OCS Study
MMS 96-0041

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

FINAL REPORT
Volume 14 of 14

Miscellaneous Taxa

U.S. Department of the Interior
Minerals Management Service
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FINAL REPORT
Volume 14 of 14

Miscellaneous Taxa

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For:

U.S. Department of the Interior
Minerals Management Service
Pacific OCS Region
770 Paseo Camarillo
Camarillo, California 93010

Under Contract No. 14-35-0001-30484

Minerals Management Service
Pacific OCS Region

July 1996

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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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ACCESS NUMBER: 30484.14

TECHNICAL SUMMARY

STUDY TITLE: Taxonomic Atlas of the Santa Maria Basin and Western Santa Barbara Channel.

REPORT TITLE: Taxonomic Atlas of the Santa Maria Basin and Western Santa Barbara Channel. Volume 14. Miscellaneous Taxa.

CONTRACT NUMBER: MMS Contract No. 14-35-0001-30484.

SPONSORING OCS REGION: Pacific.

APPLICABLE PLANNING AREA: Southern California.

FISCAL YEARS OF PROJECT FUNDING: 1990; 1991; 1992; 1993; 1994; 1995; 1996.

COMPLETION DATE OF REPORT: July 1996.

COSTS: FY 1989, $229,013; FY 1990, $150,000; FY 1991 $150,000; FY 1993 $150,000; FY 1995 $45,371.

CUMULATIVE PROJECT COST: $724,384.

PROJECT MANAGER: Andrew L. Lissner.

AFFILIATION: Science Applications International Corporation.

ADDRESS: 10260 Campus Point Drive, San Diego, California 92121.

PRINCIPAL INVESTIGATORS*: James A. Blake, Andrew L. Lissner.

KEY WORDS: Marine invertebrates, Brachipoda, Echiura, Sipuncula, Echinodermata, Crinoidea, Ophiuroidea, Asteroidea, Echninoidea, Holothuroidea, Hemicordata, Enteropneusta, Cordata, Urocordata, Ascidacea, taxonomy, California, Santa Maria Basin, Santa Barbara Channel, continental shelf.

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 14 are to provide keys, descriptions, and illustrations to the miscellaneous taxa of the Santa Maria Basin and Western Santa Barbara Channel. This volume treats the brachiopods, echiurans, sipunculans, crinoids, ophiuroids, asteroids, holothuroids, enteropneusts, and ascideans.

DESCRIPTION: Volume 14 includes a treatment of the brachiopods, echiurans, sipunculans, echinoderms, enteropneusts (hemichordates), and ascideans (urochordates). The eleven 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: A total of 97 species and 73 genera are included as representatives of 6 phyla: Brachiopoda (7 genera, 9 species), Sipuncula (4 genera and species), Echiura (4 genera, 3 species), Crinoidea (1 genus and species), Asteroidea (8 genera and species), Ophiuroidea (14 genera, 19 species), Echinoidea (4 genera and species), Holothuroidea (16 genera, 28 species), Enteropneusta (4 genera and species), and Ascidiacea (12 genera, 16 species). For the Ophiuroidea, a lectotype was designated for *Amphiura granulata* and the species was transferred to the genus *Amphichondrius. Amhioplus hexacanthus* was determined to be a synonym of *Dougaloplus amphacanthus.* Three new species of ascidians were described in a separate paper (Lambert, 1993).

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 Los Angeles Museum of Natural History is also being examined. The total number of species treated in the entire Taxonomic Atlas (14 volumes) may exceed 1,000 species.

Volume 14 represents the conclusion of the Atlas. Included in this volume are representatives of 6 different coelomate phyla: Brachiopoda, Sipuncula, Echiura, Echinodermata, Hemichordata (Enteropneusta), and Urochordaa (Ascidiacea). Five classes of the Echinodermata are included: Crinoidea, Asteroidea, Ophiuroidea, Echinoidea, and Holothuroidea. A total of 97 species and 73 genera are included among these various coelomate phyla distributed as follows: Brachiopoda (7 genera, 9 species), Sipuncula (4 genera and species), Echiura (4 genera, 3 species), Crinoidea (1 genus and species), Asteroidea (8 genera and species), Ophiuroidea (14 genera, 19 species), Echinoidea (4 genera and species), Holothuroidea (16 genera, 28 species), Enteropneusta (4 genera and species), and Ascidiacea (12 genera, 16 species). Each species is fully described and illustrated, with keys produced that allow users to identify the fauna. For the Ophiuroidea, a lectotype was designated for *Amphiura granulata* and the species was transferred to the genus *Amphichondrius. Amhioplus hexacanthus* was determined to be a synonym of *Dougaloplus amphacanthus.* Three new species of ascidians, *Molgula napiformis, Boltenia polyplacoderma,* and *Styela tesseris* were described in separate paper (Lambert, 1993: Proc. Calif. Acad. Sci. 48).

