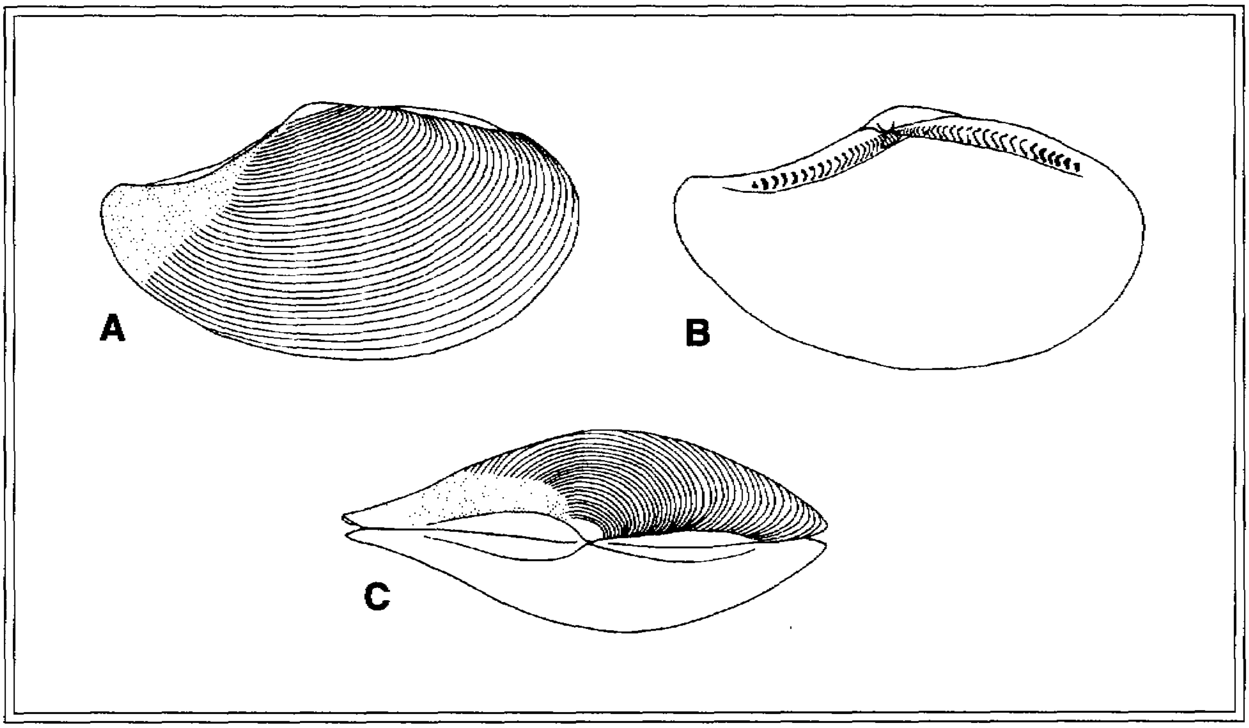

**Figure 5.10.** *Nuculana taphria*: A, exterior of right valve; B, interior of left valve; C, dorsal view of both valves.

### *Nuculana pontonia* (Dall, 1890)

Figure 5.11

*Leda pontonia* Dall, 1890: 257.

**Material Examined.** California, Santa Maria Basin, Phase I, Sta.BSS-92 (444 m).—Holotype (see below).

**Description.** Shell thin, with a pointed rostrum. Sculpture of fine rounded commarginal riblets, becoming obsolete on central slope. Escutcheon very wide, deep. Rostrum pointed. Periostracum light olive to brown, dull to silky. Length to 18 mm.

**Type Locality and Type Specimens.** Near the Galápagos Islands, Ecuador, 817 fathoms; Holotype, USNM 96943.

**Distribution.** San Diego, California (33° N) to the Gulf of Panama (6° N) [USNM] and the Galápagos Islands, in 1,150 - 3,000 m.

**Literature.** Gooch and Schopf (1972), Rokop (1979).

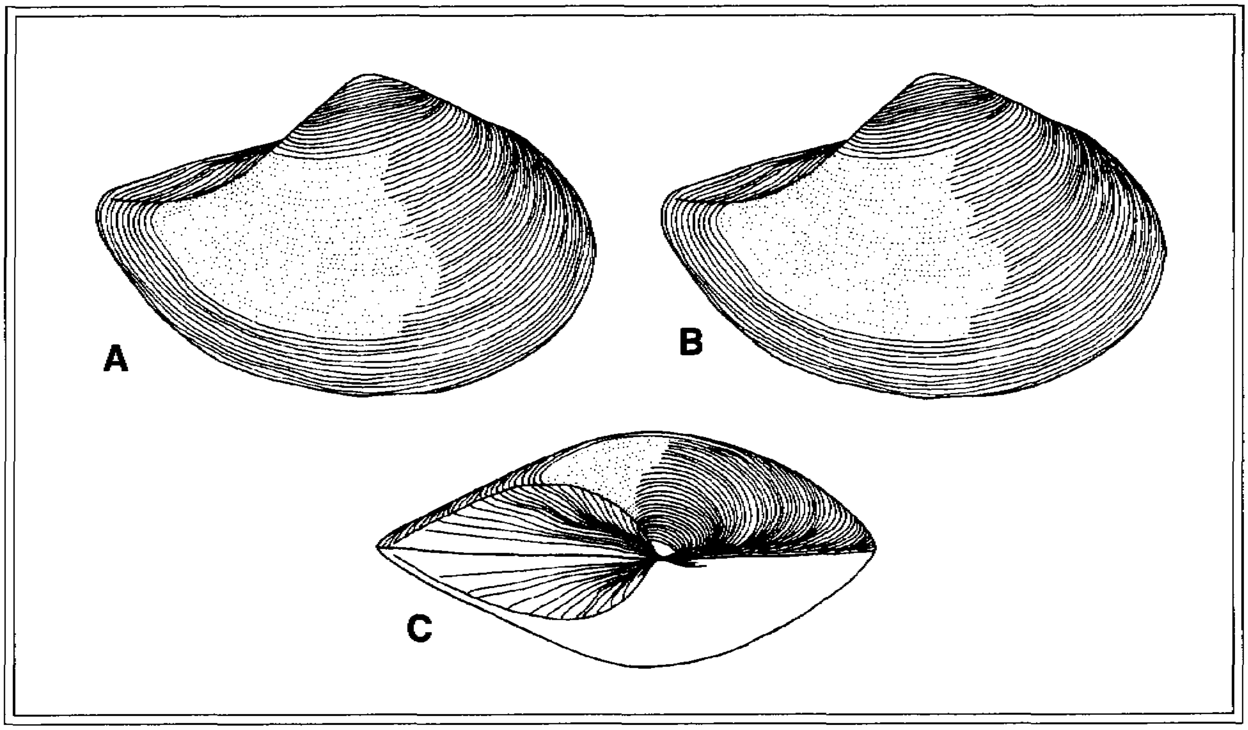

**Figure 5.11.** *Nuculana pontonia*: A, exterior of right valve; B, interior of left valve; C, dorsal view of both valves.

## Family Tindariidae Scarlato and Starobogatov, 1971

**Diagnosis.** Shell robust, inflated and subequilateral. Periostracum thick, adherent. Sculpture absent, or of commarginal lirae or riblets. Umbones prominent, prosogyrate. Hinge plate wide and strongly arched, with a continuous series of taxodont teeth. Ligament opisthodetic and external. Adductor muscle scars subequal. Pallial line obscure; sinus absent. Byssal gland small. Mantle lobes unfused. Siphons absent, but inhalant region of mantle edge with elongate papillae. Foot with divided papillated planar sole. Gill protobranch, oblique with respect to anterior-posterior axis, with few, widely spaced, thick filaments. Labial palps small, with few ridges on inner surface; palp proboscides elongate. Alimentary canal with large type 1 stomach lined with cuticle; three ducts to the digestive diverticula; style-sac conjoined to mid-gut; intestine looping once to right of stomach; rectum passing through ventricle of heart.

### Genus *Tindaria* Bellardi, 1875

*Tindaria* Bellardi, 1875. **Type species** (M): *T. arata* Bellardi, 1875. Pliocene, Italy.

**Diagnosis.** Shell solid, inflated, ovate. Periostracum adherent. Sculpture commarginal lirae or riblets, often obsolete. Umbones prosogyrate. Hinge plate arched and strong. Taxodont teeth in continuous series, minute in central section. Ligament opisthodetic and external, with a section sunken into a groove. Siphons absent; mantle with conspicuous papillae bordering incurrent region. Labial palps small. Gills small and oblique.

**Remarks.** These solid little shells are difficult to identify, and though the teeth are in a continuous series, the subumbonal ones may be minute. Named from the Greek proper name *Tyndaraeus*, a king of Sparta, but the gender is feminine.

### *Tindaria kennerlyi* (Dall, 1897)

Figure 5.12

*Malletia (Tindaria) kennerlyi* Dall, 1897: 11.
*Tindaria dicofania* Dall, 1916: 13, *nom. nud.*; Dall, 1916: 401.
*T. martiniana* Dall, 1916: 13, *nom. nud.*; Dall, 1916: 401.

**Material Examined.** California, Santa Maria Basin, Phase I, Sta.BSS-78 (762 m).—Holotype (see below).

**Description.** Shell elongate, subequilateral; posterior end rounded; dorsal margin straighter than in other species. Sculpture of numerous minute commarginal striae becoming obsolete on ends. Length to 5 mm.

**Type Locality and Type Specimens.** Off the coast of Washington, 559 fathoms; Holotype, USNM 123497.

**Distribution.** Cape Flattery, Washington (48° N), to San Diego, California (33° N) and in the Gulf of California, in 762 - 2,500 m.

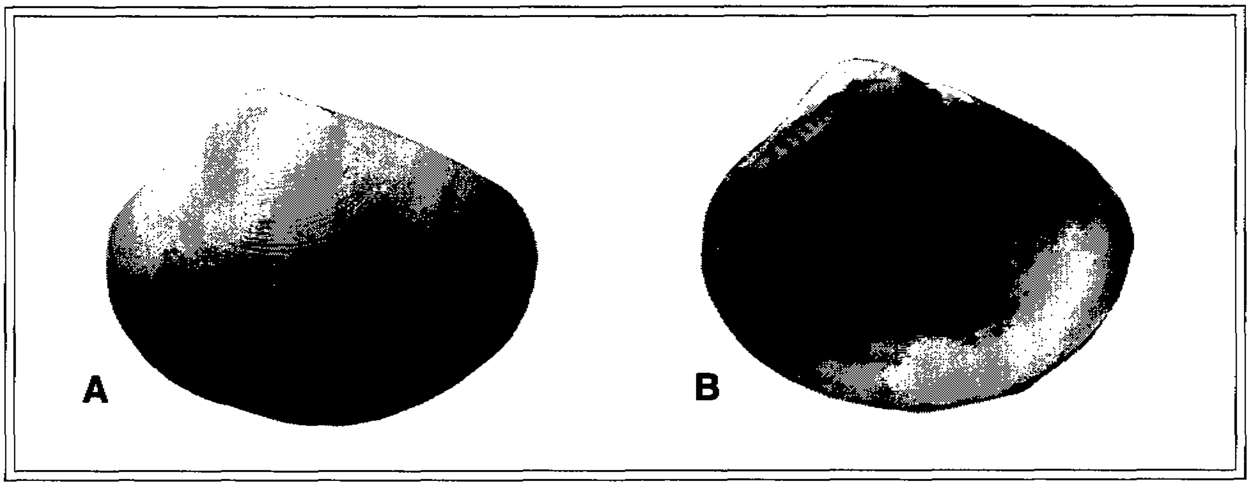

**Figure 5.12.** *Tindaria kennerleyi*: A, exterior of left valve; B, interior of right valve.

## Family Neilonellidae J. A. Allen, 1978

= Saturniidae J. A. Allen and Hannah, 1987, *non* Boisduval, 1837

**Diagnosis.** Shell aragonitic, homogeneous or crossed-lamellar; interior porcelaneous, rarely subnacreous. Subequilateral to inequilateral, rather inflated, venerid shaped. Periostracum thin, dull, adherent. Sculpture commarginal. Anterior and posterior gapes absent. Hinge plate with taxodont teeth in two series, sometimes separated by narrow plain area, without resilifer. Ligament external, opisthodetic to amphidetic, weak. Pallial sinus large. Foot with papillated, planar sole. Siphons present, inhalant and exhalant fused. Hypobranchial glands absent. Gills protobranch, with many plates. Labial palps large, with many ridges; palp proboscides narrow and long. Alimentary canal with type 1 stomach; three ducts leading to digestive diverticula; style sac not fused to mid-gut; intestine passing through ventricle of heart.

The family may be related to the Nuculanidae, but the lack of a resilifer supports its separation. They differ from the Malletiidae in being smaller and in lacking conspicuous gapes, and from Tindariidae in having siphons and a short gap in the dentition under the beaks (except in *Austrotindaria*). There are three living genera with approximately 35 species. Known from the Jurassic and present in all oceans, especially in deep water in soft substrata.

**Literature.** J. A. Allen (1978: 390-392), Knudsen (1970), Sanders and Allen (1977, 1985).

### Genus Neilonella Dall, 1881

*Saturnia* Seguenza, 1877, *non* Schrank, 1802. **Type species** (M): *Nucula pusio* Philippi, 1844. Pliocene, Mediterranean.

*Neilonella* Dall, 1881. **Type species** (OD): *Leda (Neilonella) corpulenta* Dall, 1881. Recent, Caribbean.

*Pseudoneilonella* Laghi, 1986, *nom. nov. pro Saturnia* Seguenza, *non* Schrank.

**Diagnosis.** Shell thick, inequilateral, inflated. Posterior end produced. Periostracum thin, adherent. Sculpture of commarginal riblets. Umbones prominent, opisthogyrate. Hinge plate wide; taxodont teeth heavy, continuous or separated by narrow subumbonal area. Ligament opisthodetic, mostly external, portion under beaks sunken. Pallial line obscure; pallial sinus unclear. Mantle lobes not fused, except in forming 2 small siphons. Labial palps large; palp proboscides wide. Alimentary canal with type 1 stomach; intestine curving to right.

The generic level taxonomy within this family is far from settled, and *Pseudoneilonella* may not be a synonym of *Neilonella* (T. R. Waller, letter, 3 November 1995).

A very widely distributed deep-water genus, comprising some 30 species. This genus occurs as early as the Eocene, and may date from the Jurassic. The name is from the Greek diminutive *Neilos*, the river Nile; the gender is feminine.

### *Neilonella ritteri* (Dall, 1916)

Figure 5.13

*Tindaria ritteri* Dall, 1916a: 13, *nom. nud.*; 1916b: 401.

*Tindaria californica* Dall, 1916a: 13, *nom. nud.*; 1916b: 401.

**Material Examined.** California, Santa Maria Basin, Phase II, Sta.R-3 (409 m), R-7 (565 m).

**Description.** Shell ovate-elongate, robust, inflated; anterior end sharply rounded; posterior end produced, pointed. Surface smooth, or with weak commarginal striae. Periostracum dark brown. Length to 12 mm.

**Type Locality and Type Specimens.** Off La Jolla, California, 191-293 fathoms; Holotype, USNM 209396. The type specimen of *Tindaria californica* is a juvenile of this species.

**Distribution.** Santa Barbara (34.4° N) [USNM] to La Jolla (32.7° N) [USNM], California, in 366 - 565 m.

## Family Sareptidae Stoliczka, 1871

**Diagnosis.** Shells inflated, thin, ovate to elongate. Ligament partly internal, in a resilifer. Siphons present; pallial line with sinus. Adductor muscles subequal. Hypobranchial gland present. Labial palps large; palp proboscides narrow. Foot thick, with divided plantar papillated sole. Gills tranverse, with few gill plates. Alimentary canal consisting of large stomach and long, coiled intestine; style-sac and mid-gut conjoined.

**Remarks.** As pointed out by Maxwell (1988), Sareptidae is the first family-group name available for this complex. Thus, if the poorly known, deep-water *Sarepta* is included here, that must be the family name. Three subfamilies are present in the eastern Pacific.

### Genus *Yoldia* Möller, 1842

*Yoldia* Möller, 1842. **Type species** (SD ICZN Opinion 769, 1966): *Y. hyperborea* Torell, 1859, = *Nucula hyperborea* Gould, 1841, *ex* Lovén MS. Recent, North Atlantic.

**Diagnosis.** Shell thin to robust, inequilateral, subovate. Posterior end produced, usually gaping. Hinge plate not strong; small taxodont teeth in 2 subequal series. Resilifer large. Pallial sinus deep.

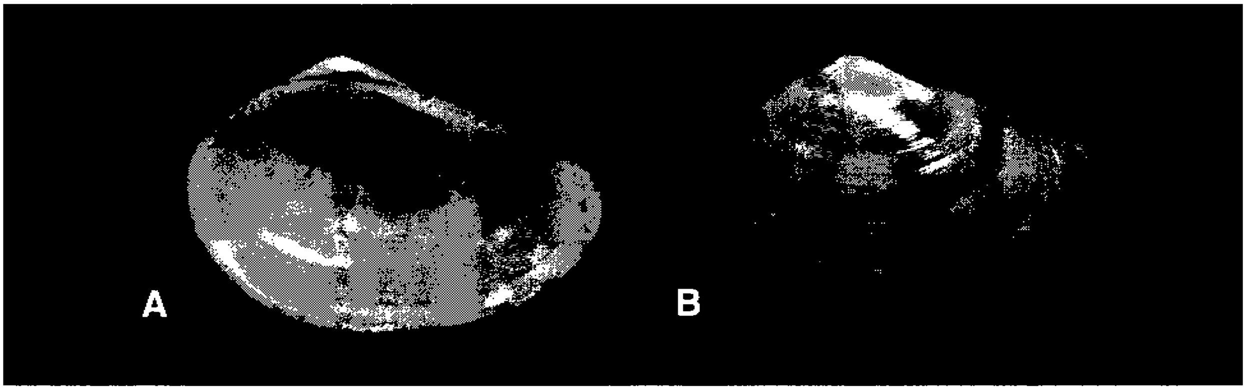

**Figure 5.13.** *Neilonella ritteri*: A, interior of right valve; B, exterior of left valve.

## *Yoldia seminuda* Dall, 1871

Figure 5.14

*Nucula arctica* Broderip and G. B. Sowerby I, 1829: 359, *non* J. E. Gray, 1824.

*Yoldia seminuda* Dall, 1871: 153.

*Yoldia scissurata* Dall, 1897: 8, *nom. nov. pro Nucula arctica* Browerip and G. B. Sowerby I, *non* J. E. Gray.

*Yoldia ensifera* Dall, 1897: 9.

*Yoldia ensifera plena* Dall, 1908: 256.

*Yoldia (Cnesterium) strigata* Dall, 1909: 104.

*Yoldia (Cnesterium) excavata* Dall, 1925: 31.

**Material Examined.** California, Santa Maria Basin, Phase I, Sta.BSS-6 (109 m); Phase II, Sta. PJ-9 (169 m).—Holotype (see below).

**Description.** Shell compressed, thin, elongate, subequilateral; posterior end with slightly recurved, blunt to slightly pointed rostrum; postero-dorsal keel low to raised. Oblique ribs present on one or more slopes, widely spaced. Periostracum adherent, shiny, frequently banded with light and dark. Length to 40 mm.

**Type Locality and Type Specimens.** St. Paul's Harbor, Kodiak, Alaska; Holotype, USNM 107678.

**Distribution.** Arctic and northwestern Pacific. Beaufort Sea, Alaska (71° N), St. Lawrence Island, Bering Sea (63° N) to San Diego, California (32.7° N); in 15 - 375 m.

**Literature.** Heath (1937: pls. 6, 8), Lubinsky (1980: 21), N. MacGinitie (1959: 154-155), Scarlato (1981: 201-202), Stasek (1965).

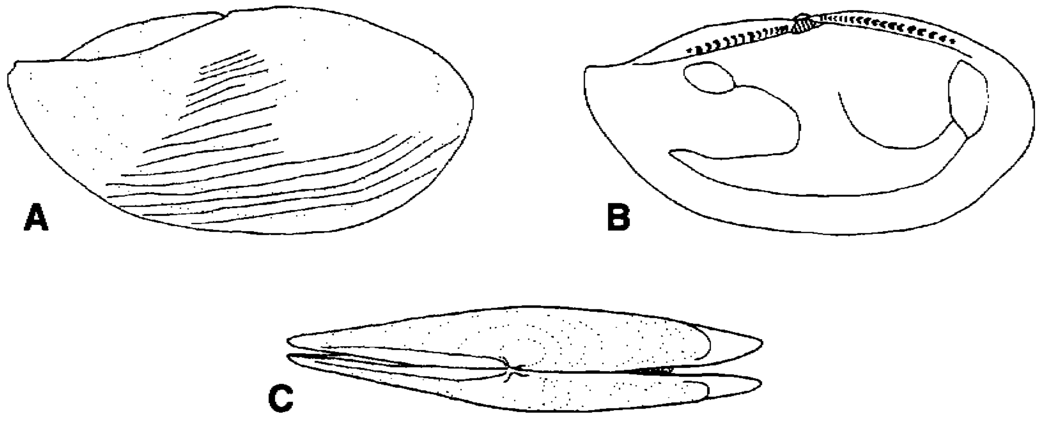

**Figure 5.14.** *Yoldia seminuda*: A, exterior of left valve; B, interior of right valve; C, dorsal view of both valves.

## Subclass Pteriomorphia Beurlen, 1944

**Diagnosis.** Shell aragonitic, calcitic, or nacreous. Variable in shape, rounded to trapezoidal, usually inequilateral, equivalve to subequivalve. Periostracum thick, usually hirsute. Hinge plate weak; dentition variable, sometimes obsolete. Ligament amphidetic or opisthodetic, external, occasionally with internal section in a resilifer. Dimyarian or monomyarian. Mantle lobes usually not fused, lacking siphons. Gills eleutherorhabdic or synaptorhabdic. Foot vestigial or absent. Adult usually byssate.

**Remarks.** The subclass is known from the Ordovician and includes a diverse array of bivalves, including ark shells, mussels, oysters and scallops, as well as less well-known forms. Although diverse in form and adapted to a wide variety of niches, the subclass represents a single phylogenetic unit accepted both by paleontologists and malacologists. Groupings of pteriomorphans that excluded the Arcoida were termed the Dysodonta or Anisomyaria. The specialised modification of the mussel species associated with deep-water hydrothermal vents displays some important specializations, but it is clearly a mytilid. One recent review proposes three major divisions and includes them in the subclass Autobranchia, as first delimited by Soviet researchers. Here I follow a more conservative course and retain the well-known name for the subclass.

The group is notable for the development and variations of shell form and the structure of the ligament. There is a strong tendency to lie on one valve, associated with at least a transitional byssate state, and for atrophy of the foot. The monomyarian condition, also typical of the subclass, has evolved independently in several lineages. Other characters are hypertrophy of the lips to form a cover over the mouth, and the strong development of the mantle margins, which are usually supplied with sensory organs, with the inner fold modified to form a wide pallial curtain. This allows wide opening of the valves while maintaining control of access to the pallial chamber. Several genera have developed elaborate projecting periostracal structures, particularly the Arcacea. In the Mytilidae, these are secondary, adventitious structures.

## Order Mytiloida Férussac, 1822

**Diagnosis.** Shell inequivalve, usually equilateral and inflated. Periostracum well developed, usually thick, often with secondary adventitious projecting structures. Umbones anterior, prosogyrate. Sculpture absent, or with radial ribs predominating, sometimes divided into distinct regions. Hinge plate usually weak, edentate, occasionally with small dysodont teeth, striations, or tubercles. Ligament opisthodetic, alivincular, external, attached to nymph. Anterior adductor muscle small or evanescent, usually heteromyarian, rarely monomyarian. Pallial line simple. Mantle lobes not fused, except for exhalant aperture, which may be supplied with a small siphon. Rarely, mantle fusion is more extensive, leaving only a small ventral aperture and a small siphon. Mantle folds without ocelli. Majority of species byssate in adult.

**Remarks.** Very widely distributed, especially in shallow water, although also present in the deepest, hadal regions; a few groups have penetrated into brackish and fresh waters. The order contains one living superfamily and family with approximately 250 species. The majority are byssally attached epifauna, but shallow infauna are also known, and a few species bore into rock or shell.

## Superfamily Mytiloidea Rafinesque, 1815

**Diagnosis.** Shell equivalve, strongly inequilateral; umbones anterior, prosogyrate. Periostracum thick, usually dark colored and adherent, commonly with secondarily formed, sparse setae. Ligament opisthodetic, external on pseudonymph. Sculpture absent, or various. Anterior adductor small to minute; posterior adductor elongate. Hinge plate feeble, edentate, or with small tubercles. Adult usually byssate.

**Remarks.** This group comprises the mussels, usually epifaunal, byssally attached species, frequently forming dense beds on solid substrata in the intertidal zone, but also byssally attached on muddy foreshores. Other representatives are nestlers, and one group contains active borers.

### Family Mytilidae Rafinesque, 1815

**Diagnosis.** Shell aragonitic and calcitic, with outer layer of simple calcite and an inner layer of sheet nacre. Strongly inequilateral, thin and inflated. Umbones prosogyrate, prominent, at or near anterior end. Periostracum thick, usually highly colored or black, frequently secondarily hirsute. Sculpture absent, or mainly radial, frequently in several zones. Hinge plate narrow, usually weak and edentate, or with crenulations forming dysodont teeth; vertical crenulations or tubercles may also be present. Ligament external, alivincular and opisthodetic, sunken into groove and attached to a nymph. Rarely ligament with internal resilium set into shallow depression. Heteromyarian, with reduced anterior adductor muscle; rarely monomyarian, with total loss of anterior adductor muscle. Interior of valves nacreous. Pallial line simple, feebly impressed. Scars from pedal musculature strongly impressed. Mantle lobes usually not extensively fused, except to separate the posterior exhalant aperture, which may be siphonate. Rarely with extensive mantle fusion, leaving small byssal aperture. A siphonal septum projecting from ventral part of exhalant opening helps to separate suprabranchial chamber. Labial palps long and narrow. Foot digitiform, with byssal groove. Adult byssate. Alimentary canal with type 3 stomach, with clustered groups of ducts leading to digestive diverticula; style-sac conjoined to mid-gut; intestine usually looped, usually passing through ventricle of heart.

### Genus *Modiolus* Lamarck, 1799

*Modiolus* Lamarck, 1799. **Type species** (T): *Mytilus modiolus* Linnaeus, 1758. Recent, North Atlantic.

**Diagnosis.** Shell inequilateral, elongate and oblique, medially inflated. Umbones anterior, but not terminal. Dorsal margin straight or curved. Sculpture absent or rarely concentrically striated. Periostracum varnished, often hirsute. Hinge edentate, but small dysodont tubercles may be present near anterior end of ligament. Ligament external, opisthodetic, frequently sunken into groove, attached to narrow resilial ridge. Interior nacreous and sometimes flushed with color. Byssate.

**Remarks.** An easily recognized group, commonly called horse mussels, widely distributed both in temperate and warm shallow seas. Usually semi-infaunal in sand or mud, with the posterior end of the shell protruding from the substratum.

### *Modiolus neglectus* Soot-Ryen, 1955

Figure 5.15

*Modiolus neglectus* Soot-Ryen, 1955: 64.

**Material Examined.** California, Santa Maria Basin, Phase I, Sta.BSS-21 (49 m); Phase II, Sta. R-8 ( 90 m), PJ-15 (155 m).

**Description.** Shell quadrangular, very inflated, with produced, flanged posterodorsal margin; anterior end not strongly produced. Periostracum varnished, with obscure radial striae on central slope; posterior slope sharply defined, with hirsute periostracum; setae simple. Length to 130 mm.

**Type Locality and Type Specimens.** San Diego, California; Holotype, LACM.

**Distribution.** Mugu, California (34° N) to Outer Gorda Bank, Baja California Sur, Mexico (27° N), in 15 - 155 m.

### Genus Amygdalum Mühlfeld, 1811

*Amygdalum* Mühlfeld, 1811. **Type species** (M): *A. dendricum* Mühlfeld, 1811. Recent, Caribbean.

**Diagnosis.** Shell thin, frequently hyaline. Periostracum thin and adherent. Sculpture absent. Hinge plate weak. Ligament small, attached to slight resilial ridge.

**Remarks.** Members of the genus usually live colonially in a nest of byssal threads and adhering particles. The name is derived from the Latin *amygdala*, an almond; although almond is feminine, this derived generic name has been treated as neuter.

**Literature.** J. F. Allen (1955), Wilson and Hodgkin (1967).

### *Amygdalum pallidulum* (Dall, 1916)

Figure 5.16

*Modiolus (?politus) pallidulus* Dall, 1916a: 18, *nom. nud.*; Dall, 1916b: 404.

**Material Examined.** California, Santa Maria Basin, Phase I, Sta.BSS-22 (99 m); Phase II, Sta. R-1 (91 m), PJ-8 (142 m), PJ-16 (130 m).

**Description.** Shell thin, translucent and compressed. Sculpture absent. Periostracum brilliantly polished, irridescent. Ventral region opaque, white to yellowish, with yellow striations on central and dorsal slopes. Length to 34 mm.

**Type Locality and Type Specimens.** Off Morro Bay, California; Holotype, USNM 212746.

**Distribution.** Trinidad Harbor, California (41° N), to Acapulco, Guerrero, Mexico (17° N) in 40 - 400 m.

**Remarks.** This species was described by Dall (1916a) as differing from the Caribbean *A. politum* (Verrill and Smith, 1880) only in being smaller and in not being as golden-yellow in color. Clearly, their relationship should be reevaluated.

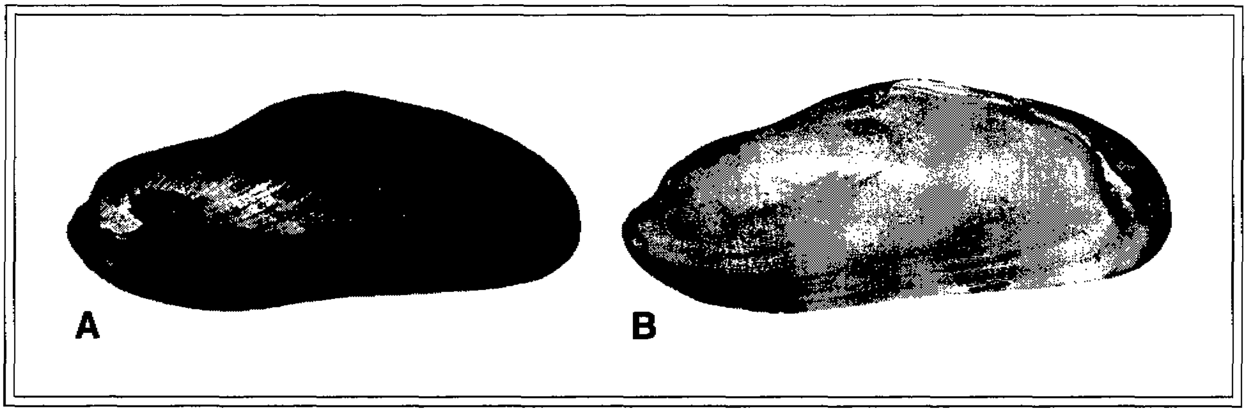

**Figure 5.15.** *Modiolus neglectus*: A, exterior of left valve; B, interior of right valve.

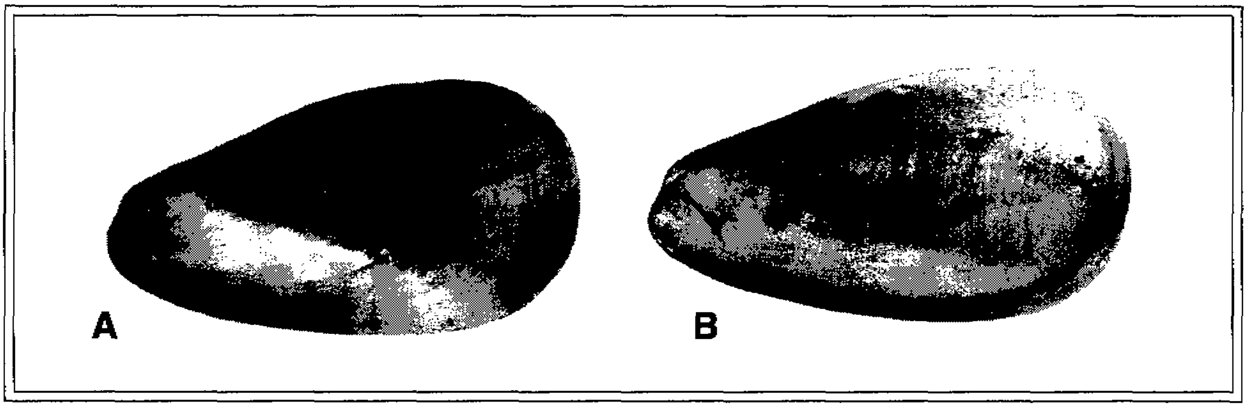

**Figure 5.16.** *Amygdalum pallidulum*: A, exterior of left valve; B, interior of right valve.

### Genus *Crenella* Brown, 1827

*Crenella* Brown, 1827. Type species (M): *C. elliptica* Brown, 1827, = *Mytilus decussatus* Montagu, 1808. Recent, North Atlantic.

*Nuculocardia* d'Orbigny, 1853. Type species (OD): *N. divaricata* d'Orbigny, 1853. Recent, Caribbean.

**Diagnosis.** Shell inequilateral, tumid, equivalve and small. Umbones not prominent, prosogyrate, with prodisoconch clearly demarcated. Periostracum thin, adherent. Sculpture of fine radial lirae, divaricating laterally, and some fine commarginal lirae, resulting in a decussate appearance. Hinge plate weak, with one or more small tubercles under beaks. Ligament opisthodetic, external, but sunken in groove.

## *Crenella decussata* (Montagu, 1808)

Figure 5.17

*Mytilus decussatus* Montagu, 1808: 69.

*Nuculocardia divaricata* d'Orbigny, 1842: pl. 27.

*Crenella? inflata* Carpenter, 1864: 313.

*Crenella yokoyamai* Nomura, 1932: 74.

*Crenella ecuadoriana* Pilsbry and Olsson, 1941: 55.

*Crenella decussata laticostata* Scarlato, 1960: 65.

**Material Examined.** California, Santa Maria Basin, Phase I, Sta.BSS-36 (492 m); Phase II, Sta. R-4 (92 m), R-8 (90 m)

**Description.** Shell ovate, inflated, with conspicuous radial riblets, which may bifurcate ventrally. Length to 10 mm.

**Type Locality and Type Specimens.** Off the coast of Scotland; type not found, possibly BMNH.

**Distribution.** Arctic and circumboreal. Beaufort Sea, Alaska (70° N), south through the Gulf of California and to northern Peru (3.5° S) (Olsson, 1961), and the Galápagos Islands (1° N) ; in Atlantic from North Carolina to the Caribbean and south to the British Isles; south to Japan in northwestern Pacific; in the intertidal zone - 492 m.

**Remarks.** Attempts to recognize two taxa here, a northern, coarsely sculptured species and a southern species with finer, more bifurcating ribs, quickly fall apart. This species-complex would prove an interesting topic for more detailed study.

**Literature.** F. R. Bernard (1979: 24), Lubinsky (1980: 24), E. J. Moore (1983: 71-72), Ockelmann (1959: 51-52), Olsson (1961: 130), Scarlato (1981: 220-222), Soot-Ryen (1955: 80-81).

### Genus *Solamen* Iredale, 1924

*Solamen* Iredale, 1924. Type species (M): *M. rex* Iredale, 1924. Recent, Australia.

*Megacrenella* Habe, 1955. Type species (OD): *Crenella* (*Megacrenella*) *tamurai* Habe, 1955: 26, = *C. columbiana* Dall, 1897. Recent, northeastern Pacific.

**Diagnosis.** Shell larger than *Crenella*, thin and inflated. Umbones prominent, anterior. Periostracum thin and dehiscent. Sculpture of radial bifurcating riblets. Hinge plate very thin, lacking dyssodont teeth. Ventral anterior margin vertically crenulate. Ligament long.

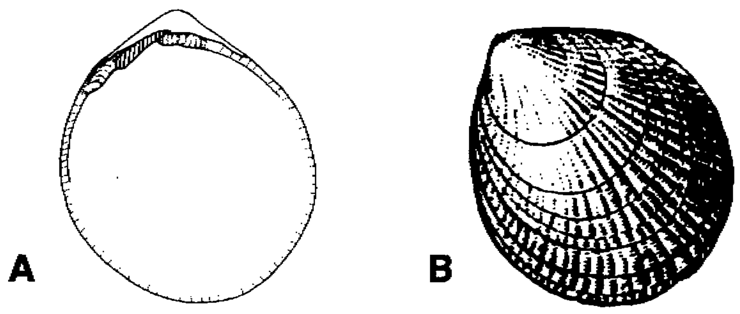

**Figure 5.17.** *Crenella decussata*: A, interior of left valve; B, exterior of left valve.

### *Solamen columbianum* (Dall, 1897)

Figure 5.18

*Crenella columbiana* Dall, 1897: 4.

*Crenella leana* Dall, 1897: 4.

*Crenella megas* Dall, 1902: 559.

*Crenella rotundata* Dall, 1916a: 20, *nom. nud.*—Dall, 1916b: 406.

*Crenella tamurai* Habe, 1955.

**Material Examined.** California, Santa Maria Basin, Phase I, Sta.BSS-6 (109 m); Phase II, Sta. R-1 (98 m), R-6 (100 m).—Holotype (see below).

**Description.** Shell highly inflated, oval. Sculpture of very fine radial striae, and minute, irregular commarginal striae. Length to 25 mm.

**Type Locality and Type Specimens.** Port Orchard, Puget Sound, Washington; Holotype, USNM 107630.

**Distribution.** Bering Sea; Cook Inlet, Alaska (60° N), to Panama Bay (8° N) and east to Siberia and northern Japan, in 20 - 500 m.

**Literature.** Scarlato (1981: 224), Soot-Ryen (1955: 82-83)

### Genus *Gregariella* Monterosato, 1883

*Gregariella* Monterosato, 1883. **Type species** (M): *Modiolus sulcatus* Risso, 1826, *non* Lamarck, 1805, = *M. barbatellus* Cantraine, 1835. Recent, Mediterranean.

*Botulina* Dall, 1889. **Type species** (M): *Modiola opifex* Say, 1825. Recent, North Atlantic.

**Diagnosis.** Shell elongate, inflated. Umbones incurved, orthogyrate. Anterior end smooth or with commarginal ribs; posterior end with radial riblets, hirsute behind keel. Hinge plate weak, with dysodont teeth. Ligament opisthodetic, external. Inner shell margins crenulate.

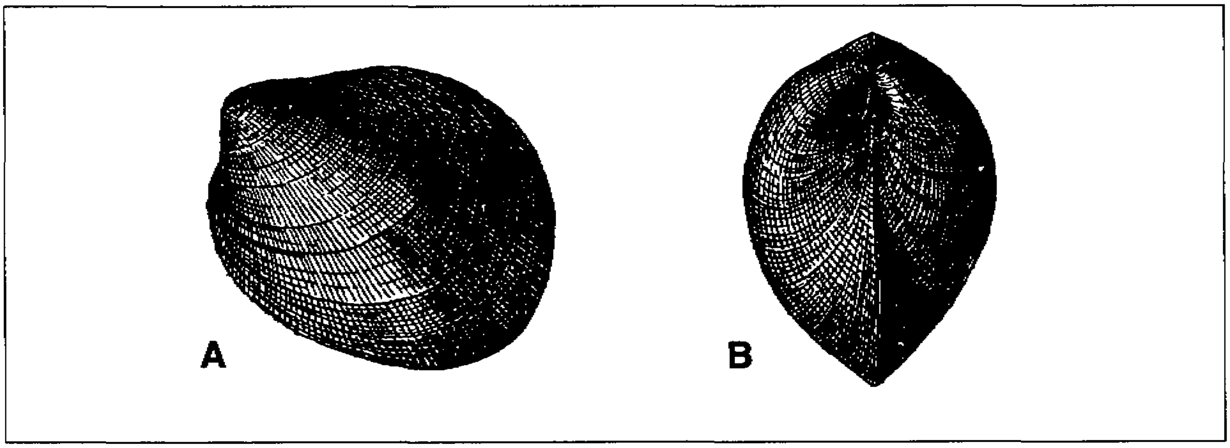

**Figure 5.18.** *Solamen columbianum*: A, exterior of left valve; B, dorsal view of both valves.

### *Gregariella coarctata* (Carpenter, 1857)

Figure 5.19

*Crenella coarctata* Carpenter, 1857: 123, *ex* Dunker MS.
*Modiolaria denticulata* Dall, 1871: 154.

**Material Examined.** California, Santa Maria Basin, Phase I, Sta.BSS-6 (109 m).

**Description.** Shell subquadrate, inflated. Umbones anterior, inflated. Anterior end with irregular commarginal ribs; posterior slope with strong radial and weak commarginal ribs, giving it a somewhat cancellate appearance. Periostracum thick, adherent, hirsute posteriorly, with compound setae. Length to 23 mm.

**Type Locality and Type Specimens.** Mazatlán, Mexico; Holotype, BMNH (unnumbered).

**Distribution.** Monterey, California (37° N) throughout the Gulf of California and south to Callao, Peru (13° S) and the Galápagos Islands (1° S), in the intertidal zone - 100 m. Usually boring in a calcareous substrate or nestling.

**Literature.** Kleemann (1986b), E. J. Moore (1983: 72), Soot-Ryen (1955: 76- 79).

## Order Limoida Waller, 1978

**Diagnosis.** Shell calcitic and aragonitic, subequilateral, equivalve, usually higher than long. Compressed to inflated, not pleurothetic. Umbones widely separated by triangular cardinal area. Sculpture variable, radial riblets predominant, occasionally with imbricated scales. Byssal notch small or absent. Monomyarian. Hinge line short and straight, hinge plate not developed, edentate, sometimes with tubercles. Ligament with resilium in short, shallow resilifer.

**Remarks.** Limids were included as a superfamily associated with the Anomiacea because of their monomyarian condition, until it was established that loss of the anterior adductor muscle has occurred independently in several lines of the Pteriomorpha. It is likely that the order Limoida is distantly related to, but more ancient than the true oysters, anomiids and pectinids, being known from the Carboniferous. The salient anatomical features include the hypertrophy of the mantle edges with the development of long tentacles. The foot has rotated some 180° in relation to the visceral mass and shell, a situation that has been considered analogous to torsion in gastropods. The order contains one superfamily.

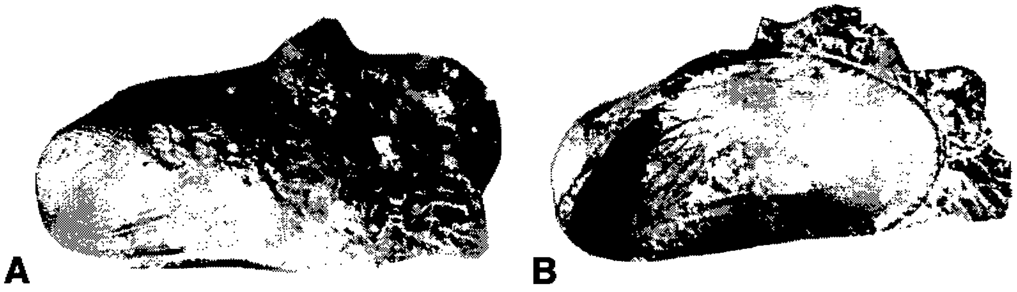

**Figure 5.19.** *Gregariella coarctata*: A, exterior of left valve; B, interior of right valve.

## Superfamily Limoidea Rafinesque, 1815

**Diagnosis.** Shell ovate to subtrigonate, usually oblique. Umbones prominent, separated by triangular cardinal area. Periostracum thin and dehiscent. Sculpture absent, or of radial ribs or lirae. Hinge line straight, usually prolonged into lateral auricles. Hinge plate weak, edentate, or with feeble tubercles. Right valve with small byssal notch. Ligament external but deeply sunken into a central resilifer. Monomyarian. Byssate.

### Family Limidae Rafinesque, 1815

**Diagnosis.** Shell aragonitic and calcitic; outer layer with a distinct microstructure derived from foliated calcite, and inner cross-lamellar layer. Subequilateral, higher than broad, frequently oblique. Periostracum thin, frequently abraded. Umbones prominent, separated by triangular cardinal area. Sculpture absent, or of radial riblets or strong radial ribs, frequently with imbricated scales. Hinge line straight, prolonged into lateral auricles, the anterior sometimes reduced or absent. Hinge plate edentate, or, in some foreign groups, with tubercles, assuming a taxodont appearance. Ligament external, alivincular and sunken in central triangular resilifer. Monomyarian. Byssate. Foot variable, short to long and slender. Mantle lobes not fused; inner fold forming pallial curtain, which may be fused anteriorly; middle fold with long tentacles; outer fold with ocelli and photoreceptors. Gills filibranch, plicate and synaptorhabdic. Labial palps small. Lips hypertrophied, covering the mouth with interdigitating or fused folds. Alimentary canal with type 4 stomach, with clustered ducts leading to the digestive diverticula; style-sac conjoined to mid-gut; intestine passing through ventricle of heart.

### Genus *Limatula* Wood, 1839

*Limatula* Wood, 1839. Type species (SD Gray, 1847): *Pecten subauriculata* Montagu, 1808. Recent, northeastern Atlantic.

**Diagnosis.** Shell thin, fragile, subequilateral, elongate to ovate and inflated. Umbones subcentral, protruding, separated by narrow cardinal area. Periostracum thin and dehiscent. Sculpture of radial striae or riblets, frequently with a larger central pair. Valves not gaping. Hinge line straight and short; auricles small, subequal. Hinge plate weak and edentate. Ligament in small subumbonal resilifer. Byssate.