STUDY PRODUCT: Blake, J.A., P.H. Scott and A.L. Lissner (Editors). 1996. Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and Western Santa Barbara Channel. Volume 14. Miscellaneous Taxa. A final report prepared by Science Applications International Corporation, for the U.S. Department of the Interior, Minerals Management Service, Pacific OCS Region, Camarillo, CA. OCS Study MMS 96-0041. Contract No. 14-35-0001-30484.

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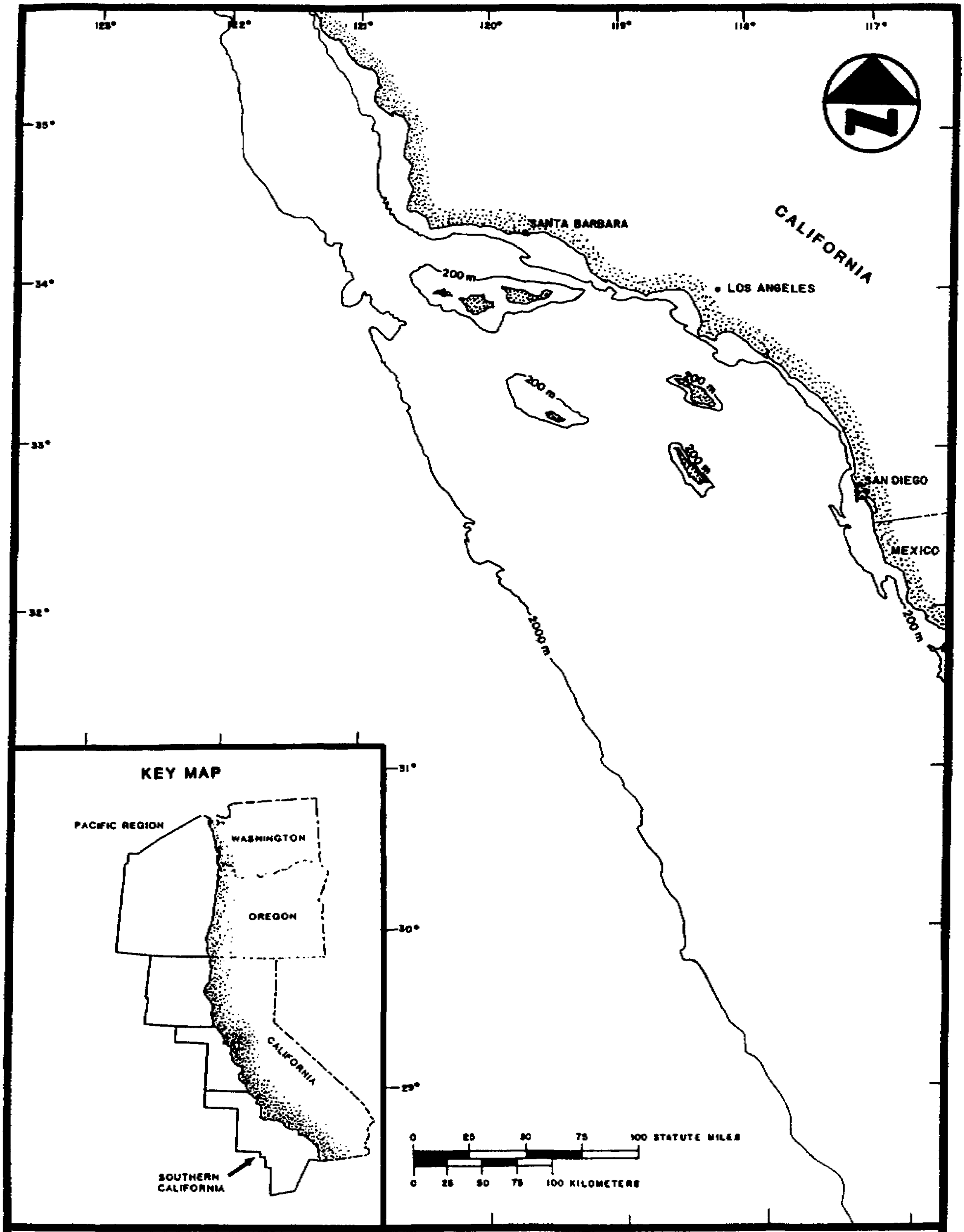
[*] P.I's affiliation may be different than that listed for Project Manager(s).



Southern California Planning Area Indicating the Taxonomic Atlas Study Region.

50272-101

REPORT DOCUMENTATION PAGE

1. REPORT NO. MMS 96-0041

2.

3. Recipient's Accession No.

4. Title and Subtitle
Taxonomic Atlas of the Santa Maria Basin and Western Santa Barbara Channel. Volume 14. Miscellaneous Taxa.

5. Report Date
July 1996

6.