### *Limatula saturna* F. R. Bernard, 1978

Figure 5.20

*Limatula (Limatula) saturna* F. R. Bernard, 1978: 71.
*Limatula californica* F. R. Bernard, 1988: 227.
*Limatula macleani* F. R. Bernard, 1988: 227.
*Pecten subauriculatus* Montagu, *auctt., non* Montagu, 1808.

**Material Examined.** California, Santa Maria Basin, Phase I, Sta.BSS-42 (100 m); Phase II, Sta. R-4 (92 m).

**Description.** Shell broad, from straight to slightly oblique; ears proportionately larger than those of *Limatula attenuata*. Height to 16 mm.

**Remarks.** This is the common shallow-water *Limatula* of California and Puget Sound, previously assigned to *L. subauriculata*. The form later named by F. R. Bernard from California, *L. californica*, cannot be distinguished from material from British Columbia in any way I can discern. *Limatula macleani* was based on a specimen from deep water with fine sculpture. This species merits comparison with *L. vladivostokensis* (Scarlato, 1955) from the western Pacific.

**Distribution.** Albatross Bank, Kodiak Island, Alaska (56.5° N) [SBMNH], to Cabo San Lucas, Baja California Sur (22.9° N) [CAS], in 30 - 675 m.

**Literature.** Hertlein and Strong (1946a: 68, as *Lima subauriculata*).

## Order Osteroida Férussac, 1822

**Diagnosis.** Shell almost entirely foliated calcite; shape variable, depending on substratum. Frequently strongly inequivalve, usually pleurothetic, either free, byssally attached, or cemented. Shell margin occasionally with interlocking processes. Hinge edentate or with strong teeth. Ligament alivincular or multivincular. Dimyarian or monomyarian. Foot reduced or absent.

**Remarks.** The oysters and scallops appear very different, but a number of anatomical and developmental features point to a shared ancestry, and it is likely that oysters descended from the scallop-like Triassic Pseudomonotidae, or perhaps earlier. Two suborders are represented in the northeastern Pacific.

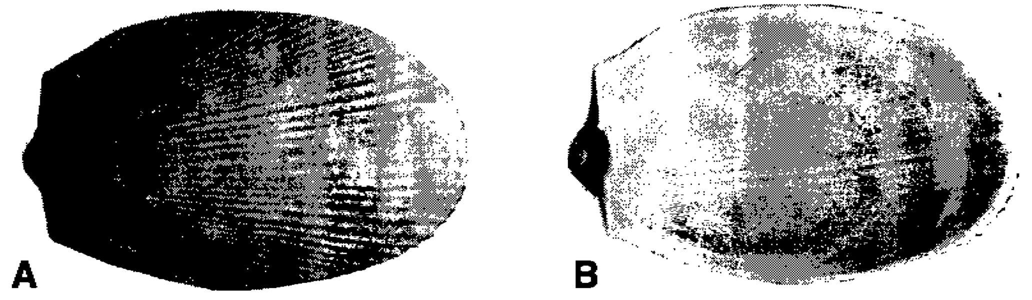

**Figure 5.20.** *Limatula saturna*: A, exterior of left valve; B, interior of right valve.

## Superfamily Pectinoidea Rafinesque, 1815

**Diagnosis.** Shell subequilateral, pleurothetic on right valve. Right valve with byssal notch, which may be absent in adults. Hinge line straight, auriculate. Ligament alivincular; resilium centrally non-fibrous, laterally fibrous.

**Remarks.** This very widely distributed superfamily contains approximately 500 living species and many more extinct species. The evolutionary relationships of a number of groups of living scallops were analyzed by Waller (1991), and the following treatment follows his groupings as applied to species in the northeastern Pacific. I also appreciate his advice and that of H. H. Dijkstra on this superfamily.

Four living families are recognized, two of which are represented in the northeastern Pacific.

**Literature.** Pelseneer (1931), Waller (1972, 1991), Yonge (1973).

### Family Pectinidae Rafinesque, 1815

**Diagnosis.** Shell primarily calcitic, with an outermost prismatic layer on right valve at least in early stages, a prominent foliated calcite layer and, inside the pallial line, a crossed-lamellar aragonite layer (absent in some). Outline orbicular to subtriangular. Pleurothetic on the right valve, with byssal notch and ctenolium, at least in early growth stages. Hinge line straight, prolonged by auricles. Ligament amphidetic, alivincular, with a thick triangular resilium having a dark-brown non-fibrous central part and a fibrous lateral part. Monomyarian, with large, subcentral posterior adductor muscle. Mantle lobes not fused; inner fold forming a pallial curtain with guard tentacles; middle fold with tentacles and ocelli. Labial palps small. Lips hypertrophied. Ctenidia filibranch, eleutherorhabdic. Alimentary canal with type 4 stomach; style sac conjoined to mid-gut; intestine passing through ventricle of heart.

Collectively known as scallops, the family contains brightly colored shells that have received much attention from collectors because of their beauty, and from paleontologists due to their importance in Tertiary and Quaternary marine biostratigraphic correlation. This very large family arose in the Triassic and includes at least 300 living species in 50 genera and subgenera, cosmopolitan in distribution and extending from intertidal to hadal zones. The generic name *Pecten* changes stem in forming the family name Pectinidae.

The taxonomy of scallops is difficult, and systematists do not yet agree on how to assign species to genera and subfamilies. In some cases, the identification of species is complicated by the existence of numerous intermediate forms, particularly in the genus *Chlamys*, which appears to be in a period of active speciation. There is common agreement that several ancestral stocks are involved, and we are witnessing convergent evolution. This makes minor features, such as shell microsculpture, important diagnostic criteria, whereas shell shape and gross ornamentation may not be as important. Even such a dramatic adaptation as cementation to the substratum has occurred independently in several unrelated groups. A full appreciation of the systematic arrangement can only be obtained by review of the world Cenozoic fossil record, so a conservative arrangement, using anatomical and conchological criteria, is adopted here.

The family is characterized by several structures at the antero-dorsal margin. The **byssal notch** is a deep indentation in the right auricle. The **byssal sinus** is a shallower indentation in the left auricle. The **byssal fasciole** is a track left by the developing byssal notch. The **ctenolium** is a comb-like series of denticles along the ventral margin of the byssal notch, which separates the strands of the byssus and mechanically strengthens byssal attachment and prevents rotation. Whereas juveniles are usually byssally attached, adults are commonly free-living; some give up their byssal attachment and become cemented to the substratum.

The anatomy of scallops is rather conservative and uniform. The most characteristic feature is the hypertrophy of the posterior adductor muscle, which occupies a subcentral position, and the disappearance of the anterior muscle. While the labial palps are small, the lips are hypertrophied, forming a cover with many pores over the mouth. This structure may help to retain the mucous food string in the mouth. The anatomy of the gill and alimentary canal suggest the family is primarily adapted to clear water and fine food particles.

All species are epifaunal, bysally attached or lying free on the right valve; one northeastern Pacific genus is permanently cemented. Many species are notable for their energetic but rather inaccurate swimming by clapping the valves vigorously together, propelled by the water jet expelled on each side below the bases of the auricles. Widely distributed from the intertidal zone to abyssal depths. Frequently locally abundant and covering extensive areas, several species support extensive commercial exploitation.

### Genus *Chlamys* Röding, 1798

*Chlamys* Röding, 1798. **Type species** (SD Herrmannsen, 1847): *Chlamys cinnabarina* Röding, 1798, = *Ostrea islandica* Gmelin, 1791. Recent, North Atlantic.

**Diagnosis.** Shell subequivalve, higher than long, with anterior auricles larger than posterior. Byssal notch moderately deep to very deep, with persistent ctenolium. Sculpture of radial ribs, increasing in number by branching or intercalation, and commonly with scales or spines.

**Remarks.** Members of this genus conform to a conservative pattern, but with variable development of external sculpture. The relationships among the species, and the degree of morphological variation, have not been resolved. Internal shell characters, such as pallial scars, hinge structures, and accessory scars, are difficult to see, so identification is based on external sculpture and color. Microsculpture details also offer valuable distinguishing criteria.

### *Chlamys hastata* (G. B. Sowerby II, 1842)

Figure 5.21

*Pecten hastatus* G. B. Sowerby II, 1842: 72.

*Pecten comatus* Valenciennes, 1846: pl. 18, *non* Münster, *in* Goldfuss, 1833

*Pecten rastellium* Valenciennes, 1846: pl. 19, *non* Lamarck, 1819.

*Pecten hericius* Gould, 1850: 345.

*Pecten hericeus, auctt., nom. null.*

*Pecten altiplicatus* Conrad, 1857: 191.

*Pecten (Chlamys) lawsoni* Arnold, 1906: 117.

*Pecten islandicus pugetensis* Oldroyd, 1920: 136.

*Pecten newcombi* Oldroyd, 1938: [2], *nomen nudum.*

*Chlamys hastata ellisi* Hertlein and Grant, 1972: 190.

**Material Examined.** California, Santa Maria Basin, Phase I, Sta.BSS-6 (109 m).

**Description.** Left valve with 8-20 primary radial ribs with strong, imbricated spines. Interspaces with 1-10 coarsely scaled, intercalary riblets and fine, striose microsculpture. Anterior auricle with many strongly imbricated radial ribs. Right valve with 12-24 rounded primary ribs, similar to left valve, but with only 3-4 intercalary riblets. Anterior auricle large, with 7-10 imbricated radial riblets. External color variable, usually pink to yellow, often radially or concentrically streaked. Height to 80 mm.

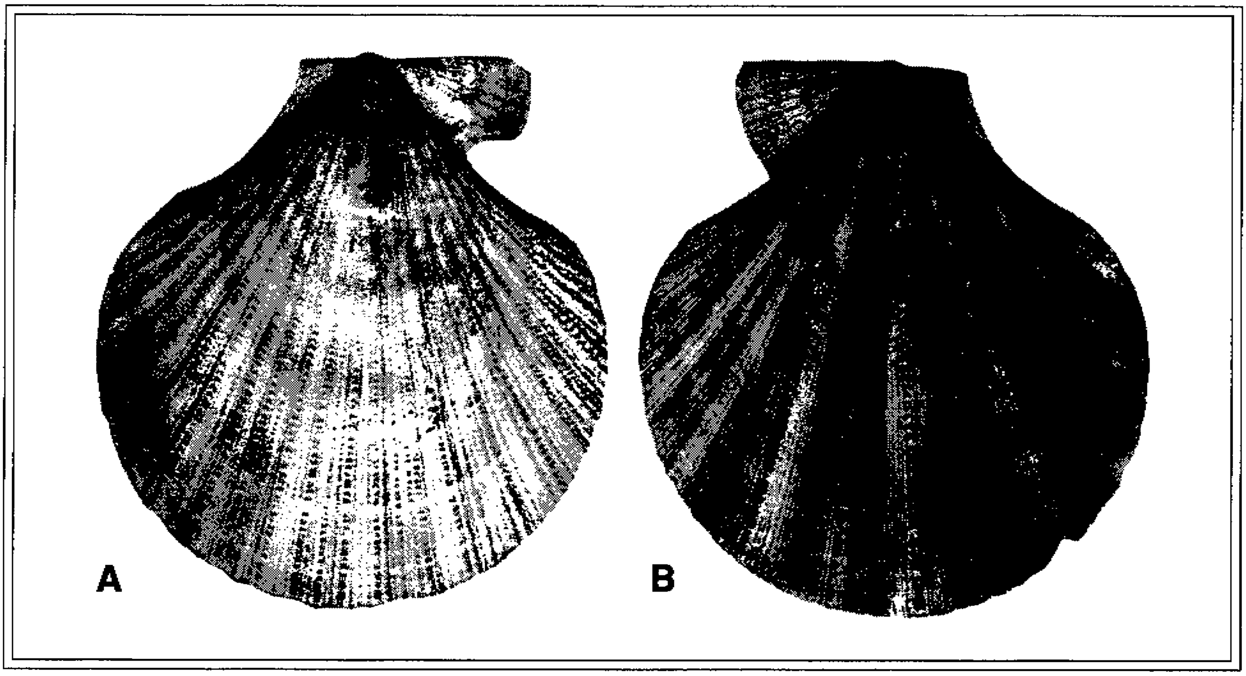

**Figure 5.21.** *Chlamys hastata*: A, exterior of right valve; B, exterior of left valve.

**Type Locality and Type Specimens.** San Diego, California; Holotype, BMNH (unnumbered)

**Distribution.** Kenai Peninsula, Alaska (59.5° N), to San Diego, California (33° N), in the intertidal zone - 160 m.

**Remarks.** A very variable species, many with short to nearly absent spines and drab coloration are found throughout the range, usually on muddy substrates. Specimens from protected waters of British Columbia, Washington and California that have a pronounced reticulated microsculpture were named *C. pugetensis*. Individuals with developed spines and fine coloration are from hard substrates and usually are covered with sponge.

Some workers may chose to recognize two geographic subspecies, *C. hastata hericia* (Gould, 1850) from the Gulf of Alaska to Puget Sound and *S. h. hastata* (G. B. Sowerby II, 1843) from the Washington to San Diego. The latter has fasciculated ribs in the right valve and ribs of three orders in the left valve. The ribs are more subdued in the northern subspecies.

**Literature.** Bloom (1975), Buck (1988), C. A. Cooke (1988), Grau (1959: 85-91), Gregg (1938), Hodgson and N. J. Bourne (1988), E. J. Moore (1984: 22-24), R. G. B. Reid and Rauchert (1970), Rombouts (1991: 12-13), Stasek (1963: 198), Strathmann (1987: 331-332), Vassallo (1973), Waller (1991: 21).

### Genus *Leptopecten* Verrill, 1897

*Leptopecten* Verrill, 1897. **Type species** (OD): *Pecten monotimeris* Conrad, 1837, = *P. latiauritus* Conrad, 1837. Recent, northeastern Pacific.

**Diagnosis.** Shell thin, forwardly slanting, of low convexity; left valve more convex than right. Ribs simple, non-branching, low, rounded. Posterior auricles larger than anterior. Byssal notch deep; ctenolium with prominent teeth.

### *Leptopecten latiauratus* (Conrad, 1837)

Figure 5.22

*Pecten latiauratus* Conrad, 1837: 238.

*Pecten latiauritus, auctt., nom. null.*

*Pecten monotimeris* Conrad, 1837: 238 (first reviser: Bernard, 1983).

*Pecten tunica* R. A. Philippi, 1844: 100.

*Pecten latiauritus fucicolus* Dall, 1898: 710.

*Pecten (Chlamys) latiauritus fragilis* Arnold, 1903: 112, *non P. fragilis* Defrance, 1825.

*Pecten (Chlamys) latiauritus bellilamellatus* Arnold, 1906: 108.

*Pecten (Chlamys) latiauritus cerritensis* Arnold, 1906: 129.

*Pecten (Chlamys) latiauritus delosi* Arnold, 1906: 130.

**Material Examined.** California, Santa Maria Basin, Phase I, Sta.BSS-

**Description.** The thin, almost hyaline and oblique valves, with 9-20 shallow radial corrugations, distinguish this species. The interspaces have fine commarginal lamellae that carry over the ribs; ribs may have a central groove. Auricles broad, but short. Exterior color usually brown-grey, rarely orange, maculated with white or brown chevron-shaped marks, rarely entirely white. Height to 50 mm.

**Type Locality and Type Specimens.** San Diego, California; Holotype, ANSP.

**Distribution.** Point Reyes, California (38° N) to Cabo San Lucas, Baja California Sur (23° N) and throughout the Gulf of California , in intertidal pools to 250 m.

**Literature.** G. R. Clark (1971), Coe (1932: 60-62, 1945), Grau (1959: 107-113), Haderlie and D. P. Abbott (1980: 366), Hertlein and Strong (1946a: 59-60), McPeake and Glantz (1982), E. J. Moore (1984: 43-44), Rombouts (1991: 26).

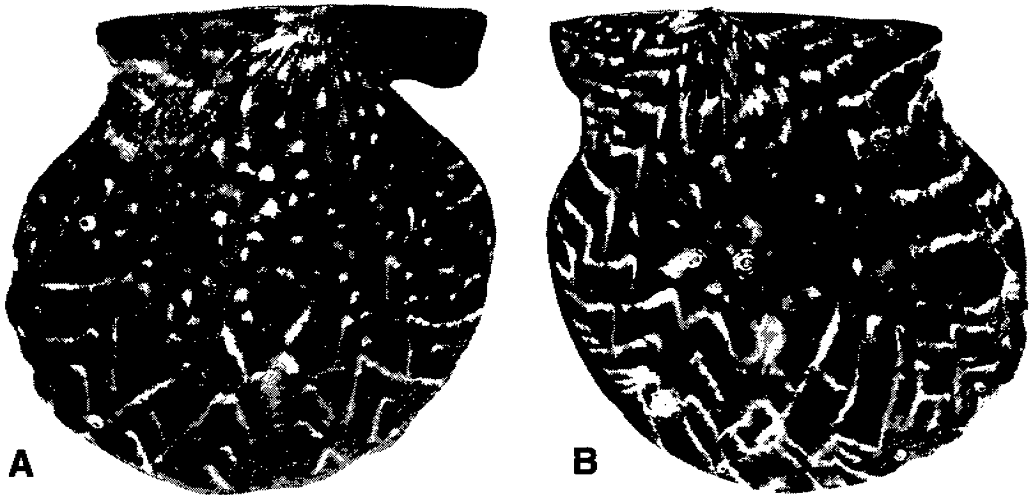

**Figure 5.22.** *Leptopecten latiauratus*: A, exterior of right valve; B, exterior of left valve.

### Genus *Delectopecten* Stewart, 1930

*Delectopecten* Stewart, 1930. **Type species** (OD): *Pecten (Pseudamussium) vancouverensis* Whiteaves, 1893. Recent, northeastern Pacific.

**Diagnosis.** Shell thin, biconvex, subequivalve. Surface not sculptured, or with commarginal and radial striae; intersections frequently with small, imbricated spines or pustules. Umbonal region may be concentrically undulated. Posterior auricles merged into rest of shell.

### *Delectopecten vancouverensis* (Whiteaves, 1893)

Figure 5.23

*Pecten (Pseudamussium) vancouverensis* Whiteaves, 1893: 133.

*Pecten randolphi* Dall, 1897: 86.

*Pecten whiteavesi* Orcutt, 1915: 183 [?*ex* Dall MS], *nom. nud.*

*Pecten (Pseudamusium) randolphi tillamookensis* Arnold, 1906: 139.

*Pecten (Pseudamusum) arces* Dall, 1913: 592.

*Cyclopecten argenteus* F. R. Bernard, 1978: 66.

**Material Examined.** California, Santa Maria Basin, Phase I, Sta.BSS-13 (197 m), BSS-20 (396 m); Phase II Sta. R-9 (410 m).

**Description.** Shell colorless, thin and translucent, often with an oily, iridescent sheen. Left valve more convex than right. Valves weakly undulated, more pronounced on umbones. Both valves with numerous minute radial and equidistant commarginal lirae, and with short, imbricated spines at the intersections, more conspicuous towards anterior and posterior margins. Some specimens almost smooth. Auricles large; anterior auricle of right valve with 4-9 imbricated radial riblets. Byssal notch deep, rounded. Height to 45 mm.

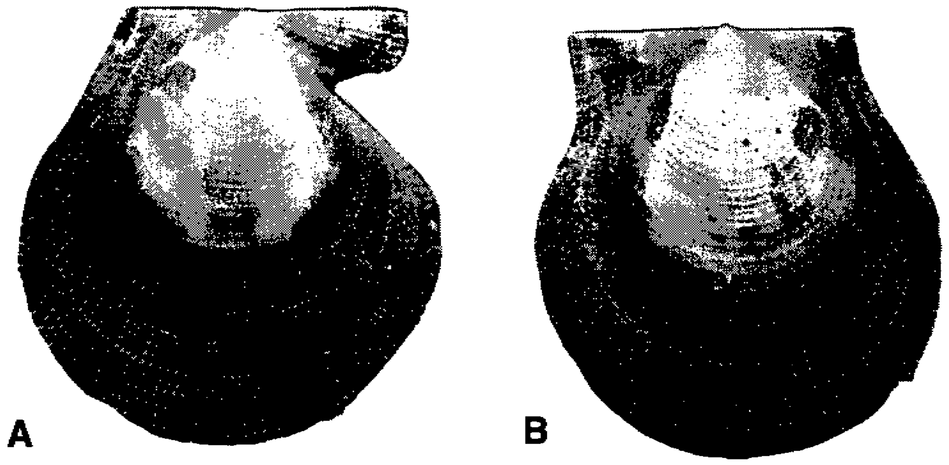

**Figure 5.23.** *Delectopecten vancouverensis*: A, exterior of right valve; B, exterior of left valve.

**Type Locality and Type Specimens.** Foward Inlet, Quatsino Sound, Vancouver Island, British Columbia, 10-20 fathoms; Holotype not found.

**Distribution.** Bristol Bay, Alaska (58° N) into the Gulf of Alaska to Prince William Sound, Alaska (61°N), south to Isla Cedros (28° N) and Isla San Benitos (28° N) Baja Calif. [Norte], and off Guaymas, Sonora, Mexico (28°N), in 45 - 2,000 m.

**Remarks.** A byssate nestler on mud, usually associated with large silicious sponges and sometimes with large crustaceans.

**Literature.** Grau (1959: 40-42, 44-47), E. J. Moore (1984: 16-18), Okutani *et al.* (1989: 72), Rombouts (1991: 76, 78), Scarlato (1981: 260-261).

## Subclass Heterodonta

### Family Lucinidae Fleming, 1828

**Diagnosis.** Shell aragonitic, with prismatic outer, cross-lamellar middle, and complex cross-lamellar inner layers. Outline usually rounded, subequaliteral, equivalve. Umbones central. Sculpture absent, or of commarginal or radial ribs. Periostracum inconspicuous, dehiscent. Lunule clearly impressed, subsymetrical. Ligament opisthodetic, parivincular, external, but usually deeply sunken into groove. Hinge plate weak; dentition variable, usually with 3 cardinal teeth in each valve; lateral teeth weak or absent, rarely duplicated in left valve. Pallial sinus absent. Dimyarian; anterior adductor muscle scar elongate. Mantle lobes with small fusion setting off posterior exhalant aperture, sometimes prolonged with an invaginable pseudosiphonal tube. Gills synaptorhabdic and homorhabdic, thick; outer demibranch lost. Foot vermiform, with distal bulb. Labial palps small. Alimentary canal with type 4 stomach; ducts to the digestive diverticula clustered into 2 or 3 groups; intestine passing through ventricle of heart.

**Remarks.** The family is found in fine sediments of high organic contents and is deeply infaunal. It probably represents a monophelytic and widely distributed lineage, comprising a rather complex assemblange of species sharing similar anatomical structures. The group is divided into four living subfamilies, two present in the northeastern Pacific.

### Genus *Parvilucina* Dall, 1901

*Parvilucina* Dall, 1901. **Type species** (OD): *Lucina tenuisculpta* Carpenter, 1864, = *Parvilucina mazatlanica tenuisculpta* (Carpenter, 1864). Recent, California.

**Diagnosis.** Shell strongly inflated, small. Sculpture strongest on central slope, consisting of fine commarginal lirae and radial striae. Ligament marginal. Hinge plate weak. Inner ventral shell margin finely crenulate.

### *Parvilucina tenuisculpta* (Carpenter, 1864)

Figure 5.24

*Lucina tenuisculpta* Carpenter, 1864a: 642; 1865f: 57.

**Material Examined.** California, Santa Maria Basin, Phase I, Sta.BSS-79 (98 m); Phase II, R-2 (161 m), R-4 (92 m).—Holotype (see below).

**Description.** Shell subcircular, beaks low, hinge line slightly curved; sculpture of fine commarginal striae weak overlain by weak radial ribs, almost obsolete in some material; surface deeply etched in many specimens. Inner ventral margin weakly crenulate. Lunule shallow, narrow, in both valves. Hinge narrow, evenly arcuate; lateral teeth weak. Length to 13 mm.

**Type Locality and Type Specimens.** Vancouver Island, British Columbia; Holotype, USNM 5244.

**Distribution.** Kodiak Island (57.3° N) [CAS] and Galena Bay, Prince William Sound, Alaska (60.9° N) [LACM], to Isla Cedros, Baja California [Norte] (28.2° N), in the subtidal zone to 300 m, in mud of high organic content, where it may occur in dense colonies. Recorded as early as the Miocene in California.

**Literature.** Felbeck *et al.* (1981), U. S. Grant and Gale (1931: 288-289), Hickman (1994: 53-55), G. F. Jones and Thompson (1984), E. J. Moore (1988: 14-15), R. G. B. Reid and Brand (1986).

### Genus *Lucinoma* Dall, 1901

*Lucinoma* Dall, 1901. **Type species** (OD): *Lucina filosa* Stimpson, 1851. Recent, New England.

**Diagnosis.** Shell large, lenticular to subcircular; posterior end truncate. Sculpture of regularly spaced commarginal lamelliform riblets, and fine commarginal lirae. Umbones depressed. Periostracum thin and adherent. Lunule lanceolate. Hinge plate narrow, with two teeth in each valve. Anterior adductor muscle scar elongate and divergent. Ventral inner shell margin smooth.

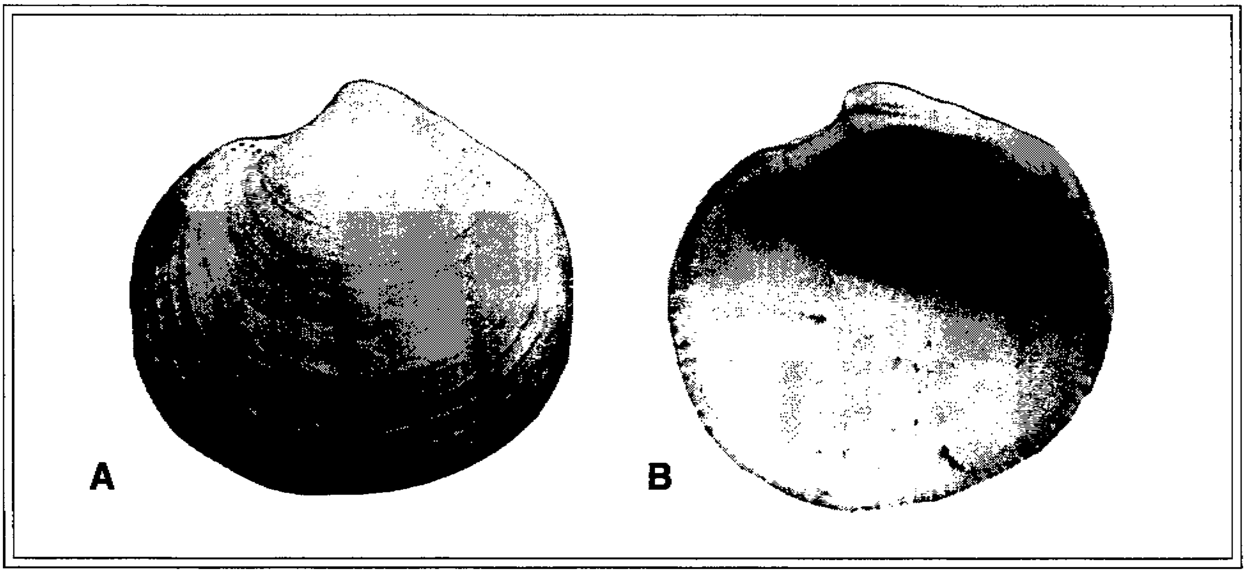

**Figure 5.24.** *Parvilucina tenuisculpta*: A, exterior of left valve; B, interior of right valve.

### *Lucinoma annulatus* (Reeve, 1850)

Figure 5.25

*Lucina annulata* Reeve, 1850: sp. 17.
*Lucinoma densilineata* Dall, 1916: 27, *nom. nud.*
*Lucinoma annulata densilineata* Dall, 1919: 249.

**Material Examined.** California, Santa Maria Basin, Phase I, Sta.BSS-21 (49 m); Phase II, Sta. R-4 (92 m).—Holotype (see below).

**Description.** Shell orbicular, only moderately inflated. Sculpture of sharp, widely spaced commarginal lamellae. Periostracum thin, light to dark tan, dehiscent. Lunule lanceolate and deeply impressed. Length to 82 mm.

**Type Locality and Type Specimens.** California; Holotype, BMNH 1963121.

**Distribution.** Kodiak Island and Prince William Sound, Alaska (60° N), to the Gulf of California as far north as Guaymas, Sonora, Mexico (28° N), in 25 to 750 m.

**Literature.** Distel and Felbeck (1987), Felbeck *et al.* (1981), E. Moore (1988: 17).

## Family Thyasiridae Dall, 1900 [1895]

**Diagnosis.** Shell aragonitic, with composite prismatic outer, cross-lamellar middle, and complex cross-lamellar inner layers. Outline rounded to subtrigonal or subquadrangular, frequently oblique. Equivalve, with small, subcentral prosogyrate umbones. Periostracum inconspicuous, adherent. Sculpture absent, or of commarginal lirae, frequently with radial sulci or folds demarcating the posterior slope. Lunule broad and clearly demarcated. Ligament opisthodetic, parivincular, external but deeply sunken into groove. Hinge plate weak, edentate, or with tubercles or striations. Pallial line entire. Dimyarian; posterior adductor scar rounded to elongate; anterior scar extremely elongate and merged with the pallial line. Mantle lobes with small fusion setting off the posterior exhalant aperture. Gills synaptorhabdic and homorhabdic, filaments thickened. Foot long and vermiform, with distal secretory bulb. Labial palps small. Alimentary canal with type 4 stomach; ducts to the digestive diverticula collected into 2-3 clusters; intestine piercing ventricle of heart.

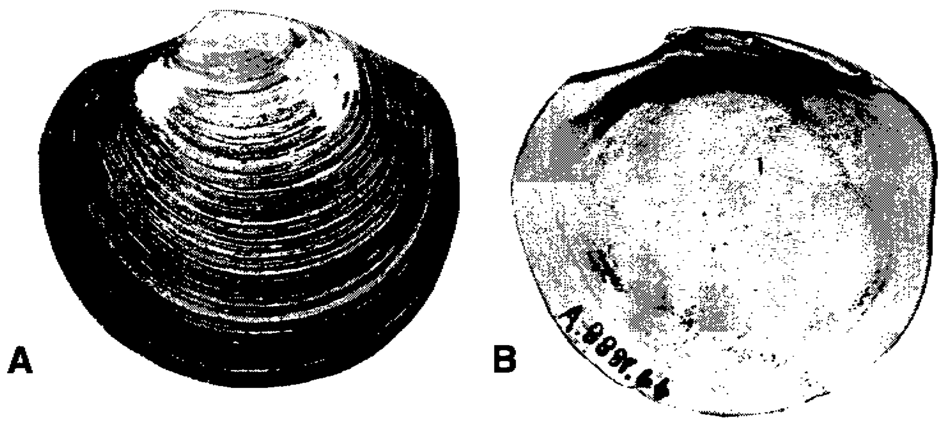

**Figure 5.25.** *Lucinoma annulatus*: A, exterior of left valve; B, interior of right valve.

### Genus *Thyasira* Lamarck, 1818, *ex* Leach MS

*Thyasira* Lamarck, 1818, *ex* Leach MS. **Type species** (OD): *Amphidesma flexuosa* Lamarck, 1818, = *Tellina flexuosa* Montagu, 1803. Recent, Europe.

*Axinus* Sowerby, 1821. **Type species** (OD): *Axinus angulatus* J. Sowerby, 1821, = *Tellina flexuosa* Montagu, 1803.

*Cryptodon* Turton, 1827. **Type species** (OD): *Axinus amplicatus* J. Sowerby, 1821, = *Tellina flexuosa* Montagu, 1803.

**Diagnosis.** Shell subcircular to trigonate, frequently oblique. Equivalve, usually higher than long. Sculpture feeble, commarginal. Posterior set off by one or more strong radial furrows. Umbones prosogyrate. Lunule indistinct; escutcheon long and narrow. Hinge plate weak, edentate, frequently tuberculate and with minute pseudocardinal in the left valve.

**Remarks.** The genus is well represented in oxygen poor environments with free hydrogen sulfide. The majority of species are variable in shape, leading to numerous needless synonyms. There is direct development of the young in a protective capsule and emergence as a benthic juvenile. The eggs are large and invested with a sticky membrane.

### *Thyasira flexuosa* (Montagu, 1803)

Figure 5.26

*Tellina flexuosa* Montagu, 1803: 72.
*Lucina sinuata* Lamarck, 1818: 543.
*Axinus angulatus* J. Sowerby, 1821: 11.
*Axinus unicarinatus* Nyst, 1835: 6.
*Ptychina biplicata* Philippi, 1836: 15.
*Lucina gouldii* Philippi, 1845: 74.
*Axinus sarsii* Philippi, 1845: 91.
*Axinus flexuosa rotunda* Jeffreys, 1881: 701.
*Axinus flexuosa polygona* Jeffreys, 1882: 248.
*Cryptodon barbarensis* Dall, 1890: 261.
*Thyasira cygnus* Dall, 1916: 26, *nom. nud.*; 1916a: 409.

**Material Examined.** California, Santa Maria Basin, Phase I, Sta.BSS-22 (99 m); Phase II, R-7 (565 m).

**Description.** Shell small, milk white, highly inflated; periostracum inconspicuous. Umbones prominent, slightly prosogyrate. Sculpture of commarginal striae, posterior end separated by radial sulcus, deeper in adults. Hinge plate feeble, broad, with obscure cardinal tubercle in left valve. Length to 12 mm.

**Type Locality and Type Specimens.** Types not found, possibly at BMNH.

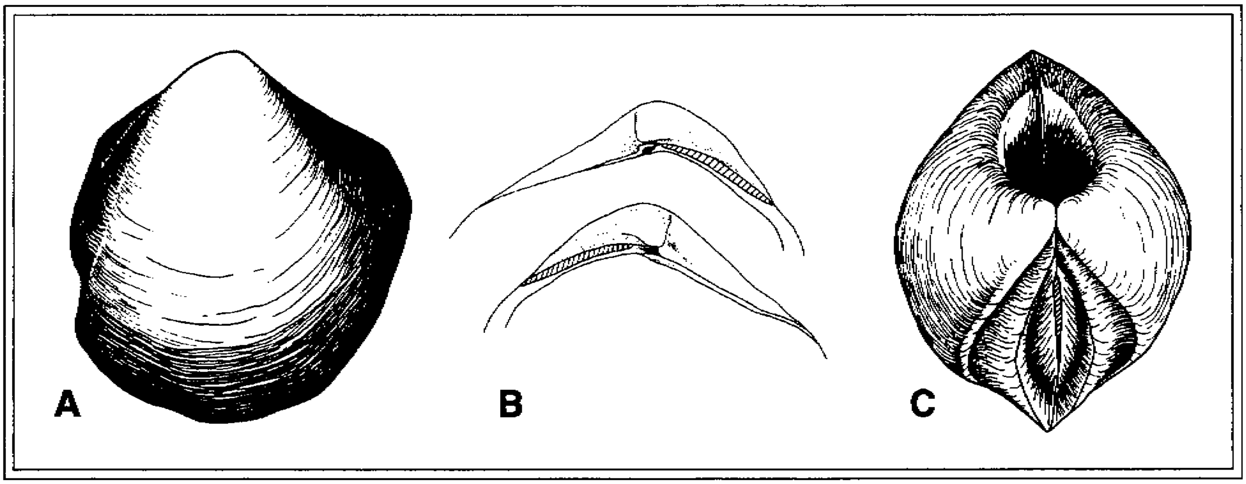

**Figure 5.26.** *Thyasira flexuousa*: A, exterior of right valve; B, details of hinge, left valve lower, right valve above; C, dorsal view of both valves.

**Distribution.** Circumboreal and Panarctic. In west American from the Beaufort Sea (71°N) and Chukchi Sea (65° N), Alaska, to San Pedro, California (36° N), and to the Gulf of California; south to North Africa in the eastern Atlantic, to Virginia in the western Atlantic, and to Hokkaido, Japan, in the western Pacific, in 20 to 3,000 m, in fine mud.

**Literature.** Bernard (1972: 35-36, 1979), Bresciani and Ockelmann (1966), Dando and Southward (1986), Le Pennec *et al.* (1988), López and Mejuto (1987), Lubinsky (1980: 38), N. MacGinitie (1959: 171-172), E. Moore (1988: 24), Ockelmann (1958: 100-110, 1961), Scarlato (1981: 310-312), Tebble (1966: 79), Theroux and Wigley (1983: 27-28).

### *Axinodon* Verrill and Bush, 1898

*Axinodon* Verrill and Bush, 1898. **Type species** (OD): *Axinodon ellipticus* Verrill and Bush, 1898. Recent, northwestern Atlantic.

*Tomburchus* Harry, 1969. **Type species** (OD): *Aligena redondoensis* T. Burch, 1941. Recent, California.

**Diagnosis.** Shell ovate, rather inflated, longer anteriorly. Posterior slope not set off by radial sulcus. Umbones depressed, prosogyrate. Ligament slightly sunken, attached to nymph. Lunule absent; escutcheon well impressed. Hinge plate feeble, with central tubercle in the left valve, smaller in the right valve.

**Remarks.** The genus is widely distributed in shallow to deep water and contains thyasirids with no strong radial sulcus setting off the posterior slope.

### *Axinodon redondoensis* (T. Burch, 1941)

Figure 5.27

*Aligena redondoensis* T. Burch, 1941: 50.

**Material Examined.** California, Santa Maria Basin, Phase I, Sta.BSS-22 (99 m); Phase II, Sta. PJ-7 (123 m).

**Description.** Shell minute and inflated. Sculpture absent. Periostracum thin, with patches of adherent ferruginous coating. Umbones depressed, prosogyrate. Posterior end not set off by radial sulcus. Lunule absent; escutcheon well defined. Hinge plate narrow, with central tubercles, large in the left valve. Length to 3 mm.

**Type Locality and Type Specimens.** Redondo Beach, California.

**Distribution.** Cape Foulweather, Oregon (45° N), to Redondo Beach, California (34° N) in 120 - 200 m.

### Genus *Axinopsida* Keen and Chavan, in Chavan, 1951

*Axinopsis* G. O. Sars, 1878, *non* Tate, 1868. **Type species** (OD): *Axinopsis orbiculata* G. O. Sars, 1878, = *Cryptodon suborbicularis* A. Adams, 1862. Recent, North Sea.

*Axinosida* Keen and Chavan, in Chavan, 1951, *nom. nov. pro Axinopsis* G. O. Sars, 1878, *non* Tate, 1868.

**Diagnosis.** Shell thin, pellucid, discoid, marginally compressed, but centrally tumid, subequilateral. Lunule margins concave. Hinge plate weak; right valve with recurved projecting pseudocardinal denticle.

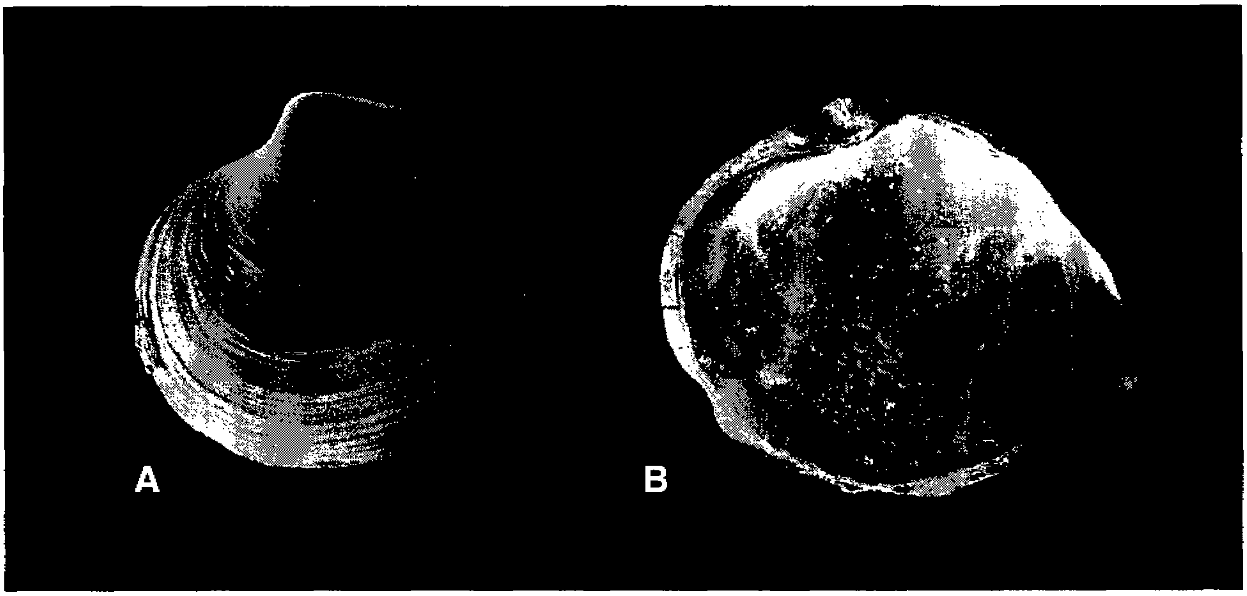

**Figure 5.27.** *Axinodon redondoensis*: A, exterior of left valve; B, interior of right valve.

### *Axinopsida suborbicularis* (A. Adams, 1862)

Figure 5.28

*Cryptodon (Clausina) suborbicularis* A. Adams, 1862: 227.
*Cryptodon serricatus* Carpenter, 1864a: 643.
*Axinopsida viridis* Dall, 1901: 819.

**Material Examined.** California, Santa Maria Basin, Phase I, Sta.BSS-34 (492 m); Phase II, Sta. R-3 (409 m), PJ-14 (134 m), PJ-16 (130 m).

**Description.** Shell compressed, lenticular; periostracum silky yellow to green. Umbones prominent; lunule feeble. Right valve with strong central tooth. Length to 8 mm.

**Type Locality and Type Specimens.** North Atlantic, types not found, possibly at BMNH.

**Distribution.** Circumboral and panarctic. Point Barrow, Alaska (71° N) to Isla Cedros, Baja California Norte (28° N), in the western Pacific from Kamchatka Peninsula to northern Japan, and in the western Atlantic from Labrador and Baffin Island, in the low intertidal zone to 275 m, in mud.

**Remarks.** This highly plastic species has caused difficulties for west American workers. *Axinopsis viridis* was through to be proportionately longer than *A. serricata*, but names for similar pairs of high and long specimens have been proposed in Japan and the in the North Atlantic. The earliest name for North Pacific material appears to be *A. suborbicularis* (A. Adams, 1862), from Japan, a variable species, also known as *A. subquadratus* (A. Adams, 1862), which I believe to be identical. Review of large series of specimens throughout the range reveal no pattern in the outline, except the elongate form appears more frequent in very fine sediment. It is preferable to use the senior synonym from northern Japan. At least in the eastern Pacific, southern specimens are smaller than northern material.

**Literature.** Bernard (1979: 32-33), Lubinsky (1980: 37), N. MacGinitie (1959: 172), E. Moore (1988: 25-26), Ockelmann (1958: 111-113), Scarlato (1981: 313-315), Theroux and Wigley (1983: 26).

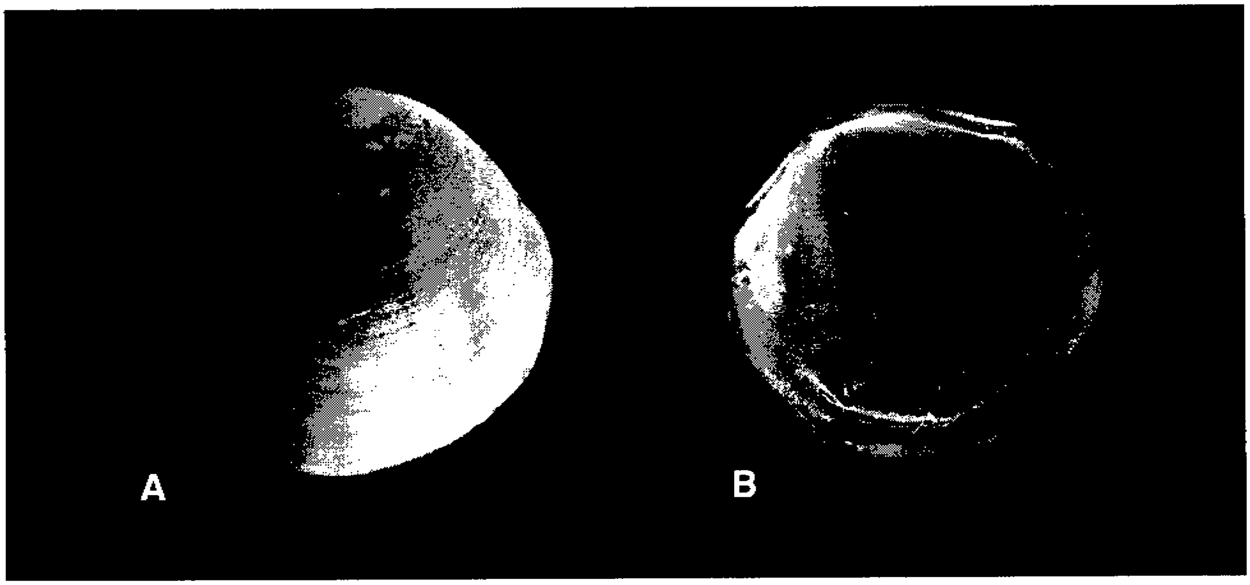

**Figure 5.28.** *Axinopsida suborbicularis*: A, exterior of left valve; B, interior of right valve.

## Genus *Adontorhina* Berry, 1947

*Adontorhina* Berry, 1947. **Type species** (OD): *Adontorhina cyclia* Berry, 1947. Pleistocene - Recent, California.

**Diagnosis.** Shell thin and suborbicular, compressed to inflated. Umbones prominent and prosogyrate. Sculpture absent, except for commarginal growth lines. Lunule margin concave. Hinge plate strong with obscure and variable ridges or tubercles on reflected lunule and escutcheon margins. Ligament internal.

**Remarks.** The genus is often confounded with specimens of *Axinopsida*, with which it frequently occurs, but it is readily separated by the absence of a cardinal tooth, and from *Thysira* by the absence of a posterior sulcus. The external appearance is also much like *Axinulus* and *Leptaxinus*, but the peculiar interlocking granulations of the hinge of *Adontorhina* are distinctive.

### *Adontorhina cyclia* Berry, 1947

Figure 5.29

*Adontorhina cyclia* Berry, 1947: 260.

**Material Examined.** California, Santa Maria Basin, Phase I, Sta.BSS-36 (492 m), BSS-50 (591 m); Phase II Sta. PJ-1 (98 m), PJ-4 (393 m).—Holotype (see below).

**Description.** Shell suborbicular and thin. Sculpture absent. Lunule and escutcheon obscure. Hinge plate edentate, but with posterior and anterior tuberosities that may be granulate. Length to 3 mm.

**Type Locality and Type Specimens.** San Pedro, California (Pleistocene); Holotype, CAS 61460.

**Distribution.** Kasitsna Bay, Alaska (54° N), to San Pedro, California (34° N), in 12 to 3,000 m, in sand and mud.

**Literature.** Jones (1965), Jones and Thompson (1986), E. Moore (1988: 25), Scott (1986).

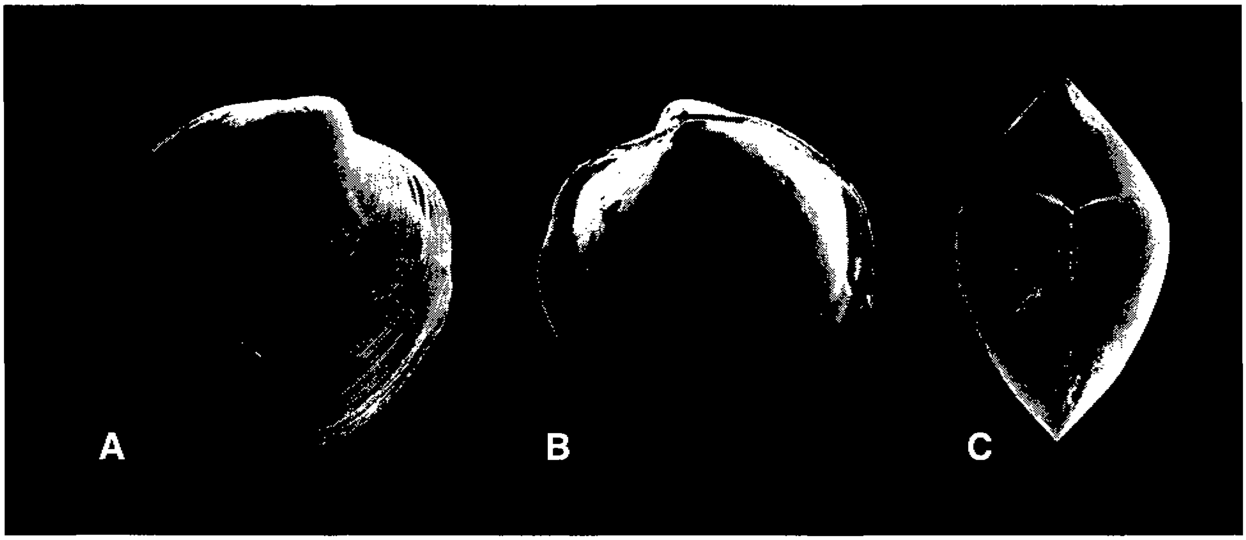

**Figure 5.29.** *Adontorhina cyclia*: A, exterior of right valve; B, interior of right valve; C, dorsal view of both valves.

## Superfamily Carditoidea Fleming, 1828

**Diagnosis.** Shell thick and inflated, usually inequilateral. Umbones prominent. Periostracum thick, generally hirsute. Ligament external, opisthodetic, parivincular, on a strong nymph. Hinge plate wide, arched. At least 2 subequal cardinal teeth present in each valve; lateral teeth remote, usually tuberculate, occasionally absent. Lunule small and deep; escutcheon obscure.

**Remarks.** The superfamily dates from the Devonian and includes two living families of thick, generally radially ribbed shells, with a particularly strong hinge plate and a uniform dentition pattern. Shallow infauna, generally byssate. Most species brood their young. One family is represented in the northeastern Pacific.

### Family Carditidae Fleming, 1828

**Diagnosis.** Shell aragonitic, with cross-lamellar outer and complex cross-lamellar inner layers. Solid, rounded to trapezoidal, equivalve. Sculpture of strong radial ribs. Lunule small and deep. Umbones prominent, prosogyrate. Periostracum often hirsute. Hinge plate wide; left valve with 2 cardinal teeth; right valve with 3 cardinal teeth. Lateral teeth weak or absent. Ligament external, opisthodetic and parivincular, with small resilium. Dimyarian. Pallial line entire. Mantle lobes not fused, except for small posterior exhalant aperture. Siphons absent. Gills synaptorhabdic, homorhabdic. Labial palps small. Foot wedge shaped; byssal groove marked. Alimentary canal with type 4 stomach; ducts to the digestive diverticula concentrated into 3-4 groups; style-sac joined to mid-gut; intestine usually passing through ventricle of heart.

**Remarks.** The sole family of bivalves to demonstrate sexual dimorphism associated with brooding. Two genera have developed a special incubatory chamber in the shell, but the majority of species brood in the pallial chamber. All representatives are shallow infauna, particularly of warm and tropical seas.

### Genus *Cyclocardia* Conrad, 1867

*Cyclocardia* Conrad, 1867. **Type species** (SD Stoliczka, 1871): *Cardita borealis* Conrad, 1831. Recent, northwestern Atlantic.

*Arcturus* Gray, 1839, *ex* Humphrey MS, *non* Berthold, in Latreille, 1827. **Type species** (M): *Cardita borealis* Conrad, 1831.

**Diagnosis.** Shell trigonal to cordiform, thick. Periostracum thick, hirsute in many, polished in some. Sculpture of strong radial ribs and commarginal lirae. Umbones small. Hinge plate wide and short. Two oblique cardinal teeth present in left valve; anterior cardinal of right valve obsolete.

#### ***Cyclocardia ventricosa*** **(Gould, 1850)**

Figure 5.30

*Cardita ventricosa* Gould, 1850: 276.

*Venericardia (Cyclocardia) stearnsii* Dall, 1903: 225.

*Cardita ventricosa redondoensis* T. Burch, in J. Burch, *ex* J. Burch MS: 1944: 14.

*Cardita (Cyclocardia) ventricosa montereyensis* Smith and Gordon, 1948: 172.

**Material Examined.** California, Santa Maria Basin, Phase I, Sta.BSS-59 (216 m), BSS-95 (198 m); Phase II, Sta. PJ-7 (123 m), PJ-21 (143 m).—Syntypes (see below).

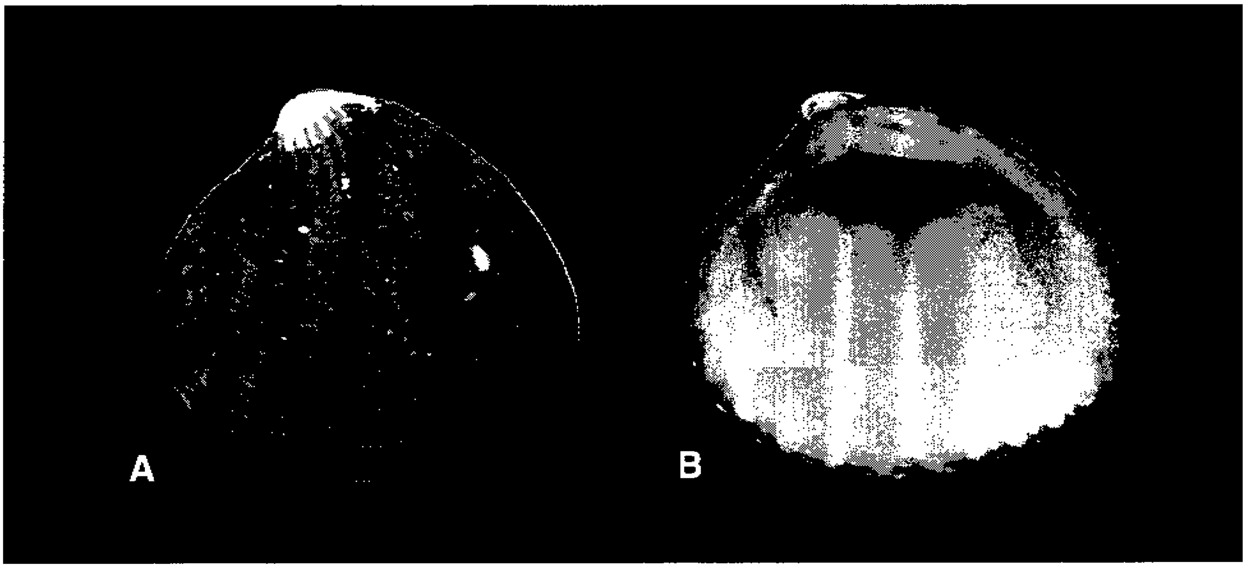

**Figure 5.30.** *Cyclocardia ventricosa*: A, exterior of left valve; B, interior of right valve.

**Description.** Oval to trigonal, thick, thicker than *C. barbarensis*. Sculpture of low, broad, nodose, radial ribs, but less prominent than those of *C. baylei*; ribs not becoming obsolete on anterior slopes, as in *C. barbarensis*. Periostracum light to dark brown, densely hirsute with radially arranged setae. Hinge plate wide, teeth heavy. Lunule small but clearly defined. Length to 15 mm.

**Type Locality and Type Specimens.** Puget Sound, Washington; Syntypes, USNM 3373.

**Distribution.** Galena Bay (61° N) and Cook Inlet (60° N) Alaska, to Punta Rompiente, Baja California (28°N), in 20 - 260 m.

**Literature.** Coan (1977: 380-382), Jones (1963), Popov (1983: 48), Stasek (1962, 1963: 199), Yonge (1969).

### *Cyclocardia barbarensis* (Stearns, 1890)

Figure 5.31

*Venericardia barbarensis* Stearns, 1890: 214.

**Material Examined.** California, Santa Maria Basin, Phase I, Sta.BSS-89 (471 m); Phase II, Sta. R-9 (410 m).—Lectotype (see below).

**Description.** Shell rounded, thin, relatively compressed. Sculpture of low radial ribs, becoming obsolete around anterior, posterior and vental edges. Periostracum dark brown, fibrous, with few, small setae. Umbones small, prosogyrate. Hinge plate narrow; teeth strong. Lunule poorly defined. Length to 15 mm.

**Type Locality and Type Specimens.** Off Santa Rosa Island, California, 276 fathoms; Lectotype, USNM 104045.

**Distribution.** Santa Barbara Island, California (34° N), to Santa Rosa Island, California (34° N) in 350 - 2,211 m.

**Literature.** Coan (1977: 376-377), Jones (1963).

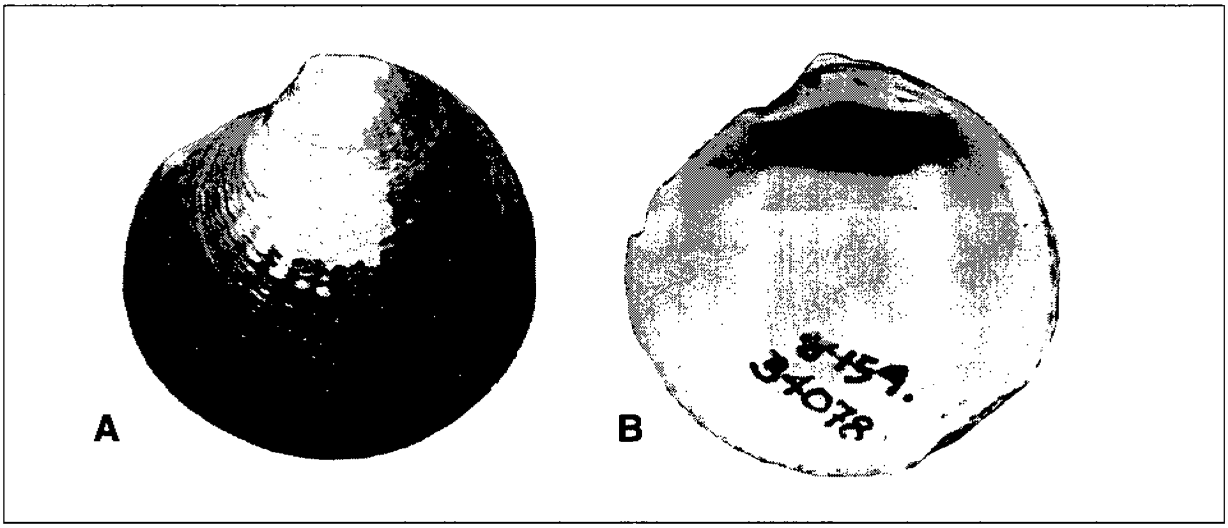

**Figure 5.31.** *Cyclocardia barbarensis*: A, exterior of left valve; B, interior of right valve.

## Superfamily Chamoidea Lamarck, 1809

**Diagnosis.** Shell thick, aragonitic, occasionally with calcitic outer layer. Strongly inequilateral and inequivalve, cemented at least at one stage to the substrate by the right or left valve. Usually distorted and idiomorphic. Umbones prosogyrate, becoming submerged in shell. Sculpture prominent, but frequently eroded, consisting of commarginal and radial frills or spines, often different in each valve. Ligament external, parivincular and opisthodetic, set on a heavy nymph. Hinge plate heavy, generally thickened by obscure and ponderous tubercles and corresponding pits.

### Family Chamidae Blainville, 1825

**Diagnosis.** Shell thick, aragonitic, with cross-lamellar outer and complex cross-lamellar inner layer, occasionally with an additional external calcitic layer. Inequilateral, usually distorted and idiomorphic. Strongly inequivalve, with cupped attached and lid-like free valve. Cemented to substrate at least during part of life. Sculpture developed, usually with elongate spines or imbricated frills. Umbones prosogyrate, migrating away from the margin due to tangential growth. Ligament external, split, early portions not functional due to direction of shell growth. Hinge plate wide, with typical heterodont dentition in the juvenile, becoming overgrown by tubercles to accomodate tangential growth. Dimyarian, with subequal adductor muscles. Foot small. Mantle lobes fused, with pedal gape and two posterior apertures. Gills large, synaptorhabdic plicate, or heterorhabdic. Labial palps small to large. Alimentary canal with type 5 stomach; style-sac joined to the mid-gut; intestine passing through ventrical of heart.

## Genus *Chama* Linnaeus, 1758

*Chama* Linnaeus, 1758. **Type species** (SD Children, 1823; ICZN Opinion 484, 1957): *Chama lazarus* Linnaeus, 1758. Recent, Indo-Pacific.

**Diagnosis.** Shell irregular, very inequivalve, with cupped left and flat right valve. Left valve cemented to substrate. Umbones recurved, prosogyrate, unequal; left valve usually with deep subumbonal chamber. Sculpture of foliaceous commarginal frills. Right valve commarginal lamellae or spines, frequently eroded. Adult hinge plate strong with ponderous tubercles.

### *Chama arcana* Bernard, 1976

Figure 5.32

*Chama pellucida* Broderip, *auctt., non* Broderip, 1835.

*Chama arcana* Bernard, 1976: 14.

**Material Examined.** California, Santa Maria Basin, Phase I, Sta.BSS-25 (390 m).—Holotype (see below).

**Description.** Shell orbicular, much distorted. Cemented by left valve. Left valve cupped; right valve nearly flat. Sculpture of commarginal lamellae. Interior margin minutely crenulate. Hinge plate irregular, with obscure tubercles. Length to 60 mm.

**Type Locality and Type Specimens.** Newport Bay, California; Holotype, LACM 1723.

**Distribution.** Pacific Grove, California (37° N), to Bahía Magdalena, Baja California Sur (25° N), and in the Gulf of California, in the intertidal zone - 390 m.

**Literature.** Bernard (1976:14-15), Gill (1985: 28-29), Haderlie and D. P. Abbott (1980: 368), Skoglund (1991a), Taylor and Kennedy (1969).

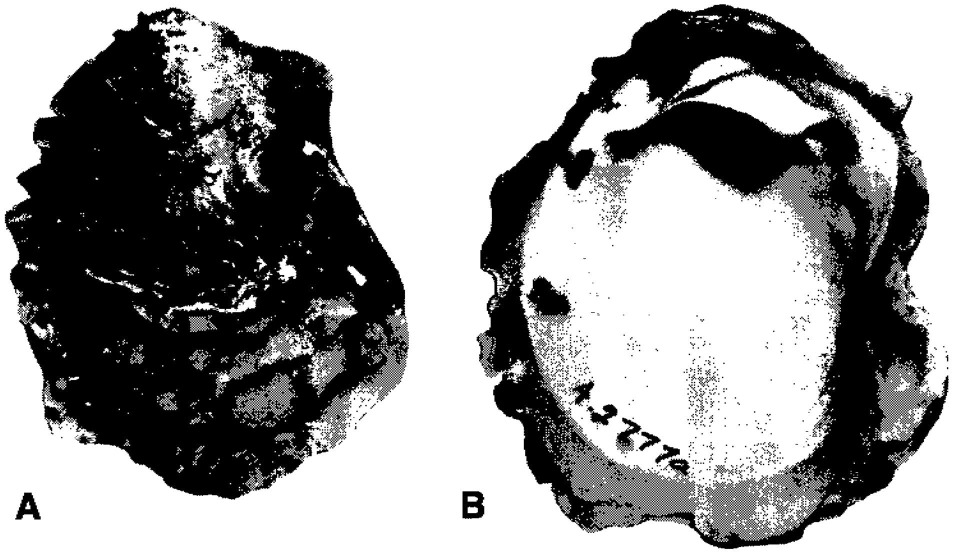

**Figure 5.32.** *Chama arcana*: A, exterior of right valve; B, interior of left valve.

### Genus *Pseudochama* Odhner, 1917

*Pseudochama* Odhner, 1917. **Type species** (SD Gardner, 1926): *Chama cristella* Lamarck, 1819. Recent, Indo-Pacific.

**Diagnosis.** Similar to *Chama*, but attached by the right valve.

**Remarks.** For a long time this genus was merged with *Chama* either completely, or as a subgenus. Beside the valve of attachment, consistent differences in the hinge or sculpture cannot be found. However, juveniles show differences in the dentition, but the constraints of spiral growth impose a similar pattern on the two genera. There is no suggestion that settlement may be by either valve and is consistent in the two genera. The genus is often colonial and may be found in large fused masses and clusters on rocky reefs.

### *Pseudochama exogyra* (Conrad, 1837)

Figure 5.33

*Chama exogyra* Conrad, 1837: 256.

**Material Examined.** California, Santa Maria Basin, Phase I, Sta.BSS-1 (98 m), BSS-16 (591 m).

**Description.** Shell ovate, usually distorted. Broadly cemented by deeply cupped right valve; left valve flattened, lid-like. Sculpture of uneroded specimens of small commarginal lamellae and irregular spines. Interior white, sometimes blushed with pink. Inner shell margin smooth. Hinge plate irregular, with tubercles. Length to 40 mm.

**Type Locality and Type Specimens.** Santa Barbara, California; Syntypes BMNH 1961.5.20.155.

**Distribution.** Monterey Bay, California (36.7° N), to Cabo San Lucas, Baja California Sur (23° N), in the intertidal zone - 591 m.

**Literature.** Bernard (1976: 26-27), Hertz and Skoglund (1991), Kellogg (1915: 669-671), Haderlie and D. P. Abbott (1980: 368), Yonge (1967).

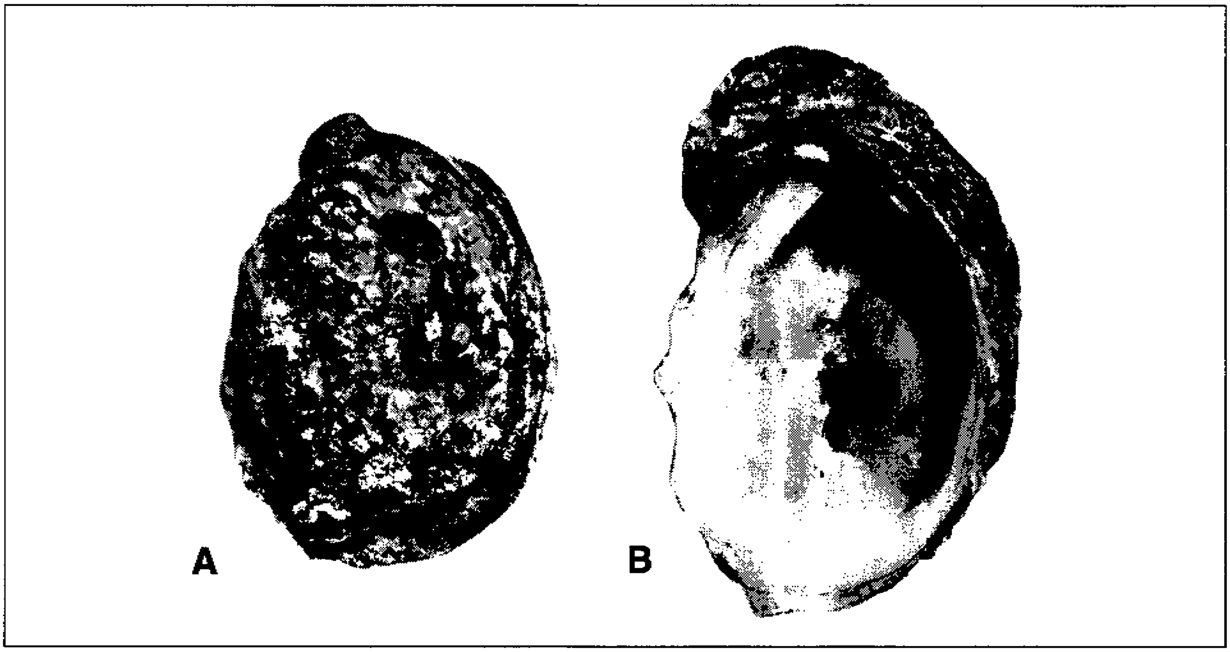

**Figure 5.33.** *Pseudochama exogyra*: A, exterior of left valve; B, interior of right valve.

## Superfamily Galeommatoidea J. E. Gray, 1840

= Leptonacea J. E. Gray, 1847; Erycinacea Deshayes, 1850; Chlamydoconchacea Dall, 1884

**Diagnosis.** Shell aragonitic, small to minute, partly to entirely covered by mantle lobes in some. Hinge plate with small cardinal tubercles; lateral teeth obscure to well developed. Ligament mainly external, frequently with small resilium. Usually byssate.

**Remarks.** The superfamily, known from the Cretaceous, may be polyphyletic and comprises small to minute species, containing many symbiotic and commensal forms, usually associated with large infaunal invertebrates.

### Family Galeommatidae J. E. Gray, 1840

= Ephippiodontidae Scarlato and Starobogatov, 1979

**Diagnosis.** Shell aragonitic, ovate to rounded, thin, small, inequilateral, equivalve, internal in some. Sculpture absent. Periostracum thin, dehiscent. Hinge plate edentulous or variable, with cardinal tubercles; lateral teeth obscure, marginal, usually bent. Ligament variable, usually external opisthodetic, with a small internal resilium in an obscure resilifer. Dimyarian; adductor muscles subequal. Foot well developed, with byssal groove. Mantle lobes extensively fused, with large pedal aperture and small posterior exhalant opening. Mantle usually extending over exterior of shell. Ctenidia synaptorhabdic, homorhabdic; outer demibranch usually absent. Labial palps small. Alimentary canal with type 4 stomach; ducts to digestive diverticula in 2 clusters; style sac separate from mid-gut; intestine passing through ventricle of heart.

**Remarks.** The majority of members are less than 10 mm, and many are far smaller. Many are commensal with large sedentary or burrowing invertebrates, thus achieving the protection of a deep infaunal habitat in spite of the absence or small size of the siphons. The family has secondarily developed an anterior-posterior mantle current. It is also likely that the ventilatory current of the host brings additional food to these filter-feeding species. Identification depends greatly on the external appearance of the living animal and details of the hinge plate. The foot has a planar sole and is usually adapted for active crawling, rather like a gastropod. In many species, the mantle is greatly protrusible and may cover the external shell; the anterior mantle may carry two tentacles. The family is known back to the Eocene.

#### New Genus, New Species A

Figure 5.34

**Material Examined.** California, Santa Maria Basin, Phase I, Sta.BSS-83 (444 m), BSS-85 (113 m); Phase II, Sta. R-2 (161 m), R-3 (409 m), R-5 (154 m).

**Description.** Shell extremely thin, fragile, transparent; subequilateral, posterior slightly longer, anterior end slightly flared. Sculpture predominately irregular radial striae, few commarginal growth striae. Beaks low, wide.

Mantle papillated, reflected, covering entire shell; fused posteriorly forming an exhalent siphon and anteriorly forming an inhalent siphon. Long mantle papillae extend well past shell margins. Foot vermiform, without heel; long byssal groove extending to tip of smooth foot tip.

**Distribution.** Known from the Santa Barbara Channel, California and the Barkely Sound, British Columbia (attached to *Brissaster*).

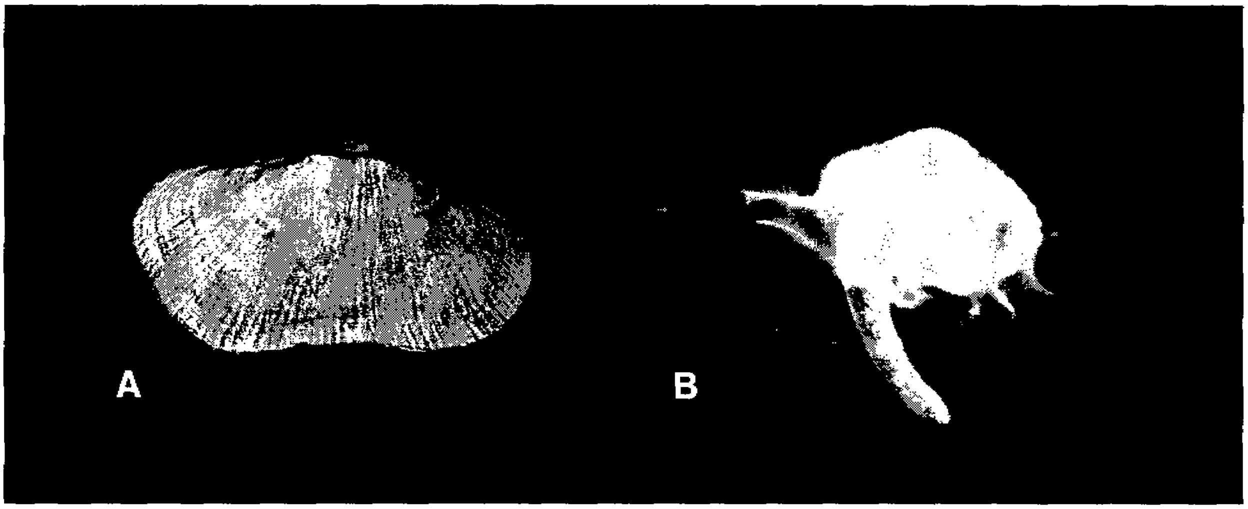

**Figure 5.34.** Galeommatidae new genus, new species A: A, interior of left valve; B, exterior of living animal from the left side.

**Remarks.** This new genus and species were discovered simulaneously by the author and Diarmaid Ó Foighil in British Columbia, Canada, and the author in Santa Barbara. British Columbia specimens were collected on echinoid specimens, whereas California specimens have yet to be associated with a host. The genus and species will be described in a forthcoming publication authored by both investigators.

## Family Lasaeidae J. E. Gray, 1842

= Kelliidae Forbes and Hanley, 1849; Erycinidae Deshayes, 1850; Montacutidae W. Clark, 1855; subfamilies Borniinae, Mysellinae, Orobitellinae, Thecodontinae F. R. Bernard, 1983

**Diagnosis.** Shell aragonitic, thin to translucent, small to minute, inequivalve, rounded to elongate, inflated. Sculpture absent, rarely with radial riblets or commarginal lirae, occasionally with both. Umbones prominent, prosogyrate, submedial to posterior. Prodissoconch demarcated, minute. Periostracum thin. Hinge plate strong, variable, stained red or purple. Right valve with strong lateral teeth, fitting into grooves in, right valve, and with single, conical cardinal tooth. Ligament opisthodetic, parivincular, attached to small nymph. Resilium feeble, in small, obscure resilifer. Interior frequently stained brown or purple. Dimyarian; muscle scars subequal. Byssate. Mantle lobes not fused, except for small posterior exhalant aperture. Inner mantle fold hypertrophied, covering much of shell exterior and projecting to form anterior hood. Mantle current anterior to posterior. Ctenidia synaptorhabdic, usually homorhabdic; outer demibranch reduced or absent. Labial palps small. Foot long, compressed, with planar sole. Byssate. Alimentary canal with type 4 stomach; ducts of digestive diverticula concentrated on right wall of stomach; style sac not joined to mid-gut; intestine passing through ventricle of heart.

**Remarks.** Mostly minute parasitic or commensal forms. Most actively move using the planar sole of the foot. Following Boss (1982) I can find no consistent characters with which to separate the Erycinidae, Kelliidae and Monticutidae from this family. Until such characters can be delineated I have chosen to combine all members of these families into the Lasaeidae. The family is recorded as early as the Cretaceous.

### Genus *Rochefortia* Velain, 1877

*Rochefortia* Velain, 1877 (31 Dec.). **Type species** (M): *R. australis* Velain, 1877. Recent, Indian Ocean.

**Diagnosis.** Shell small, subtrigonal to elliptical, subequilateral to strongly inequilateral. Umbones opisthogyrate. Left valve edentate; right valve with 2 subequal diverging cardinals Right valve overlapped by left valve.

**Remarks.** Several *Rochefortia* species are common members of the benthic infauna from Alaska to the equator. They have been observed as free-living individuals or associated commensally with a wide variety of invertebrate hosts.

The size and structure of the labial palps is a key anatomical character for discriminating between species. Several species have elongate palps which have few sorting grooves, while others have trigonal palps with many sorting grooves. The gills of all *Rochefortia* species consist of only one demibranch, with the outer demibranch absent, however *Mysella (Montacutona)* possesses a vestigial outer demibranch (Morton 1971). The number of gill filaments also can be useful in separating species.

*Rochefortia* has often been combined with *Mysella* Angas, 1877, however the two subequal diverging cardinal teeth in the former are distinctive.

The genus is recorded back to the Pliocene.

### *Rochefortia compressa* Dall, 1913

Figure 5.35

*Rochefortia compressa* Dall, 1913: 596.

**Material Examined.** California, Santa Maria Basin, Phase I, Sta.BSS-26 (590 m); Phase II, Sta. PJ-15 (155 m).—Holotype (see below).

**Description.** Shell of medium size, length to 10 mm; beaks prominent, inequilateral, longer anteriorly, subquadrate; compressed; very thin, fragile; white to transparent; periostracum adherent, very thin, transparent, dull to silky; surface rough but without sculpture, with minute commarginal growth striae.

Hinge plate very weak; left valve with 2 slight cardinal teeth below beaks; right valve edentulous, but with very weak lateral projection on either side of beaks, projections fit into left valve between cardinal teeth and dorsal margin; resilifer very small; adductor scars subovate, weakly impressed; pallial line weakly impressed.

**Type Locality and Type Specimens.** Bahia Concepcion, Baja California Sur, Mexico. Holotype: USNM 21445.

**Distribution.** Santa Barbara, California (34.4° N) [SBMNH], throughout the Golfo de California [LACM] to Bahía Culebra, Costa Rica (10.6° N) [Skoglund Collection] and possibly south to Zorritos, Peru (3.7° S) (Olsson, 1961), in 5 - 590 m.

**Literature.** Keen (1971: 142), Olsson (1961: 234).

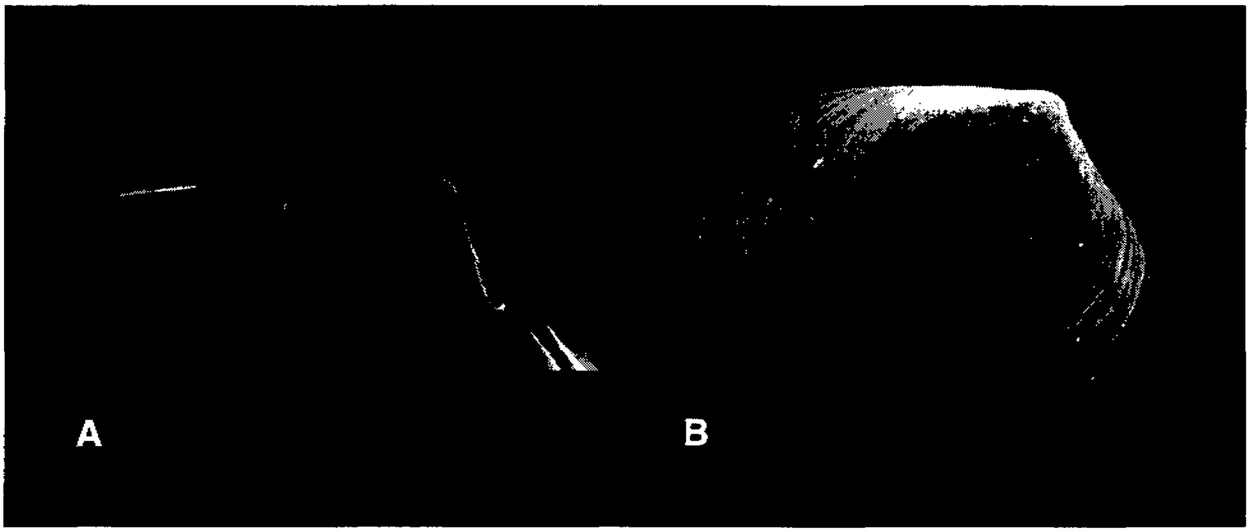

**Figure 5.35.** *Rochefortia compressa*: A, detail of hinge in right valve; B, exterior of left valve.

### *Rochefortia grippi* Dall, 1912

Figure 5.36

*Rochefortia grippi* Dall, 1912: 128.

**Material Examined.** California, Santa Maria Basin, Phase I, Sta.BSS-21 (49 m); Phase II, Sta. R-8 (90 m).—Holotype (see below).

**Description.** Shell small; equilateral, ovate/elongate, anterior and posterior margins evenly rounded; moderately inflated; thin; white; periostracum thin, adherent, silky to shiny, medium-brown; surface without sculpture, but with commarginal growth striae; beaks prominent. Length to 5 mm.

Left valve with 2 small cardinal teeth of equal size, one on each side of resilifer, both parallel to dorsal margin; resilifer very small, with an obscure lithodesma; adductor scars weakly impressed; pallial line weakly impressed.

Anatomy in distinct contrast to *Mysella tumida*. Gill filaments numerous, about 31, narrowly spaced. Adductor muscles ovate, sub-equal. Labial palps large, elongate; sorting grooves on palps well demarcated, almost forming separate fingers.

**Type Locality and Type Specimens.** California, off San Diego, 16-20 fm. Holotype: USNM 214363 (holotype has brooding larvae).

**Distribution.** Esperanza Inlet, Vancouver Island, British Columbia (49.8° N) [LACM], to San Diego (32.7° N) [USNM], California, in 10 - 120 m.

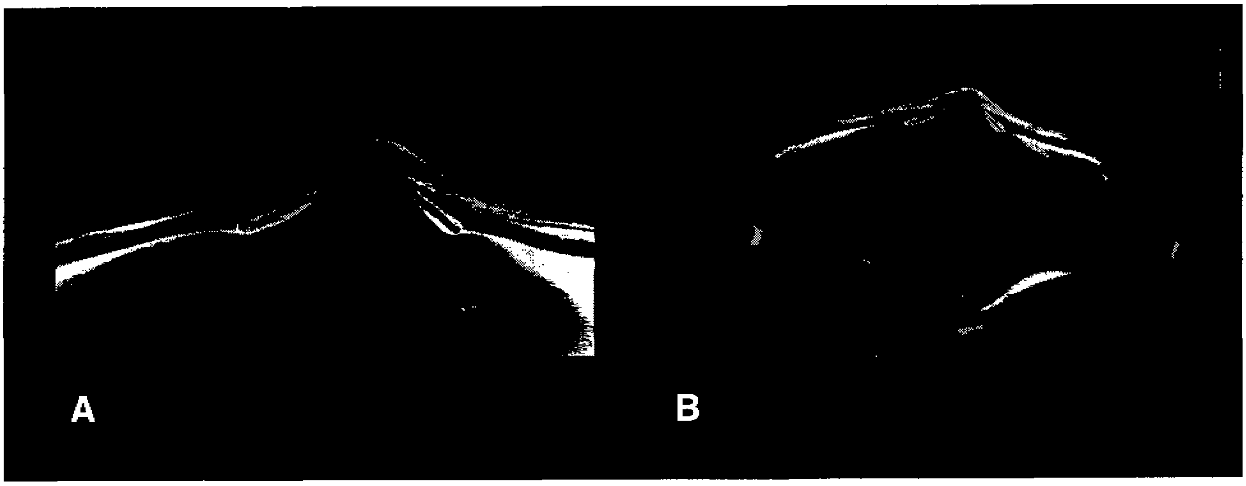

**Figure 5.36.** *Rochefortia grippi*: A, detail of hinge in right valve; B, exterior of left valve.

### *Rochefortia tumida* (Carpenter, 1864)

Figure 5.37

*Tellimya tumida* Carpenter, 1864: 602, 611, 643.

*Mysella aleutica* Dall, 1899: 881, 892, 896, pl. 87, fig. 8.

*Rochefortia ferruginosa* Dall, 1916: 29, *nom. nud.*; 1916a: 411

**Material Examined.** California, Santa Maria Basin, Phase I, Sta.BSS-64 (59 m); Phase II, Sta. R-1 (98 m), R-8 (308 m).—Holotype (see below).

**Description.** Shell small, length to 4 mm; ovate to subquadrate; inequilateral, anterior longer, evenly rounded; posterior truncate; inflated to moderately compressed; shell very thick for small size; white to dark brown; periostracum thick, adherent, light to dark brown, generally eroded from beaks; surface smooth except for commarginal growth striae; beaks prominent, extending almost to posterior margin.

Right valve with 2 sturdy cardinal teeth, one on each side of resilifer; posterior tooth projecting ventrally from beaks, anterior tooth projecting from beaks parallel to dorsal margin; left valve without cardinal teeth but with slight lateral projection on either side of beaks, projections fit into left valve between cardinal teeth and dorsal margin; resilifer of moderate size; adductor scars subequal, ovate/elongate, moderately impressed, posterior scar slightly longer and more elongate than anterior; pallial line moderately impressed.

Gill filaments are few, about 26, widely spaced; an obvious demarcation present between ascending and descending lamellae. Foot relatively large, compressed. Labial palps small, trigonal, with few sorting grooves. Adductor muscles unequal, with elongate, curved anterior adductor and small, ovate posterior adductor muscle.

**Type Locality and Type Specimens.** Washington, Puget Sound, Strait of Juan de Fuca. Holotype USNM 5242.

**Distribution.** Beaufort Sea, Alaska (71°) to San Diego, California (33°N); in the Gulf of California at Puerto Peñasco, Sonora, Mexico (31°N); intertidal - 308 m.

**Literature:** F. R. Bernard (1979: 39-40), U. S. Grant and Gale (1931: 301), Hertlein and Grant (1972: 239-240), Maurer (1967a, c, 1969), E. J. Moore (1992: 9), Ó Foighil (1985b), Ó Foighil and Eernisse (1987), Scott (1987), Strathmann (1987: 333-334).

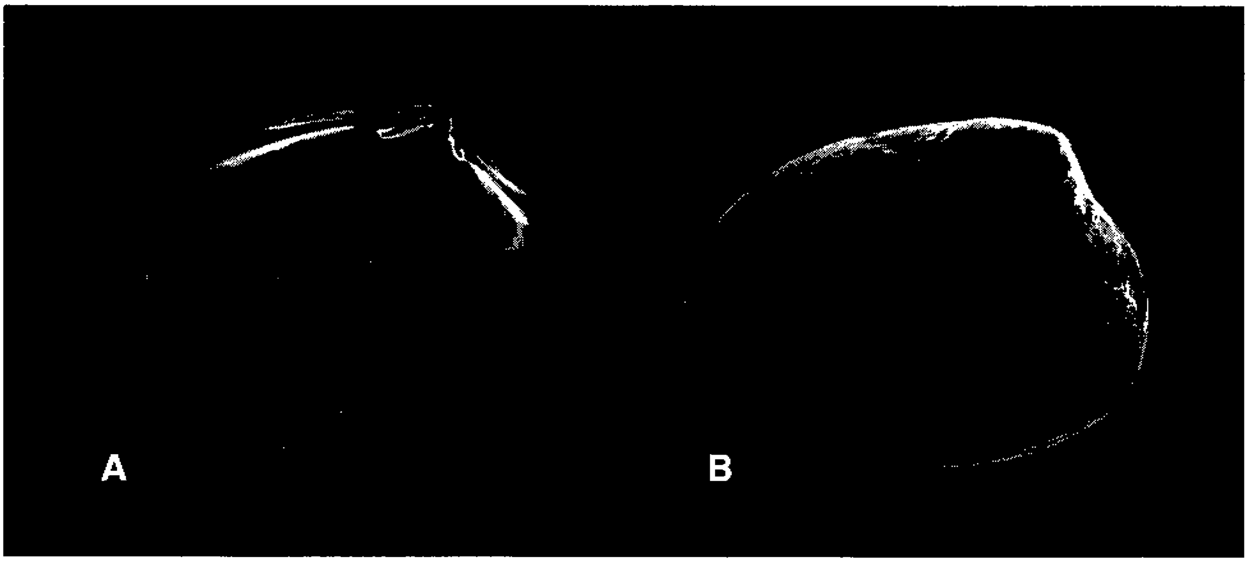

**Figure 5.37.** *Rochefortia tumida*: A, interior of right valve; B, exterior of left valve.

### ***Rochefortia*** **sp. A**

Figure 5.38

**Material Examined.** California, Santa Maria Basin, Phase II, Sta.R-1 (91 m).

**Description.** Shell subovate, very thin, fragile, compressed. Inequilateral, anterior much longer. Anterior and posterior ends broadly rounded. Sculpture of very fine commarginal striae. Periostracum very thin, transparent. Umbones small, not produced. Right valve with 2 very small, subequal, diverging cardinal teeth. Length to 5 mm.

**Distribution.** Off Coos Bay, Oregon (43.3° N) [SBMNH], to San Diego (32.7° N) [SBMNH], California, from intertidal to 91 m.

### ***Rochefortia*** **sp. B**

Figure 5.39

**Material Examined.** California, Santa Maria Basin, Phase I, Sta.BSS-73 (98 m); Phase II, Sta. R-4 (92 m)

**Description.** Shell subquadrate, thin, fragile, compressed. Inequilateral, anterior longer. Anterior and posterior ends truncate. Sculpture of heavy irregular commarginal ribs. Periostracum thin, often covered with ferruginous mud. Umbones small, not produced. Right valve with 2 small, subequal, diverging cardinal teeth. Length to 5 mm.

**Distribution.** Santa Maria (35.1° N) [SBMNH], to San Diego (32.7° N) [SBMNH], California, from 45 - 165 m.

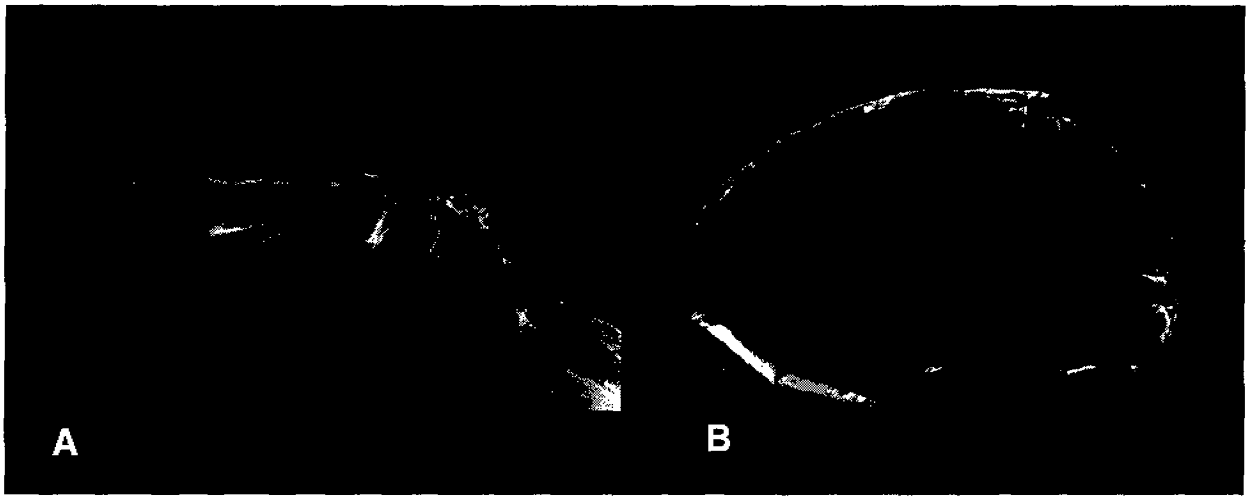

**Figure 5.38.** *Rochefortia* sp A: A, detail of hinge in right valve; B, interior of right valve.

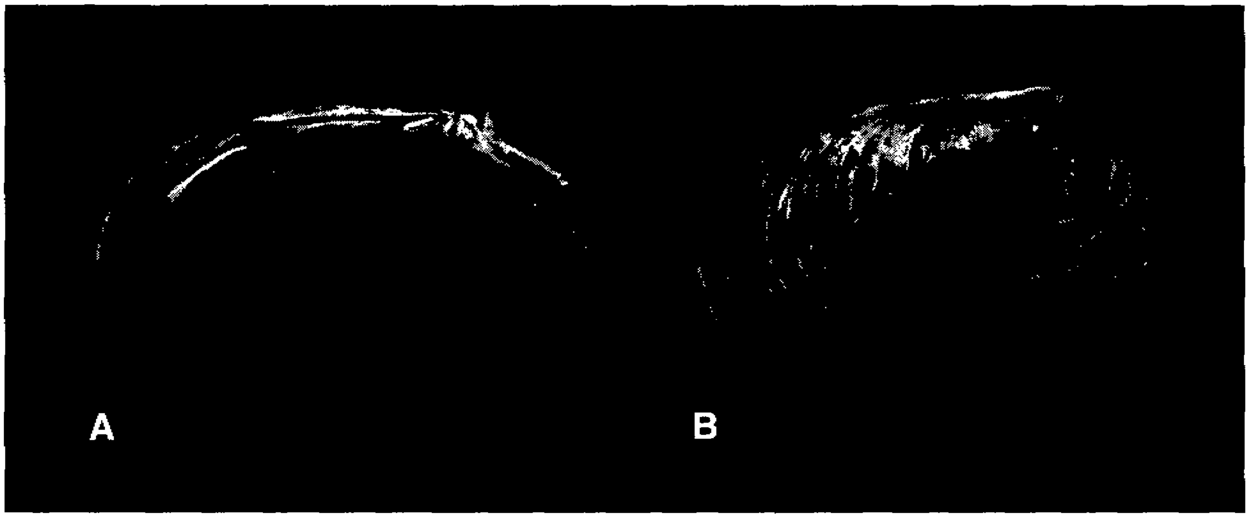

**Figure 5.39.** *Rochefortia* sp. B: A, interior of right valve; B, exterior of left valve.

## ***Rochefortia* sp. C**

Figure 5.40

**Material Examined.** California, Santa Maria Basin, Phase I, Sta.BSS-21 (49 m); Phase II, Sta. R-1 (91 m), PJ-7 (123 m), PJ-15 (155 m).