7. Author(s)
James A. Blake, Paul H. Scott and Anderw L. Lissner (editors)

8. Performing Organization Rept. No.

9. Performing Organization Name and Address

Science Applications International Corporation
10260 Campus Point Drive
San Diego, California 92121

10. Project/Task/Work Unit No.

11. Contract(C) or Grant(G) No.
(C) 14-35-001-30484
(G)

12. Sponsoring Organization Name and Address

Mineral Management Service, U. S. Department of the Interior,
Pacific OCS Region, 770 Paseo Camarillo
Camarillo, California 93010

13. Type of Report & Period Covered
Final 14 of 14 volumes,
9/89 to 7/96

14.

15. Supplementary Notes

Contributing authors: Mary Bergen, Debra Hart, Gordon Hendler, F. G. Hochberg, Andrew Lissner, Gretchen Lambert, John F. Pilger, Paula S. Winchell, Keith H. Woodwick.

16. Abstract (Limit: 200 words)

Volume 14 represents the conclusion of the Atlas. Included in this volume are representatives of 6 different coelomate phyla: Brachiopoda, Sipuncula, Echiura, Echinodermata, Hemichordata (Enteropneusta), and Urochordaa (Ascidiacea). Five classes of the Echinodermata are included: Crinoidea, Asteroidea, Ophiuroidea, Echinoidea, and Holothuroidea. A total of 97 species and 73 genera are included among these various coelomate phyla distributed as follows: Brachiopoda (7 genera, 9 species), Sipuncula (4 genera and species), Echiura (4 genera, 3 species), Crinoidea (1 genus and species), Asteroidea (8 genera and species), Ophiuroidea (14 genera, 19 species), Echinoidea (4 genera and species), Holothuroidea (16 genera, 28 species), Enteropneusta (4 genera and species), Ascidiacea (12 genera, 16 species). Each species is fully described and illustrated, with keys produced that allow users to identify the fauna. For the Ophiuroidea, a lectotype was designated for *Amphiura granulata* and the species was transferred to the genus *Amphichondrius*. *Amhioplus hexacanthus* was determined to be a synonym of *Dougaloplus amphacanthus*. Three new species of ascidians, *Molgula napiformis, Boltenia polyplacoderma,* and *Styela tesseris* were described in separate paper (Lambert, 1993: Proc. Calif. Acad. Sci. 48).

17. Document Analysis a. Descriptors

Marine invertebrates, Brachipoda, Echiura, Sipuncula, Echinodermata, Crinoidea, Ophiuroidea, Asteroidea, Echninoidea, Holothuroidea, Hemicordata, Enteropneusta, Cordata, Urocordata, Ascidacea, taxonomy, California, Santa Maria Basin, Santa Barbara Channel, continental shelf.

b. Identifiers/Open-Ended Terms

Taxonomic Atlas, Keys to species, faunal guide, marine ecology, crustaceans, marine benthos.

c. COSATI Field/Group

18. Availability Statement
Unlimited

19. Security Class (This Report)
Unclassified

20. Security Class (This Page)

21. No. of Pages
302

22. Price

(See ANSI-Z39.18) *See Instructions on Reverse*

OPTIONAL FORM 272 (4-77)
(Formerly NTIS-35)
Department of Commerce

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Acknowledgments

This study was funded by the Pacific Outer Continental Shelf Region of the U.S. Department of the Interior, Minerals Management Service, Washington, D.C., under Contract No. 14-35-0001-30484. Ms. Marie Murphy of the Santa Barbara Museum of Natural History provided graphic design and production assistance for this volume. Ms. Adele Smith, also of the Santa Barbara Museum, assisted with editing and production of this volume.

List of Acronyms

AMNH	American Museum of Natural History, New York, USA.
ANSP	Academy of Natural Sciences, Philadephia, USA.
BLM	Bureau of Land Management.
BMNH	The Natural History Museum, London, U.K.
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.
CAMP	California Phase II Monitoring Program (by MMS).
CASIZ	California Academy of Sciences, Department of Invertebrate Zoology, San Francisco, California, USA.
LACM	Natural History Museum of Los Angeles County, Los Angeles, California, USA.
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA.
MMS	United States Minerals Management Service.
SCAMIT	Southern California Association of Marine Invertebrate Taxonomists.
SBMNH	Santa Barbara Museum of Natural History, Santa Barbara, California, USA.
SCCWRP	Southern California Coastal Waters Research Project
SDNHM	San Diego Natural History Museum, San Diego, California, USA.
SSB	S. Stillman Berry Collection, now housed at the Santa Barbar Museum of Natural History.
SIO	Scripps Institute of Oceanography, La Jolla, California, USA.
UCSB	University of California, Santa Barbara, USA.
USNM	United States National Museum. A historical designation for the National Museum of Natural History (NMNH), Smithsonian Institution, Washington, D.C., USA.
ZMUC	Zoological Museum, University of Copenhagen, Denmark.