**Description.** Shell ellipsoid, inequilateral, moderately inflated, thin, without external sculpture. Beaks prominent, almost to posterior margin, opisthogyrate. Cardinal teeth small, anterior tooth larger. Length to 4 mm.

**Distribution.** Santa Maria Basin to Los Angeles Harbor, California, in 49 - 155 m.

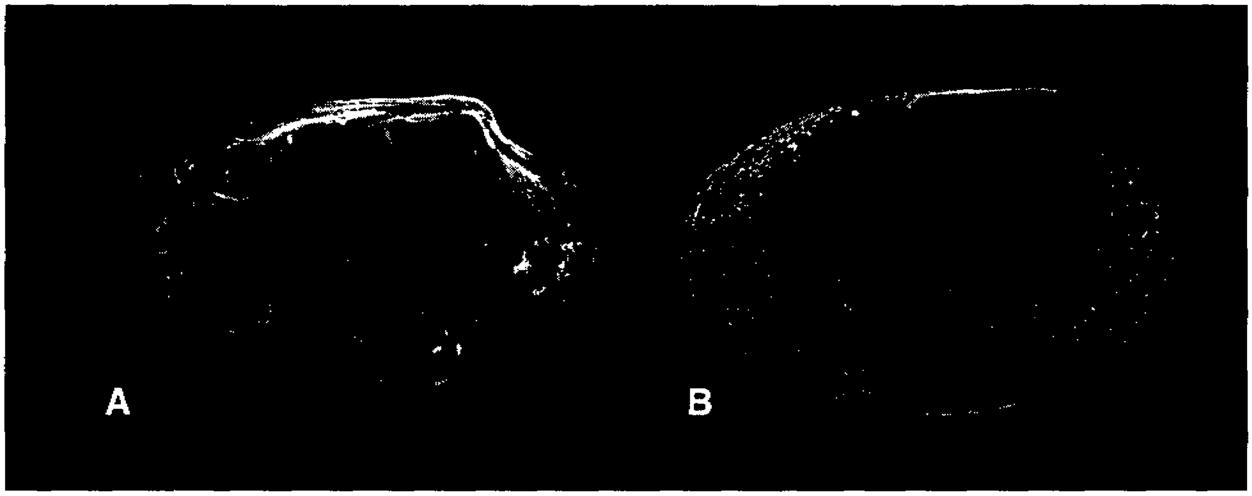

**Figure 5.40.** *Rochefortia* sp. C: A, interior of right valve; B, exterior of left valve.

## Superfamily Cardioidea Lamarck, 1809

**Diagnosis.** Shell aragonitic, subtrigonate to subquadrate, inequilateral, usually solid, inflated, and equivalve. Periostracum thin, frequently abraded. Sculpture predominently radial. Hinge plate variable, usually with 2 conical cardinal teeth; laterals short and distant; dentition evanescent or absent in adult of a few taxa. Ligament external, on strong nymph, opisthodetic, parivincular, sunken into groove. Dimyarian.

### Family Cardiidae Lamarck, 1809

**Diagnosis.** Shell aragonitic, with outer fibrous prismatic, cross-lamellar middle, and complex cross-lamellar inner layers. Ovoid to rounded, equivalve and inflated, frequently higher than wide. Sculpture of radial ribs, sometimes spinose or frilled; sculpture absent in few. Periostracum thin and adherent. Umbones prominent. Hinge plate wide, with 2 conical, hooked cardinal teeth in each valve. Cardinal teeth cruciform when valves interlocked. Left valve with 1 anterior and 1 posterior lateral tooth; right valve with 1 anterior and 1 or 2 posterior lateral teeth. Ligament short, external, opisthodetic, in a groove. Dimyarian, with subequal adductor muscles. Mantle lobes with wide pedal opening, occasionally with small area of fusion setting off exhalant aperture; small siphons sometimes present. Foot long and geniculate. Gills synaptorhabdic, plicate and heterorhabdic. Labial palps small and narrow. Alimentary canal with type 5 stomach; ducts to digestive diverticula numerous, in right and left clusters; style-sac joined to mid-gut; intestine passing through ventricle of heart.

### Genus *Nemocardium* Meek, 1876

*Nemocardium* Meek, 1876. **Type species** (SD Sacco, 1899): *Cardium semiasperum* Deshayes, 1858. Eocene, France.

**Diagnosis.** Sculpture of radial ribs and striae, usually stronger on posterior slope; central slope sometimes nearly smooth; ribs on posterior slope often spinose; inner ventral margin crenulate.

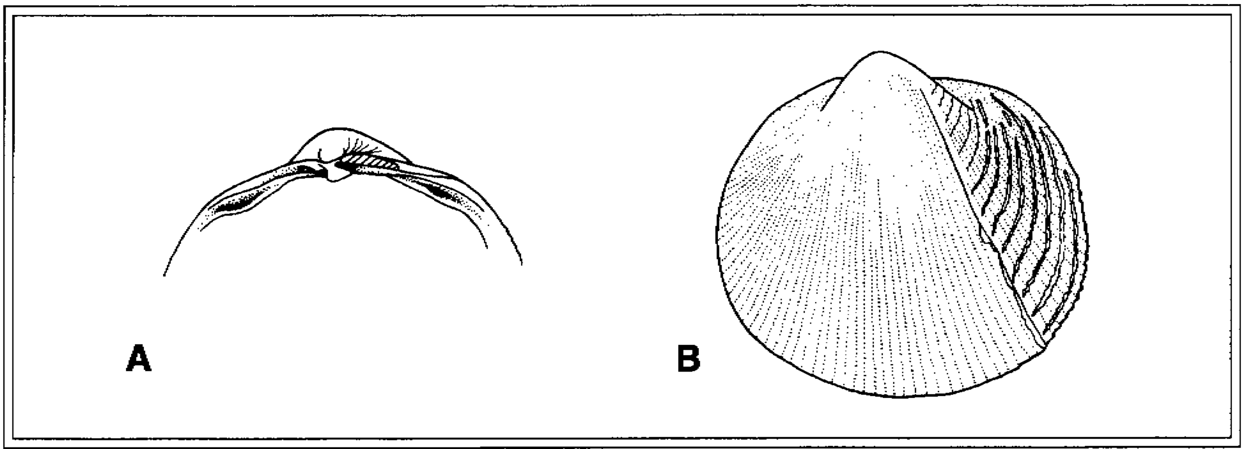

**Figure 5.41.** *Nemocardium centifilosum*: A, detail of hinge in right valve; B, exterior of left valve.

### *Nemocardium centifilosum* (Carpenter, 1864)

Figure 5.41

*Cardium (?modestum var.) centifilosum* Carpenter, 1864a: 611; 1866: 209.
*Cardium richardsoni* Whiteaves, 1878: 468.

**Material Examined.** California, Santa Maria Basin, Phase I, Sta.BSS-73 (98 m), BSS-102 (99 m); Phase II, Sta. R-4 (92 m), R-8 (90 m).

**Description.** Shell ovate, thin and inflated. Sculpture of posterior slope cancellate, with about 20 radial ribs, separated from central slope by a raised radial rib. Central and anterior slopes with 40 or more fine radial riblets. Umbones prominent, subcentral. Inner margin finely crenulate. Length to 25 mm.

**Type Locality and Type Specimens.** Catalina Island, California; Holotype USNM 15262.

**Distribution.** Kodiak Island, Alaska (58° N), to Punta Rompiente, Baja California Sur (27.7° N), in the intertidal zone to 150 m.

**Literature.** Fischer-Piette (1977: 6), Schneider (1992).

## Superfamily Veneroidea Rafinesque, 1815

**Diagnosis.** Shell aragonitic, inequilateral and equivalve. Umbones anterior, prosogyrate. Ligament opisthodetic, parivincular, on nymph. Hinge plate broad; teeth strong, with up to 3 cardinal teeth in each valve; lateral teeth present or absent.

### Family Veneridae Rafinesque, 1815

**Diagnosis.** Shell aragonitic, usually with a composite prismatic outer, homogenous or cross-lamellar middle, and complex cross-lamellar inner layers. Usually thick, ovate to suborbicular or subtrigonate, inequilateral and equivalve. Umbones prosogyrate, subcentral to anterior. Periostracum inconspicuous, frequently abraded. Sculpture absent or of strong commarginal or radial ribs, sometimes spinose or lamellate. Lunule and escutcheon usually present. Ligament external, opisthodetic, parivincular on strong nymph. Hinge plate wide, with three cardinal teeth in each valve, generally thickened and bifid. Lateral teeth variable, frequently absent. Foot large, compressed, with byssal groove. Pallial line entire, usually with deep pallial sinus. Mantle edge with 4 folds; lobes fused leaving large pedal opening; posterior openings usually with short, united siphons. Gill large, synaptorhabdic, plicate and heterorhabdic. Labial palps small and triangular. Alimentary canal with type 5 stomach; numerous ducts to the digestive diverticula; style-sac joined to mid-gut; intestine passing through ventricle of heart.

### Genus *Compsomyax* Stewart, 1930

*Compsomyax* Stewart, 1930. Type species (OD): *Clementia subdiaphana* Carpenter, 1864. Recent, Puget Sound, Washington.

**Diagnosis.** Shell thin and porcellaneous. Sculpture of weak commarginal striae. Posterior right cardinal tooth strong and bifid; lateral teeth absent.

### ***Compsomyax subdiaphana* (Carpenter, 1864)**

Figure 5.42

*Clementia subdiaphana* Carpenter, 1864a: 640; 1865e: 56.

*Saxidomus gibbosus* Gabb, 1869: 58.

*Callista subdiaphana pedroana* Arnold, 1903: 144.

*Clementia obliqua* Jukes-Browne, 1913: 59.

**Material Examined.** California, Santa Maria Basin, Phase I, Sta.BSS-21 (49 m); Phase II, Sta. R-1 (91 m); R-8 (90 m).—Holotype (see below).

**Description.** Shell subquadrangular, very inflated and thin. Sculpture of weak commarginal striae. Periostracum thin, with adherent sand grains in living material. Umbones anterior, prosogyrate. Hinge plate feeble; posterior cardinal tooth of right valve valve bifid. Pallial sinus large. Length to 85 mm.

**Type Locality and Type Specimens.** Puget Sound, Washington; Holotype, USNM 4541.

**Distribution.** Cook Inlet, Gulf of Alaska (61° N), to Bahía San Quintín, Baja California [Norte] (30° N), in 2 - 500 m, in soft mud, frequently in areas with high organic content. Recorded as early as the late Miocene in western North America.

**Literature.** Fischer-Piette and Vukadinovic (1972: 165), Hertlein and Grant (1972: 269-270), Jukes-Browne (1914), L. S. Smith and Davis (1965), Williamson (1893), Woodring (1926).

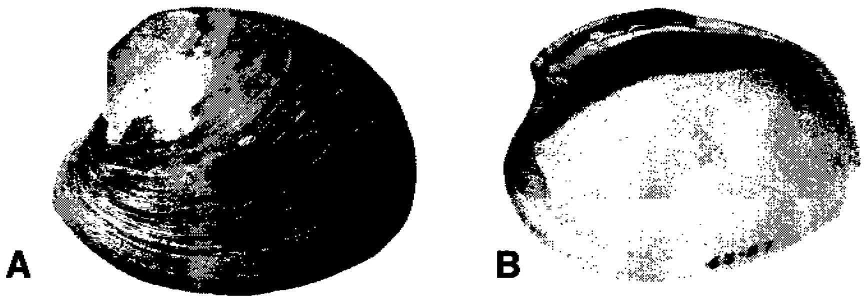

**Figure 5.42.** *Compsomyax subdiaphana*: A, exterior of left valve; B, interior of right valve.

## Superfamily Tellinoidea Blainville, 1814

**Diagnosis.** Shell rounded to subtrigonal or elongate, inequilateral, compressed, equivalve in most. Periostracum thin and adherent. Sculpture variable, usually commarginal. Ligament opisthodetic and parivincular, either external set on nymph, or internal in resilifer. Hinge plate strong, usually with 2 cardinal teeth in each valve. Lateral dentition may be present, or vestigial. Pallial sinus impressed; pallial sinus strongly developed. Dimyarian. Unique cruciform muscles present at base of siphons.

**Remarks.** The Tellinoidea arose in the Triassic and comprise one of the largest bivalve superfamilies, with numerous groups adapted to a wide variety of shallow water, infaunal habitats. Cosmopolitan in distribution, but especially abundant in tropical regions. Many forms are particularly important ecologically because of their abundance, and a number of species are important food sources. Among the most attractive of bivalves, their elegant shells are frequently brightly colored. Four living families with approximately 550 species are recognized. All the families are represented in the northeastern Pacific.

### Family Tellinidae Blainville, 1814

**Diagnosis.** Shell aragonitic, with prismatic outer, cross-lamellar middle, and complex cross-lamellar inner layers. Usually with rounded anterior end and an elongate posterior end, equivalve to inequivalve, occasionally with posterior flexure. Sculpture variable, commarginal and subdued. Periostracum thin, varnished. Ligament external, on weak, elongate nymph. Hinge plate narrow; 2 cardinal teeth in each valve; lateral teeth, when present, stronger in the right valve. Dimyarian; adductor muscles subequal. Foot compressed, broad and linguiform. Pallial line strong; pallial sinus deep, frequently differing in the two valves. Gills synaptorhabdic. Mantle lobes fused, with large pedal gape and long, separate siphons. Labial palps large and triangular. Alimentary canal with type 5 stomach; numerous ducts to digestive diverticula; style-sac joined with mid-gut; intestine passing through ventricle of heart.

### Genus *Tellina* Linnaeus, 1758

*Tellina* Linnaeus, 1758. **Type species** (SD Children, 1823): *Tellina radiata* Linnaeus, 1758. Recent, Caribbean.

**Diagnosis.** Shell elongate, compressed. Hinge plate with 2 cardinal teeth in each valve and with lateral teeth in one or both valves, sometimes ephemeral. Often brightly colored and elegantly sculptured.

### ***Tellina modesta* (Carpenter, 1864)**

Figure 5.43

*Angulus modestus* Carpenter, 1864b: 681; 1865f: 56.

*Angulus modestus obtusus* Carpenter, 1864b: 639; 1865f: 56, *non Tellina obtusa* J. Sowerby, 1817.

*Tellina (Oudardia) buttoni* Dall, 1900: 326, *nom. nov. pro T. obtusa* Carpenter, *non* J. Sowerby.

**Material Examined.** California, Santa Maria Basin, Phase II, Sta.PJ-7 (123 m).—Lectotype (see below).

**Description.** Shell small, elongate, moderately inflated, generally with internal radial riblet just behind anterior adductor muscle scar. Periostracum highly polished; sculpture absent to weakly commarginal. Color white. Length to 20 mm.

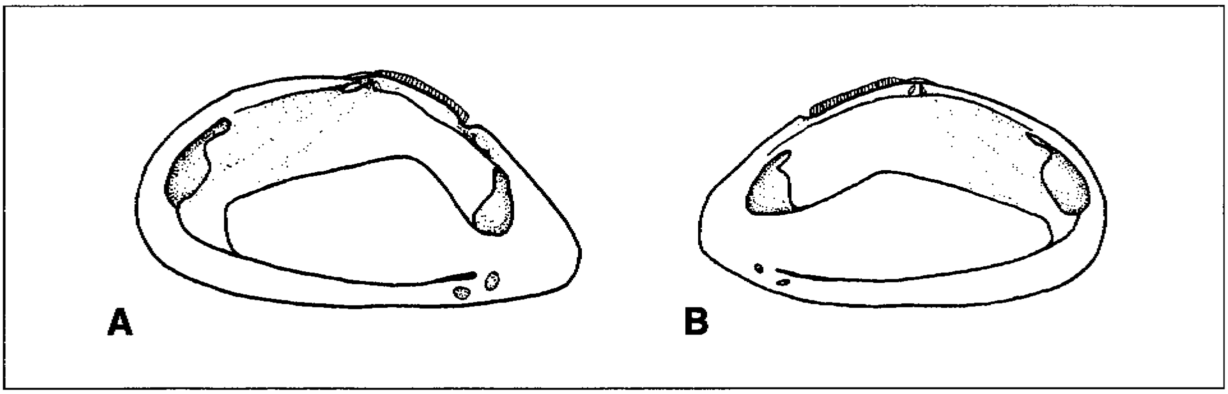

**Figure 5.43.** *Tellina modesta*: A, interior of right valve; B, interior of left valve.

**Type Locality and Type Specimens.** Puget Sound, Washington; Lectotype, USNM 4245.

**Distribution.** Cook Inlet, Alaska (60° N), to Bahía San Bartolome, Baja California Sur (28° N) in the intertidal zone to 100 m, in fine sandy sediments in bays or open coast.

**Literature.** Coan (1971), Mauer (1967a-c, 1969).

### *Tellina carpenteri* Dall, 1900

Figure 5.44

*Angulus variegatus* Carpenter, 1864b: 629; 1864e: 423, *non Tellina variegata* Gmelin, 1791.

*Tellina (Angulus) carpenteri* Dall, 1900: 320, *nom. nov. pro T. variegatus (Carpenter), non Gmelin.*

*Tellina (Moerella) arenica* Hertlein and Strong, 1949: 68.

**Material Examined.** California, Santa Maria Basin, Phase I, Sta.BSS-85 (113 m), BSS-86 (197 m).—Holotype (see below).

**Description.** Shell elongate, inflated, pink or rose-colored, lacking an internal radial riblet. Sculpture absent or of fine commarginal striae. Habitat influences the form, those from offshore situations are pale and compressed, while those from shallow bays are more inflated and brightly colored. Length to 20 mm.

**Type Locality and Type Specimens.** Neah Bay, Washington; Lectotype, USNM 15467b.

**Distribution.** Sitka, Alaska (57° N), to San Pedro, California (34° N), and in deeper water south to Corinto, Nicaragua (12° N), in the intertidal zone to 450 m.

**Literature.** Coan (1971: 15-16), Hertlein and Strong (1949: 68-69).

### Genus *Macoma* Leach, 1819

*Macoma* Leach, 1819. **Type species** (M): *Macoma tenera* Leach, 1819, = *Tellina calcarea* Gmelin, 1791. Recent, North Atlantic.

**Diagnosis.** Shell ovate to subtrigonal, inaequilateral. Sculpture usually absent, or weakly commarginal. Periostracum thin, frequently abraded. Two cardinal teeth in each valve; lateral teeth absent. Pallial sinuses discrepant, longer in left valve.

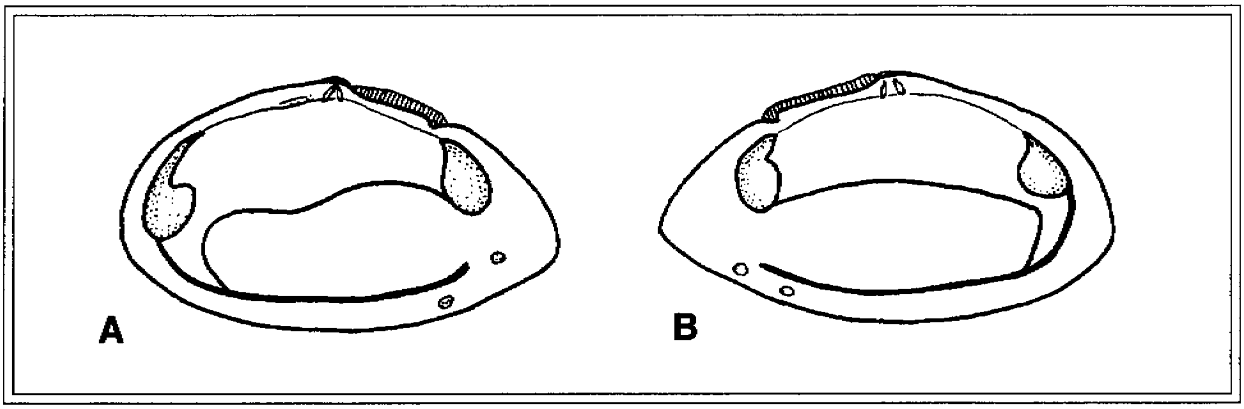

**Figure 5.44.** *Tellina carpenteri*: A, interior of right valve; B, interior of left valve.

## *Macoma yoldiformis* Carpenter, 1864

Figure 5.45

*Macoma yoldiformis* Carpenter, 1864b: 639; Carpenter, 1865f: 55.

**Material Examined.** California, Santa Maria Basin, Phase I, Sta.BSS-21 (49 m); Phase II, Sta. R-8 (90 m), PJ-17 (126 m).—Lectotype (see below).

**Description.** Shell elongate, thin, and very inflated shell; postero-dorsal margin produced into flange. Periostracum thin, adherent. Pallial sinus is mostly detached from pallial line, approximately equal in size in each valve. Length to 25 mm.

**Type Locality and Type Specimens.** Neah Bay, Washington; Lectotype, USNM 4507.

**Distribution.** Sitka, Alaska (57° N) [RBCM], to Bahía San Bartolome, Baja California Sur (28° N), in the intertidal zone to 100 m, in bays and protected foreshores in sand or mud. Recorded as early as the Pliocene in the eastern Pacific. It is possibly related to *M. wilcoxi* Hall and Ambrose, 1916, from the Miocene of California.

**Literature.** Coan (1971: 33-34), Dunnill and Ellis (1969: 30-33).

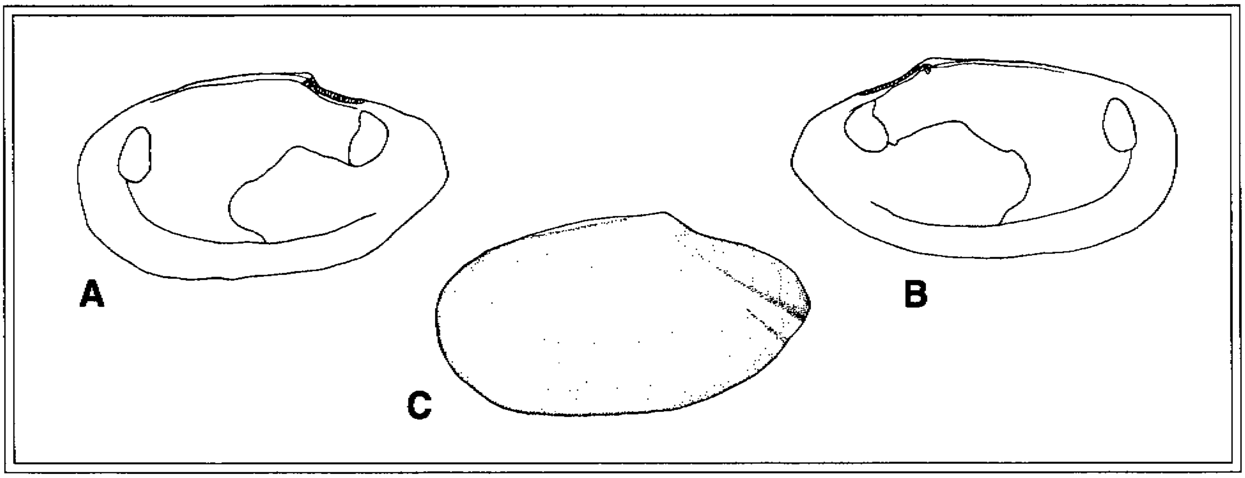

**Figure 5.45.** *Macoma yoldiformis*: A, interior of right valve; B, interior of left valve.

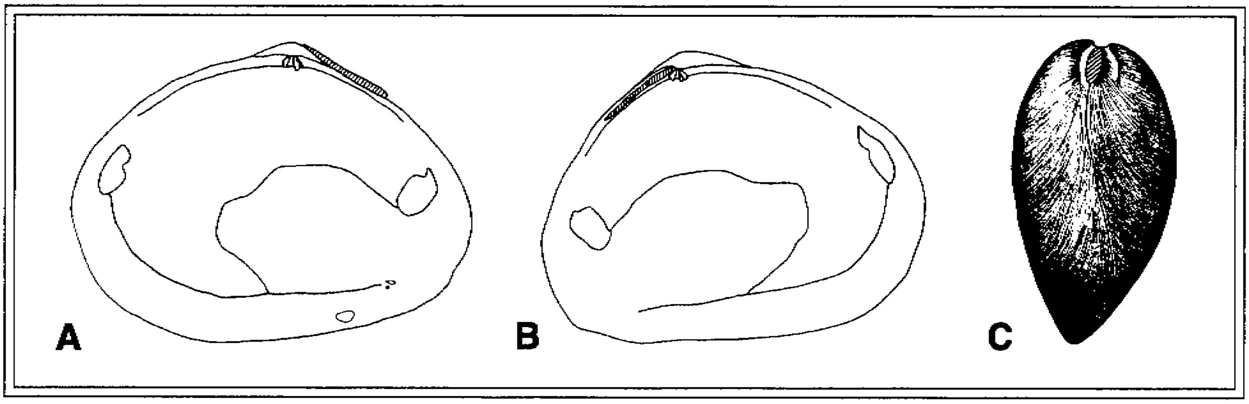

**Figure 5.46.** *Macoma carlottensis*: A, interior of right valve; B, interior of left valve; C, posterior view of both valves.

### *Macoma carlottensis* Whiteaves, 1880

Figure 5.46

*Macoma carlottensis* Whiteaves, 1880: 196B.

*Macoma leptonoidea* Dall, 1895: 33.

*Macoma inflatula* Dall, 1897: 11.

*Macoma quadrana* Dall, 1916: 37, *nom. nud.*; Dall, 1916a: 414.

**Material Examined.** California, Santa Maria Basin, Phase I, Sta.BSS-55 (590 m), BSS-89 (471 m); Phase II, Sta. PJ-9 (169 m).

**Description.** Shell trigonal to elongate, thin, more inflated anteriorly. Periostracum adherent, polished, usually straw-colored. Pallial sinus larger in left valve. Length to 30 mm.

**Type Locality and Type Specimens.** Virago Sound, Graham Island, Queen Charlotte Islands, British Columbia; Lectotype, NMC 316.

**Distribution.** Lituya Bay, Alaska (59° N), to Islas Los Coronados, Baja California [Norte] (32° N) in the subtidal zone to 1,550 m, in mud or fine sand. Also known in the Pleistocene of California.

**Literature.** Bright (1988), Coan (1971: 35-37), Dunnill and Ellis (1969: 13-15).

## Family Bernardinidae Keen, 1969

**Diagnosis.** Shell small to minute, solid, equivalve and subequilateral. Lunule and escutcheon absent. Hinge plate prominent, with 2 or 3 large cardinal teeth and 2 or more lateral teeth. Ligament mostly internal in obscure resilifer.

### Genus *Halodakra* Olsson, 1961

*Halodakra* Olsson, 1961. **Type species** (OD): *Circe subtrigona* Carpenter, 1857. Recent, California.

**Diagnosis.** Shell ovate to suborbicular, inequilateral; posterior end produced. Sculpture absent, or of commarginal striae. Posterior area with chevron-shaped color markings. Umbones prosogyrate. Lunule obscure or demarcated. Hinge plate strong with 1 to 3 cardinal teeth; lateral teeth sometimes present. Ligament internal in shallow resilifer. Juvenile byssate.

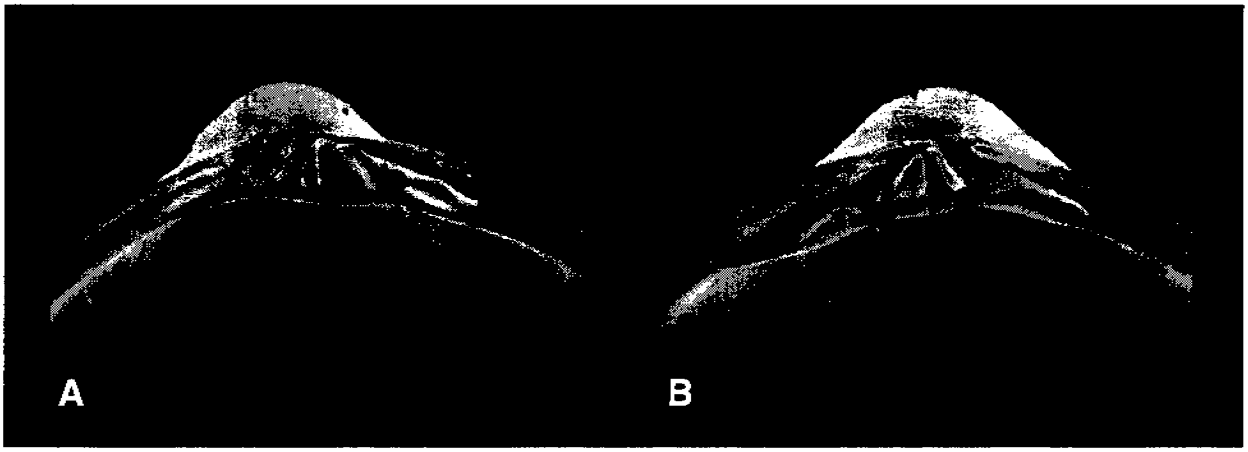

**Figure 5.47.** *Halodakra salmonea*: A, hinge of left valve; B, hinge of right valve. (after Coan, 1984).

### *Halodakra salmonea* (Carpenter, 1864)

Figure 5.47

*Psephis salmonea* Carpenter, 1864: 641.
*Crassatella marginata* Keep, 1887: 179, *ex* Carpenter MS.
*Psephidia brunnea* Dall, 1916: 34, *nom. nud.*; 1916a: 413.

**Material Examined.** California, Santa Maria Basin, Phase I, Sta.BSS-22 (99 m).

**Description.** Shell ovate to subtriangular; posterior end produced. Sculpture of commarginal striae. Color usually reddish, rarely white, generally with blush of brown on umbo. Length to 5 mm.

**Type Locality and Type Specimens.** San Diego, California; Lectotype, USNM 15578.

**Distribution.** Banks Island, British Columbia (53.5° N) to Rocas Alijos, Baja California (25° N), in 20 - 99 m, among rubble in rocky areas.

**Literature.** Coan (1984: 231-233), Howard (1953).

## Order Myoida Goldfuss, 1820

**Diagnosis.** Shell aragonitic, subequilateral to strongly inequilateral, equivalve or inequivalve. Sculpture absent to highly developed in some groups. Umbones not prominent. Lunule and escutcheon obscure or absent. Ligament external, or internal in resilifer or prominent chondrophore. Occasionally with lithodesma. Hinge plate edentate, or with pseudocardinal tubercle in each valve.

## Superfamily Hiatelloidea J. E. Gray, 1824

**Diagnosis.** Shell aragonitic, thick, quadrate to trapezoidal, frequently irregular or distorted, inflated, equivalve. Sculpture absent, or of irregular commarginal striae. Periostracum thick, usually layered and bridging hinge region. Ligament external parivincular and mainly opisthodetic, attached to strong nymph. Hinge plate strong, often edentate, but with obscure denticles or ephemeral tubercles. Some genera byssate.

## Family Hiatellidae J. E. Gray, 1824

**Diagnosis.** Shell aragonitic, with prismatic outer, homogenous middle, and complex cross-lamellar inner layers. Shell usually thick; outline ovate to elongate, with extensive gape. Sculpture absent, or weakly commarginal. Periostracum strongly developed, dehiscent, usually covering mantle edge and prolonged into siphonal sheath. Ligament external, opisthodetic and parivincular. Hinge plate irregular, with 1 or 2 submarginal denticles possibly ephemeral. Dimyarian, with subequal adductor muscle scars. Pallial line deeply impressed, frequently discontinous; pallial sinus variable. Ctenidia synaptorhabdic and homorhabdic, usually extending into exhalant siphon. Foot usually small, digitiform, with byssal groove, many groups byssate when adult. Mantle lobes extensively fused, usually thick, with small pedal aperture and fourth pallial aperture in some. Siphons large, fused for most of length. Alimentary canal with type 4 stomach; ducts to digestive diverticula in 3 clusters; style-sac conjoined with mid-gut; intestine passing through ventricle of heart.

**Literature.** Keen (1969x), Lamy (1924-1925), Tryon (1869), Yonge (1971).

### Genus *Hiatella* Bosc, 1801

*Hiatella* Bosc, 1801, *ex* Daudin MS. Type species (SD Winckworth, 1932): *Hiatella monoperta* Bosc, 1801, *ex* Daudin MS, = *Mya arctica* Linnaeus, 1767. Recent, Norway.

*Saxicava* Fleuriau de Bellevue, 1802. Type species (M): *S. striata* Fleuriau de Bellevue, 1802, = *Mya arctica* Linnaeus, 1767.

**Diagnosis.** Shell ovate to trapezoidal, usually distorted, chiefly nestling, but able to enlarge its home somewhat by mechanical action. Inequilateral and equivalve, usually gaping. Sculpture absent, or feebly commarginal, rarely with 1 or 2 posterior radial rows of spines in juvenile. Hinge plate weak and irregular, usually with 1 or more cardinal denticles sometimes lost in adult. Byssate.

### ***Hiatella arctica* (Linnaeus, 1767)**

Figure 5.48

*Mya arctica* Linnaeus, 1767: 1113.

*Mytilus pholadis* Linnaeus, 1771: 548.

*Saxicava orientalis* Yokoyama, 1920: 106.

[there are many more synonyms throughout the world].

**Material Examined.** California, Santa Maria Basin, Phase I, Sta.BSS-20 (396 m); Phase II, Sta. R-4 (92 m).

**Description.** Shell usually distorted; sculpture of irregular commarginal growth lines. Umbones prominent, prosogyrate, near anterior end. Some individuals with 1 or 2 external radial ridges on posterior slope that may be spinose, particularly on small specimens. Periostracum thin, not investing white or red tipped siphons. Small, distinct lunule present. Ligament attached to weak nymph. Hinge plate feeble; right valve with one ephemeral denticle, 2 in left valve, but may be erroded and lost. Length to 78 mm.

**Type Locality and Type Specimens.** Norway, types possibly at the Linnean Society of London.

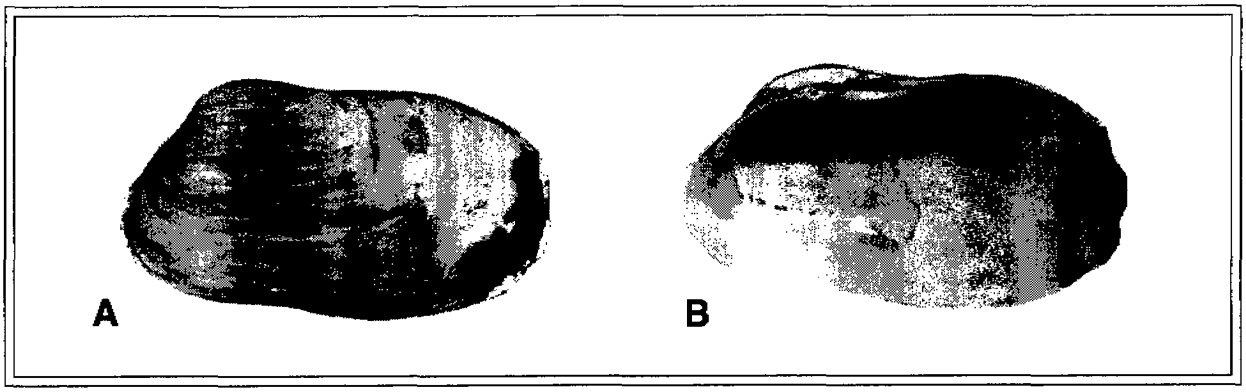

**Figure 5.48.** *Hiatella arctica*: A, exterior of left valve; B, interior of left valve.

**Distribution.** Point Barrow, Alaska (71° N) along the west American coast to Chile, in the intertidal zone to 800 m.

**Remarks.** This highly variable species is the dominant byssally attached bivalve of Arctic and boreal regions. There is tantilizing evidence that there is more than one species in this genus: eggs of two colors (red and pinkish cream), two post-larval forms (oval and triangular), and siphon tips of two colors (red and white). Unfortunately, these traits have not been correlated with with shell morphologies or type material. Full taxonomic understanding of this genus is a problem that cries out for attention with modern methodologies grounded in sound nomenclature and with type specimens.

Strauch (1968, 1970, 1971) found that size of this species is correlated with water temperature and can be used to estimate paleotemperatures, but other workers are not as certain of this (Rowland and Hopkins, 1971).

**Literature.** Ali (1970), Barrois (1879), F. R. Bernard (1979: 56-57), Beu (1971), N. MacGinitie (1959: 190-191), Narchi (1973), Ockelmann (1959: 135-142), Yonge (1971). For additional references, see Clapp and R. Kenk (1963).

### Genus *Saxicavella* Fischer, 1878

*Saxicavella* P.-H. Fischer I, 1878. **Type species** (M): "*Mytilus plicatus* Gmelin, *ex* Chemnitz MS," Montagu, 1808, *non* Gmelin, 1791, = *Saxicavella jeffreysi* Winckworth, 1930; ICZN *Code* Art. 70c. Recent, northeastern Atlantic.

**Diagnosis.** Shell small, elongate, rhomboidal, thin, slightly gaping. Umbones not prominent. Periostracum dehiscent. Ligament short, prominent, mostly external, on very short nymph just posterior to beaks. Siphons absent. Pallial line continuous; pallial sinus absent.

**Remarks.** The name is a diminutive based on the Latin *saxum*, a stone, and *cavator*, an excavator; the gender is feminine. This genus occur back to the Late Paleocene or Eocene.

### *Saxicavella nybakkeni* P. H. Scott, 1994

Figure 5.49

*Saxicavella nybakkeni.* P. H. Scott, 1994: 65

**Material Examined.** California; 10 lots of southern and central California.

**Description.** Short, rhomboidal. Posterior end longer, broad; posterior gape wide. Surface smooth, with commarginal growth striae. Ligament small, deeply sunken, not protruding. Periostracum tan, adherent. Length to 10 mm.

**Remarks.** The juveniles of this species are brooded in an external pouch between the inner and outer mantle folds. It is somewhat similar to the Caribbean *S. sagrinata* Dall and Stimpson, 1901, which has a granular shell suface, narrower beaks, a small cardinal tubercle, and a shallow nymph.

**Distribution.** San Francisco (37.7° N) [CAS] to San Diego (32.7° N) [SBMNH], California, in 31-61 m.

**Literature.** P. H. Scott (1994).

### *Saxicavella pacifica* Dall, 1916

Figure 5.50

*Saxicavella pacifica* Dall, 1916a: 42, *nom. nud.*; 1916b: 416.

**Material Examined.** California, Santa Maria Basin, Phase I, Sta.BSS-76 (387 m).

**Description.** Shell rhomboidal-elongate, narrow anteriorly, longer, broad posteriorly. Sculpture of feeble commarginal growth lines. Periostracum thin, tan, adherent. Posterior slope set off by obscure radial ridge. Posterior gape small. Hinge plate with minute cardinal denticle in right valve in juveniles, overgrown in larger specimens. Ligament distinct, external, protruding. Length to 8 mm.

**Remarks.** This species is similar to the European *S. jeffreysi* Winckworth, 1930, differing in being more rhomboidal, with a narrower anterior end and a proportionately broader posterior end.

**Type Locality and Type Specimens.** Off Pt. Loma, California, 120-131 fathoms; Holotype, USNM 209912.

**Distribution.** Vancouver Island, British Columbia (49.8° N) [LACM], to San Diego, California (32.7° N) [CSDOMP], in the subtidal zone to 100 m, nestling in cobbles or burrows, occasionally in kelp holdfasts.

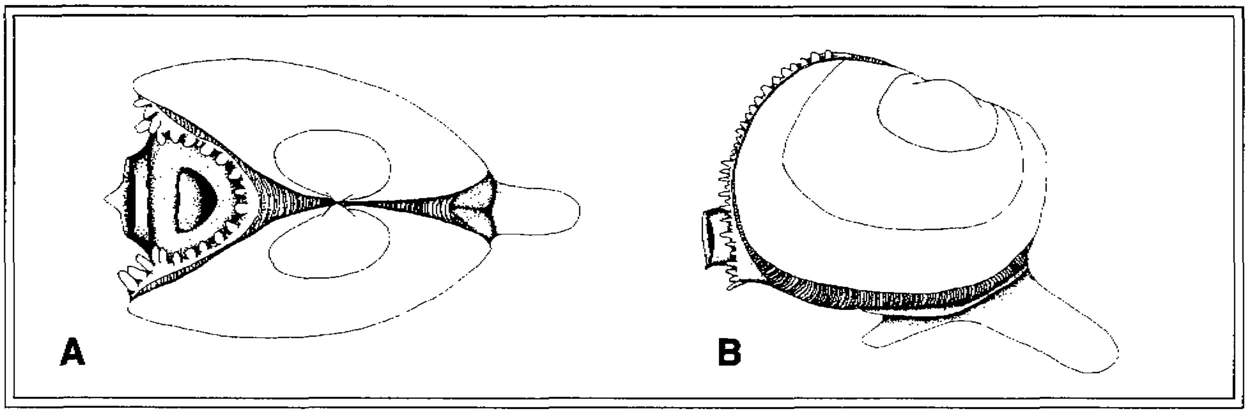

**Figure 5.49.** *Saxicavella nybakkeni*: A, dorsal view of living animal; B, lateral view of living animal. (after Scott, 1984).

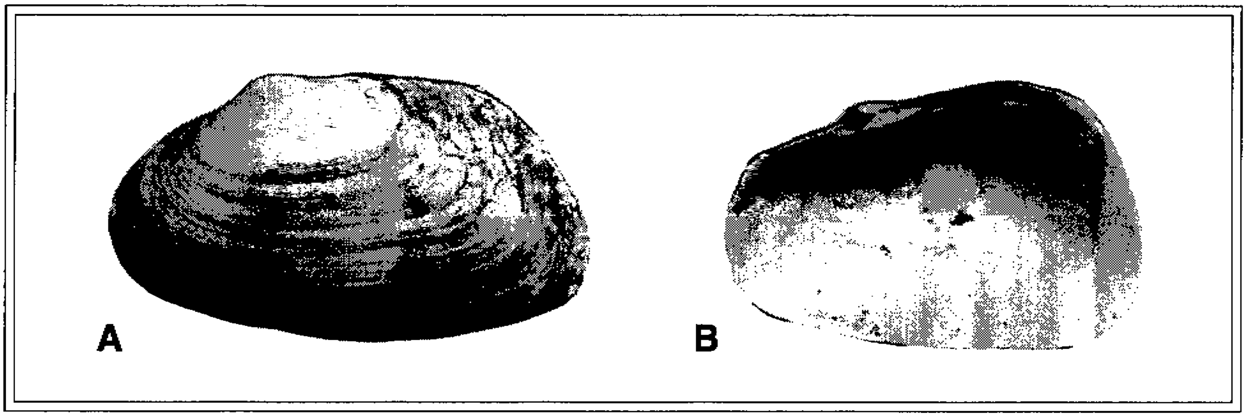

**Figure 5.50.** *Saxicavella pacifica*: A, exterior of left valve; B, interior of right valve.

## Subclass Anomalodesmata Dall, 1889

**Diagnosis.** Shell aragonitic, ovate to elongate, equivalve to strongly inequivalve. Periostracum thin, adherent, occasionally with radial rows of pustules or adherent grains. Ligament opisthodetic, sometimes vestigial, usually with internal section in resilifer or chondrophore, generally with supporting lithodesma. Hinge plate thickened, edentate, or with pseudocardinal tubercle. Gills eulamellibranch, reduced or absent in some forms.

## Order Pholadomyoida Newell, 1965

**Diagnosis.** Shell aragonitic, in 3 layers, ovate to subtrigonal, strongly inequilateral with anterior umbones. Periostracum thin, frequently pustulate, or with cemented sand grains. Ligament external, opisthodetic, parivincular on nymph; internal ligament in resilifer. Hinge plate thickened, edentate, sometimes with amorphous tubercles.

### Superfamily Pandoroidea Rafinesque, 1815

**Diagnosis.** Shell slightly to markedly inaequivalve, inequilateral, compressed to medially inflated. Interior nacreous. Periostracum adherent, frequently granulated. Sculpture absent or commarginal, rarely radial. Ligament external, feeble; valves bridged by periostracum; internal ligament strong, in resilifer, sometimes supported by elongate lithodesma along antero-posterior axis. Hinge plate edentate, or with tubercles, usually buttressed. Some groups byssate in adult.

## Family Pandoridae Rafinesque, 1815

**Diagnosis.** Shell aragonitic, with prismatic outer, lenticular nacre middle, and sheet nacre inner layers. Outline inaequilateral, compressed, markedly inequivalve; right valve flat; left valve convex and overlapping. Sculpture absent or of commarginal lirae. Periostracum thin, occasionally with radial lirae. Ligament external, amphidetic. Hinge plate absent, but with tooth-like crural ridges or lamina, on either side of resilifer. Interior nacreous. Pallial line simple, frequently broken. Dimyarian; adductor muscle areas subequal. Foot with byssal groove, but adult not byssate. Mantle lobes not extensively fused, with large pedal aperture, 2 short siphons and fourth pallial aperture. Gills heterorhabdic; outer demibranch with reduced descending lamella. Labial palps long, narrow. Alimentary canal with type 4 stomach; ducts to digestive diverticula; style-sac conjoined to mid-gut; intestine passing through ventricle of heart.

### Genus *Pandora* Hwass, 1795

*Pandora* Hwass, 1795. Type species (SD Children, 1823): *Pandora rostrata* Lamarck, 1818, = *Solen inaequivalvis* Linnaeus, 1758. Recent, Mediterranean.

**Diagnosis.** Shell strongly inequilateral; right valve flat; left valve convex. Hinge plate vestigial, with crural ridges bordering resilifer. Lithodesma usually present. Sculpture of irregular commarginal growth lines only. Interior nacreous. Siphons very short.

### ***Pandora bilirata* Conrad, 1855**

Figure 5.51

*Pandora bilirata* Conrad, 1855: 267, 1857: 73.

*Pandora (Kennerlia) bicarinata* Carpenter, 1864b: 638; 1864e: 603.

*Pandora delicatula* G. B. Sowerby II, 1874: sp. 17.

*Pandora granulata* Dall, 1915: 449.

*Pandora (Kenerlyia) pseudobilirata* Nomura and Hatai, 1940: 87.

**Material Examined.** California, Santa Maria Basin, Phase II, Sta.R-8 (308 m).

**Description.** Shell elongate-ovate. Anterior end sharply rounded; posterior end rounded, not attenuate, with 1 to 3 strong radial ribs on left valve. Length to 15 mm.

**Type Locality and Type Specimens.** California, types not located, possibly lost.

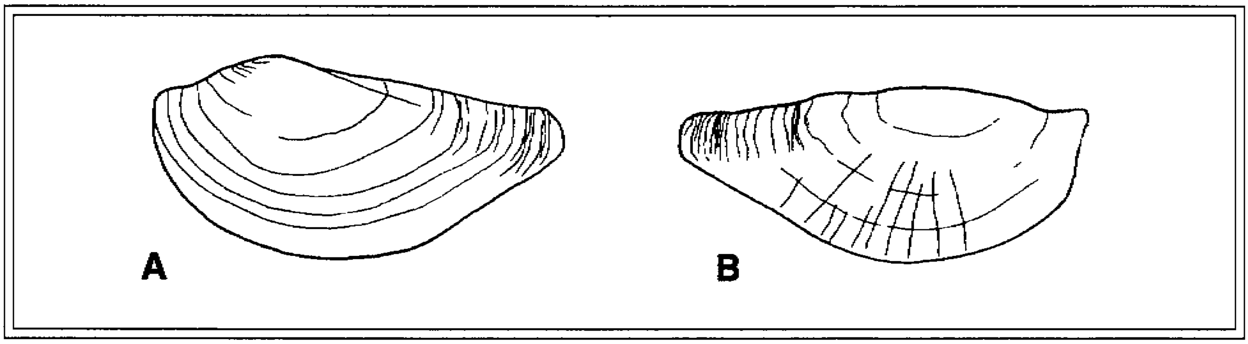

**Figure 5.51.** *Pandora bilirata*: A, exterior of left valve; B, exterior of right valve.

**Distribution.** Kukak Bay (58° N) [CAS] and Prince William Sound (60° N), Alaska, to the Gulf of California, and in the northwest Pacific from the Kurile Islands to Honshu, Japan; in the subtidal zone to 308 m, in mud. Also known as early as the Pliocene of California.

**Literature.** U. S. Grant and Gale (1931: 261), Hertlein and Grant (1972: 335-336), Hertlein and Strong (1946: 97), Keen (1971: 289).

## Family Lyonsiidae Fischer, 1887

**Diagnosis.** Shell aragonitic, with prismatic outer, lenticular nacre middle, and sheet nacre inner layers; some also with homogeoeous middle layer. Outline suborbiculate to elongate, inequilateral and subequivalve, usually thin and fragile. Umbones prosogyrate, anterior. Valves overlapping ventrally. Sculpture feeble, variable. Periostracum thin to extremely thick, dehiscent, often with adherent particles. Ligament opisthodetic; resilium in marginal resilifer, supported by short to elongate lithodesma. Hinge plate irregular, edentate. Dimyarian; adductor muscle scars small and subequal. Pallial line impressed; pallial sinus small. Mantle lobes fused; pedal aperture large to small; fourth pallial aperture present; siphons short and separate. Foot large and compressed in *Lyonsia*, small and veneriform in *Entodesma* and *Mytilimera*, with byssal groove; adult byssate. Gills heterorhabdic; outer demibranch reflected, with descending lamella only. Labial palps long and narrow. Alimentary canal with type 4 stomach; style-sac conjoined to mid-gut; intestine passing through ventricle of heart.

### Genus *Lyonsia* Turton, 1822

*Lyonsia* Turton, 1822. Type species (M): *Mya striata* Montagu, 1815, = *Mya norwegica* Gmelin, 1791. Recent, North Sea.

*Bentholyonsia* Habe, 1952. Type species (OD): *Allogramma (B.) teramachii* Habe, 1952. Recent, Japan.

**Diagnosis.** Shell thin, inequilateral, equivalve, with small posterior gape. Hinge plate feeble, edentate. Exterior and interior nacreous. Periostracum with radial ridges and often with adherent sand grains, particularly in young specimens. Lithodesma large.

#### ***Lyonsia californica* Conrad, 1837**

Figure 5.52

*Lyonsia californica* Conrad, 1837: 248.

*Osteodesma nitidum* Gould, 1853: 390.

*Lyonsia gouldii* Dall, 1915: 453.

*Lyonsia californica haroldi* Dall, 1915: 453.

*Lyonsia californica nesiotes* Dall, 1915: 453.

*Mya striata* Montagu, 1815: 188, *auctt., non* Montagu.

**Material Examined.** California, Santa Maria Basin, Phase II, Sta.R-8 (90 m).

**Description.** Shell elongate, thin, translucent. Anterior end approximately 30% of length. Posterior end broadly attenuate. Periostracum thin, generally light in color, with fine, widely spaced radial lirae. Length to 35 mm.

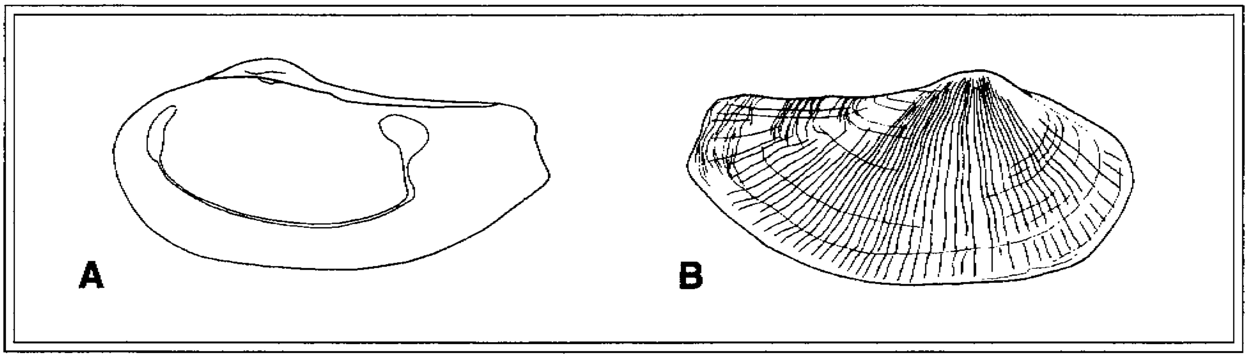

**Figure 5.52.** *Lyonsia californica*: A, interior of right valve; B, exterior of right valve.

**Type Locality and Type Specimens.** California; types not found, possibly lost.

**Distribution.** Kodiak Island, Alaska (58° N) [CAS, LACM], to Acapulco, Mexico (17° N) and in the Gulf of California, in the subtidal zone to 100 m, in mud.

**Remarks.** Small specimens tend to have more sand particles adhering to their periostracum. It is possible that *L. gouldii* may prove to be a distinct southern species or subspecies, but no characters have been advanced that reliably separate it.

**Literature.** Haderlie and D. P. Abbott (1980: 395), Mauer (1967c, 1969), Narchi (1968).

## Superfamily Thracioidea Stoliczka, 1870 [1830]

**Diagnosis.** Shell aragonitic, thin, inequilateral; right valve often larger and overlapping left valve. Umbones posterior, orthogyrate. Surface usually granulated; periostracum variable. External ligament opisthodetic, parivincular, seated on nymph. Resilium in an oblique resilifer or chondrophore, supported by lithodesma. Hinge plate weak, edentate. Interior porcellanous, chalky, or subnacreous.

### Family Thraciidae Stoliczka, 1870 [1830]

**Diagnosis.** Shell aragonitic, with outer and inner homogenous layers; never nacreous, although iridescence shows on eroded beaks of some specimens. Shell very fragile and brittle. Outline quadrate to rounded, subequilateral. Right valve often more convex and overlapping left. Posterior end gaping. Umbones median or posterior, perforated in some. Sculpture absent, occasionally with commarginal or oblique undulations. Surface frequently granulated; periostracum variable. External ligament, when present, opisthodetic, parivincular; resilium, when present, in oblique resilifer or chondrophore, supported by small to large laterially oriented lithodesma. Hinge plate weak, edentate. Dimayrian; anterior adductor muscle scar elongate; posterior scar rounded. Pallial sinus present. Foot small, with byssal groove. Adult not byssate. Mantle lobes fused, with small pedal and fourth pallial apertures. Siphons long and separate. Ctenidia plicate, ascending lamellae of outer demibranchs not present. Labial palps broadly triangular. Alimentary canal with type 4 stomach; style-sac joined to mid-gut; intestine passing through ventricle of heart.

### Genus *Thracia* Blainville, 1824

*Thracia* J. Sowerby, 1823, *ex* Leach MS, *nomen nudum*; Blainville, 1824, *ex* Leach MS. **Type species** (M): *Mya pubescens* Pultney, 1799. Recent, North Sea.

*Osteodesma* Blainville, 1827, *ex* Deshayes MS. **Type species** (SD Dall, 1903): *Anatina myalis* Lamarck, 1818, = *Thracia pubescens* Pulteney, 1799.

**Diagnosis.** Shell ovate, thin, inflated, inequivalve; right valve larger than left. Umbones prominent, orthogyrate; umbo of right valve sometimes perforate from contact. Posterior gape large. Ligament mostly external. Projecting resilium in some; lithodesma present in many, but sometimes inconspicuous in adult. Hinge plate weak, edentate.

### ***Thracia trapezoides* Conrad, 1849**

Figure 5.53

*Thracia trapezoides* Conrad, 1849: 723.

*Thracia kanakoffi* Hertlein and Grant, 1972: 338.

**Material Examined.** California, Santa Maria Basin, Phase I, BSS-94 (96 m). Phase II, Sta.R-8 (90 m).

**Description.** Shell trapezoidal, inflated. Anterior end rounded; posterior end truncate, set off by shallow radial sulcus and ridge. Right valve slightly larger. Pustules especially prominent on posterior slope. Umbones wide and depressed; right umbo sometimes perforate. Periostraum dark brown. Length to 65 mm (to 130 mm in Pliocene material).

**Type Locality and Type Specimens.** Astoria, Oregon (Miocene); Holotype, USNM 3604.

**Distribution.** Cook Inlet (60° N), to Isla Cedros, Baja California Sur, (28° N), in 11 to 200 m, in sand and mud.

**Literature.** Coan (1990: 30-31).

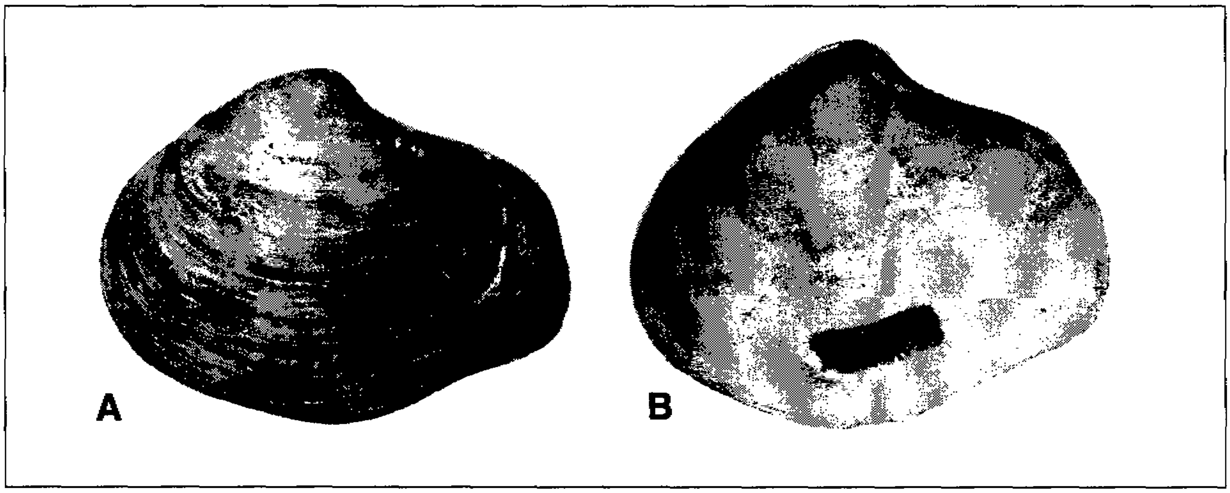

**Figure 5.53.** *Thracia trapezoides*: A, exterior of left valve; B, interior of right valve.

## Family Periplomatidae Dall, 1895

**Diagnosis.** Shell aragonitic, with prismatic outer, lenticular nacreous middle, and sheet nacre inner layers, and with prismatic myostraca. Outline ovate to elongate; thin and fragile. Markedly inequivalve, with right valve more convex and overlapping left. Umbones prominent, usually with radial fissure. Sculpture weak, usually with commarginal undulations, rarely with radial ridges. Periostracum thin and adherent, frequently with cemented sand grains. External ligament obsolete; resilium in butressed chondrophore, usually supported by lithodesma. Mantle lobes extensively fused, with small pedal and fourth pallial apertures. Siphons long and separate. Foot small, elongate not byssate. Dimyarian; anterior adductor muscle scar crescent-shaped; posterior adductor rounded. Ctenidia strongly plicate; outer demibranch with descending lamella only. Labial palps narrow and elongate. Alimentary canal with type 4 stomach; style-sac joined with mid-gut; intestine passing through ventricle of heart.

### Genus *Periploma* Schumacher, 1817

*Periploma* Schumacher, 1817. **Type species** (M): *Periploma inaquivalvis* Schumacher, 1817, = *Corbula margaritacea* Lamarck, 1801. Recent, Florida.

**Diagnosis.** Shell ovate to elongate or rhomboidal, thin, inequivalve; right valve more inflated, overlapping left. Anterior end rounded; posterior end truncate. Umbones opisthogyrate, with radial fissure. Surface granulate or pustulate. Hinge plate weak, with large chondrophore in each valve supported by rib or clavicle. Lithodesma usually present. Interior subnacreous.

#### ***Periploma discus* Stearns, 1890**

Figure 5.54

*Periploma discus* Stearns, 1890: 222.

**Material Examined.** California, Santa Maria Basin, Phase I, BSS-21 (49 m); Phase II, Sta. R-8 (90 m).—Holotype (see below).

**Description.** Shell discoidal, equilateral; posterior end slightly produced, spout-like. Sculpture of feeble commarginal growth lines and radial rows of pustules. Chondrophore narrow and subvertical. Length to 45 mm.

**Type Locality and Type Specimens.** San Pedro, California; Holotype, USNM 105391.

**Distribution.** Monterey Bay, California (36.7° N) to Isla Herradura, Costa Rica (9° N), in the low intertidal zone to 40 m, in sand.

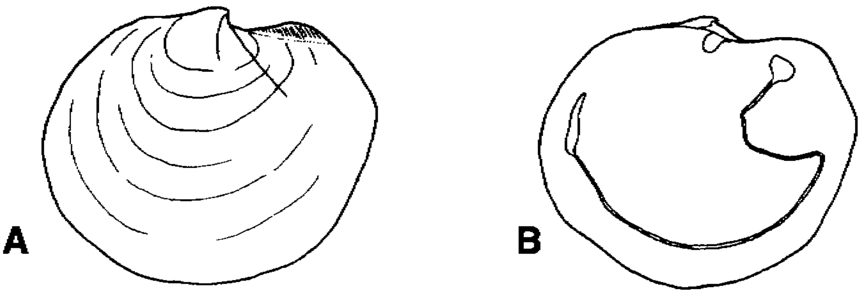

**Figure 5.54.** *Periploma discus*: A, exterior of left valve; B, interior of right valve.

## Superfamily Verticordioidea Stoliczka, 1871

**Diagnosis.** Shell aragonitic, inflated, ovate to subquadrate, inequilateral and subequivalve. Umbones anterior, incurved. Sculpture usually radial; surface granulate or with minute spines, rarely smooth. Periostracum thin, adherent. Hinge plate edentate, frequently with 1 or 2 pseudocardinal tubercles and occasionally with lateral teeth. Ligament opisthodetic; resilium with supporting lithodesma. Lunule usually developed.

### Family Verticordiidae Stoliczka, 1871

**Diagnosis.** Shell aragonitic, with prismatic outer, lenticular nacreous middle, and sheet nacre inner layers. Outline ovate to trapezoidal to quadrate, inflated, inequilateral. Umbones incurved. Periostracum thin and adherent, usually granulate. Radial sculture usually present, often of riblets or lirae, rarely with broad undulations. Lunule well demarcated; escutcheon obscure. Ligament opisthodetic, weak; periostracum bridging valves; resilium in irregular resilifer, supported by lithodesma. Hinge plate feeble, sinuous, occasionally thickened, or with 1 or 2 conical pseudocardinal tubercles. Dimyarian; adductor muscle scars subequal. Foot digitiform or laterally compressed, often weakly byssate in adult. Mantle lobes fused, with large pedal aperture and arenophilic radial glands on margins; exhalant and inhalant apertures with short siphonal ring with large sensory tentacles. Pallial line obscure; pallial sinus absent. Ctenidia eulamellibranch, hypertrophied, with outer demibranch consisting of descending lamella only; inner demibranch reduced. The gills horizontally aligned and attached to lateral membrane, forming septum separating the exhalant chamber. Labial palps mostly small; lips enlarged forming an oral hood. Alimentary canal with large cuticular stomach and oesophagus with strongly muscularised walls; 2 ducts to digestive diverticula; style-sac joined to mid-gut; intestine passing through ventricle of heart. Simultaneously hermaphroditic.

### Genus *Dalliocordia* Scarlato and Starobogatov, 1983

*Dalliocordia* Scarlato and Starobogatov, 1983. Type species (OD): *Lyonsia alaskana* Dall, 1895. Recent, eastern Pacific.

**Diagnosis.** Shell ovate, inflated and thin. Periostracum with sparse radial lirae. Sculpture limited to minute commarginal striae, granules absent. Umbones prominent, prosogyrate. Ligament sunken into groove. Hinge plate feeble, sinuate and edentate, but with obscure central tubercle. Lithodesma large. Ctenidia absent.

### ***Dalliocordia alaskana* (Dall, 1895)**

Figure 5.55

*Lyonsiella alaskana* Dall, 1895: 703.

**Material Examined.** California, Santa Maria Basin, Phase I, BSS-9 (398 m), BSS-33 (396 m); Phase II, Sta. R-3 (291 m).—Holotype (see below).

**Description.** Shell oval, inflated, thin and hyaline. Sculpture limited to distant radial lirae on periostracum and irregular growth lines. Umbones recurved, prominent. Hinge plate feeble; lithodesma large. Length to 30 mm.

**Type Locality and Type Specimens.** SW of Sitka, Alaska (55° 20'N, 136° 20'W), 1569 fathoms; Holotype, USNM 123500.

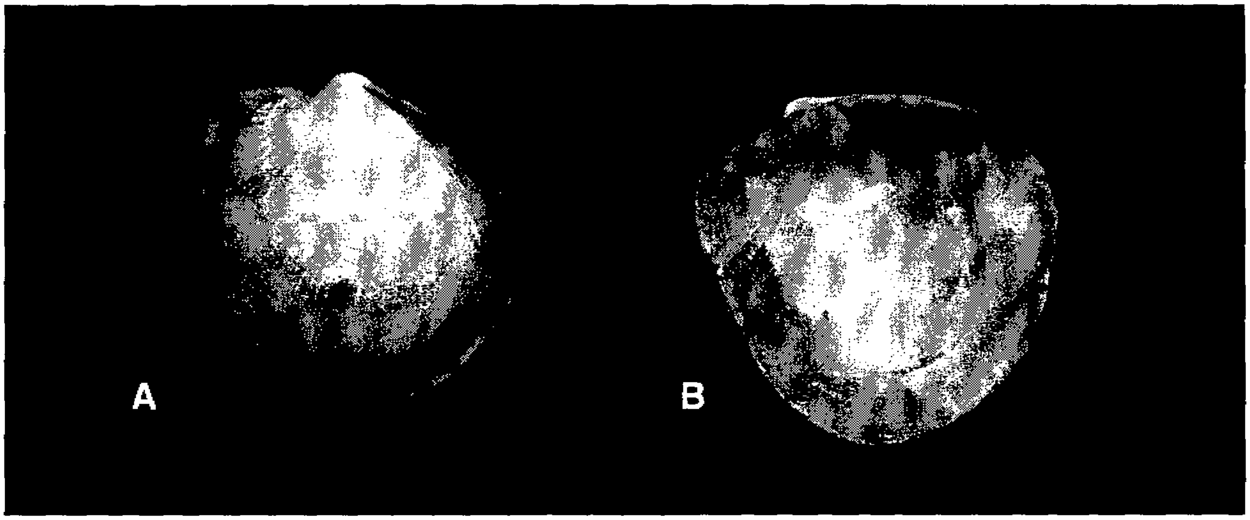

**Figure 5.55.** *Dalliocordia alaskana*: A, exterior of valve; B, interior of right valve.

**Distribution.** Sitka, Alaska (55° N) to Santa Catalina Island, California (33° N) in 291 to 3,570 m, in fine mud.

**Literature.** F. R. Bernard (1974: 103-109), Knudsen (1970: 129-132).

## Order Septebranchida Pelseneer, 1888

**Diagnosis.** Shell aragonitic, inequilateral, ovate to elongate. Umbones subcentral. Anterior end rounded; posterior end truncate or rostrate. Sculpture absent or various. Periostracum adherent, usually bridging valves. Ligament mostly external; resilium small, in vestigial resilifer, usually supported by lithodesma. Hinge plate weak, edentate, or with more or less developed cardinal tubercles and/or lateral ridges. Ctenidia reduced or absent.

**Remarks.** This "order," known from the Cretaceous and containing three superfamilies, is almost certainly polyphyletic. Early workers followed Dall (1886b) and Pelseneer (1888), who believed that a continuous series of modifications were represented from *Lyonsia*, with typical eulamellibranch ctenidia, through the Verticordiidae with reduced ctenidia, to the entirely gill-less Cuspidariidae. Differences in shell structure and anatomy, however, do not support this, and the similarities are rather due to convergence engendered by carnivorous macrophagy.

## Superfamily Cuspidarioidea Dall, 1886

**Diagnosis.** Shell thin, ovate to subtrigonate; posterior end usually produced. Sculpture variable, surface occasionally granulate. Ligament external; small resilium supported by a lithodesma. Hinge plate narrow, edentate, sometimes with small pseudocardinal tubercles and lateral ridges.

## Family Cuspidariidae Dall, 1886

**Diagnosis.** Shell aragonitic, with homogeneous inner and outer layers. Inflated in shape, inequilateral; anterior end rounded; posterior end drawn out into tubular rostrum. Umbones subcentral, orthogyrate. Subequivalve, with right valve smaller. Periostracum thin, usually dehiscent, bridging valves, frequently granulate. Sculpture absent, sometimes radial or commarginal. Ligament external, sunken into a small resilifer, supported by lithodesma. Pallial line simple; pallial sinus vestigial. Foot digitiform, directed anteriorly. Mantle lobes fused, with small anterior pedal gape. Siphons united at base and with 7 prominent sensory tentacles; exhalent siphon short and eversible; inhalent siphon relatively large and extensible to capture prey. Foot digiform, with byssal grove. Adult not byssate. Gills absent; pallial cavity separated by muscular septum. Labial palps minute, lips enlarged. Alimentary canal with type 2 stomach, with cuticular lining and muscularized walls; 2 ducts to digestive diverticula; style-sac in separate caecum; intestine passing through ventricle of heart.

### Genus *Cuspidaria* Nardo, 1840

*Neaera* Griffith, 1834, *non* Robineau-Desvoidy, 1830. **Type species** (M): *Neaera chinensis* Griffith, 1834. Recent, China.

*Cuspidaria* Nardo, 1840. **Type species** (M): *Cuspidaria typica* Nardo, 1840, = *Tellina cuspidata* Olivi, 1792. Recent, Adriatic.

**Diagnosis.** Shell globular, thin; posterior end produced into tubular rostrum. Umbones subcentral, inequivalve. Periostracum thin. Sculpture absent or feeble commarginal striae. Ligament with narrow, sunken external portion and resilium in deep, oblique resilifer, supported by lithodesma. Hinge plate narrow, with variable pseudocardinal tubercules and lateral teeth. Septum typically with 4 pairs of ostia.

### ***Cuspidaria parapodema*** **F. R. Bernard, 1969**

Figure 5.56

*Cuspidaria parapodema* F. R. Bernard, 1969: 2232.

**Material Examined.** California, Santa Maria Basin, Phase I, BSS-31 (200 m), BSS-59 (216 m); Phase II, Sta. R-9 (410 m), PJ-1 (145 m).—Holotype (see below).

**Description.** Shell thin and fragile, translucent. Periostracum dull, frequently with coating of sediment. Rostrum somewhat longer than that of *C. (C.) apodema*. Hinge plate weak; posterior lateral tooth in right valve long and curved. Length to 17 mm.

**Type Locality and Type Specimens.** Off Redondo Beach, California (33° 49.5'N, 118° 26.2'W), 172 fathoms; Holotype, LACM.

**Distribution.** Point San Luis, California (35.2° N) to Bahía Elena, Costa Rica (11° N), in 50 to 410 m, in mud.

**Literature.** F. R. Bernard (1974: 41-43).

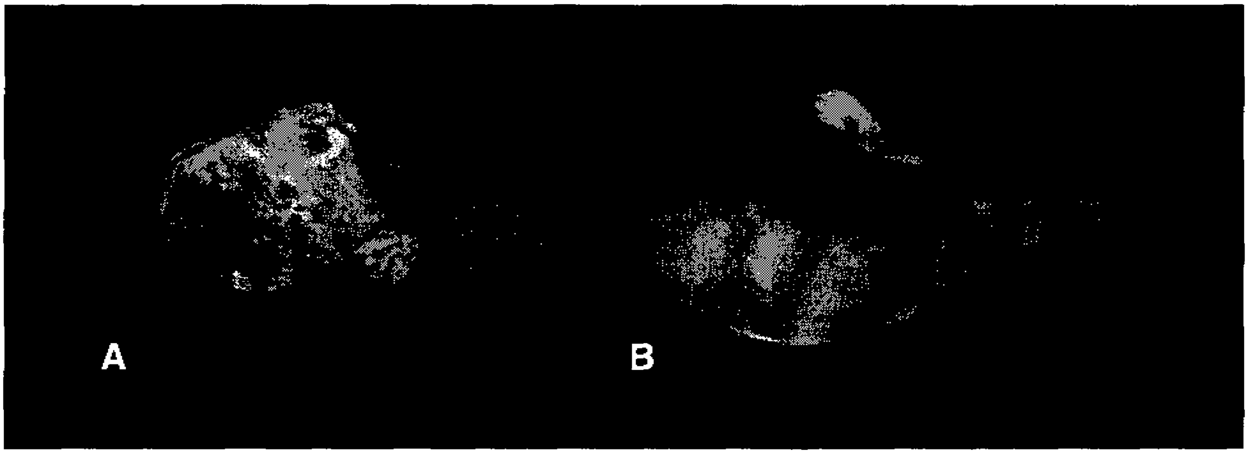

**Figure 5.56.** *Cuspidaria parapodema*: A, exterior of left valve; B, interior of right valve.

### Genus *Cardiomya* A. Adams, 1864

*Cardiomya* A. Adams, 1864. Type species (M): *Neaera gouldiana* Hinds, 1843. Recent, Indo-Pacific.

**Diagnosis.** Shell inflated, globular to ovate, with posterior rostrum. (The anterior portion of the shell, apart from the rostrum, is here referred to as the "disk.") Sculpture of disk of radial riblets or lirae, rarely with commarginal sculpture. Right valve with posterior lateral denticle may be obsolete. Resilifer deep and subvertical. Septum with 4 pairs of ostia and an extra lateral attachment to each valve posteriorly.

### *Cardiomya pectinata* (Carpenter, 1864)

Figure 5.57

*Neaera pectinata* Carpenter, 1864b: 637; 1865f: 54.
*Cuspidaria (Cardiomya) californica* Dall, 1886: 296.
*Cardiomya oldroydi* Dall, in Oldroyd, 1924: 33.
*Cardiomya isolirata* F. R. Bernard, 1969: 2231.

**Material Examined.** California, Santa Maria Basin, Phase I, BSS-86 (197 m); Phase II, Sta. PJ-15 (155 m), PJ-21 (143 m).

**Description.** Disk ovate to elongate; rostrum long and narrow. Sculpture of sharp, well-spaced, narrow, equal-sized radial ribs. Length to 40 mm.

**Remarks.** Young specimens have an elongate disk. As the animal grows, the disk becomes rounded, and the rostrum is proportionately longer. In northern waters, where the species attains the largest size, the species was named *pectinata*, based on a small specimen, and *oldroydi*, based on a large specimen, while young specimens were identified as *californica*. In southern waters, the species generally does not attain as large a size, and most material has been labeled *californica*, with only the occasional large specimen being labeled *pectinata*. Occasional specimens may have radial sculpture extending onto the rostrum, and this was named *isolirata* by Frank Bernard. There seems some merit in dividing this species into two subspecies, southern material having on average a more elongate disk.

**Type Locality and Type Specimens.** Puget Sound, Washington; Holotype, USNM 4506.

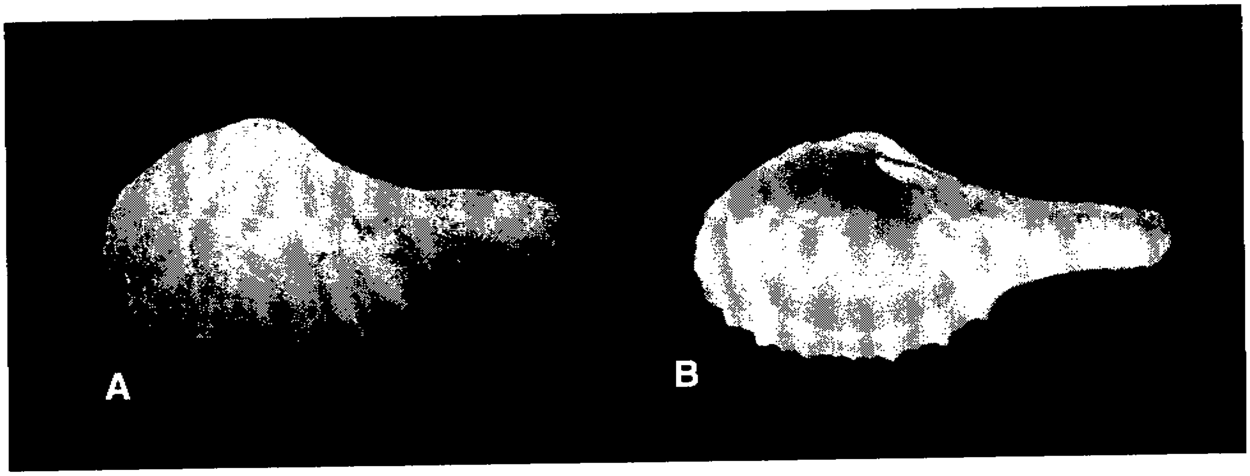

**Figure 5.57.** *Cardiomya pectinata*: A, exterior of left valve; B, interior of right valve.

**Distribution.** Prince William Sound, Alaska (60° N) to Acapulco, Guerrero, Mexico (17° N), and the Galápagos Islands (1°N), in 5 - 640 m, in sand and mud.

**Literature.** F. R. Bernard (1974: 50-52, 59, 61-64), Gustafson *et al.* (1986), Strathmann (1987: 341-342).

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# 6. CLASS CEPHALOPODA

by

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## Introduction

Cephalopods are soft-bodied mollusks which have a well developed head and a circumoral crown of mobile appendages that bear suckers and/or hooks. The mouth has a chitinous, beak-like set of jaws and a tongue-like radula with rows of teeth. An external shell occurs only in *Nautilus* while in all other cephalopods the shell is enveloped by the mantle and either reduced in size or completely absent. Water is expelled via a funnel from the mantle cavity which aids in locomotion and eliminates waste products. With the exception of *Nautilus* all cephalopods have a single pair of gills. They possess a well developed central nervous system and the brain is protected by a cartilaginous cranium. Large eyes and a diversity of sense organs are characteristic of the group. Extensive experimental work has been conducted in documenting both learning and other complex behaviors.

The cephalopod skin is the most complex in all the mollusk groups. Numerous sacs of pigment (chromatophores), reflective platlets (iridophores) and refractive platlets (leucophores) are present in the surface layers of the skin. Superficial muscles allow these animals to control skin texture with a diversity of papillae patterns. Cephalopods are capable of rapid changes in colors and patterns. They are known for the ability to cryptically match the color and texture of their surrounding environment. In addition, they are able to produce bold contrasting color patterns used for courtship, territorial and other behavioral displays.

Sexes are separate and in many genera either the male or female is considerably larger than the opposite sex. Spermatophores are used to transfer sperm to the female and fertilization is internal. Cephalopod eggs are heavy with yolk and development is direct. Egg capsules vary in length from 1 - 40 mm. The eggs of benthic cephalopods are laid singly, braided into a festoon or incorporated into gelatinous "fingers or strings" and all are attached to the substrate. Development time varies from a few weeks to many months. Eggs spawned by squids and sepiolids are not attended, whereas female octopuses brood their eggs until they hatch.

Hatchlings from large egg species stay on the bottom and immediately move or crawl away as miniature adults. Hatchlings from benthic species with small eggs typically go into the plankton where they can continue to feed and grow for up to several months before settling to the bottom. Metamorphosis does not occur nor are there discrete larval stages. These planktonic hatchlings are termed "paralarvae" by some workers to reflect this feature. Most cephalopods live for six months to several years at the most. The majority are semelparous and die after spawning or brooding their eggs.

Cephalopods are active predators that feed mainly on crustaceans, other mollusks, worms and fishes. In turn they are a major component in the diet of toothed whales, pinnipeds, marine birds, and larger fishes, including sharks. Off the west coast of North America *Loligo opalescens* are caught for human consumption on a commercial basis. Several octopus species are used for food or bait along coastal California but do not support a sustainable fishery.

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Approximately 800 species of living cephalopods are currently recognized. They are exclusively marine and occur in a wide diversity of habitats, in depths from the surface to over 5000 m. Adults range from about 2 cm to over 20 m long and weigh from 1 g to over 1000 kg.

Cephalopod systematics is currently in a state of flux. The earlier monographs by Berry (1912, 1949, 1953a), Pickford (1964), Voss and Pearcy (1990) and others dealing with the west coast fauna are in need of considerable revision. Much of the species specific work cannot be adequately addressed until the genus group names have been revaluated and rediagnosed using consistent, modern terminology.

## Collection and Preservation

Deep water benthic cephalopods traditionally are collected using commercial or scientific bottom trawls. More recently these animals have been observed live and then collected either by remote or manned submersibles. In shallower depths, octopuses are collected by divers using nets or other devices. A variety of irritants, such as vinegar, ammonia, copper sulfate, or quinaldine, often have to be used during capture to cause specimens to emerge from their dens in rocky areas.

Following collection, animals should be kept alive in running sea water or placed in ice chests filled with chilled sea water until they can be studied or preserved. For identification purposes it is important to examine animals while still alive to record characteristic skin textures (papillae patterns) and color patterns. Whenever possible color photographs should be taken of live animals for comparison with preserved specimens. If animals are dead when they arrive on deck or following capture they should be chilled but not frozen until they can be fixed. If at all possible, specimens should not be frozen because that process destroys a number of key characters used for identification.

Due to their large size, heavy musculature and lack of skeleton, cephalopods, especially octopods, are notoriously difficult to fix and preserve. Animals should be relaxed by slowly adding ethyl alcohol to their sea water. Other narcotizing agents also may be used such as magnesium choride. When the animal no longer responds to prodding it is ready to be fixed in 10% buffered formalin. Cephalopods normally are fixed for periods of a day to several days depending on their size. In the case of very large specimens, the buffered formalin should be injected into the body cavity to enhance the fixation of internal organs.

Fixation should be done in large pans that will accommodate the entire length of the specimen being treated and allow it to be completely immersed. Only the smallest species should be fixed in jars because this process may distort specimens, especially large octopuses. Also, once tissues harden specimens they often cannot be removed without breaking the jar. Small, live squids and sepiolids can be placed directly into 10% formalin without narcotization. The contractions of the body pull fixative into the mantle cavity and result in excellent preparations. At the time of fixation, if animals are completely muscle dead, they will harden into postures which induce distortions of body proportions, especially arm lengths. Unless material is to be used for DNA studies they should not be fixed in alcohol. If DNA study is anticipated a portion of each specimen, such as an arm tip or fin, should be cut off, prior to fixation, and placed in 95% ethyl alcohol.

Following fixation, rinse specimens in fresh water for at least 24 hours to remove most of the formalin. Rinse briefly in alcohol prior to final preservation. The majority of cephalopods are preserved for long term storage in 70% ethyl alcohol (preferred) or 45-55% isopropyl alcohol. Gelatinous species, such as the cirrate or finned octopods, should be retained in 5% formalin for long term storage. Specimens should be positioned with the body down and the arms up so bubbles are not trapped in the mantle cavity. Small to medium size specimens are stored in vials and small jars. Glass or plastic buckets with snap lids are used for medium to large specimens. Extremely large specimens must be stored in stainless steel, plastic or fiberglass tanks. For additional details and information on fixation, preservation, and curation of cephalopods see Roper and Sweeney (1983).

## Laboratory Study

Depending on the nature of the study, live cephalopods often are easier to identify than preserved specimens. The identification of preserved cephalopods typically involves a number of counts, measurements and indices. A list of standard features used in morphometrics is provided below.

A more detailed resolution of species and relationships involves the study of internal anatomy. Features such as the configuration of the digestive and reproductive tracts, and the morphology of beaks, radulae and spermatophores should be characterized. Resolution of some characters, such as the funnel organ, often are aided by the use of aqueous methylene blue to enhance visibility.

Whenever possible additional elements such as the size and shape of spawned egg capsules should be noted because clutches of eggs occasionally are trawled up separate from the adults. The presence of spawned eggs indicates the presence of a species in a given region and helps to advance our understanding of spawning seasons and habits of cephalopods found along the west coast.

Roper and Voss (1983) provide guidelines for the description of cephalopods. Their publication also is helpful in understanding procedures and terminology used in identifying squids, sepiolids and octopuses.

## Terms for Measurements and Counts

| | |
|---|---|
| **AL.** | arm length |
| **AL Formula.** | longest to shortest arm lengths (by arm pair) |
| **AW.** | arm width |
| **DL.** | diverticulum length |
| **E Count.** | number of mature ovarian or spawned eggs |
| **EL.** | length of chorion capsule of egg |
| **EStL.** | length of egg stalk |
| **G Count.** | number of gill lamellae per outer demibranch |
| **GL.** | gill length |
| **HW.** | head width |
| **ML.** | mantle length |
| **MW.** | mantle width |
| **S Count.** | number of suckers on each arm |
| **Sp Count.** | number of spermatophores in storage sac |
| **SpL.** | spermatophore length |
| **SpRL.** | spermatophore reservoir length |
| **TCS Count.** | number of suckers on each tentacle club |
| **TL.** | total length |
| **TOL.** | length of terminal organ complex (= penis) |
| **TW.** | total weight |
| **WD.** | web depth |
| **WD Formula.** | deepest to shallowest web depths (by sector) |

# Indices (percentages)

**AMI** (arm mantle index) = AL ÷ ML x 100

**AWI** (arm width index)= widest arm ÷ ML x 100

**CLI** (calamus length index) = CL ÷ LL x 100

**CiLI** (cirri length index= CiL ÷ ML x 100

**D/AS** = diameter (lateral arm span), measured from arm tip to arm tip

**DLI** (diverticulum length index) = DL ÷ TOL x 100

**ELI** (egg capsule length index) = egg capsule length ÷ ML x 100

**FFLI** (free funnel length index) = FFL ÷ FL x 100

**FLI** (funnel length index) = FL ÷ ML x 100

**FOLI** (funnel organ length index) = FOL (median limb) ÷ FL x 100

**HWIw** (head width index) = HW ÷ MW x 100

**LLI** (ligula length index) = LL ÷ length hectocotylized arm x 100

**MWI** (mantle width index) = MW ÷ ML x 100

**OAI** (opposite arm index) = length hectocotylized arm ÷ length opposite arm x 100

**SDIe** (enlarged sucker diameter index) = diameter largest enlarged sucker ÷ ML x 100

**SDIed** (SDIe, distal field, in cirrates) = SDe in distal field ÷ ML x 100

**SDIep** (SDIe, proximal field, in cirrates) = SDe in proximal field ÷ ML x 100

**SDIn** (normal sucker diameter index) = diameter largest normal sucker ÷ ML x 100

**SpLI** (spermatophore length index) = SpL ÷ ML x 100

**SpRI** (spermatophore reservoir length index) = SpRL ÷ SpL x 100

**StyLI** (stylet length index) = StyL ÷ ML x 100

**TCLI** (tentacle club length index) = TCL ÷ TL x 100

**TLI** (tentacle length index) = TL ÷ ML x 100

**TOLI** (terminal organ length index) = TOL ÷ ML x 100

**WDI** (web depth index) = deepest web sector ÷ length longest arm x 100

# Glossary

**Accessory nidamental glands.** (see nidamental glands).

**Acetabulum.** The lumen of a sucker; muscular contraction produces the suction.

**Anal flaps.** A pair of fleshy flaps or finger-like papillae that arise at the sides of the anus; species which lack ink also lack anal flaps.

**Arm formula.** Comparative length of the arms expressed numerically in decreasing order, e.g., 3.2.4.1.

**Beak.** A pair of horny, parrot beak-like structures present in the mouth; consists of an upper and lower beak (see buccal mass).

**Buccal lappet.** Small, triangular flaps formed by the tips of buccal membrane and the muscular membrane supports; may bear suckers.

**Buccal mass.** The muscular mass associated with the mouth which contains the beaks, radula, and anterior salivary glands.

**Buccal membrane.** Thin web of tissue that encircles the mouth in squids, reinforced by 6-8 buccal supports.

**Buccal suckers.** Small suckers on the buccal lappets.

**Calimus.** The conical projection on the copulatory organ of octopods at the proximal terminus of the spermatophore groove, distal to the last sucker (see copulatory organ, ligula).

**Chromatophores.** Pigment-filled organelles in the skin of cephalopods; consists of cytoelastic sacs under individual nervous control that collectively provide the background color and color patterns in cephalopods.

**Circumoral appendages.** The eight arms and two tentacles that arise from the head and encircle the mouth of cephalopods.

**Cirri.** Elongate, fleshy, finger-like projections along the lateral edges of the oral surface of the arms, especially in cirrate octopods.

**Cone.** The single central projection on the rachidian tooth (see cusp; = mesocone).

**Copulatory organ.** The modified groove-like tip of the hectocotylized arm of mature male octopuses; consists of a calamus and ligula (= end organ).

**Corneal membrane.** The thin, transparent skin that covers the eyes of myopsid and sepioid cephalopods.

**Cusp.** One or more lateral projections on each side of the rachidian tooth; symmetrically or asymmetrically arranged (see cone).

**Dactylus.** The distal or terminal section of the tentacle club, often characterized by suckers of reduced size.

**Festoon.** A braided string or strand of octopus eggs.

**Finger.** A sausage-like capsule containing eggs of loliginids.

**Fin lobe.** The portion of each fin that protrudes anteriorly from the anterior point of attachment of the fin to the mantle.

**Fins.** The pair of muscular flaps that arise along the dorsolateral surface of the mantle of squids, cuttlefishes, vampyromorphs, and cirrate octopods; used for locomotion, steering and stabilization.

**Fin Support Cartilage.** Cartilaginous support for fins in cirrate octopods, consists of a U- or V-shaped rod or is saddle-shaped (= shell vestige, pteropallial cartilage).

**Funnel.** The ventral, conical tube through which water is expelled from the mantle cavity during locomotion and respiration.

**Funnel locking cartilage**. The cartilaginous socket-like pad that contains a variously shaped groove, pit, pocket or depression on each ventrolateral side of the posterior part of the funnel that locks into the mantle component of the apparatus during locomotion (see mantle locking-apparatus).