1. THE BRACHIOPODA

by

F.G. Hochberg[1]

Introduction

Brachiopods or "lamp shells" are a phylum of exclusively marine invertebrates. The phylum is characterized by the presence of a lophophore, a tentacle bearing structure used for feeding and respiration. The lophophore unites the brachiopods with several other phyla, namely the Phoronida and the Bryozoa or Ectoprocta. Brachiopods are solitary animals enclosed in a bivalved shell and typically are either attached to a hard substrate or anchored in a soft substrate by a tough, flexible stalk or pedicle. A diversity of brachiopods in the two classes, Inarticulata and Articulata, is illustrated in Figure 1.1.

Approximately 350 species of living brachiopods are known which is but a small fraction of the more than 20,000 extinct species described in the literature. The fossil record for brachiopods dates back at least 600 million years. Off the coast of California brachiopods range in depths from the intertidal to several thousand meters. Adults range in length from 1-100 mm.

Morphology and Anatomy

Shell morphology with a focus on fossil forms is documented in an extensive literature summarized in Moore (1965). Details of internal anatomy are know for relatively few living species. Most anatomical and histological studies are 50-100 years old but still remain the principal original sources of information and illustrations (for reviews see Hyman, 1959; Williams and Rowell, 1965; and Rudwick, 1970). The literature on functional morphology is reviewed in James *et al.* (1992). Some of the key features used in systematics are briefly summarized below. Additional details can be found in the references listed above.

Shells. The brachiopod shell is composed of two separate valves that are bilaterally symmetrical but dissimilar. The valves are oriented dorsal and ventral in reference to the body unlike in bivalve mollusks in which the valves are oriented lateral to the animal inside. In life the ventral valve in articulates typically is uppermost in reference to the substrate to which they are attached. The ventral valve, often termed the pedicle valve, is generally larger and deeper than the dorsal valve. It contains the hole or foramen, through which the pedicle protrudes. The dorsal, or brachial valve, contains the lophophore and the supporting loop.

Brachiopods are identified principally on descriptions of the size, shape, sinuosity and sculpture of the valves. Visually they are identified by figures which illustrate dorsal, ventral, lateral and end views. Shapes are expressed by a comparison of ratios of lengths to widths or depths to widths. The sinuosity of valves is described based on the anterior and lateral commissures. Simple folding patterns as used in the following text are illustrated in Figure 1.3B. External valve surfaces may be smooth or textured with radiating ribs, concentric growth lines, spines and a diversity of other features. Valves may be pitted with canals or punctae which are seen as tiny holes in the shell (Figure 1.12E). The presence of muscle attachment scars leave characteristic patterns on the internal surfaces of valves (Figs. 1.2C and D, 1.5D).

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The valves are either locked together posteriorly by teeth and sockets (Class Articulata) or held together solely by muscle (Class Inarticulata). The articulation of teeth and sockets in the hinge of articulate brachiopods is important in diagnosing various taxa in the class.

There is a complex and rather formidable terminology that covers in minute detail every feature used to describe brachiopod shells (see Moore, 1965).

Pedicle. Most brachiopods are attached to a hard substrate or anchored in soft sediments by a cylindrical stalk or pedicle which emerges from the posterior end of the shell (Figs. 1.1, 1.2). In a few cases, such as *Neocrania*, the pedicle is absent. In inarticulates the pedicle emerges between the two valves but in the articulates it emerges from the beak of the ventral valve through a hole or foramen. The foramen is formed by the partial closure of the delthyrium by the deltidial plates. The opening is described as being either complete or incomplete.

Lophophore. The lophophore develops as an outgrowth of the anterior body wall. It projects into and fills the greater part of the mantle cavity. The lophophore is lined along its entire length with ciliated tentacles. It functions for both feeding and respiration.

Compared with other lophophorate phyla (e.g., Phoronida, Bryozoa) brachiopod lophophores come in a tremendous diversity of shapes and sizes. Specific named patterns characterize the various higher taxa. The evolution of lophophore shape and efficiency involves increasing lengths and complexity in bending to accommodate more tentacles (Figure 1.3A). The lophophore is supported by a calcareous loop or brachidium (Figs. 1.1D, 1.2D).

Mantle. The mantle of brachiopods is patterned with a series of coelomic channels or sinuses. These mantle canals may leave impressions on the inner surfaces of the valves or may be seen through the shell in live animals or wet preserved specimens. Mantle canal patterns are characteristic generic features (Figure 1.2E).

In addition, spicules may be present in the mantle tissue of some brachiopods. The presence or absence of spicules is another character used at the generic level and above.

Reproduction

Sexes are separate in most brachiopods, although a few genera, such as *Platidia*, are hermaphrodites. Sexual dimorphism appears to be absent. Two pairs of gonads (dorsal and ventral) develop from cells lining the coelom. When mature they expand greatly to fill the space within the mantle. The majority of brachiopods studied do not appear to have a breeding cycle, although a few exhibit distinct spawning seasons. When spawning occurs sperm and eggs are released and pass into the mantle cavity where they are then carried to the exterior in exhalent currents. Fertilization in these cases is external. In a number of cases ova are retained in the mantle cavity and following internal fertilization the embryos undergo extended development in a brood pouch.