**Funnel organ**. The superficial pad or patch of glandular tissue on the internal surface of the funnel; the shape is genus or species specific (= Verrill's organ).

**Funnel valve**. The semilunar muscular flap on the inner, dorsal surface near the distal opening of the funnel.

**Gill lamellae**. The leaf-like, convoluted components of the gill through which gas exchange occurs.

**Gladius**. The feather-like or rod-shaped chitinous support structure in the dorsal midline of squid (= pen).

**Hectocotylized arm(s)**. One (or more) arm(s) of male cephalopods modified for transfer of spermatophores to the female; modifications may involve suckers, sucker stalks, protective membranes, or trabeculae. Either the entire arm may be modified, or only its distal portion. Functions as the copulatory or intromittent organ (see calimus, ligula; = hectocotylus, = nuptial arms).

**Infundibulum**. The exposed flat ring that functions as the adhesive surface of a sucker.

**Ink sac**. The organ that manufactures and stores the ink in cephalopods; the sac is embedded in the digestive gland, it lies along the intestine and empties via a duct into the rectum.

**Keel**. (A) A flattened, membranous muscular extension along the aboral surface of some arms to render them more hydrodynamic; (B) one or two expanded muscular membranes on the tentacular club of some groups. Functions to streamline and support the arms and tentacles during swiming (= swimming keel).

**Kölliker organs**. Minute, bristle-like structures that cover the skin of planktonic octopod paralarvae.

**Lateral ridge**. A ridge or fold of skin around the lateral mantle of some octopods.

**Ligula**. The spatulate to spoon-shaped structure at the tip of the hectocotylized arm in male octopods (see calimus, hectocotylus).

**Mantle**. The fleshy tubular or sac-like body of cephalopods; contains the viscera; provides propulsion through jet-like expulsion of water (see mantle cavity).

**Mantle cavity**. The hollow part of the mantle which contains the gills and viscera.

**Mantle locking apparatus**. The snap-like ridge and socket components which connect the mantle dorsally to the head and/or ventrally to the funnel. Three components may be present: 1) nuchal or head locking-cartilage (sepiolids); 2) mantle locking-cartilage (button, all squids) and 3) funnel locking-cartilage (socket, all squids). The apparatus serves to lock the mantle to the funnel and head during locomotion, so water is expelled only through the funnel and not around the mantle opening

**Mantle locking cartilage**. The button-like cartilaginous pad variously shaped as a ridge, knob or swelling on each side of the ventrolateral, internal surface of the mantle that locks into the funnel component of the apparatus during locomotion (see mantle locking-apparatus).

**Manus**. Central portion of the tentacle club between the dactylus distally and the carpus proximally.

**Nidamental glands**. Two large, cylindrical glands and 2 smaller accessory glands in mantle cavity of female squids; secrete gelatinous material which envelopes the fertilized eggs as they are extruded.

**Nuchal locking cartilage**. The oblong, cartilaginous pad in the posterior dorsal surface of the head of most squids; articulates with a complimentary structure on the inner surface of the anterodorsal part of the mantle (see mantle locking-apparatus).

**Ocellus**. A pigmented spot or patch, usually consisting of a central locus and concentrated dark chromatophores; with one or more concentric rings of chromatophores or iridophores.

**Olfactory organ**. A sensory pit, bump or papilla-like protuberance on the posterolateral surface of each side of the head; function presumed to be olfactory.

**Pallial aperature**. The slit-like opening to the mantle cavity, situated on the ventral surface of the mantle.

**Papillae**. Soft, muscular, finger-like extensions of the skin.

**Paralarva**. A young cephalopod of the first post-hatching growth stage that is pelagic in near-surface waters and that has a distinctly different mode-of-life from that of older conspecific individuals.

**Patch and groove system**. The reticulate pattern seen in the skin, especially the dorsal mantle, of some species of octopuses.

**Pedicel**. A short, cylindrical stalk that supports a sucker in squids and cuttlefishes.

**Photophore**. Simple or complex light organs that produce bioluminescence by intrinsic (self-generated biochemical reaction) or extrinsic (bacterial) means.

**Pocket**. An open depression in the anteroventral surface of the head of sepioids into which the feeding tentacles are retracted when not in use.

**Protective membrane**. Thin web-like fold of the integument along the lateral angles of the oral surface of the arms and tentacle clubs lateral to the suckers, typically supported by trabeculae (see below).

**Rachidian tooth**. The central tooth in a row of 7 teeth in the radula; a heterodont rachidian tooth has a large central cone and 1 or more lateral cusps may be present (see cone, cusp, radula).

**Rachis**. The thickened central axis that usually extends the entire length of the gladius. Free rachis is the portion that does not support the vanes (see gladius, vane).

**Radula**. The chitinous, ribbon-like structure in the mouth of cephalopods containing transverse rows typically composed of: 1 rachidian tooth (centrally located); 2 lateral teeth and 1 marginal tooth (on each side); 1 marginal plate (at the end of each row of teeth) (see rachidian tooth).

**Secondary web**. The narrow membrane that connects the primary web to the arms in some cirrate octopods.

**Seminal recepticle**. A bulbous structure in the buccal region of some female cephalopods (e.g., loliginids), for the retention of viable sperm until they are required for fertilization (= bursa copulatrix).

**Shell Vestige**. see fin support cartilage, stylets, gladius.

**Spermatophore**. A tubular structure manufactured by male cephalopods for packaging sperm.

**Spermatophore pad**. A fleshy patch of tissue, usually in the mantle cavity of some female cephalopods (e.g., loliginids), to which spermatophores adhere after mating until fertilization occurs.

**Spermatophore sac**. The elongate, membranous container at the terminus of the the male reproductive tract that stores mature spermatophores (= Needham's sac).

**Stylets**. A pair of small keratinized or calcified rods embedded in the wall of the dorsal mantle of some octopods.

**Suckers**. Muscular, suction-cup structures on: a) the oral surfaces of the arms; b) the tentacle clubs; and rarely c) on the buccal membrane of cephalopods. Suckers may be stalked, placed on muscular rods that contract (squids and cuttlefishes); or sessile, embedded without stalks on the oral surface of the arms (octopuses) (see acetabulum, infundibulum).

**Sucker ring**. Chitinous ring that encircles and provides rigidity to the opening of suckers of squids and cuttlefishes; may be smooth, serrated or denticulate.

**Tail**. The posterior extension of the mantle, frequently elongate. Fins or tapered terminations of fins may extend posteriorly along the tail.

**Tentacles**. Elongate, stalked circumoral appendages of cuttlefishes and squids used to capture prey; distal ends contain clubs with suckers (or hooks); tentacle stalks usually devoid of suckers.

**Tentacle club**. Terminal portion of a tentacle; armed with suckers (or suckers and/or hooks), used for capturing prey.

**Terminal Organ**. The duct and organ complex at the distal end of the male reproductive tract; contains a diverticulum (= penis).

**Trabeculae**. Muscular rods that support the protective membranes on the arms and tentacle clubs of squids.

**Vane**. Thin lateral expansion of the gladius that arises from the rachis (see rachis).

**Web**. A thin membranous sheet of skin that extends between the arms of many cephalopods (especially octopods), giving an umbrella-like appearance when the arms are spread out.

**Web formula**. Comparative depths of the web sectors expressed alphabetically in decreasing order, e.g., B.C.D.A.E.

# Key to the Orders of Cephalopoda

1A. Ten circumoral appendages (8 arms plus 2 tentacles); arms with stalked suckers; body rounded to elongate with fins; with an internal shell (gladius or pen) .......... 2

1B Eight circumoral appendages; arms with sessile suckers; body ovoid, not elongate .......... Order Octopoda

2A Tentacles retractile into small pockets between arms 3 and 4; eye membrane absent; mantle rounded, less than 50 mm long; mantle free all around; fins semicircular, almost as long as mantle, with broad free lobe; arms short, circular in transverse section; dorsal arms hectocotylized .......... Order Sepiolioidea; Family Sepiolidae; *Rossia pacifica*

2B Tentacle not retractile into pockets; eye covered by transparent membrane; tentacle clubs narrow and without fixing apparatus, suckers large and in 4 rows; arms with 2 rows of suckers; arm lengths unequal, ventral pair long and broad; left ventral arm of male hectocotylized; fins less than half mantle length, fins triangular, length equal to width; mantle elongate and tapered, length not exceeding 150 mm; mantle attached; arms long, angular in transverse section .......... Order Teuthoidea; Family Loliginidae; *Loligo opalescens*

# List of Species

Family Sepiolidae
    *Rossia pacifica* Berry, 1911
Family Loliginidae
    *Loligo opalescens* Berry, 1911
Family Octopodidae
    *Benthoctopus leioderma* (Berry, 1911) new combination
    *Benthoctopus robustus* Voss and Pearcy, 1990
    *Graneledone boreopacifica* Nesis, 1982
    *Octopus dofleini* (Wülker, 1910)
    *Octopus rubescens* Berry, 1953
    *Octopus californicus* (Berry, 1911)

# Description of Species

## Family Sepiolidae Leach 1817

**Diagnosis.** Mantle short, broad, sac-like, stubby; fins separated, rounded; mantle locking apparatus simple, straight; shell, if present, chitinous; ink sac present or absent; light organ on ink sac present or absent.

## Subfamily Rossinae Appelloff 1898

**Diagnosis.** Anterior margin of dorsal mantle free; articulating with ovate nuchal cartilage; gladius present; one or both dorsal arms hectocotylized; web relatively narrow, not forming sheath around tentacles at base; glandular luminescent organ associated with ink sac absent; fins moderate to large size, auriculate in front.

### Genus *Rossia* Owen, 1834

**Type Species:** *Rossia palpebrosa* Owen, 1834.

**Diagnosis.** Animals robust. Web greater than 1/2 arm length between arms 3 and 4. Sessile arms short; suckers spherical, arranged in 2-4 rows; greatly enlarged suckers absent in middle part of arms. Tentacles entirely retractile; clubs wide, not bent; suckers on clubs, medium to large size, typically arranged in 6-12 rows. Both dorsal arms hectocotylized; suckers reduced in size; protective membranes on modified parts of hectocotylized arms well developed, separated from sucker stalks by deep groove. Gladius much reduced. Ink sac present. Anal flaps present. Papilliform glands on sides of rectum absent. Spermatophores with thick, non coiling sperm cord.

### ***Rossia pacifica* Berry, 1911**

Figure 6.1

*Rossia pacifica* Berry, 1911:591. —Berry, 1912a: 290-293, pls. 41(figs. 1-6), 42(fig. 1), 43(figs. 2-4), 44(figs. 1, 5). —Sasaki, 1914: 598-599; 1920: 188-189. —Berry, 1921: 353.—Sasaki, 1929: 154-157, textfigs. 92-94, pl. 16(figs. 3-6).—Johnson and Snook, 1927: 579-580, fig. 679. —Kondakov, 1941: 217, 219, fig. 3. —Akimushkin, 1965: 156-159, figs. 45, 46. —Taki, 1965: 314. —Mercer, 1969: 270. Iverson and Pinkas, 1971: 105, fig. 50.—Okutani, 1973: 92-93, textfig. 22. —Okutani, 1975: 28. —Okutani, 1977: 40-41, fig. 20. —Okutani, 1980: 24-25, fig. 22. —Hochberg and Fields, 1980: 431-432, pl. 134(figs. 17.1a, b). —Taki, 1981: 240. —Clarke, 1986: 217, figs. 116A, 120A. —Okutani et. al., 1987: 85, pl. 25(figs. A-C). —Nesis, 1987: 125, fig. 26K, L. —Hochberg, 1987: 293, fig. 14.6.

? *Rossia* sp. —Berry, 1912a: 417.

*Rossia borealis* Sasaki, 1913:243.

**Material Examined.** California: —1 female (immature), 15 mm ML; Ventura Co, Pt. Mugu, off Mugu Pier, 30-50 ft [9-15 m]; coll. Conboy and party, 5 December 1962; SBMNH 51570 [*ex* MacGinitie collection]. —3 males (submature and mature), 21-29 mm ML; Santa Barbara Co, 2 mi S of Santa Barbara, 200 ft [61 m]; coll. F.G. Hochberg and P.H. Scott, station 1, 29 September 1986; SBMNH 60036. —1 female (mature), 40 mm ML; Santa Barbara Co, 1.5 mi S of Santa Barbara, 29 fm [53 m]; coll. F.G. Hochberg and P.H. Scott, station 2, 29 September 1986; SBMNH 60018. —2 females (immature and submature), 34 and 36 mm ML; western Santa Barbara Channel, off Ellwood Beach, 34°20'N, 119°50'W, 36 fm [66 m]; coll. S. Anderson, 27 June 1979; SBMNH 42487. —2 females (submature and mature), 35 and 44 mm ML; western Santa Barbara Channel, off Naples, 110-120 fm [200-220 m]; coll. R. Hazard, F/V *Eagle B*, 10 September 1974; SBMNH 44065 [beak voucher]. —2 females (submature and mature), 39 and 46 mm ML; western Santa Barbara Channel, off Naples, 120 fm [220 m]; coll. R. Hazard, F/V *Eagle B*, 24 August 1974; SBMNH 44066. —1 female (mature), 45 mm ML; western Santa Barbara Channel, off Hendrys Beach, 61 m; coll. D. Ibara and F.G. Hochberg, 27 May 1967; SBMNH 60039 [dicyemid voucher]. —1 male (mature) + 1 female (submature), 30 and 35 mm ML; Santa Cruz Island, off W end of island, 110 fm [201 m]; coll. P. Brophy, F/V *Eagle B*, 1967; SBMNH 47505.

Oregon: —Lincoln Co., 35 mi W of Depoe Bay, 44°47.8'N, 124°23.7'W, 110-128 m; coll. R/V *Andrea*, station 1498-42, 9 August 1942; SBMNH 60013 [*ex* AHF/USC]. —5 males (mature) 26-30 mm ML, off Coos Bay, 65 fm [119 m]; coll. F.G. Hochberg, 20 July 1965; SBMNH 47504.

Washington: —5 females (immature - mature), 30-45 mm ML; Seattle, Elliott Bay, off mouth of Duwamish River, 45 fm [82 m], coll. R. Anderson, C/V *Chasina*, 5 June 1992; SBMNH. —1 clutch spawned eggs; Seattle, Seattle Aquarium; coll. R. Anderson, 17 July 1993; SBMNH.

Alaska: —2 females (submature), 22, 35 mm ML; Port Dick; coll. R. Baxter, 25 June 1985; SBMNH 60029.

**Description.** *Body* moderately large (TL to 105 mm; TW mature males 10-15 g, mature females 20-30 g). Females longer, more robust and heavier than males (ML mature males 25-35 mm, mature females 25-55 mm). *Mantle* firm and muscular, short; shape subcylindrical, longer than wide (MWI 63-100); dorso-ventrally flattened, rounded posteriorly; mantle in males widest anteriorly, in females width uniform. Anterior dorsal mantle margin free with short angular medial projection; ventral margin weakly concave. *Mantle-locking apparatus* small; nuchal cartilage ridge- like plug, longer than funnel socket, slightly curved, twice as long as wide, shape elliptical, stongly narrowed posteriorly; funnel cartilage three times as long as wide, shape elongate-rectangle with prominent raised margins, sides parallel, located one on either side of funnel base. *Fins* large, muscular, almost as long as mantle (FiLI 60-72); shape semi-lunar or subcordate, broad, 1/2 to 2/3 as wide as long (FiWI 110-<u>130</u>-180); anterior lobes free, do not reach edge of anterior mantle margin; attached to middle of body, more or less oblique to general body plane.

*Gladius* slender, much shorter than mantle; shape lanceolate in males, more spatulate in females; vane thin and delicate, moderately wide, starts near middle of rachis and continues beyond tip of rachis, bluntly rounded posteriorly.

*Head* large, narrower than mantle (HWI 88-112); dorso-ventrally compressed. *Eyes* large, prominent, oval; lower lids free, orbit semi-lunar, lids concentric; lacrymal pore distinct. *Olfactory papillae* prominent. *Funnel* stout, thick walled; broad at base, slender, conical, truncate at apex; free for most of length, often projects beyond base of ventral arms. *Funnel valve* large, rounded, located midway between anterior tip of funnel organ and free margin of funnel. *Funnel organ* prominent, fleshy; single large median V-shaped pad with apical projection and 2 broad, elongate-pyriform lateral pads. *Anal flaps* long, appear flattened or blade-like. *Buccal membrane* thick, 7 lappets present without suckers; ventral 2 lappets originate very close together; marginal projections undiscernable.

*Arms* medium length (ALI 42-58; AMI 86-<u>120</u>-128), stout; lengths unequal, arm pair 1 always shortest, formula typically 3.2.4.1 or rarely 3.4.2.1; aboral surface of arm rounded, sucker bearing surface flat. *Arm suckers* arranged in densely crowded diagonal rows; 3-4 per row medially; 2 per row basally and distally on all arms; sucker number about 80. Pedicles short. Suckers spherical to subglobular, oblique; sucker openings minute, typically circular in males, occasionally narrow and slit-like; chitinous rings well developed with smooth, entire margins. Suckers smaller (SDIn 3.3-4.2) and more uniform in size (arrangement essentially alike on all arms) in females than in males (SDIn 6.4-7). In males suckers distinctly enlarged in mid-portion of arm pairs 2-4; largest and most densely packed on arms 2 or 3. On arms of both males and females marginal suckers larger than mesial suckers and suckers in middle of arms largest, gradually decreasing distally; size subequal in all rows at same point on arm. *Web* well developed, broad or deep between arms 3 and 4, covers base of tentacles; very shallow to rudimentary between other arms, absent between ventral arms. *Swimming keels* present along aboral surface of all arms, especially prominent on arms 3; keel on arms 4 extends from tentacle sheath to arm tip. *Protective membranes* weakly developed, very narrow, associated with pedicle bases of suckers.

*Hectocotylized arms* - dorsal arm pair in mature males; arms short (HcLI ), often strongly recurved dorsally. *Suckers* on hectocotylized arms greatly reduced in size (HSDI 2.2) 1/3 as large as those on lateral arms; 4 suckers per row basally, reduced to 2 per row distally; sucker number about 65-75 per arm. Pedicle bases enlarged and transversely compressed to form series of prominent transverse folds or ridges. *Protective membrane* narrow on inside of dorsal arms, wider and more prominent aborally; ventral protective membrane broad on outside of arms, extends distally along arm more than 1/2 distance to tip; deep longitudinal groove defined by membranous fold along 2/3 of outside arm length. In mature males, thickened ridge of glandular tissue on inside lateral edge of each dorsal arm, extends about 1/2 length of arm in mid region.

*Tentacles* retractile into shallow pockets between arms 3 and 4; 2-3 times longer than body when extended (TLI 173-200-333); oral surface of tentacle stalk flattened with distinct medial groove, aboral surface rounded; stout, as thick as arms. *Tentacle clubs* well defined, elongate (TCLI ), slightly wider than stalk, crescent-shaped to lanceolate; sucker bearing surfaces bordered with 2 protective membranes - ventral membrane narrow, marginal and dorsal membrane broad, originates proximal to club and extends to dorsal tip, flap absent. *Tentacle club suckers* arranged in 6-8 oblique rows medially and 2-3 longitudinal rows at base. Suckers minute, crowded; sizes unequal; largest located near base of club, gradually decreasing in size ventrally and distally; cup-shaped, flattened on one side, with wide apertures; chitinous rings with numerous (about 45) small blunt teeth; surrounded by broad papillate band. Pedicles moderately long.

*Gills* long, narrow, leaflets thin; with 22-25 lamellae per outer demibranch. Tip of gills not attached to mantle wall.

*Beaks* small, robust; upper beak rostrum about 1/3 hood width; lower beak - with pronounced tooth or projection on shoulder, rostral length about 1/4 hood length, crest walls parallel without posterior indentation. *Radula* with 7 teeth; rachidean tooth - without lateral cusps; lateral teeth 1 and 2 - similar in shape, tall, narrow, with very high cusp; marginal tooth - elongate, saber-like.

*Female* reproductive tract - single oviduct on left side. *Nidamental glands* very large, similar in size, in contact along entire inner surfaces; accessory nidamental glands present, small, appear darker at maturity. Spermatophores deposited on left side in funnel pocket or nuchal pocket. *Spawned eggs* large, nearly transparent, with pointed apex (capsule 9 mm long, 5 mm wide). Hatchlings large, benthonic.

*Male* reproductive tract; terminal organ - elongate, tubular, thin walled. *Spermatophores* small (length 6-16 mm; SpLI 42-48); ensiform; head highly convoluted; sperm whorls not spirally coiled; reservoir stout (SpWI 37-48); unarmed; maximum number present 65-85 (typically between 20-30).

*Skin* smooth, without papillae. *Color in life* dark red-brown to violet, darker dorsally on head, arms and mantle; ventral mantle and underside of fins lightly pigmented to almost white; occasionally appearing light opalescent gray-green or iridescent blue or green. Single median dorsal mantle dark spot and dark eyes present in dymantic display. *Color in alcohol* brownish buff, densely punctate dorsally and on fins and to lesser degree ventrally, laterally and on underside of fins with purplish chromatophores; funnel entirely unpigmented.

**Type Locality and Type Specimens.** Pacific Ocean - Alaska, [Alexander Archipelago], vicinity of Yes Bay, Behm Canal, [1 mi off Cannery Point], 39-45 fm [71-82 m].

*Holotype:* USNM 214323 [SSB 21]; no longer extant.

*Paratypes:* —8 specimens; from same lot as holotype; USNM 214323 [SSB 21], no longer extant.—1M (immature) + 1F (immature), 28 and 28 mm ML; from same lot as holotype; CASIZ 018796 [SSB 21; SU 2125; CASIZ type nos. 495 and 496].

**Distribution.** Boreal; wide spread in North Pacific from Korea, Japan and Sea of Japan north through Sea of Okhotsk, Kurile Islands and SE Kamchatka to Aleutian Islands, Bering Sea, Gulf of Alaska south to southern California (34°N). Neretic in shallow coastal waters; depths of capture in the eastern North Pacific range from 10-250 m; in the western North Pacific from 100-600 m. The animals typically live buried in soft sand and mud bottoms.

**Etymology.** Specific name recognizes the species abundance and distribution in the North Pacific Ocean.

**Common Name.** North Pacific bobtail squid

Also referred to as the short squid (Johnson and Snook 1927); stubby squid (Brocco 1971; Hochberg and Fields 1980; Anderson 1991); Pacific bob-tailed squid (Tomiyama and Hibiya 1978); bottle-tailed cuttlefish (Okutani 1980); bob-tail cuttlefish (Okutani *et al.* 1987).

**Biology.** In spite of its abundance in the Eastern North Pacific relatively little is known about *Rossia pacifica*. The biology has been extensiverly studied in Puget Sound (Washington, USA and British Columbia, Canada). The species was first studied in detail by Brocco (1971). Brocco analyzed the morphometrics of specimens collected in Canada off Vancouver Island. He described the beaks, radula, male and female genitalia for the first time. Sasaki (1913, 1929) described in detail Japanese specimens identified as the same species. The life history was documented by Summers (1985a, b) and Summers and Colvin (1989).

*Rossia pacifica* is semelparous and has a 2-year life cycle; 18-19 months from hatching to death and 5-6 months of embryonic development (Summers, 1985). Typically two age classes are present in field samples. Growth is dimorphic and accelerates with age. Ovarian development begins at 24 mm ML in females and 50% of males are mature with spermatophores at 26 mm ML.

*Rossia* lives in low densities wherever it occurs along the coast. Brocco (1971) and others have indicated that the squid spends long periods during the day on the bottom covered in sand. Sand gluing behavior, typical of other sepiolids, has been observed but it is brief and transient. The squid emerge from the substrate and become active shortly after sunset. Nocturnal or crepuscular activity pattern well developed by 6 months of age (Summers and Colvin, 1989).

Polychaete worm, mysids and caprellid amphipods utilized by juveniles. Shrimps (especially *Pandalus danae*) and other small crustaceans preferred by adults (Brocco, 1971; Summers, 1985). Can be maintained easily in the laboratory.

Mating has been described by Brocco (1971) and Anderson (1991). During copulation the male orients his body ventral and posterior to the female and grasps her with the lateral and ventral arms. The dorsal hectocotylized arms are wrapped over the openings of the pallial cavity of the female. Spermatophores are deposited on the left side in the funnel pocket or nuchal valve pocket. In mated females the sperm bulbs (spermatangia) are evident just beneath the colorless skin in the nuchal region.

Eggs are laid when water temperatures warm to 11°C. The ovary of unspawned females contains about 130 mature eggs, each measuring 4-5 mm in diameter (Summers and Colvin, 1989). The capsules of spawned eggs are spherical in shape and measure 8-9 mm in length and 5 mm in width. They are nearly transparent or colorless. They are attached to the substrate by a disk at one side while the other end of the capsule is drawn out into a point (Fig. ). Clutches of 25-50 eggs are laid at one time which represents about 35% of the females body weight. The spawning process may be repeated over a several week period. The egg mass from a single female may contain 80-100 eggs attached in a single mass 2-3 layers of eggs deep. Spawning occurs in late spring and early summer (April - June) or late summer and fall (August - October). Adults die in late spring to early summer within days of spawning.

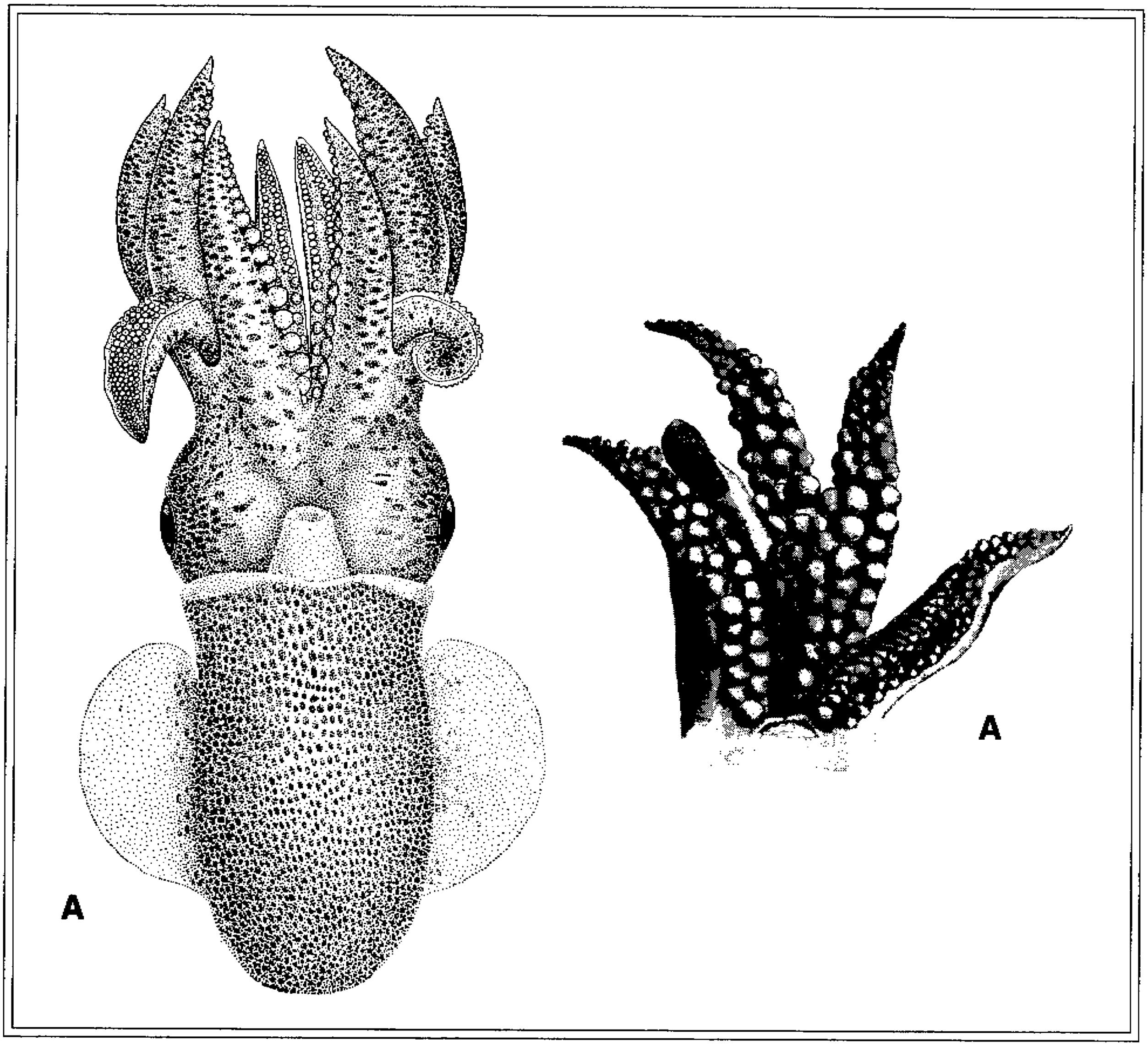

**Figure 6.1** *Rossia pacifica*: A, ventral view; B, male - oral view of right arms. (after Berry, 1912a).

Vitellogenesis and development of oocytes have been examined in *Rossia pacific* from the western North Pacific (Aisenshtadt, 1969, 1971). The ultrastructure of spermatozoa of *R. pacifica* from Puget Sound was studied by Fields and Thompson (1976).

Development takes 5-6 months. Hatching is reported to take place at the end of the year and according to Summer and Colvin (1989) it is keyed to the new moon. Hatching is protracted and episodic and may extend over 2 months. Hatchlings are benthonic and are large, measuring about 6-8 mm ML. Early life, the first 6 months, is characterized by low growth. Growth is dimorphic and accelerates with age. Sexual maturity and sexual dichotomy appears in last half of life span. Growth may cease in both sexes during the last few weeks of life.

**Parasites.** Apicomplexa: *Aggregata* sp. (Hochberg, pers. obs.). Dicyemida: *Dicyemennea brevicephaloides* Bogolepova-Dobrokhotova; *D. filliformis* Bogolepova-Dobrokhotova [=D. parva Hoffman]. For review see Hochberg (1990).

## Family Loliginidae d'Orbigny, 1848

**Type Genus:** *Loligo* Schneider, 1784.

**Diagnosis.** Mantle muscular, elongated; anteriorly projecting rostrum present at edge of dorsal mantle. Fins posterior, extend to posterior of body; posterior end of mantle conical. Tentacle club with 4 rows of suckers; without fixing apparatus. Anterior eye chamber covered with transparent cornea; connecting to exterior through tiny anterior pore ("lachrymal pore"). Buccal membrane with 7 lappets each with 2 rows of tiny suckers; seminal receptacle present on membrane of female. Photophores present or absent. Right oviduct absent. Paired nidamental glands and accessory nidamental glands present. Inshore, neretic squids; benthic spawners

### *Loligo* Schneider, 1784

**Type Species:** *Loligo vulgaris* Lamarck, 1799.

**Diagnosis.** Fins posterior; eggs small to moderate size (<4 mm) contained in sausage-shaped gelatinous capsule; arm sucker ring dentition variable; hectocotylus without ventral crest; hectocotylization consists of reduced sucker size and elongation of pedicles to form papillae on either dorsal or both dorsal and ventral rows; light organs absent; spermatophores with short cement body; spermatophores implanted around mouth or occasionally in mantle cavity. (Subgenus undetermined).

**Etymology.** Derived from the Latin, "*loligo*" meaning squid.

### ***Loligo opalescens* Berry, 1911**

Figure 6.2

*Loligo stearnsii* Hemphill, 1892:51 (*nomen nudum*). —Hoyle, 1897:370. —Williamson, 1905:129. —Kelsey, 1907:42.

*Ommastrephes tryoni* Keep, 1904:271, 351 (no description; not of Gabb). —Keep, 1910:297.

*Loligo pealii* non Le Sueur. —Jenkins and Carlson, 1903:264.

*Loligo opalescens* Berry, 1911:591-592. —Berry, 1912a:294-297, pls. 43(figs. 5-8), 44(figs. 2-4), 45, 46(figs. 4 and 5)

**Material Examined.** California:—3 males (mature), 140-163 mm ML, western Santa Barbara Channel, off Santa Barbara, 170 m, coll. H. Durrah,— 1957, SBMNH 45866.—1 male (mature), 135 mm ML, western Santa Barbara channel, off Gaviota, 155 m, coll. P. Brophy, F/V *Eagle B*, 19 July 1967, SBMNH 45981 [beak voucher].—1 male (mature) + 1 female (mature), 127 and 126 mm ML, western Santa Barbara Channel, 10 mi west of Santa Barbara, 120 m, coll. D. Ibara, F/V *Eagle B*, 22 July 1967, SBMNH 60067.—1 male (mature) + 3 females (mature), 110 and 142-152 mm ML, off Santa Cruz Island, coll. CDFandG, station 75-A3-45, 23-24 May 1975, SBMNH 60065. —10 males (mature) + 1 female (mature), 155-181 and 163 mm ML, coll. CDFandG, station 80-CFI, date unknown, SBMNH 60060.—12 males (immature and mature) + 3 females (immature), 57-181 and 55-67 mm ML, locality unknown, coll. CDFandG, station 76-A7-70, date unknown, SBMNH 60061.—1 clutch spawned egg capsules, Pt. Mugu, USNMC base, off Mugu Pier, 10-12 m, coll. G.E. and N. MacGinitie et al., 7 January 1963, SBMNH 45836.—1 clutch spawned egg capsules, Pt. Mugu, USNMC base, off Mugu Pier, 12 m, coll. G.E. and N. MacGinitie *et al.*, 13 March 1963, SBMNH 45844.

**Description.** *Body* medium size, slender (TL over 300 mm; TW to 130 g in males, to 90 g in females). Males larger and more robust than females (ML to 190 mm in males, to 170 mm in females). *Mantle* thin, muscular; shape elongate cylindrical, longer than wide (adult lengths greater than 5 times width), wider medially; tapered to acute point posteriorly. Anterior dorsal mantle margin free with elongate medial rostrum; ventral mantle margin deeply emarginate with prominent lateral angles on each side of funnel. *Mantle locking apparatus* well developed; mantle cartilage slender, elongate ridge; funnel cartilage simple elongate socket with raised, reflexed margins. *Fins* large, about 1/2 as long as mantle; shape sagittate, slightly lobed anteriorly, obtusely angled anterior to middle; about 1/2 as wide as long; margins thin, entire.

*Head* small, compact, narrower than body; squarish; ornamented by 3 parallel, longitudinal folds of integument, correspond to cartilaginous ribs of rostrum. *Eyes* large, prominent; do not protrude. *Funnel* large, broad, short; funnel valve large, terminal. *Funnel organ* V-shaped with oval lateral pads. *Buccal membrane* with 7 lappets, each with 2 distinct rows of minute suckers, 7-9 suckers per row, lateral ventral lappets with 10-12 suckers per row in females; sucker rings with 5-6 irregular, squarish teeth; inner buccal membrane thickened with rugose cushion surrounding beaks. *Seminal receptacle* present in region of buccal membrane of females.

*Gladius* long, thin, ends posteriorly in blunt point; vanes well demarcated from rachis, broadly lanceolate, widest about 1/4 distance from posterior tip; free rachis moderately short, slender, ends anteriorly in acute point; rachis with marginal fusiform thickenings. Gladius vanes wider in females than males.

*Arms* slender, short; shorter in males than females; lengths unequal, arm pair 1 considerably shorter; formula 3=2.4.1. *Web* membrane rudimentary between arms pairs 1-3, absent between ventral arms; web extends as prominent keel along aboral margins of dorsal arms; oral margins of arms 2 bluntly carinate, arms 3 obscurely so; prominent flesh keel along aboral margins of arms 2 and 3, keel extends to arm tips; ventral arms with broad, prominent web along aboral margin ensheating base of tentacle; similar but less well-developed keel extends along oral surface of ventral arms. Membranous *swimming web* present along oral, sucker bearing surface of all arms; strengthened by numerous, slender transverse trabeculae alternating with pedicels. *Arm suckers* small, kettle-shaped; biserial, alternately arranged on short conical pedicels; margins of cupules hood-like; sucker rings with 9-12 bluntly rounded, truncate teeth on upper margin; papillary area wide and very prominent.

*Hectocotylized arm* - distal 30% of left ventral arm modified in males (HcLI 29-40); left ventral arm stouter and broader than right ventral arm; proximally about 19-20 pairs of normal suckers; at about row 20, suckers in both rows progressively reduced in size, their pedicels tall, glandular with triangular bases; suckers of dorsal row more strongly affected; pedicels and suckers decrease in size distally; at about rows 30-40, suckers of ventral row and pedicels resume their normal appearance; in area where ventral suckers become normal, dorsal suckers become minute and on very small triangular pedicels to arm tip.

*Tentacles* moderately long; highly contractile. *Tentacle club* medium size, narrow and unexpanded to slightly lanceolate, with prominent keel and narrow swimming web. *Tentacle club suckers* in 4 rows; marginal 2 rows of suckers very small; mesial suckers much larger; sucker rings with 30-35 small, bluntly conical teeth.

*Gills* very long, lamellae thin; with 65-70 lamellae per outer demibranch.

*Spermatophores* short, slender (SpLI 5.7-7.2-8.3); bulk of length occupied by sperm reservoir (SpRLI 60-75 in males smaller than 100 mm ML; 75-85 in larger males); prominently armed with numerous fine crochettes.

*Nidamental glands* large, equal in size; accessory nidamental glands of mature females distended, bright yellow-orange in color. *Eggs* small (lengths 2.0-2.5 mm); 200-300 eggs embedded in gelatinous matrix of capsules or "egg fingers"; *egg fingers* spindle-shaped (lengths 50-80-200 mm, widths 10-12 mm); stalk end tapered to adhesive base. Squid migrate inshore in dense aggregations to mate and spawn; egg capsules clustered together in large "mops".

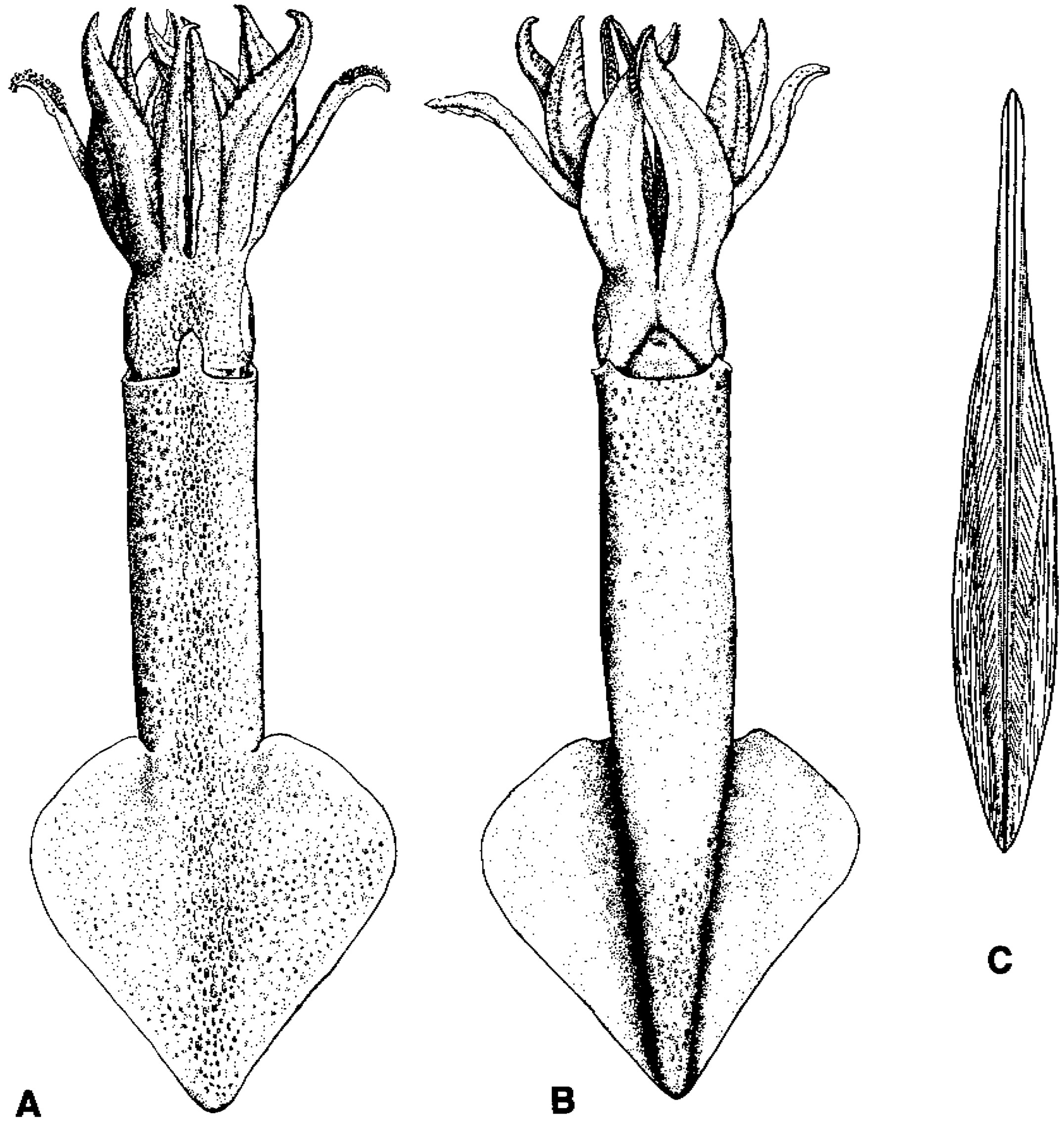

**Figure 6.2.** *Loligo opalescens.* A, dorsal view of mature male holotype (USNM); ventral view of mature male holotype (USNM); C, gladius of male (USNM). (after Berry, 1912a).

*Skin* smooth, without papillae. *Color in alcohol* pale buff, with numerous distinct brownish chromatophores scattered over dorsal surface. *Photophores* absent in mantle cavity.

*Hatchlings* large (ML 2.5-2.7-3.2 mm); mantle cylindrical, length 1.5-2.0 times width; fins small, subterminal, oval in outline, wider than long. Dorsal mantle with 6 large chromatophores in mid region (1+2+2+1 pattern), plus 11 small ones, 3 on midline and 3-4 laterally on each side of mantle; ventral mantle with about 40 small chromatophores randomly scattered or arranged in irregular transverse rows; dorsal head with 6 large chromatophores in 3 pairs (2+2+2 pattern) plus 3 small ones; ventral head with 6 large chromatophores in 2 groups of 3 posterior to eyes plus 6 small ones; arms 1 and 2 without chromatophores; arms 3 and 4 with 2 chromatophores in single row aborally; tentacle stalks with 6-8 chromatophores in single row aborally; base of dorsal arms with 1 small chromatophore; base of ventral arms with 3 small chromatophores; funnel without chromatophores

**Type Locality and Type Specimens.** Pacific Ocean - Washington, Puget Sound; coll. shrimp fishermen,— 1908. *Holotype:* male, 132 mm ML; CASIZ 017970 [SSB 101; SU 2076; CASIZ type no. 547]. *Paratype:* 1 female, 146 mm ML; USNM 214388 [SSB 101]; from same lot as holotype. *Paratype:* 1 male, 126 mm ML; USNM 816384 [SSB 101]; from same lot as holotype.

**Distribution.** Endemic to waters of the California Current. Range from British Columbia, Canada (50°N) to southern tip of Baja California, Mexico (22°N). Migrate into shallow water (15-35 m) to spawn; distribution away from spawning grounds not know.

**Etymology.** Named for the characteristic opalescent color of the body of live animals.

**Common Name.** Opalescent inshore squid (see Roper *et al.*, 1984).

Also referred to as the market squid, common squid, opalescent squid, sea arrow, calamary and calamari (see Hochberg and Fields, 1980).

**Parasites.** Dicyemida: *Dicyemennea nouveli*. Platyhelminthes (Cestoda): *Pelichnibothrium speciosum*, phyllobothrid type 4, unident pseudophyllidean. Nematoda: unident. philometroid. Annelida (Polychaeta): *Capitella capitata ovincola* (in gelatinous matrix of egg capsules). For review see Hochberg (1990).

### Order Octopoda Leach, 1818

## Key to Species of Octopoda

1A. Skin of body smooth with distinct lateral ridge; gills with 11-12 lamellae per outer demibranch; enlarged suckers absent; arms 2-3 times mantle length; copulatory organ large, about 20% of length of hectocotylized arm ........ *Benthoctopus leioderma*

1B. Skin papillate; arms 3-5 times mantle length; males with 1 or more enlarged suckers on all or some arms; eggs small; hatchlings planktonic ........ *Octopus* ........ 2

2A. Mantle length greater than 200mm, weight typically exceeds 50kg; skin with large folds or truncate papillae; field of 6-8 enlarged suckers present in males on lateral arms; copulatory organ large, about 20% length of hectocotylized arm; gills with 12-15 lamellae per outer demibranch; eggs medium size, capsule length 6-9mm, spawned in festoons ........ *Octopus dofleini*

2B. Mantle length less than 200mm ........ 3

3A. Mantle length less than 100mm, weight typically less than 250g; funnel organ W-shaped; skin with small pointed papillae; white spots present on dorsal mantle; funnel organ W-shaped, limbs equal; 1-2 enlarged suckers present in males on all arms; copulatory organ small, about 10% length of hectocotylized arm; gills with 10-13 lamellae per outer demibranch; eggs small, capsule length 2.5-4mm, spawned in festoons; hatchlings planktonic ........ *Octopus rubescens*

3B. Mantle length less than 150mm, weight to 600g; funnel organ VV-shaped, limbs unequal; crop diverticulum absent; copulatory organ 15-20% length of hectocotylized arm; gills with 12-13 lamellae per demibranch; eggs large, capsule length 14-17mm, spawned singally; hatchlings benthonic ........ *Octopus californicus*

### Family Octopodidae Orbigny, 1840

### Subfamily Bathypolypodinae Robson, 1928

**Diagnosis.** Mid-depth to deep-water octopods; suckers biserial; suckers tubular, infundibulum reduced in diameter, rim thick and muscular; enlarged suckers may be present in males; copulatory organ well developed; posterior salivary glands not greatly reduced in size; crop diverticulum reduced or absent; anal flaps absent; ink sac absent; distal oviducts very long; eggs very large (capsule length up to 35 mm), planktonic hatchlings absent; radula octopus-like to degenerate; gills small, with reduced number of lamellae.

**Discussion.** As currently defined and perceived, three genera are placed in this subfamily, namely: *Bathypolypus* Grimpe, 1921; *Benthoctopus* Grimpe, 1921; and *Teretoctopus* Robson, 1929. A fourth, monotypic genus, *Grimpella* Robson, 1928, has occasionally been aligned in this subfamily but the type needs to be reexamined critically in light of the recent redescription of *G. thaumastocheir* by Stranks (1988). *Benthoctopus* originally was placed by Robson (1932) in the subfamily Octopodinae.

## Genus *Benthoctopus* Grimpe, 1921

*Atlantoctopus* Grimpe, 1921.

**Type Species:** *Octopus piscatorum* Verrill, 1897; by original designation (Grimpe, 1921: 299).

**Diagnosis.** Deep-water octopods; arms short to medium length, 2.5-4 times ML; eyes small; ligula short, narrow, slightly to moderately excavated, never laminate; crop diverticulum present, but reduced in size; radula with unicuspid or multicuspid rachidian; body entirely smooth, mantle and ocular papillae absent; gills with 7-12 lamellae per outer demibranch.

**Etymology.** Name derived from the Greek *benthos* meaning "depth of the sea" in reference to the deep dwelling habits of octopuses in this group.

### ***Benthoctopus leioderma*** **(Berry, 1911) new combination**

Figure 6.3

*Octopus leioderma* Berry, 1911:590-591. —Berry, 1912:288-289, pl. 35(fig. 1), pl. 40(figs. 4 and 5).

*Benthoctopus hokkaidensis* (Berry)— Pickford and McConnaughey manuscripts.

**Material Examined.** Neotype, see below.

**Description.** *Body* small to moderate size (TL to 210 mm, TW to 148 gm); females larger than males. *Mantle* medium size (ML 50-70 mm [Nesis, to 100 mm]); short, plumb and firm, truncately rounded, widest posteriorly (MWI 63-89). *Stylets* present, non-mineralized. *Head* short (HWIw 86-105), broad; neck region slightly constricted. *Eyes* small, do not protrude. *Pallial aperture* narrow. *Funnel* slender, long (FLI 30-58), extending well past base of arms. W-shaped; inner limbs partially adnate, outer limbs 1/2 length of inner limbs.

*Web* moderately well developed (WDI 14-24); sectors unequal, formula typically B.A=C.D.E or C.B.D.A.E, ventral sector distinctly shallowest; web membranes along ventral sides of arms broad and well developed. *Arms* stout, short (ALI 64-68); about 2.5-3.5 times ML (AMI 224-374); lengths unequal, formula 1.2.3.4, ventral pair always shortest. *Suckers* small (SDIn 7-8); numerous, well separated medially and transversely; often partially embedded in flesh of arms; infundibulum flared, smooth; enlarged suckers absent. *Sucker counts* R1/85-102, R2/88-92, R3(males)/58-61, L3(males and females)/82-87, R4/80-92. *Hectocotylized arm* - right arm 3 (HAMI 127-139); distinctly shorter than opposite arm (OAI 69- 89); spermatophoric groove well developed; HASC 58-61 suckers, OASC 82-87. *Copulatory organ* medium to large (LLI 11-18); ligula elongate, conical, distinctly recurved, margins thick and fleshy, copulatory groove narrow, deep, with numerous transverse striae; calamus small (CLI 12-20), conical.

*Gills* medium length (GLI 27); with 1-12 lamellae per outer demibranch.

*Internal organs* not described. *Ink sac* absent, but duct present.

*Terminal organ* large (TOI 35).

Mature ovarian *eggs* large (capsule length 14-17 mm; spawned eggs 17-18 mm). *Hatchlings* presumed benthonic.

*Skin* soft, smooth, with distinct keel-like lateral mantle fold; small simple papillae on dorsal surface of head and neck; 1 large papilla over each eye; row of 4 papillae between eyes. *Color* in life uniform pinkish tan, web and arms darker reddish purple; patch and groove system absent. *Color* in alcohol dorsal mantle pale tan, gray buff or brownish red; arms and web darker; ventral mantle lighter.

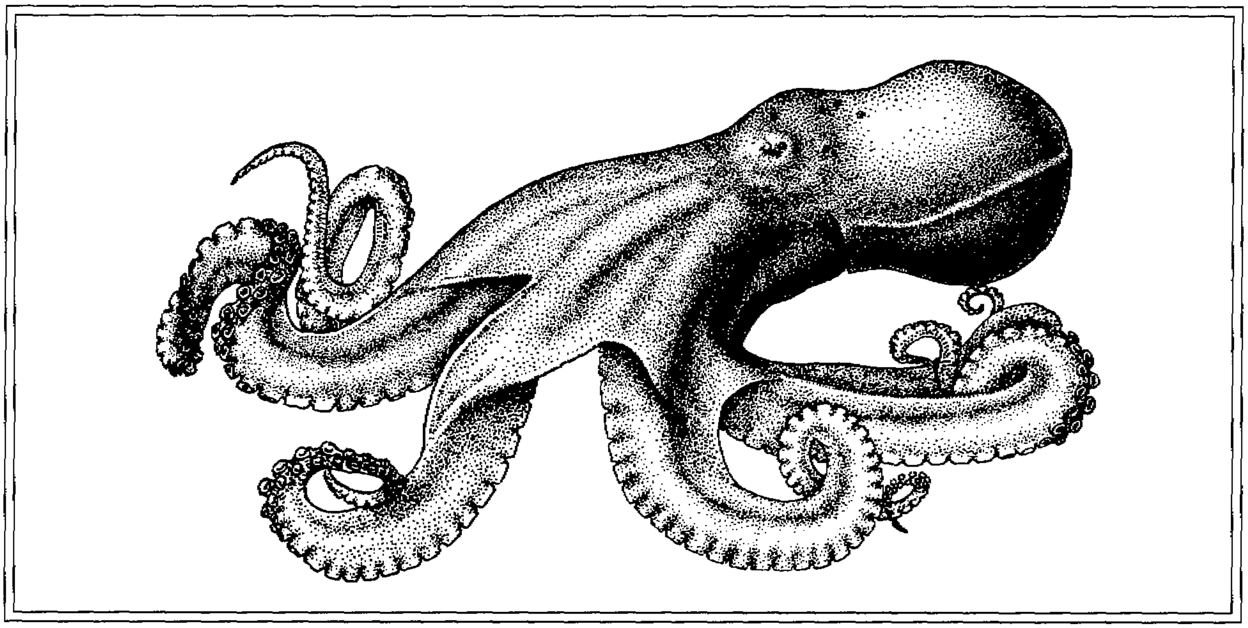

**Figure 6.3.** *Benthoctopus leioderma*: lateral view of living animal. (after Berr, 1912a).

**Type Locality and Type Specimens.** Eastern North Pacific Ocean, USA, Alaska, Shelikof Strait, [Cape Uyak, S 10°W, 5.8 mi], 106-112 fm [194-205 m]; USBCF *Albatross*, station 4293. *Holotype* - female (immature), 44 mm ML; USNM 214322 [SSB 137], no longer extant. *Neotype* - Female (immature), CASIZ 031369 [SSB 173, SU 2132]; preserved in alcohol in good condition.

**Neotype Locality.** Eastern North Pacific Ocean, USA, Gulf of Georgia, Alaska, 111-170 fm [203-310 m]; USBCF *Albatross*, station 4194.

**Distribution.** Reported to occur in the Sea of Okhotsk, Bering Sea and Kurile Islands through Alaska south to California (Monterey Bay). Known to occur in moderate depths from 90-500m, on muddy sand bottoms.

**Etymology.** Name derived from the Greek *leios* and *derma* meaning "smooth skin".

**Common Name.** None.

**Discussion.** The above diagnosis is based on Berry's original description and figures, plus examination of two specimens identified by Voss in the NMNH (USNM) and additional comparative material in the collections of the YPM and SBMNH. The holotype is no longer extant and Berry did not designate any paratypes. Two juvenile specimens from the same lot as the holotype were recorded by Berry in his card file. One of these, a female (USNM 214664) was not found in July of 1985. An additional female specimen resides in the collections of the CASIZ. Although mentioned but not measured by Berry in his original description it is herein designated as the neotype for *Octopus leioderma*.

None of the specimens available to Berry were dissected for his original description, hence the presence or absence of an ink sac was not determined. Robson (1932: ) felt that, based on general appearance and body proportions, *Octopus leioderma* was closely related to *Benthoctopus hokkaidensis*. The neotype and comparative material which can be referred to this species were found to lack an ink sac and hence the species herein is transferred to the genus *Benthoctopus*.

**Biology.** Little is known of the biology of this species.

**Parasites.** Two undescribed dicyemid species have been recorded from specimens collected off Oregon and Vancouver Island, Canada (Hochberg and McConnaughey, unpubl.).

## ***Benthoctopus robustus* Voss and Pearcy, 1990**

Figure 6.4

*Benthoctopus robustus* Voss and Pearcy, 1990:67-69, figs. 9a-h, 10a-e.

*Polypus januarii* not Hoyle. — Hoyle, 1904:18.

**Material Examined.** Canada:—*Paratype* 1 male (mature), 114 mm ML; British Columbia, Queen Charlotte Island, 140 nautical mi off Tasu Sound, 52°27.4'N, 135° 34.4'W, 3660 m; coll. E. Houde, sablefish trap, 16 October 1978, USNM 730895.

Oregon:—*Holotype* 1 male (mature), 137 mm ML; off Newport, eastern portion of Cascadia Abyssal Plain, 44°38.5'N, 126°03.8'W, 2800 m; coll. R/V *Acona*, station NAD22, 1 June 1963, USNM 729994.—1 male (immature), 85 mm ML; SW of Columbia River mouth, 45°44'N, 124°54'W, 1189 m; coll. W. Pereyra and Alton, BCF-AEC Project, M/V *Commando*, 72 ft shrimp trawl, 28 August 1963, YPM 13218.

Mexico:—1 female (gravid), 125 mm ML; off Baja California del Norte, 30°57.9'N, 119°08.0'W, 3840 m; coll. C. Hubbs and party, R/V *Melville*, station MV-69-VI-5A, free vehicle setline and trap, 16-17 December 1969, SBMNH 42224.

**Description.** *Animal* large. *Mantle* compact, robust, muscular (ML to 142 mm), rounded, longer than wide (MWI 77-80). *Head* small, narrow (HWI 48-51); distinct neck region absent. *Eyes* small, do not protrude. *Pallial aperture* narrow. *Funnel* large, long; free for half its length; aperture small. *Funnel organ* very large; W-shaped; limbs wide, lateral limbs equal to or slightly longer than median limbs, median limbs round.

*Web* heavy, deep (WDI 35); sectors subequal, formula typically D.B.C.A.E or C.B.D.A.E; membrane extends along ventral edge of arms about 2/3's their length. *Arms* moderately long (ALI 57-68); about 5 times ML; stout at base (AWI 12-16), tapered rapidly to stout, attenuated tips; lengths subequal, formula typically 4.1.2.3 or 3.2.1.4. *Suckers* small (SDIn 5.1-5.7); well separated, erect on stout bases; enlarged suckers absent. *Sucker counts* - males: arms 1 with 38-40 suckers. *Hectocotylized arm* - right arm 3 (HAMI ); shorter than opposite arm (OAI 80- 85); stouter than other arms; spermatophore groove formed by thick in-rolled web. *Copulatory organ* large (LLI 12-13); ligula elongate, conical, margins thick and fleshy, copulatory groove deep, with 14-16 transverse folds; calamus large, long (CLI 38-45), slender, sharply pointed.

*Beaks* - rostrum of upper beak very small, sharp and curved; rostrum of lower beak forms 90 angle to jaw angle. *Radula* - rachidian simple, narrow, with single small cusp on thin cutting edge; 1st laterals with tall sharp ectocone; 2nd laterals with straight inner edge; 1st marginals slender, curved, sabre-like; marginal plates present. *Digestive tract* - esophagus slender; crop with small, distinct anterior diverticulum; stomach large, muscular; caecum small; intestine inflated distally; rectum about 1/3 length of intestine; anal flaps absent; digestive gland nearly spherical. *Ink sac* absent.

*Gills* large; with 11 lamellae per outer demibranch.

*Male genitalia* (mature) - spermatophoric gland I wide, thin walled; gland II about 2/3 length of gland I, appendix present; spermatophore storage sac long, triangular, filled with relatively few, large spermatophores; terminal organ very large (TOLI 58), with long diverticulum. *Spermatophores* long; horn (oral cap) with 3 tight turns.

*Female genitalia* (mature) - not described.

*Skin* entirely smooth; lateral mantle fold absent; papillae absent on mantle, head and arms. *Color* (in life) pale pinkish. Color (in alcohol) pale tan dorsally and on aboral surface of arms; light reddish- brown on ventral side of head, around and on funnel, around eyes and on web; web margins darkish purple. Some specimens appear to be reverse countershaded.

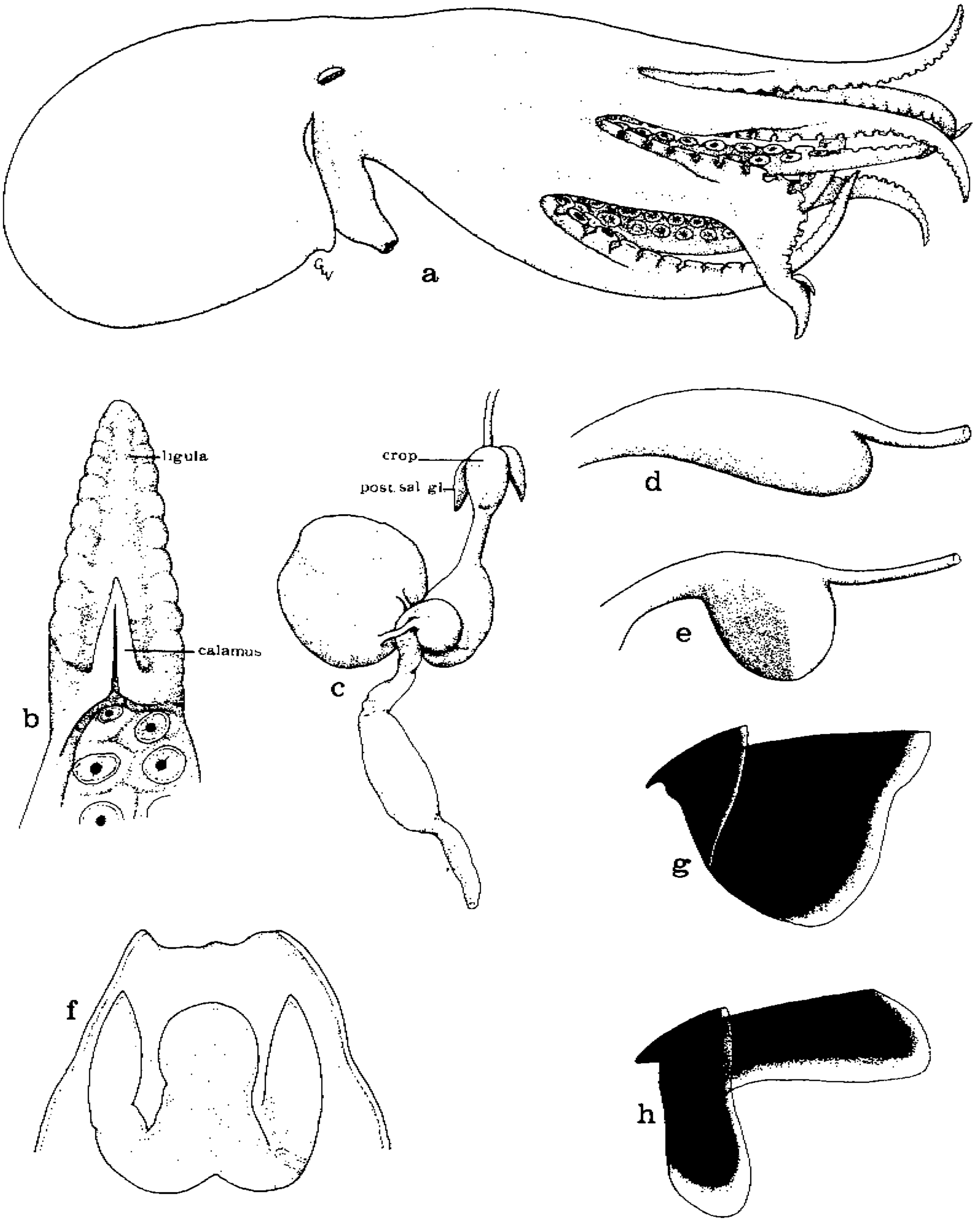

**Figure 6.4.** *Benthoctopus robustus*: A, lateral view of holotype (USNM 729994), male 137 mm ML; B, ligula; C, digestive tract of paratype (USNM 730895), male, 49 mm ML; D, crop of holotype; E, crop of paratype; F, funnel organ of holotype; G, H, upper and lower beaks of holotype. (after Voss and Pearcy, 1990).

**Type Locality and Type Specimens.** OREGON, off Newport, eastern portion of Cascadia Abyssal Plain, 44°38.5'N, 126°03.8'W, 2800 m. *Holotype* - male (mature), 137 mm ML; USNM 72994; preserved in isopropyl alcohol, in good condition. *Paratype* - male (mature), 114 mm ML; USNM 730895.

**Distribution.** Known range from Oregon to off Baja California, Mexico. Precise northern and southern limits unknown. Known depth range from 1,200-3,850 m.

**Etymology.** Specific epithet derived from Latin *robustus* meaning "hard or strong" in reference to the species' stout, muscular body.

**Common Name.** None.

**Biology.** Little is known about the biology of this rare, deep sea octopus.

**Parasites.** A undescribed species of dicyemid parasite has been discovered in the kidneys of an animal off Mexico (*Symbiotype* SBMNH 42224; Hochberg, unpubl.).

## Subfamily Graneledoninae Voss 1988

**Diagnosis.** Deep-water octopodids; suckers uniserial, small; enlarged suckers absent; ink sac absent; funnel organ V- or VV-shaped; copulatory organ small to medium size (LLI <8), calamus large (CLI >50); radula homodont, reduced or degenerate; crop simple without diverticulum; posterior salivary glands small to vestigial; spermatophores large and few in number; gills small, with reduced number of lamellae.

**Discussion.** Robson (1932:51-56) discussed the Eledoninae (*i.e.*, octopodids with a single row of suckers) and considered the subfamily to be polyphyletic. With this in mind Voss (1988a: 270) erected the new subfamily, Graneledoninae, to contain three genera, namely: *Bentheledone* Robson, 1932; *Graneledone* Joubin, 1918 and *Thaumeledone* Robson, 1930. According to Voss all three genera share the following key characters: 1) lack of an ink sac; 2) lack of a crop diverticulum; and 3) degenerate radula.

### Genus *Graneledone* Joubin, 1918

**Type Species:** *Eledone verrucosa* Verrill, 1881; by original designation (Joubin, 1918b: 39).

**Diagnosis.** Skin of dorsal mantle, head, eyes and bases of arms 1 and 2 covered with permanent rosette-like clusters of rugose cartilaginous tubercles; gills with 6-8 lamellae per outer demibranch; funnel organ large, VV-shaped; posterior salivary glands small; 1-3 large multifid papillae over each eye; radula with very large cusps on second laterals and marginals.

**Etymology.** Derived from the Latin *granum* meaning "small kernal or grain" in reference to the granule-like, cartilaginous tubercles characteristically present on the dorsum of species in this genus.

**Discussion.** Over the years several species have been placed in the genus *Graneledone* which presently are considered to belong in other genera, namely: *G. rotunda* Hoyle, 1885 [= *Bentheledone*] and *G. polymorpha* Robson, 1930 [=*Pareledone*]. In addition, several unidentified specimens have been indicated to be present in various parts of the world, namely: Gulf of Panamá in 1865- 2500 m (Hoyle, 1904; Nesis, 1982, 1987; Voss, 1988b); in 1866 m off Costa Rica (Hochberg, unpubl.) and in 1100 m off Perú (Hochberg, 1992, unpubl.).

### ***Graneledone boreopacifica*** **Nesis, 1982**

Figure 6.5

*Graneledone boreopacifica* Nesis, 1982:322, textfigs. 85k, l. — Nesis, 1985:48; — Avdeev, 1986:49; — Nesis, 1987:322, textfigs. 85J, K [translation of original description];— Nesis, 1989a:27-28. — Nesis, 1989b:1001, textfig. 2; — Hochberg, 1990:193-196.

*Graneledone pacifica* Voss and Pearcy, 1990:85-92, figs. 18a-g, 19a-h, 20a-g, tables 18, 19.

*Graneledone* sp. — Avdeev, 1982:108, 114; — Voss, 1988a: fig. 2k.

*Graneledone* sp. A. — Voss, 1988b:303, fig. 8.

*Moschites* sp. — Berry, 1917: 4.

*Moschites verrucosa* not Verrill. — Hoyle, 1904:21.

*Graneledone challengeri* not Berry— Robson, 1932:311-313 (in part), textfig. 71.

*Japetella heathi* not Berry. — Hanna, 1952:357, pl. 13(fig. 2).

**Material Examined.** Oregon: *Holotype*—1 male (mature), 85 mm ML; Cascadia Abyssal Plain near the slope, 44°52.0'N, 125°32.8'W, 2706 m; coll. R/V *Yaquina*, station Cr. 6907C haul 95, 16 July 1969, USNM 730716.— 6 juveniles, 16-42 mm ML; SW of Columbia River mouth, 45°45'N, 125°09'W, 1646 m; coll. W. Pereyra and Alton, M/V *Commando*, 70 ft semi-balloon shrimp trawl, 29 May 1964, YPM 13249.— 1 male (immature), 60 mm ML; SW of Columbia River mouth, 45°55.2'N, 125°08.8'W, 1463 m; coll. W. Pereyra and Alton, M/V *Commando*, 70ft semi-balloon shrimp trawl, 29 May 1964, YPM 13250. — 1 male (mature), 135 mm ML; SW of Columbia River mouth, 46°03.5'N, 125°05.7'W, 1463 m; coll. W. Pereyra and Alton, M/V *Commando*, 70 ft semi-balloon shrimp trawl, 30 May 1964, YPM 13256.

California:— 1 female (subadult), 100 mm ML; Humboldt Co., north of Cape Mendocino, 41°41'N, 125°19'W, 1300 m; coll. California Dept. Fish and Game, 26 May 1969, SBMNH 42223. — 2 males (immature), 60, 64 mm ML; San Francisco Co., off Farallon Islands, 2980 m; coll. J. Nybakken and party, Farallones Oceanic Research Expedition, 27 July 1991 SBMNH. — 1 female (mature), 145 mm ML; San Luis Obispo Co., off Avila near Santa Lucia Banks, 35°06.2'N, 121°38.8'W, 688-698 fm [1258-1277 m]; coll. S. Kato and party, R/V *D.S. Jordan*, tow #6, 93 ft modified Eastern otter trawl, 7 September 1976, SBMNH 64541. — 1 female (juvenile), 33 mm ML; Santa Barbara Co., south of San Miguel Island, 1036 m; SBMNH 63332. — 1 male (mature), 125 mm ML; south of Cortez Bank, 32°15'N, 119°01'W, 1050 m; coll. F/V *Calafia*, 5 October 1978, SBMNH 63333. — 1 male (mature), 95 mm ML; Monterey Co., off Monterey Bay, 36°41' N, 122°19'W, 1336-1347 m; coll. E. Anderson and party, USNS *De Steigner*, 7.5 ft McDuck beam trawl, 19 November 1975, CASIZ 031500. — 1 male (mature), 95 mm ML; Monterey Co., off Soberanes Pt., 36°28'N, 122°17'W, 1384-1409 m; coll. E. Anderson and party, USNS *De Steigner*, 7.5 ft McDuck beam trawl, 21 November 1975, CASIZ 031474. — 2 females (mature), 130 and 130 mm ML; off Bodega, 4-5 mi N of Bodega Canyon, 1197-1244 m; coll. Capt. Ed Bishop, F/V *Eagle*, 27 December 1976, CASIZ 003318. — 1 female (immature), 80 mm ML; N. Farallon Island, 10 mi SE of Farallones, SW x S1/4, 1280-1463 m; coll. F/V *N.B. Scofield*, station 155 [NBS 50B- 88], beam trawl, 12 November 1950, CASIZ 035044.

**Description.** *Body* medium to large. *Mantle* firm, muscular; short ((ML 80-145, mature males and females); moderately wide (MWI males 87-92.9-100, females 81-92.1-115); widest medially. *Head* narrower to slightly wider than mantle (HWI males 54.5-72.7-83, females 60-72.0-115); not distinctly set off from mantle. *Eyes* large, protrude very slightly; apertures small. *Funnel* large, stout (FLI ); free about 1/4 of its length (FFLI ); inner edge forms strong flap which inserts in deep pouch in inner mantle wall to form effective "locking apparatus". *Funnel organ* very large (fills almost entire length of funnel in immature animals); pads thick, orangish; VV-shape, limb widths and lengths variable.

*Web* moderately deep (WDI males 17.4-30.9, females 22.9-31.3); sectors subequal, formula C.D.B.A.E or B.C.D.A.E. *Arms* moderately long (ALI males 72-78.7-84, females 74-75.6-77); 2.3-3.4 times ML (MAI males 25-27.6-32, females 25-29.1-31); muscular, stout (AWI males 19-21.6-24 [Nesis 16-18.1-20], females 18-20.2-24), round in cross-section, taper to long slender tips; lengths subequal, formula typically 1.2.3.4, less frequently 2.1.3.4. *Suckers* small (SDIn males 4.8-7.4 [Nesis 5.6-6.3], females 4.4-7.7 [Nesis 5.2-6.7]), largest suckers in region of web insertion; well separated; urn-shaped, rim inflated and crenulated; embedded in flesh of arms; enlarged suckers absent. *Sucker counts* - male: HASC 40-48, OASC 60-94; female: arm R3 or L3/88-108.

*Hectocotylized arm* - right arm 3; shorter and more robust than opposite arm (OAI 71-82.4-86); spermatophore guide distinct (on margin of web between arms R3 and 4); spermatophore groove well developed, web broad, thickened at margin, white (devoid of chromatophores). *Copulatory organ* small (LLI 4.5-5.6-6.5); ligula short, broad, spade- or heart-shaped, copulatory groove deep with numerous low transverse laminae, often with low median, longitudinal ridge; calamus large (CLI 59-62.8-83 [Nesis 40-70]), narrow, sharply pointed.

*Gills* large, stout; with 7-8 lamellae per outer demibranch.

*Buccal mass* large; anterior salivary glands small; posterior salivary glands small, narrowly elliptical. *Beaks* - upper beak with strong deep jaw angle; lower beak with 90° jaw angle, distinct groove along lower edge of insertion plate. *Radula* - rachidian varies from multicuspid with B8 seriation to simple (homodont), almost degenerate; first lateral very small with small cusp; second lateral with large, very broad cusp; marginal with large, broad cusp. *Digestive tract* - esophagus slender; crop simple, inflated, slightly wider than esophagus, without anterior diverticulum, inner walls strongly plicate; stomach slightly larger than caecum, bipartite, anterior half muscular, thick- walled, posterior half thin-walled; caecum small; intestine short, stout, with sharp bend in proximal quarter, without bulbus; anal flaps absent; digestive gland large, rounded; paired digestive gland ducts large, thin-walled. *Ink sac* absent.

*Male genitalia* (mature) - testis not figured; spermatophoric gland I long, stout, about 2 times longer than gland II; spermatophoric gland II without appendix; spermatophore storage sac very long, stout anteriorly, tapered to elongate point posteriorly, contains few large spermatophores; terminal organ large, short and stout; diverticulum large, stout, strongly reflexed. *Spermatophores* long (SpLI 145-157.0-169), stout (SpWI 4- 5); sperm reservoir large (SpRI 41), swollen in region of sperm mass, flesh colored; cement gland dark purplish-red to maroon; oral cap (= horn) with 3-4 loose coils just prior to end.

*Female genitalia* (mature) - ovary moderately large; proximal oviducts very short, stout; oviducal glands large, round and flattened, distal half appears pleated, dark blue-gray; distal oviducts short, very swollen; genital pore small, subterminal. *Eggs* large (mature ovarian capsule length 16 mm), widest posteriorly, flesh colored with about 10-12 striations (follicular folds); stalk short, white.

*Skin* soft, loose; dorsal mantle, head and bases of arms 1 and 2 densely covered with small, round (diameter 1-4 mm) clusters of cartilaginous tubercles, each rosette-like cluster typically consists of 2-6/7-11 small blunt tubercles surrounding a larger central one; raised above body surface on low fleshy pad (in life tubercles capable of being erected as tall rugose papillae); skin between tubercles smooth; ventral mantle and ventral arms smooth without tubercles; 1-2 large papillae above each eye, each covered with small tubercles; some specimens with distinct demarcation line on lateral mantle separating light dorsal mantle from dark ventral mantle (often appears as lateral mantle fold). *Color* (in alcohol) variable, ground color pinkish-gray to reddish-brown or reddish-purple; web and oral surface of arms slightly darker; some specimens are distinctly reverse countershaded with the dorsal mantle, head and arms lighter than the dark red ventral surfaces; eyes dark colored; tubercles typically stand out as pale round spots; funnel dark, distal tip (around aperture) with light ring; lip of pallial aperture light or white; sucker bases dark, rims distinctly white (devoid of chromatophores).

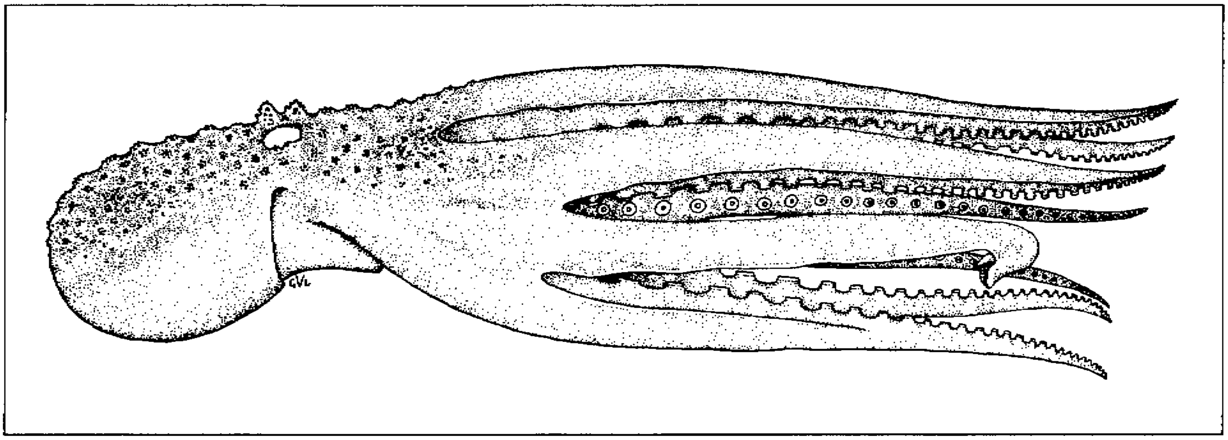

**Figure 6.5.** *Graneledone boreopacifica*: lateral view of holotype, USNM 730716, male, 85 mm ML. (after Voss and Pearcy, 1990).

**Type Locality and Type Specimens.** North Pacific Ocean, 50°04'N, 151°35'W, 1350 m. *Holotype* —male (mature), 110 mm ML; ZIN, unregistered. *Paratypes*—1 female (immature), 32 mm ML; IOAS, unregistered.— 2 males (immature), 58 and 65 mm ML; IOAS, unregistered.

**Distribution.** A boreal, lower-bathyal species recorded in the western Pacific Ocean off NE Honshu Island, Japan, in the Sea of Okhotsk and in the Eastern Pacific Ocean from Washington to southern California, USA. Ranging in depths from 1,000-3,000 m.

**Etymology.** Named in recognition of the boreal distribution of the species in the North Pacific Ocean.

**Common Name.** None.

**Discussion.** Voss and Pearcy (1990) named and described in detail *Graneledone pacifica* from the Eastern North Pacific. Their species is considered herein to be a junior synonym of *G. boreopacifica* Nesis, 1982. The holotype of *G. pacifica* is a mature male, 85 mm ML; USNM 730716, preserved in 50% isopropyl alcohol, in good condition. Additional paratypes of *G. pacifica* are in the NMNH (USNM); CAS (CASIZ 061433, 061434); RSMS (UMML) and SBMNH. The type locality of *G. pacifica* is off Oregon, Cascadia Abyssal Plain near the slope, 44°52'N, 125°32.8'W, 2,706 m. Voss and Pearcy (1990) reported that *G. pacifica* has been captured on the continental slope, slope base and eastern boundary of the Cascadia Abyssal Plain. It was not found on the Western Cascadia or Tufts plains and, hence, appears to be a species that lives near the continent wherever it occurs.

Based on the examination of additional material easily recognized as *G. boreopacifica* [= G. pacifica] in the collections of SBMNH, CASIZ and YPM, the species is confirmed to be distributed in the Eastern North Pacific as far south as southern California.

Hoyle (1904: 21) reported the presence of an animal matching the description of *Graneledone verrucosa* from 1865 m off Cape Malá in the Gulf of Panamá. Nesis (1982, 1987) and Voss (1988b), on the other hand, indicated the presence of a new species of *Graneledone* in the Gulf of Panamá. Additional specimens of an unidentified species from Costa Rica (adult, spawned egg mass and hatchlings) and Perú (spawned egg mass) are in the collections of the SBMNH (Hochberg, unpubl.). Unfortunately, Hoyle's specimen from Panamá does not appear to be extant and hence can not be compared with the above material. If these specimens prove to be *G. boreopacific* the distribution will be extended south at least to Panamá.

Hoyle (1886:104) earlier reported the presence of *Graneledone verrucosa* in 1152 m off the Kermadec Islands. Berry (1916:49-50) proposed a new name *challengeri* for the specimen off the Kermadecs based primarily on the geographic separation from the type locality of the true *G. verrucosa* which is in the Western North Atlantic (for a discussion see Voss, 1976:457). Robson (1932:311-313) confused the situation when he later treated both Hoyle's Kermadec and Panamá specimens under Berry's name. The specimen from the Kermadecs is considered to represent a species distinct from *G. boreopacifica*. Lu and Mangold (1978) recently collected large numbers of an unidentified species of *Graneledone* from the Kerguelen and Heard Islands in the Indian Ocean. Whether their specimens relate to *G. challengeri* or to *G. antarctica* has not been determined.

**Parasites.** Avdeev (1982) described two species of host specific harpacticoid copepods from the gills of specimens collected in the Western North Pacific: *Cholydiella incisa* and *Brescianiana rotundata*. Copepods have not been reported from *Graneledone* specimens in the Eastern Pacific. For review see Hochberg (1990).

## Subfamily Octopodinae

### Genus *Octopus* Cuvier, 1797

**Diagnosis.** *Adults* - small to large shallow water octopodines; mantle muscular, globose to rounded ovoid; skin with distinct patch and groove system which appears as dark trellis or reticulated pattern; dorsal mantle white spots present; frontal white spot complex present; fixed pattern of 4 long primary papillae in diamond pattern on mid-dorsal mantle; funnel organ W-shaped; water pores absent; stylets present, not mineralized; eyes not protruding; arms muscular, medium length (3-5 times ML), lateral arms longest, formula typically 2.3.4.1 or 3.2.4.1; suckers large, infundibulum large and flared; enlarged suckers present in males and females, modified non-functional suckers at tips of arms of males absent; right arm 3 hectocotylized; copulatory organ with distinct ligula and calamus; spermatophores unarmed; oviducal glands distinctly bipartite, spermatheca present, braiding chambers present; fertilization occurs in oviducal gland; eggs always laid in festoons.

*Hatchlings* - planktonic or benthonic; Kölliker bristles present. In planktonic species mantle bluntly ovoid; arms with few to many suckers, subequal throughout paralarval development.

**Type Species:** *Octopus vulgaris* Cuvier, 1797; by absolute tautonomy (see ICZN Opinion 233).

**Etymology.** Name derived from the Greek *okto* and *pous* meaning "eight footed" in reference to the animal's eight arms.

### *Octopus dofleini* Wülker, 1910

Figure 6.6

*Octopus dofleini* Wülker, 1910:7, pl. 2(figs. 1-2), pl. 3(fig. 10).

In addition, it has been placed in the genus *Paroctopus* by some workers.

**Material Examined.** California:—1 female, 253 mm ML; off San Miguel Island, 3 mi west of Richardson Rock, Elbow Bank, 34°08'N, 120°34'W, ~25 fm [45 m]; coll. E. Wike and Capt. R. Hart, F/V *Condor*, hook and line, 3 February 1993; SBMNH 143068 [photographs].—1 female, 160 mm ML; off San Miguel Island, 3 mi west of Richardson Rock, Elbow Bank, 34°08'N, 120°34'W, 300 ft [91 m]; coll. Capt. M. McCrea, F/V *Sea Hawk*, hook and line, 11 January 1996 [released 3 February 1996]; SBMNH 143069 [DNA voucher].—1 female, 190 mm ML; off San Miguel Island, 3 mi west of Richardson Rock, Elbow

Bank, 34°08'N, 120°34'W, 200-220 ft [61-67 m]; coll. Capt. R. Hart, F/V *Condor*, hook and line, 2 February 1996 [released 3 February 1996]; SBMNH 143070 [DNA voucher].—1 male, 380 mm ML; due S of Santa Barbara Harbor, 60 fm [110 m]; coll. Capt. B. Bramly, F/V *C*, commercial prawn trawl, 6 April 1996 [released 1 May 1996].

Washington: —1 female, 200 mm ML; Clallam Co., Neah Bay, mile 6.2, under rock to left of bay, intertidal [0 m]; coll. R. Anderson, by hand w/quinaldine, 25 April 1993 [maintained in aquarium until death 8 July 1993]; SBMNH 143143 [FD-246; DNA voucher]. —1 female, 255 mm ML; Clallam Co., Discovery Bay, S of Mill Point, in ballast pile adjacent to wreck of S/V *Warhawk*, 30 ft [9 m]; coll. R. Anderson, by hand w/ quinaldine, 28 October 1994 [maintained in aquarium until death 23 November 1994]; SBMNH 143144 [FD-255; DNA voucher]. —1 female, 350 mm ML; King Co., off Seattle, MeKwa Mooks Park, Jacobsen Reef, 60 ft [18 m]; coll. J. Christensen, by hand w/quinaldine, 30 October 1994 [maintained in aquarium until death 8 November 1994]; SBMNH 143145 [MD-256]

British Colombia, Canada:—1 male, 65 mm ML; Dundas Island, small islet off Armiston Point, 54°38'N, 130°55.3'W, intertidal; coll. P. Lambert and P. Kerfoot, 21 June 1974; BCPM 974-233-26.—1 female, 70 mm ML; Queen Charlotte Sound, 51°22.0'N, 128°44.4'W, 122-124 fm [223-227 m]; coll. A. Peden, 12 September 1973; BCPM 973-219-6.—1 male, 64 mm ML; W Barkley Sound, 48°44.4'N, 126°30.0'W, 461 m; coll. F.R. Bernard (Biological Station, Nanaimo), cruise 63-185, station 3, line 2, 8 September 1964; BCPM 977-336.— 1 male, 25 mm ML; Vancouver Island, William Head, 48°20'N, 123°32'W, depth unknown; coll. I.E. Cornwall, 22 May 1924; BCPM 982-60. —1 male + 1 female, 55 and 50 mm ML; Queen Charlotte Sound, 51°10'N, 129°18.8'W, 142-152 fm [260-278 m]; coll. A. Peden, 7 September 1973; BCPM 973-200-4.—1 female, 225 mm ML; off Vancouver, depth unknown; coll. S. Gabe, Vancouver Public Aquarium,— October 1973; SBMNH 143071.—1 male, 445 mm ML; off Victoria, Sealand, depth unknown; coll. S. Gabe, Vancouver Public Aquarium, 23 February 1974; SBMNH 45786

**Description.** *Adults* - Animals large (TL 945-1105-1620 mm); body large (ML 158-195-330 mm). Mantle rounded-ovate, broad (MWI 67-87-102). Head narrow (HWIw 33-41-62); neck wider than head; eyes medium size, not protruding. Funnel long (FLI 35-40). Funnel organ W-shaped, limbs broad, outer limbs typically about half as long as inner limbs (FOI 42-64).

*Web* moderately deep (WDI 17-22-28); sectors subequal, formula typically B=C=D.A.E, ventral sector always shallowest, about half as deep as deepest sector. *Arms* moderately long (ALI 70-81-84); 3-5 times ML (AMI ); subequal, formula typically 2=1.3.4. *Suckers* large (SDIn males 13-17-19, females 12-14), larger in males than females; slightly elevated, infundibulum flared with distinct radial cushions; conspicuously enlarged suckers absent.

Right arm 3 hectocotylized (HAMI ); not markedly shorter than opposite arm (OAI 80-109). *Copulatory organ* very long (LLI 20-24); ligula slender, pointed, copulatory groove tightly closed, ornamented with regularly arranged transverse rows of 6-8 papillae per row; calamus short (CLI 5-8).

*Gills* long; with 12-13-15 lamellae per outer demibranch.

*Radula* - rachidian tooth with asymmetrical B4 seriation of rachidian; marginal plates flat, without cusp; other teeth not described.

*Genitalia of mature male* - testis round; vas deferens encased in elongate tubular membrane (not spherical); spermatophoric gland long, narrow, spirally coiled and reflexed back on itself; spermatophoric gland II long, tubular, distal end blind with reflexed tip; spermatophore storage sac very long and narrow, contains very few spermatophores; apex of terminal organ (penis) short; diverticulum very long. *Spermatophores* very long (SpLI 342, 346); horn with 10-15 spiral turns.

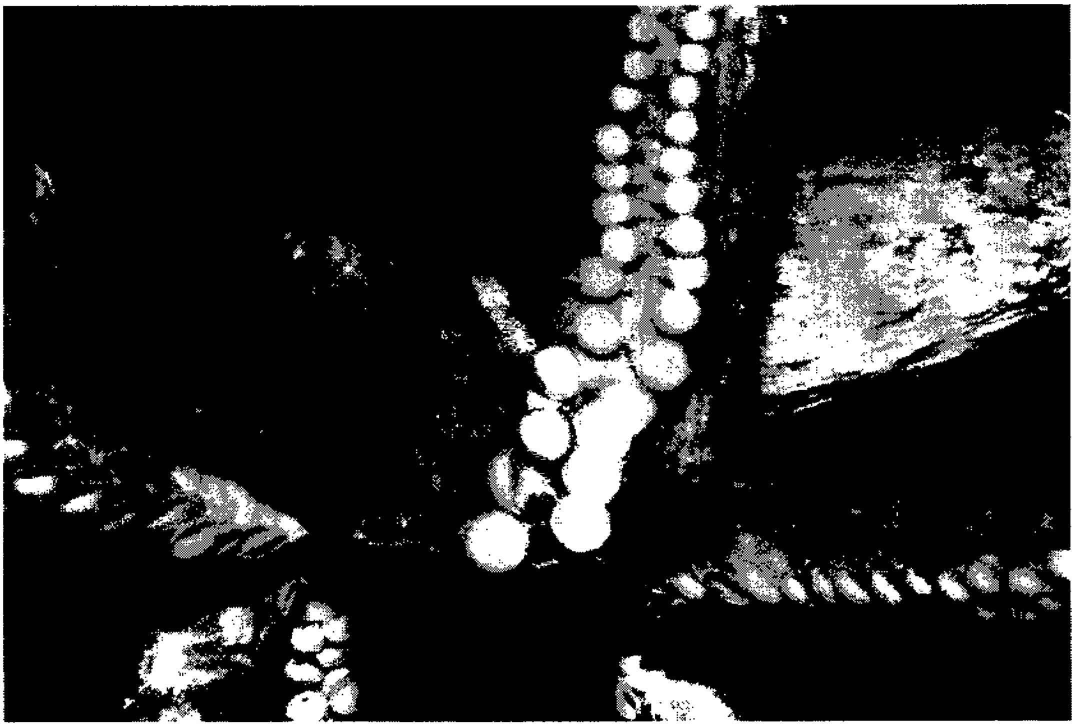

**Figure 6.6.** *Octopus dofleini*: view of living specimen. (from Morris, Abbott, and Haderlie, 1980).

*Genitalia of mature female* - ovary large, round, distended; proximal oviducts short, narrow; oviducal gland large (OGDI 23-24), bean-shaped, distinctly bipartite, proximal portion small, appears "pleated" (indicates radial chambers present), distal portion much larger, smooth and uniformly darker; proximal and distal oviducts enter and leave gland side by side at hilium; initial section of distal oviduct greatly inflated and wrapping around gland (accessory seminal receptacle). *Eggs* small (spawned capsule length 5.9-6.4 mm), stalks long (stalk length 13.8-17 mm); laid in festoons, stalks braided together. *Hatchlings* planktonic.

*Color* in formalin, dark reddish brown dorsally, often mottled with black streaks or reticulations; paler below without conspicuous dark reticulation; frontal white spot complex present; dorsal mantle white spots present; patch and groove system present, patches large, irregular-shaped oval to narrowly elongate. *Skin* in life loose, often smooth or with parallel longitudinal ridges or folds; in preservation appearing wrinkled, generally rugose or papillated dorsally; oral surface of web finely granulated; 4 primary papillae in diamond pattern on dorsal mantle, appear stellate at base; 2 large flattened primary papillae above and just behind each eye ("horn or ear-like"); single secondary papillae near front of each eye.