Details of larval development are known in only a few cases (see Reed, 1987 and Long and Stricker, 1994 for reviews of reproduction and development in west coast species). Free swimming, ciliated brachiopod larvae, known as "protegula," spend varying periods in the plankton depending on the class. In articulates the protegula are comprised of three segments. Following a brief phase in the plankton, they settle at an early stage of growth. The protegula of inarticulates consist of two segments. These larvae spend a much longer period in the plankton and are much further advanced when they settle to the bottom. At the point of settlement in both classes the valves are present, the lophophore is well developed and used for both feeding and swimming, and the pedicle is evident at the edge of the posterior mantle. Settlement may be delayed if the bottom is too deep or if the substrate first contacted is unsuitable.

Biology and Classification

The paper by James *et al.* (1992) provides the most comprehensive recent review of the biology and ecology of living brachiopods.

Overviews of brachiopod classification variously are treated in Moore (1965) and Foster (1982). Evolution of the phylum is discussed in Williams and Hurst (1977) and Wright (1979).

The identification of brachiopods from the Eastern North Pacific is in need of critical reevaluation which is beyond the scope of this chapter. Many species appear to be extremely variable not only in color but shape and sculpture which has created considerable confusion in the literature. There is a morass of synonyms in which the validity of many Recent and fossil variety and subspecies names have not been adequately reviewed in the recent literature. Bernard (1972) provides the most recent comprehensive, illustrated summary of living forms from the Eastern North Pacific. Deep-water brachiopods, including several species treated here, are covered in Cooper (1972, 1982). West coast fossils are reviewed in Hertlein and Grant (1944, 1960).

Brachiopod shells are comparable to the shells of mollusks in attracting collectors which has resulted in a proliferation of names. Brachiopods are often listed with mollusks in earlier faunal reports from a variety of locations in the Eastern North Pacific. For the purposes of this paper I have not attempted to review the extensive fossil literature. In the synonymy section for each species treated below I have attempted to list the key works to provide a chronology of spellings or mispellings of the morass of names that have been used for west coast species. For more complete citations the reader is referred to Dall (1920) and to Hertlein and Grant (1944, 1960).

Collection and Preservation

Deep-water brachiopods typically are collected utilizing bottom trawls, benthic sleds and dredges. Following collection specimens should be sorted out from the remainder of the catch and cleaned of any debris. Before epifaunal specimens are removed from their substrates observations should be made to determine whether the substrate is biological (type of organism to which they are attached; whether the organic substrate is living or dead) or inorganic (rock type). If possible, preserve small pieces of substrate along with the sample for later identification. Avoid storing large rocks with brachiopods because their shells are very fragile and subject to breakage if handled or placed together with heavy objects. Additional notes should be taken to indicate whether a given species is attached singly, in small clusters or in dense aggregations.

Most brachiopod species are dried for ease of storage and study. Identifications most often are based solely on shell morphology and do not rely on internal anatomy. However, in any given collecting program where material might be utilized for taxonomic study a subsample should be preserved in alcohol. Small brachiopods may be placed directly into 70% ethyl alcohol. Large specimens are narcotized by placing them in alcoholized sea water for several hours before they are placed into alcohol for preservation. Prior to preservation place a toothpick or small piece of cork between the valves to keep them open. Brachiopods should not be fixed or stored in formalin unless it is buffered to prevent damage to the shell.

Specimens to be prepared for anatomical study must first be decalcified in Bouin's solution or another appropriate decalcifying agent. Stained whole mounts of small, flat brachiopods (e.g., *Glottidia, Neocrania, Platidia*) are easily prepared. Larger, deep-bodied specimens need to be sectioned and stained prior to examination.