*Hatchlings* - Recent hatchlings large (ML 3-3.5 mm); arms subequal with 10-14 suckers; arms with 8-9 chromatophores in 1 row; funnel with 2+2+4+8 chromatophores; dorsal mantle midregion (over digestive gland) barren, anterior margin with band of 4-6 chromatophores, posterior region and sides with numerous chromatophores; ventral mantle barren, posterior region with 10+ chromatophores visible; dorsal head with 4+4 chromatophores, eye chromatophore number unknown; ventral head with 2 chromatophores; visceral chromatophore number unknown; silver iridophores around eyes.

**Type Locality and Type Specimens.** Japan, Hokkaido Island. *Holotype*: University Museum, Munich.

**Distribution.** San Diego, California to Japan. A boreal species restricted to the North Pacific Rim. Intertidal to 1500m, typically shallow subtidal to 100m.

**Common Name.** Giant North Pacific Octopus.

**Distribution.** Eastern North Pacific from San Diego, California to British Columbia, Canada. Depth range from 0-1500 m, typically shallow subtidal to 100 m.

**Common Name.** Giant North Pacific octopus.

**Discussion.** The above diagnosis is based on the original description, tables, and figures. Additional specimens have been examined (Hochberg, unpub.) and color photographs of numerous live animals have been studied.

Pickford's (1964) subspecific description of *Octopus dolfleini martini* for Canadian, Washington and California populations of the Giant North Pacific Octopus is not accepted. Additional critical morphometric, anatomical and behavioral work needs to be done on mature animals before they can be adequately separated from populations to the north and west.

### ***Octopus rubescens* Berry, 1953**

Figure 6.7

*Octopus punctatus* Gabb, 1862 (in part). — Wheeler, 1899:169-176.

*Polypus* sp. (young/juv.). — Berry, 1911:303-304; Berry, 1912:289.

*Polypus hongkongensis* **not** Hoyle. — Berry, 1911:302-303 (in part); Berry, 1912:280, 282-283, 333 (in part), textfig. 2, pl. 39(fig. 3).

*Polypus apollyon* Berry. — Berry, 1913:72 (in part), text fig. 1; Fisher, 1923:147-149, pl. 5; Fisher, 1925:411-414, pl. 27(figs. 1-6).

*Paroctopus apollyon* (Berry). — Robson , 1929: 202-204 ( in part), text fig. 82.

*Octopus apollyon* (Berry). — McConnaughey, 1949:12; Winkler and Ashley, 1954:24-26 (in part), text figs. 18-19.

*Octopus rubescens* Berry, 1953. — Halstead, 1965:731, 739-740; Packard and Hochberg, 1977:208-219, figs. 28, 32-33; Hochberg, 1980:204; Hochberg (1987); Hochberg and Fields, 1980:435-436, pl. 135(fig. 17.6).

**Material Examined.** Over 50 lots from California (SBMNH).

**Diagnosis.** *Body* small (TL 115-170-255 mm; adult ML 35-100 mm); *mantle* rounded to rounded-ovate; slightly longer than wide (MWI 70-83-98), widest posterior to mid mantle. *Stylets* present, non-mineralized. *Head* short, distinctly narrower than mantle (HWIw 64-76-89); separated from mantle by slightly constricted neck region; eyes large and prominent, not protruding. *Pallial aperture* wide (PAI 60-66-83). *Funnel* medium length (FLI 47), extends about 1/2 distance to web margin, broad at base tapering rapidly to slender constricted apex. *Funnel organ* W-shaped, limbs wide, narrowly separated, subequal.

*Web* thin, transparent, moderately deep (WDI 19-28); sectors nearly subequal, formula typically D.C.B.E.A; web membrane extends about 1/2 way up ventral edge of each arm. *Arms* slender, moderately long (ALI 72-75-85); 3.5-4.5 times ML (AMI 318-363-464); rapidly tapering to slender tips; lateral arms slightly longest, formula typically 2.3.4.1, dorsal pair shortest. *Suckers* moderate size (SDIn 8-11-13); widely spaced and distinctly elevated; infundibulum cup-like, slightly flared with radial cushions; 1-2 conspicuously enlarged suckers present on all but ventral arms of males (SDIe 13-17), less conspicuously enlarged on females, ventral sucker of 6th pair at web margin typically deeper and more robust but not much wider than normal suckers; sucker counts L1/164.

*Hectocotylized arm* right third arm (HAMI 258-289-329); distinctly shorter than opposite arm (OAI 72-94); spermatophore groove closely adnate, web membrane narrow; HASC 95. *Copulatory organ* moderately long (LLI 8-11); ligula well developed, elongate-conic, margins abruptly elevated, wide and fleshy, copulatory groove deep with 15-24 transverse ridges and grooves; calamus small (CLI 19).

*Gills* with 11-13 lamellae per outer demibranch; long (GLI 50). Internal anatomy not completely described. Ink sac large, conspicuous.

*Genitalia* of mature male, testis oval; vas deferens long, narrow, convoluted bound in membrane; spermatophoric gland I narrow; spermatophoric gland II with distinct bend at bluntly rounded distal blind end; spermatophore storage sac narrow, pointed, packed with numerous small spermatophores. Terminal organ small (TOI ), plump, sausage-shaped, distinctly looped; diverticulum appears absent. *Spermatophores* short ("small") (SpLI 132); horn straight or with few widely open coils.

*Eggs* small (capsule 3-4 mm long), stalks long, braided together, eggs laid in festoons.

*Skin* firm, smooth or textured with tessellate pattern of low relief, inflated or raised patches ("blister-like welts"); 4 primary papillae in diamond pattern on dorsal mantle; 1 primary papilla on mid-posterior dorsal mantle; 1 primary papilla over each eye. *Color* in life reddish on dorsal surfaces of head mantle and arms, with darker red- brown reticulate pattern; often mottled with white and with row of white spots down each side of arms; paler ventrally, often orangish; dorsal mantle white spot complex present; frontal white spot complex present; patch and groove system present, patches small, round or circular; bluish iridescence around eyes. Color in alcohol mouse gray to benzo-brown, mottled or reticulated with slate or blackish brown; ventral mantle and oral surfaces of arms avellaneous to cream buff. Ink reddish or red-brown.

*Hatchlings* planktonic, small (ML 1.7-2.0 mm); mantle globose; arms short, subequal with 4 suckers; arms with chromatophores in 2 rows; funnel with 2+2 chromatophores; dorsal mantle barren in mid region, with simple band of 6 chromatophores on anterior margin and cap of 6-8 chromatophores in posterior region; ventral mantle densely covered with 30-40 chromatophores (6-7 across); dorsal head with 2 + 4 + 4 pattern; visceral chromatophore number unknown; gold iridophores around eyes.

**Type Locality and Type Specimens.** MEXICO, Baja California del Norte, South Coronado Island, off south end of island, [26°07'N, 111°17'W], 15-17 fm [27-31 m]; coll. R/V *Orca*, station H49-167. *Holotype* —male (mature), 32 mm ML; USNM 815709, [SSB 969]; preserved in alcohol, in good condition. *Paratypes* —1 female (immature), 23 mm ML; USNM 815710 [SSB 968; from same locality as holotype].— 3 males + 5 females + 5 juveniles (mature - juveniles), 11-30 mm ML; USNM 81571 [SSB 970; from same lot as holotype].—2 females (age ?), ML unknown; [SSB 972; location unknown, presumed not extant].—2 females (immature), 12 and 23 mm ML; USNM 815712 [SSB 976; from same locality as holotype].

**Distribution.** Known to range from the mouth of the Gulf of California, Mexico to the Gulf of Alaska. Widely distributed vertically from intertidal to shallow subtidal, 0-300 m, on soft sand/mud bottoms and in rocky areas inshore and in intertidal areas.

**Etymology.** Name derived from the Latin *rubeo* meaning "I redden" in reference to the species' conspicuous red color.

**Common Name.** Red octopus.

**Discussion.** Diagnosis based on Berry's (1953) original diagnosis, his manuscript notes, measurements and figures in the archives at the USNM, discussions with Berry while he was alive; observations of live animals and reference to color photographs of live animals (see Packard and Hochberg, 1977).

The relationship of *rubescens* from the Eastern Pacific and Hoyle's *hongkongensis* from Japan in the Western Pacific needs to be compared in detail to determine if they are related or represent the same species.

**Figure 6.7.** *Octopus rubescens*: view of living specimen. (from Morris, Abbott, and Haderlie, 1980).

*Octopus rubescens* is the most common species of octopus in the Eastern North Pacific. The species typically occupies a depth range intermediate between *O. bimaculatus/bimaculoides* inshore and *O. californicus* in deeper water offshore.

**Biology.** The biology of *rubescens* was briefly reviewed Hochberg and Fields (1980) and more fully by Hochberg (in press). The species lives in rocky areas or inhabits large dead gastropod or barnacle shells, empty bottles and cans. *Octopus rubescens* has a life span of 12-18 months. It is a migratory species, moving offshore in winter months. Mating occurs at depth in the spring followed by an onshore migration prior to spawning. Depending on the size of the female from 20-50,000 small eggs are laid in the spring and fall. Color patterns have been studied by Warren *et al.* (1974), Dorsey (1976) and Packard and Hochberg (1977). Planktonic hatchlings and later stage paralarvae and juveniles have been described by Young (1972), Green (1973), Brocco *et al.* (1974), Mills (1983), Osborn (1990) and Hochberg *et al.* (1992). Paralarvae are thought to remain in the plankton for 1-2 months. Juveniles up to 20 mm ML have been reported in the plankton in large numbers (Young, 1972; Robison, pers. comm.). *Octopus rubescens* is nocturnally active and feeds principally on crustaceans, mollusks and occasionally fishes. The species is known to bite when handled or disturbed and is capable of injecting a potent toxin via the salivary proboscis (Halstead, 1949; Berry and Halstead, 1954; Oglesby, 1972; Ballering *et al.* 1972).

**Parasites.** The presence of species specific parasites, especially dicyemid mesozoans often aids in the identification of this octopus (for review of parasites and literature see Hochberg, 1990). An unusual dinoflagellate parasite which attaches to and destroys spawned eggs has recently been noted by Osborn (1990).

### *Octopus californicus* Berry, 1911

Figure 6.8

*Polypus californicus* Berry, 1911:590.

**Material Examined.** California: Paratype—male (mature), 77 mm ML; CASIZ 017971 [SSB 131; SU, CASIZ type 460].—2 females (submature), 55 and 62 mm ML; San Diego County, Soledad Mtn., SE 3.7 mi off Pt. La Jolla, 193-227 fm [353-415 m]; coll. USBCF *Albatross*, station 4323, 7 March 1904; CASIZ 024403 [SSB 135, SU 2133, CAS hypotype 530; voucher for Berry 1912].—1 female (submature), 60 mm ML; San Diego County, S 82°E, 10 mi off Pt. Loma Light House, 260-284 fm [475-519 m]; coll. USBCF *Albatross*, station 4369, 16 March 1904; CASIZ 024404 [SSB 113, SU 2118, CAS hypotype 532; voucher for Berry 1912].—4 juveniles, 11-22 mm ML; San Diego County, S 81°E, 6.2 mi off Pt Loma Light House, 130-158 fm [238-289 m]; coll. USBCF *Albatross*, station 4365, 16 March 1904; CASIZ 031371 [SSB 126, SU 2134; voucher for Berry 1912].—1 male (mature) + 2 females (mature/immature), 65 and 37, 77 mm ML; Santa Barbara Channel, 301° true, 9 mi off west point of Santa Cruz Island, 34°09'N, 120°04'W; coll. G.S. Myers, R.L. Bolin and party, Crocker-Stanford Deep Sea Expedition, P/Y *Zaca*, station 10, 13 September 1938; CASIZ 031244 and 032607 [split lot].—2 males (mature), 65, 70 mm ML; San Luis Obispo County, 50° true, W 1/4 S off San Luis Obispo Bay Light, 125-160 fm [229-293 m]; coll. M/V *N.B.Scofield*, station 116 [NBS 50B-49], 21 October 1950; CASIZ 031363.—1 male (mature) + 4 females (immature), 65 and 30-50 mm ML; San Luis Obispo County, 10 mi SW of Avila, 100 fm [183 m]; coll. E.S. Herald and party, R/V *Searcher*, 19 October 1970; CASIZ 031364.—1 male (mature), 75 mm ML; Channel Islands, Santa Catalina Island, off Isthmus Cove, 33°28'N, 118°26'W, 107-130 fm [196-238 m]; coll. G.S. Myers, R.L. Bolin and party, Crocker-Stanford Deep Sea Expedition, P/Y *Zaca*, station 25, 16 September 1938; CASIZ 031365.—1 female (juvenile), 31 mm ML; San Luis Obispo County, W of Pismo Beach, 85-110 fm [155-201 m]; coll. Ripley and Phillips, M/V *N.B. Scofield*, station 122 [NBS 50B-55], 23 October 1950; CASIZ 031367.—1 male (immature), 46 mm ML; San Luis Obispo County, 7-10 mi SW of Pt. San Luis, 70-110 fm [128-201 m]; coll. G.D. Hanna, M/V *N.B. Scofield*, station 139-149 [NBS 50B-72-82], 5-7 November 1950; CASIZ 031368.—2 males (immature) + 1 female (immature), 38, 40 and 46 mm ML; Channel Islands, 152° true, 8 mi off Anacapa Island, 128 fm [234 m]; coll. D. Goodwin, M/V *N.B. Scofield*, station 168 [NBS 51B-7], 17 February 1951; CASIZ 031370.—2 males (immature), 37, 44 mm ML; Monterey Bay, 42° true, 10 mi off Santa Cruz, 220-236 fm [402-432 m]; coll. D. Goodwin, M/V *N.B. Scofield*, station 175 [NBS 51B-14], 19 February 1951; CASIZ 031372.—1 male (juvenile), 20 mm ML; Santa Barbara County, Santa Barbara Channel, S of Goleta Pt., 34°15.3'N, 119°39.4'W, 141-228 fm [258-417 m]; coll. T. Iwamoto, M/V *Commando*, station TI-77-15 to 17, 7 July 1977; CASIZ 061054.—1 male (immature) + 2 females (immature), 37 and 31, 35 mm ML; Santa Barbara County, Santa Barbara Channel, S of Goleta Pt., 34°20.0'N, 119°50.7'W, 141-146 fm [258-267 m]; coll. T. Iwamoto, M/V *Commando*, station TI-77-15, 7 July 1977; CASIZ 069422.

**Description.** *Animals* medium size (TL 195-375 mm) short, compact and plump; *body* medium size (ML 50-100 mm); mantle muscular, broadly ovoid, almost as wide as long (MWI males 70-80, females 64-101). *Stylets* present, non-mineralized. *Head* broad, about as wide as mantle (HWIw males 75-87, females 61-86); neck slightly constricted; eyes very large, prominent, bulging in live animals. *Pallial aperture* wide (PAIw 60-80). *Funnel* large, stout, bluntly tapered (FLI 29-53); free about half its length (FFLI 51-79). *Funnel organ* VV- shaped, limbs thick, outer limbs half as long as median limbs.

*Web* moderately deep (WDI 25-31), well developed, capable of considerable in life; web extends along ventral side to tips of all arms; dorsal and ventral sectors always shallowest, web formula commonly B=C=D.A=E. *Arms* short (ALI 61-74), 2.5-3 times ML (AMI 269-360); stout, muscular, tapering to fine tips; subequal, arm formula typically 2.1.3.4. *Suckers* moderate to large size (SDIn 7-11); raised above arm surface, infundibulum flared, radial grooves indistinct; proximal 2-3 suckers uniserial; enlarged suckers (sucker number 14-23) on all arms of mature males only (SDIe 9-18). *Hectocotylized arm* right third arm (HAMI 196-247); shorter than opposite arm (OAI 70-81); spermatophore groove deep, white, interbrachial web not thickened; with 47-53 suckers. *Copulatory organ* medium size (LLI 10-22); ligula conical, narrow, groove long, deep with 50-60 transverse folds; calamus minute (CLI 2-6), pointed.

*Gills* with 12-13 lamellae per outer demibranch; gills moderately long (GLI 24- 43).

*Beaks* typical. *Radula* not described. Digestive tract with small anterior salivary glands; posterior salivary glands large, leaf like; esophagus long, narrow; anterior crop inflated, without anterior diverticulum; posterior crop wider than esophagus; stomach tripartite; caecum with single tight coil; intestine differentiated with expanded mid section; anal flaps large, stout. Ink sac small, lying in shallow groove in digestive gland.

Male reproductive tract and spermatophores not described. *Terminal organ* (penis) large (PLI 14-28), diverticulum moderately large (DLI 47-75).

Mature female, ovary large, ovoid; proximal oviducts joined in common duct where enter ovary, short free section; oviducal glands large, spherical, uniformly dark in color, braiding chambers absent; distal oviducts extend almost to anus, curved with expanded tips. *Eggs* large (capsule 14- 17 mm long), attached singly to substrate by short stalk (3-5 mm long). *Hatchlings* benthonic.

*Skin* in life appears smooth; in preserved specimens mantle, head and arm bases densely covered with large stellate tubercles or nodules; raised papillae uniformily distributed across surface of dorsal mantle, head and arms; single large unbranched papilla over each eye. *Color* in life uniform orange brown or pinkish red-brown dorsally; ventral surfaces of mantle, head and arms lighter than rest of body; eyelids gold, often with green iridophore sheen. Patch and groove system present; patches circular with faint dark reticulation. Frontal white spot complex faint; dorsal mantle white spots absent. Variegated or mottled color patterns never produced. *Ink* black.

**Type Locality.** California, vicinity of San Diego, [Point La Jolla, off Soledad Hill, SE 4.4 mi], 191-292 fms [349-534 m]; coll. USBCF *Albatross*, station 4325. *Holotype*— Male (mature), 308 mm TL [89 mm ML]; USNM 214321 [SSB 131]; no longer extant. *Paratypes* - Male (mature), 265 mm TL [77 mm ML]; CASIZ 017971 [SSB 131; CASIZ type 460]. - Male; USNM 214312b [SSB 131]; no longer extant.

**Distribution.** A boreal deep water species reported to occur from Punta Eugenia, Baja California, Mexico to the Gulf of Alaska (see discussion below). For the purposes of this paper the distribution is limited to the eastern North Pacific. Lives on soft mud and muddy sand bottoms at depths ranging from 100-900 m, highest densities occur between 200-500 m.

**Etymology.** Named for the State of California.

**Common Name.** California bigeye octopus

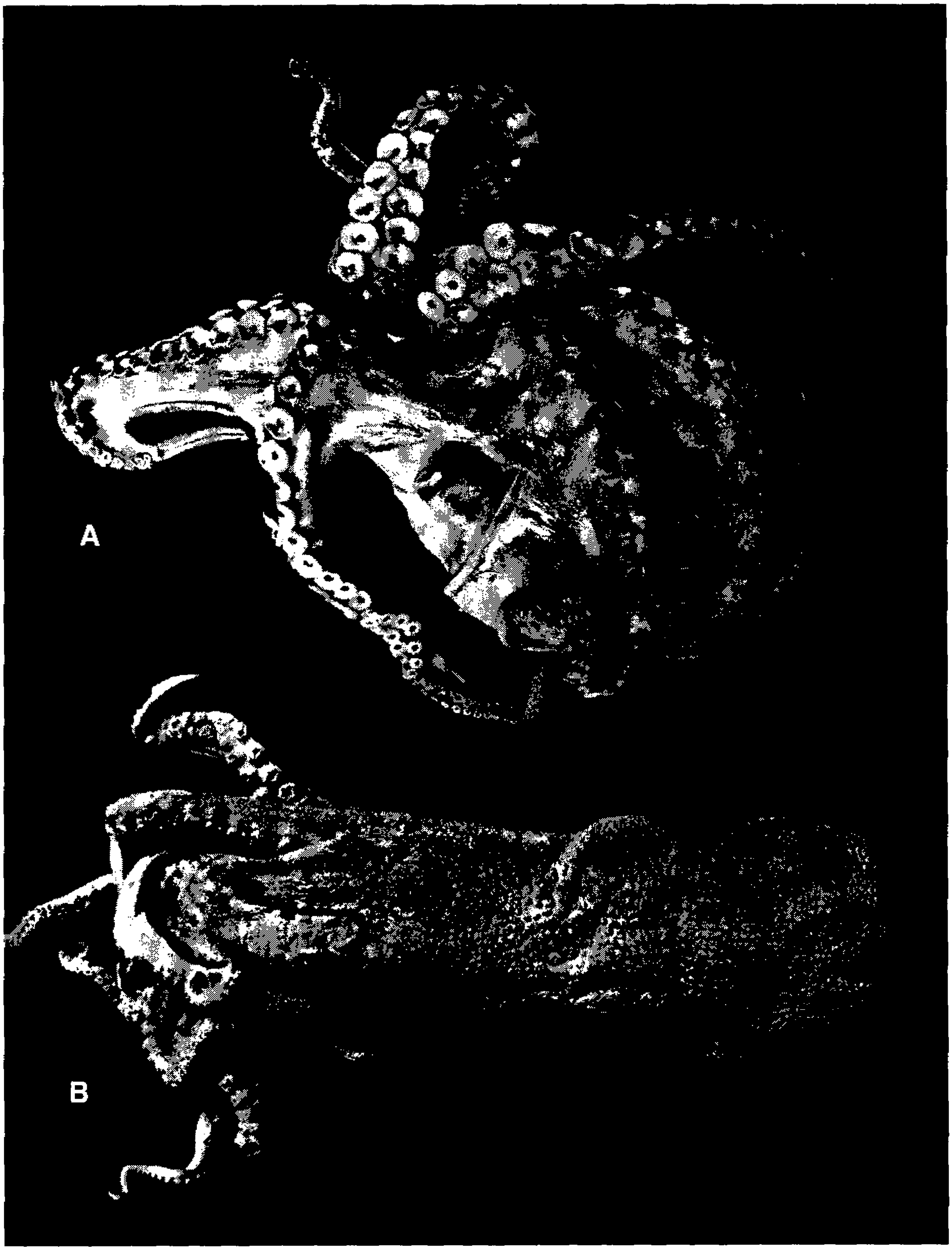

**Figure 6.8.** *Octopus californicus*: A, ventral view of large male, San Diego, California; B, dorsal view of holotype specimen (male). (after Berry, 1912a).

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# Appendix

## Lists and Maps of Stations

**Table A.1.** Position of soft-substrate stations taken during the Phase I Reconnaissance.

| Station | Latitude | Longitude | Depth (m) |
|---|---|---|---|
| 1 | 35°27.86′N | 121°05.33′W | 98 |
| 2 | 35°27.70′N | 121°06.52′W | 200 |
| 3 | 35°27.07′N | 121°10.20′W | 291 |
| 4 | 35°26.56′N | 121°14.93′W | 393 |
| 5 | 35°25.77′N | 121°21.69′W | 585 |
| 6 | 35°20.88′N | 120°59.62′W | 109 |
| 7 | 35°20.65′N | 121°02.57′W | 197 |
| 8 | 35°20.00′N | 121°06.58′W | 308 |
| 9 | 35°19.48′N | 121°10.06′W | 398 |
| 10 | 35°18.28′N | 121°18.65′W | 591 |
| 11 | 35°17.80′N | 121°22.13′W | 690 |
| 12 | 35°15.03′N | 120°57.31′W | 98 |
| 13 | 35°14.54′N | 120°59.77′W | 197 |
| 14 | 35°14.15′N | 121°02.04′W | 299 |
| 15 | 35°13.98′N | 121°04.54′W | 393 |
| 16 | 35°12.23′N | 121°16.29′W | 591 |
| 17 | 35°11.61′N | 121°22.55′W | 654 |
| 18 | 35°09.08′N | 120°56.55′W | 197 |
| 19 | 35°08.93′N | 120°59.66′W | 296 |
| 20 | 35°15.72′N | 121°04.68′W | 396 |
| 21 | 35°06.11′N | 120°44.82′W | 49 |
| 22 | 35°05.85′N | 120°50.23′W | 99 |
| 23 | 35°05.60′N | 120°55.18′W | 195 |
| 25 | 35°05.07′N | 121°00.75′W | 390 |
| 26 | 35°04.38′N | 121°15.99′W | 590 |
| 27 | 35°04.30′N | 121°19.27′W | 611 |
| 28 | 35°04.22′N | 121°19.65′W | 603 |
| 30 | 34°54.19′N | 120°47.07′W | 98 |
| 31 | 34°53.76′N | 120°52.96′W | 200 |
| 32 | 34°53.56′N | 120°56.81′W | 297 |
| 33 | 34°53.43′N | 120°59.66′W | 396 |
| 34 | 34°53.15′N | 121°04.40′W | 492 |
| 35 | 34°52.96′N | 121°10.30′W | 548 |
| 36 | 34°52.77′N | 121°15.37′W | 492 |
| 38 | 34°49.81′N | 120°52.66′W | 197 |
| 39 | 34°49.53′N | 120°56.85′W | 294 |
| 40 | 34°49.24′N | 121°00.81′W | 392 |
| 41 | 34°48.35′N | 121°19.14′W | 495 |
| 42 | 34°48.04′N | 120°47.50′W | 100 |
| 43 | 34°46.59′N | 120°52.92′W | 197 |
| 45 | 34°44.91′N | 120°59.59′W | 395 |
| 46 | 34°41.22′N | 121°13.56′W | 597 |
| 47 | 34°41.99′N | 121°10.81′W | 378 |
| 48 | 34°45.11′N | 120°52.85′W | 196 |
| 49 | 34°45.03′N | 120°56.31′W | 290 |
| 50 | 34°37.80′N | 121°01.66′W | 591 |
| 52 | 34°39.56′N | 120°47.64′W | 98 |
| 53 | 34°37.69′N | 120°50.38′W | 196 |
| 54 | 34°36.57′N | 120°52.02′W | 396 |
| 55 | 34°33.66′N | 120°56.31′W | 590 |
| 56 | 34°30.32′N | 121°01.02′W | 900 |

**Table A.1** (Continued)

| Station | Latitude | Longitude | Depth (m) |
|---|---|---|---|
| 58 | 34°34.35'N | 120°45.18'W | 99 |
| 59 | 34°33.65'N | 120°47.18'W | 216 |
| 60 | 34°33.25'N | 120°48.34'W | 275 |
| 61 | 34°33.01'N | 120°48.89'W | 345 |
| 62 | 34°30.46'N | 120°52.13'W | 582 |
| 63 | 34°26.29'N | 120°58.08'W | 930 |
| 64 | 34°33.15'N | 120°40.90'W | 59 |
| 65 | 34°31.27'N | 120°43.27'W | 107 |
| 66 | 34°30.46'N | 120°44.55'W | 201 |
| 67 | 34°30.29'N | 120°45.50'W | 282 |
| 68 | 34°29.24'N | 120°45.99'W | 390 |
| 69 | 34°22.88'N | 120°54.20'W | 927 |
| 70 | 34°29.67'N | 120°43.70'W | 200 |
| 71 | 34°29.04'N | 120°44.01'W | 306 |
| 72 | 34°28.41'N | 120°44.76'W | 401 |
| 73 | 34°28.21'N | 120°36.80'W | 98 |
| 74 | 34°26.84'N | 120°38.61'W | 201 |
| 75 | 34°26.08'N | 120°39.65'W | 293 |
| 76 | 34°25.59'N | 120°40.98'W | 387 |
| 77 | 34°22.62'N | 120°44.02'W | 578 |
| 78 | 34°18.78'N | 120°49.30'W | 762 |
| 79 | 34°24.12'N | 120°28.32'W | 98 |
| 80 | 34°22.86'N | 120°28.34'W | 196 |
| 81 | 34°21.26'N | 120°28.83'W | 294 |
| 82 | 34°18.71'N | 120°29.55'W | 394 |
| 83 | 34°17.20'N | 120°30.20'W | 444 |
| 84 | 34°13.54'N | 120°31.19'W | 394 |
| 85 | 34°25.88'N | 120°16.31'W | 113 |
| 86 | 34°24.45'N | 120°17.02'W | 197 |
| 87 | 34°21.60'N | 120°17.11'W | 299 |
| 88 | 34°17.89'N | 120°16.86'W | 393 |
| 89 | 34°13.79'N | 120°16.56'W | 471 |
| 90 | 34°09.44'N | 120°16.30'W | 375 |
| 91 | 34°11.73'N | 120°07.43'W | 540 |
| 92 | 34°08.70'N | 120°07.50'W | 444 |
| 93 | 34°07.63'N | 120°07.51'W | 357 |
| 96 | 34°22.91'N | 120°05.42'W | 296 |
| 94 | 34°24.54'N | 120°05.47'W | 96 |
| 95 | 34°23.70'N | 120°05.47'W | 198 |
| 97 | 34°22.28'N | 120°05.49'W | 393 |
| 98 | 34°12.87'N | 120°05.59'W | 561 |
| 99 | 34°11.22'N | 120°05.86'W | 540 |
| 100 | 34°08.67'N | 120°05.50'W | 443 |
| 101 | 34°07.51'N | 120°05.65'W | 357 |
| 102 | 34°59.71'N | 120°48.22'W | 99 |
| 103 | 34°59.63'N | 120°53.56'W | 197 |
| 104 | 34°59.45'N | 120°56.49'W | 294 |
| 105 | 34°59.23'N | 120°59.60'W | 392 |
| 106 | 34°58.95'N | 121°04.42'W | 492 |
| 107 | 34°58.65'N | 121°15.08'W | 573 |
| 108 | 34°58.21'N | 121°17.88'W | 492 |

Note: Sample labels from the Soft-substrate stations have several identification codes which include a station number, sample type, replicate number, and analysis type. These are as follows: 001 to 200 = the range of station numbers; BSS = Benthic Sediment Single (i.e., a non-replicated station); BSR = Benthic Sediment Replicate (three replicates taken at this station); BSV = Benthic Sediment Variance (subsamples); 01-09 = replicate numbers; TX = a taxonomy sample. Sample labels having the designation BRA, represents a sample from rocks taken as part of the hard bottom survey.

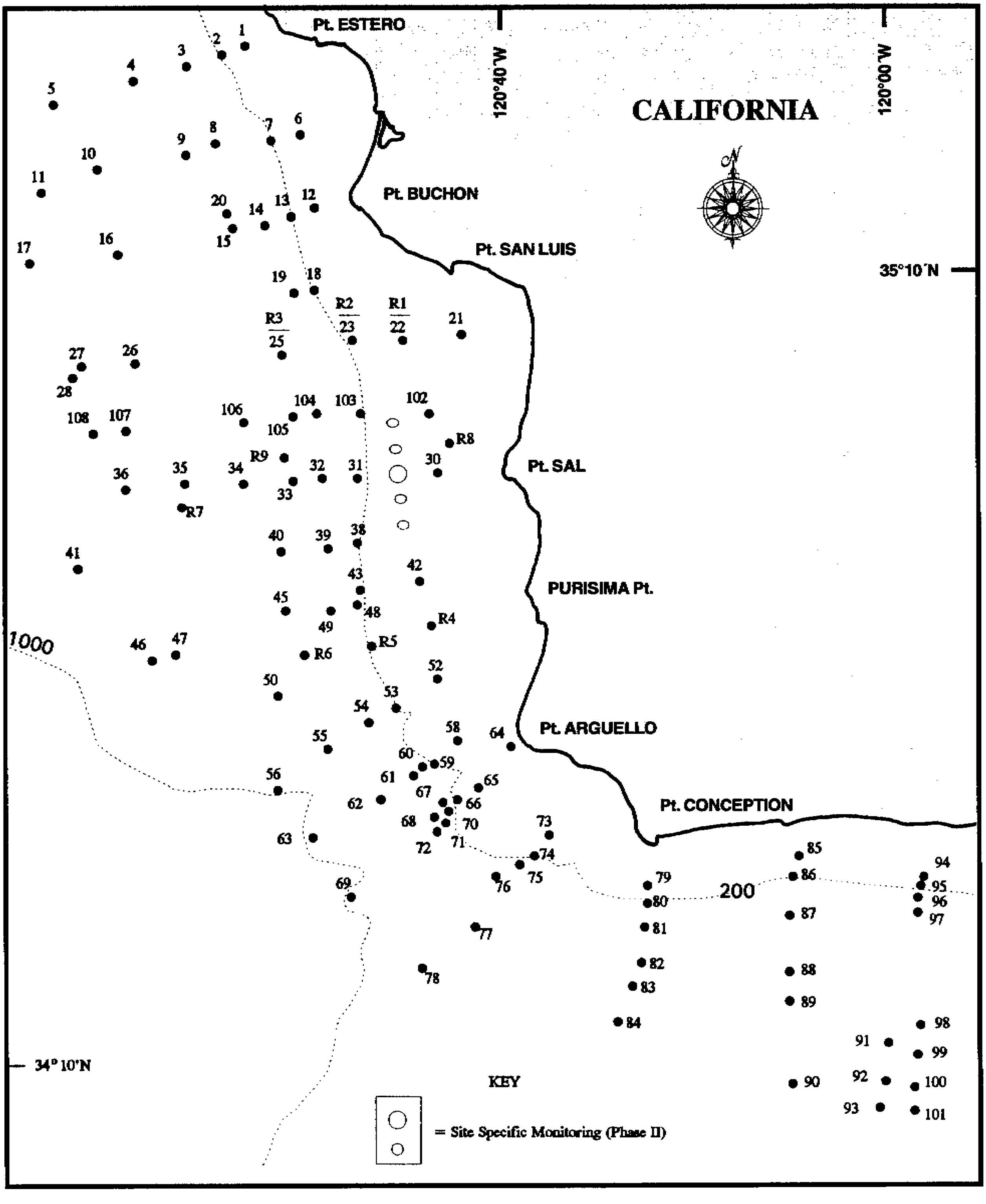

**Figure A.1.** Map showing location of soft-substrate stations from the Phase I Reconnaissance and Phase II Monitoring Programs.

**Table A.2.** Location of soft-substrate stations taken during the Phase II Monitoring Program.

| Station | Latitude | Longitude | Depth (m) |
|---|---|---|---|
| R-1 | 35°05.83′N | 120°49.16′W | 91 |
| R-2 | 35°05.50′N | 120°53.40′W | 161 |
| R-3 | 35°05.30′N | 121°00.90′W | 409 |
| R-4 | 34°43.01′N | 120°47.39′W | 92 |
| R-5 | 34°42.69′N | 120°50.83′W | 154 |
| R-6 | 34°41.40′N | 120°57.90′W | 410 |
| R-7 | 34°52.90′N | 121°10.30′W | 565 |
| R-8 | 34°55.30′N | 120°45.87′W | 90 |
| R-9 | 34°53.68′N | 120°59.12′W | 410 |
| PJ-1 | 34°55.79′N | 120°49.91′W | 145 |
| PJ-2 | 34°55.32’N | 120°49.59’W | 142 |
| PJ-3 | 34°56.26’N | 120°49.58’W | 138 |
| PJ-4 | 34°56.26’N | 120°50.24’W | 150 |
| PJ-5 | 34°55.32’N | 120°50.24’W | 152 |
| PJ-6 | 34°54.71′N | 120°49.91′W | 148 |
| PJ-7 | 34°55.79′N | 120°48.60′W | 123 |
| PJ-8 | 34°56.87′N | 120°49.91′W | 142 |
| PJ-9 | 34°55.79′N | 120°51.23′W | 169 |
| PJ-10 | 34°53.63′N | 120°49.91′W | 147 |
| PJ-11 | 34°57.95′N | 120°49.91′W | 136 |
| PJ-12 | 34°55.58′N | 120°49.91′W | 145 |
| PJ-13 | 34°56.01′N | 120°49.91′W | 144 |
| PJ-14 | 34°55.79′N | 120°49.26′W | 134 |
| PJ-15 | 34°55.79′N | 120°50.57′W | 155 |
| PJ-16 | 34°55.03′N | 120°48.99′W | 130 |
| PJ-17 | 34°56.56′N | 120°48.98′W | 126 |
| PJ-18 | 34°56.56′N | 120°50.84′W | 158 |
| PJ-19 | 34°55.03′N | 120°50.84′W | 167 |
| PJ-20 | 34°50.38′N | 120°49.91′W | 148 |
| PJ-21 | 35°01.23′N | 120°51.15′W | 143 |
| PJ-22 | 34°55.25′N | 120°49.93′W | 143 |
| PJ-23 | 34°56.33′N | 120°49.90′W | 143 |

**Table A.3.** Sampling dates of MMS Phase II Monitoring Program.

| Cruise | Date |
|---|---|
| 1-1 | October 1986 |
| 1-2 | January 1987 |
| 1-3 | May 1987 |
| 2-1 | July 1987 |
| 2-3 | October 1987 |
| 2-4 | January 1988 |
| 2-5 | May 1988 |
| 3-1 | October 1988 |
| 3-4 | May 1989 |

**Table A.4.** MMS Phase I - Locations of hard-substrate transects.

| Station | Beginning | | End | | Depth |
|---|---|---|---|---|---|
| | Latitude | Longitude | Latitude | Longitude | (m) |
| 1 A/B | 34°24.454′N | 120°01.876′W | 34°24.464′N | 120°00.878′W | 69-73.5 |
| 1 C/D | 34°24.076′N | 120°00.443′W | 34°24.184′N | 120°01.480′W | 73.5-78 |
| 2 A/B | 34°11.377′N | 120°29.318′W | 34°11.289′N | 120°28.774′W | 110-126 |
| 2 C/D | 34°10.984′N | 120°28.094′W | 34°10.780′N | 120°27.554′W | 120-123 |
| 4 A/B | 34°27.539′N | 120°40.364′W | 34°28.162′N | 120°40.189′W | 168-237 |
| 6 A/B | 34°30.246′N | 120°35.555′W | — —.— | — —.— | 54-63 |
| 6 C/D | — —.— | — —.— | 34°30.421′N | 120°34.315′W | 54-63 |
| 13 A/B | 34°42.570′N | 120°47.899′W | 34°42.107′N | 120°48.253′W | 92-100 |
| 13 C/D | 34°42.556′N | 120°48.147′W | 34°42.974′N | 120°47.424′W | 88.5-100.5 |
| 14 A/B | 34°43.589′N | 120°49.093′W | 34°42.826′N | 120°48.370′W | 96-105 |
| 14 C/D | 34°43.244′N | 120°49.406′W | 34°42.893′N | 120°48.822′W | 105-117 |
| 16 A/B | 34°46.544′N | 120°50.197′W | 34°45.912′N | 120°49.726′W | 91.5-123 |
| 17 A/B | 34°49.382′N | 120°50.768′W | 34°49.600′N | 120°50.688′W | 160.5-168 |
| 19 A/B | 34°47.833′N | 120°51.425′W | 34°47.097′N | 120°50.793′W | 148.5-177 |
| 20 A/B | 34°46.470′N | 120°50.289′W | 34°46.140′N | 120°49.885′W | 90-130.5 |
| 21 A/B | 34°47.335′N | 120°45.903′W | 34°47.548′N | 120°46.123′W | 75-90 |
| 22 A/B | 34°50.365′N | 120°48.221′W | 34°50.990′N | 120°48.365′W | 114-115.5 |
| 23 A/B | 34°49.868′N | 120°47.393′W | 34°50.003′N | 120°47.480′W | 93-102 |
| 25 A/B | 35°05.662′N | 120°47.562′W | 35°06.036′N | 120°47.652′W | 64.5-72 |
| 26 C/D | 35°11.586′N | 120°55.556′W | 35°11.555′N | 120°55.233′W | 108-111 |
| 27 A/B | 35°20.906′N | 120°59.657′W | 35°21.035′N | 120°59.603′W | 96-126 |
| 28 A/B | 35°21.539′N | 120°59.641′W | 35°21.867′N | 120°59.299′W | 96-105 |
| 29 A/B | 35°27.864′N | 121°05.331′W | 35°27.805′N | 121°05.277′W | 102-106.5 |

**Table A.5.** MMS Phase II - Locations of hard-substrate photosurvey stations.

| Station | Latitude | Longitude | Depth (m) |
|---|---|---|---|
| PH-E | 34°30.26′N | 120°42.76′W | 119 |
| PH-F | 34°30.81′N | 120°42.36′W | 105 |
| PH-I | 34°29.96′N | 120°41.68′W | 107 |
| PH-J | 34°29.82′N | 120°41.82′W | 117 |
| PH-K | 34°29.37′N | 120°42.26′W | 160 |
| PH-N | 34°29.21′N | 120°42.05′W | 166 |
| PH-R | 34°29.11′N | 120°42.67′W | 213 |
| PH-U | 34°31.48′N | 120°43.51′W | 113 |
| PH-W | 34°31.52′N | 120°45.86′W | 195 |

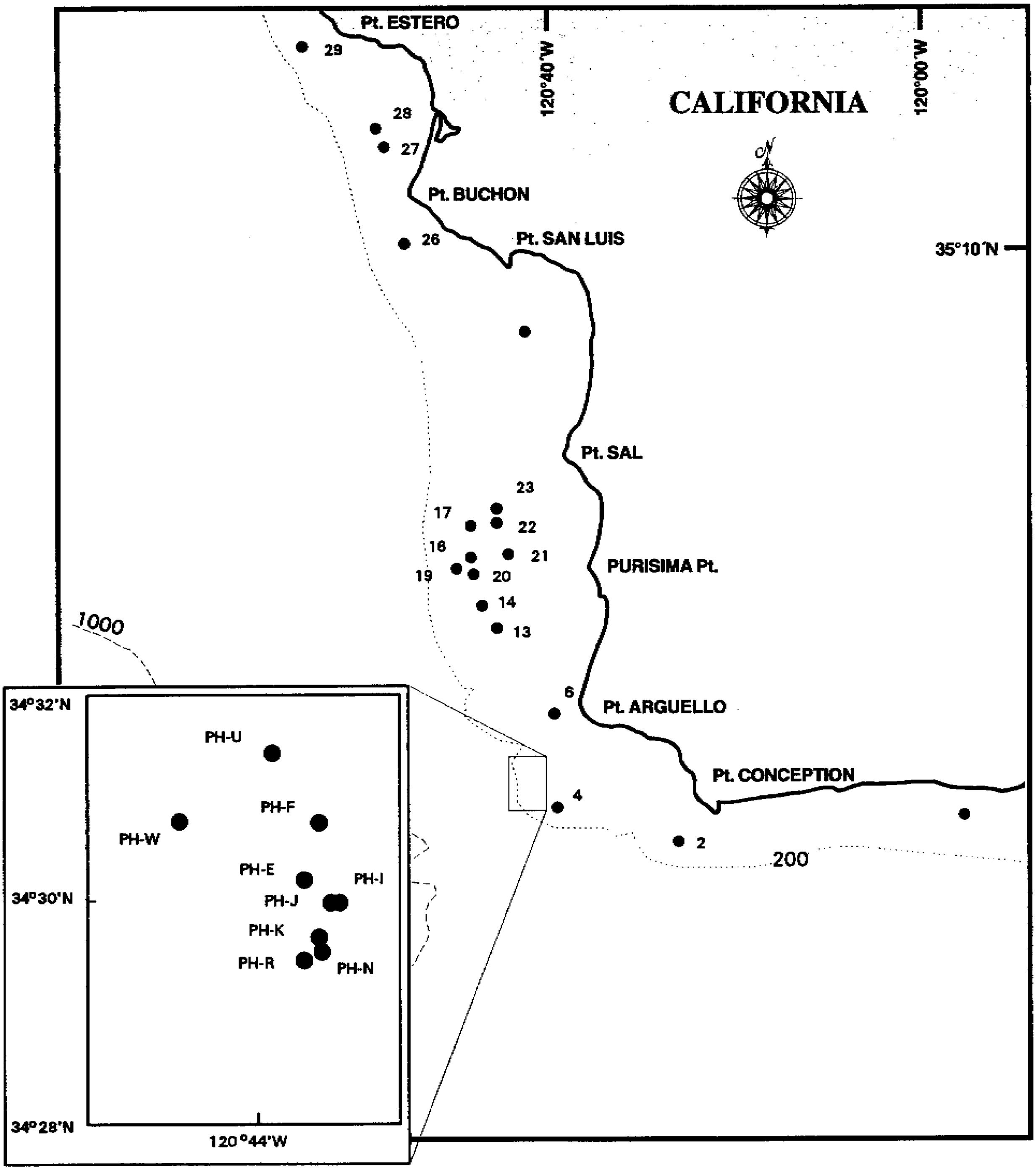

**Figure A.2.** Map showing location of hard-substrate stations from the Phase I Reconnaissance and Phase II Monitoring Programs. Phase II stations are indicated in the inset.

MARCH 3, 1849

## The Department of the Interior Mission

As the Nation's principal conservation agency, the Department of the Interior has responsibility for most of our nationally owned public lands and natural resources. This includes fostering sound use of our land and water resources; protecting our fish, wildlife, and biological diversity; preserving the environmental and cultural values of our national parks and historical places; and providing for the enjoyment of life through outdoor recreation. The Department assesses our energy and mineral resources and works to ensure that their development is in the best interests of all our people by encouraging stewardship and citizen participation in their care. The Department also has a major responsibility for American Indian reservation communities and for people who live in island territories under U.S. administration.

## The Minerals Management Service Mission

As a bureau of the Department of the Interior, the Minerals Management Service's (MMS) primary responsibilities are to manage the mineral resources located on the Nation's Outer Continental Shelf (OCS), collect revenue from the Federal OCS and onshore Federal and Indian lands, and distribute those revenues.

Moreover, in working to meet its responsibilities, the **Offshore Minerals Management Program** administers the OCS competitive leasing program and oversees the safe and environmentally sound exploration and production of our Nation's offshore natural gas, oil and other mineral resources. The MMS **Royalty Management Program** meets its responsibilities by ensuring the efficient, timely and accurate collection and disbursement of revenue from mineral leasing and production due to Indian tribes and allottees, States and the U.S. Treasury.

The MMS strives to fulfill its responsibilities through the general guiding principles of: (1) being responsive to the public's concerns and interests by maintaining a dialogue with all potentially affected parties and (2) carrying out its programs with an emphasis on working to enhance the quality of life for all Americans by lending MMS assistance and expertise to economic development and environmental protection.