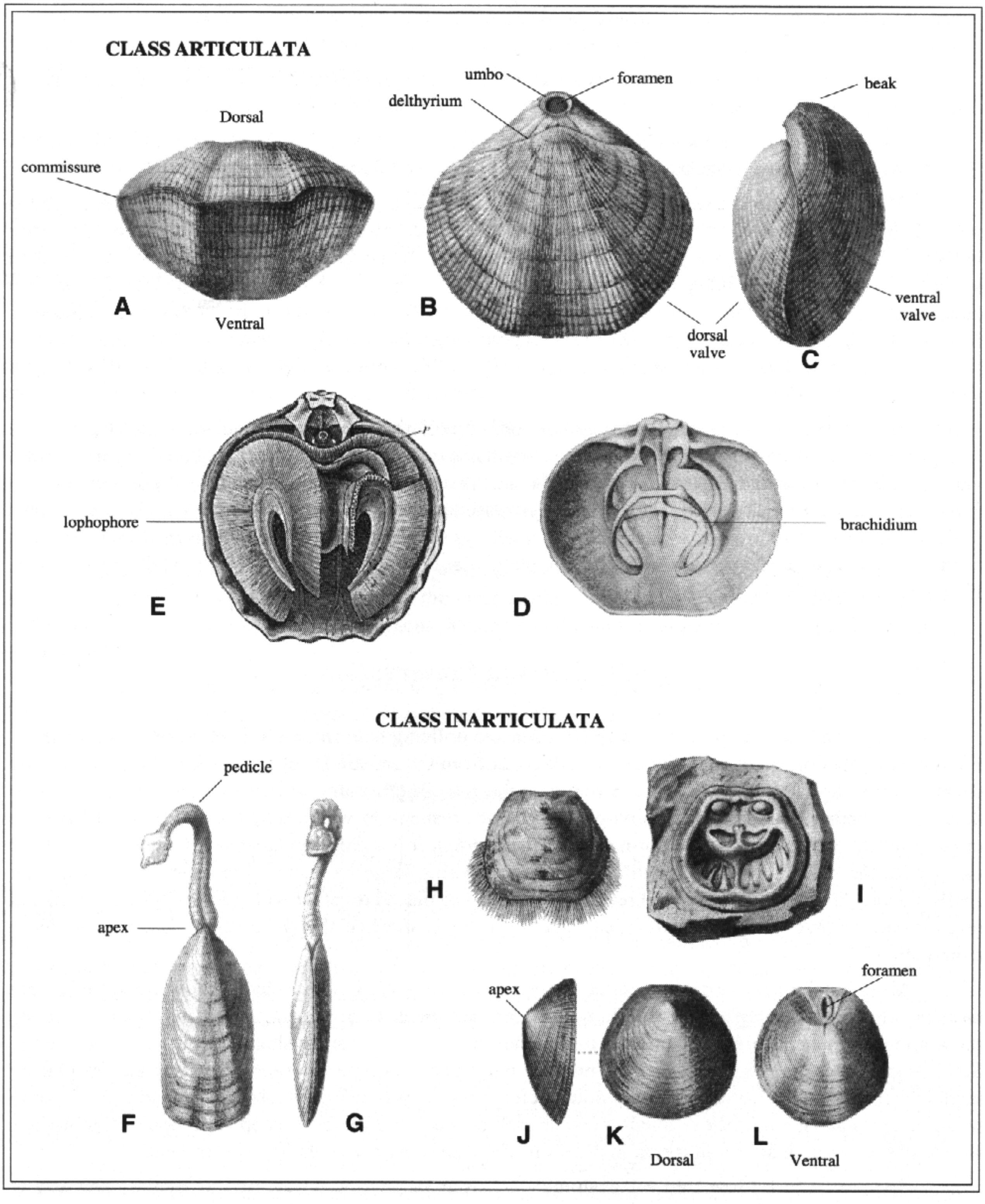

Figure 1.1. Diversity of shell types in the two classes of brachiopods - Articulata and Inarticulata. A. anterior end view; B, F, H, K, dorsal views; C, G, J, lateral views; D, E, interior view of dorsal valve; I, interior view of ventral valve; L, ventral view. A-C, *Terebratella*; D and E, *Magellania*; F, G, *Lingula*; H , I, *Crania*; J-L, *Discinisca*.

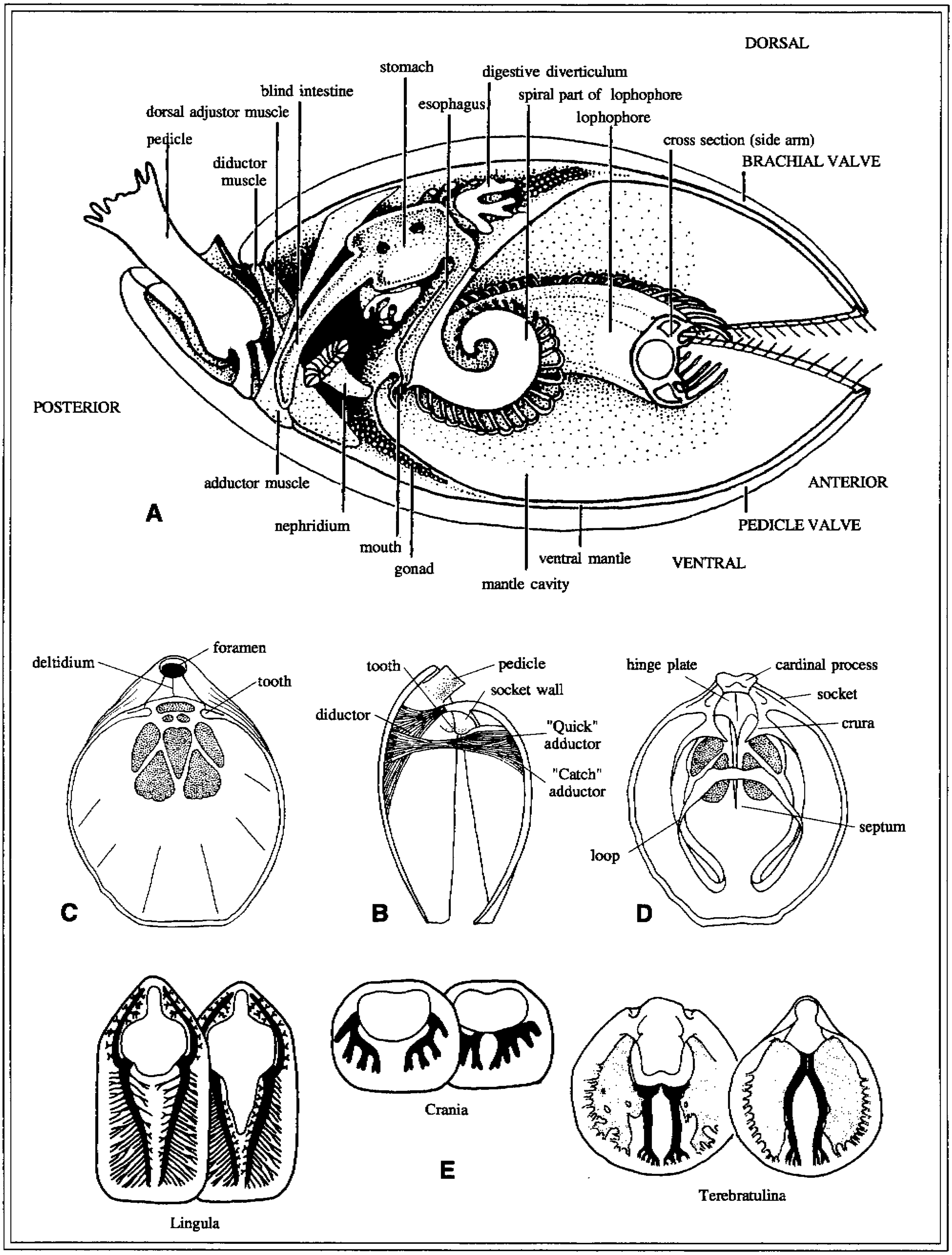

Figure 1.2. Diagramatic representations of brachiopod anatomy and morphology. A. principal organs, lateral view; B, articulation and muscle system, median section; C, D, muscle scars, shell and brachidium terminology, interior views; C, ventral or pedicle valve; D, dorsal or brachial valve; E, mantle canal patterns, often seen through the shell, in a diversity of brachiopod genera. (A , E, from Williams and Rowell, 1965; B, modified from Rudwick, 1961; C, D, modified from Davidson, 1886).

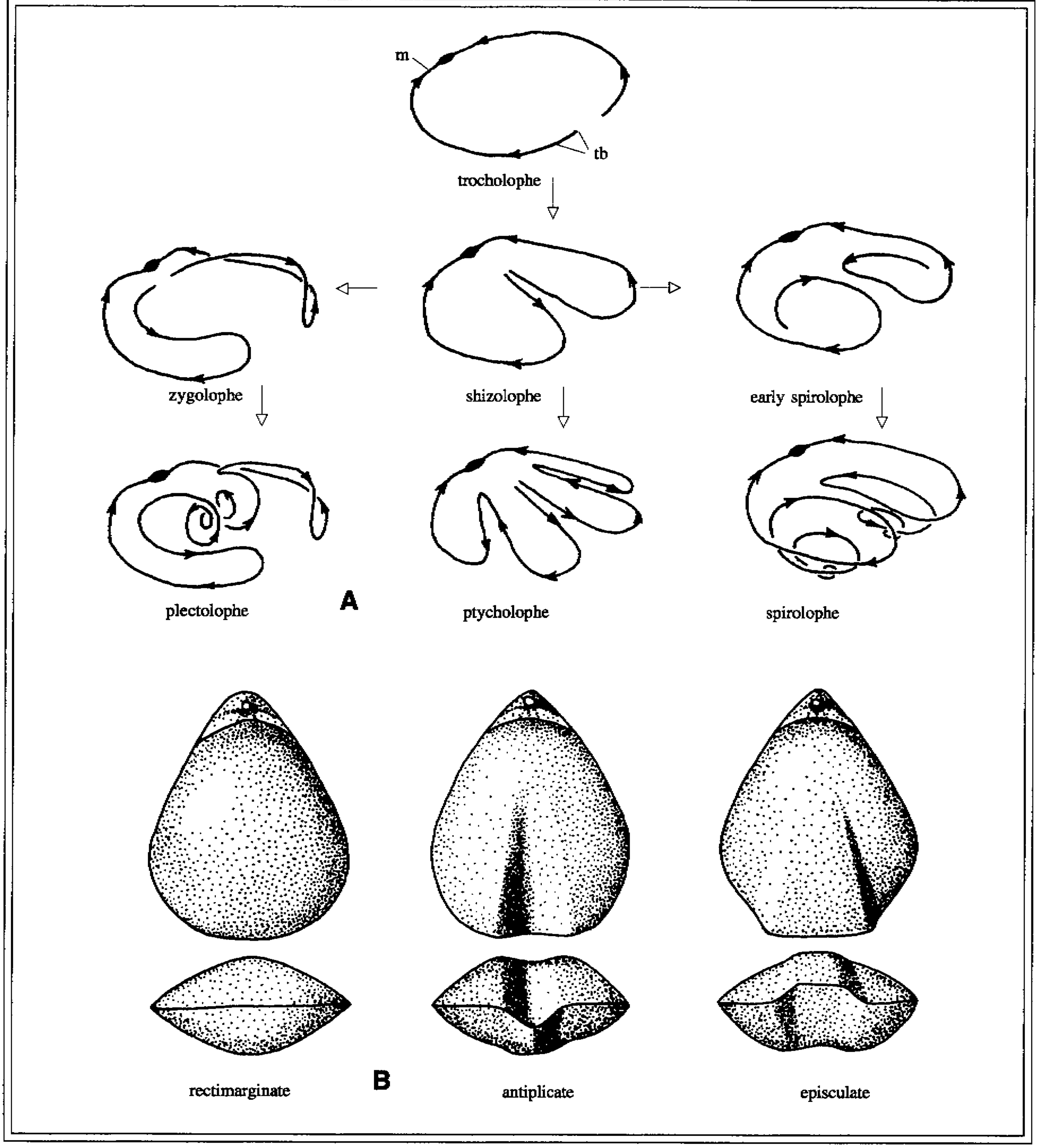

Figure 1.3. Diagramatic representations of brachiopod anatomy and morphology. A, lophophore loop patterns; B, simple types of folding patterns in the anterior commissure of the shell, anterior end views. Abbreviations: m, mouth; tb, tips of brachia. (A, from Rudwick, 1962; B, from Williams and Rowell, 1965).

Glossary

Adductor muscles. Paired muscles which, on contraction, close shell.

Adjustor muscles. Two pairs of muscles in many articulate brachiopods attached to base of pedicle and responsible for moving shell relative to pedicle.

Articulation. Interlocking of 2 valves by projections along their posterior margins; typically effected in Articulata by 2 ventral teeth filling sockets of brachial valve.

Beak. Extremity of umbo, commonly pointed.

Body cavity. Posterior coelomic space between the 2 valves, enclosed by epithelium, containing body organs (digestive system, muscles, metanephridia, etc.).

Brachial cavity. Anterior space between the valves, lined by mantle and body-wall epithelium, containing lophophore.

Brachial valve. See dorsal valve.

Brachidium. Calcareous support for lophophore in form of loop or spires.

Caeca. Outgrowths of outer mantle epithelium contained in endopunctae of shell (singular = caecum).

Cardinal process. Blade or variably shaped boss of secondary shell situated medially in posterior end of brachial valve and serving for separation or attachment of diductor muscles.

Commissure. Line of junction between the edges of the two valves.

Costa. Radial ridge on external surface of shell originating at margin of protegulal node or any coarse rib.

Costate. Shell radially ornamented by costae.

Crenulated. Scalloped or notched valve margin.

Crura. Two processes which extend from septum to give support to posterior end of lophophore; distal ends may also be prolonged into primary lamellae of spire or descending branches of loop (singular = crus).

Crural plates. Shelly plates extending medialy from the crura, sometimes fusing to floor of the dorsal valve.

Delthyrium. Median triangular aperture in margin of the ventral valve, wholly or partially used as the pedicle aperture.

Deltidial plates. Pair of shelly plates, growing medially from margins of delthyrium, partly or completely closing pedicle aperture.

Dental plates. Shelly walls supporting hinge teeth from the floor of ventral valve.

Diductor muscles. The paired muscles which, on contraction, open the shell by pulling on the cardinal process, situated on opposite side of the hinge axis from ventral areas of attachment.

Dorsal valve. Valve that contains skeletal support for lophophore and never wholly accommodates pedicle; commonly smaller than pedicle valve (= brachial valve).

Endopunctae. Minute canals which perforate interior of the shell but do not extend to external surface; occupied by caecal prolongations of the outer epithelium.

Foramen. Aperature through which the pedicle passes; typically confined to the ventral valve; aperature may be complete or incomplete.

Hinge plates. A general term for skeletal structure connected with the sockets and crura in dorsal valve.

Hinge teeth. Two principal articulating processes situated at anterolateral margins of delthyrium and articulating with dental sockets in brachial valve.

Impunctate. Shell not perforated by minute canals or holes (see punctate).

Loop. Delicate shelly loop-like support for lophophore, exending anteriorly from crura as closed apparatus; generally ribbon-like with or without supporting septum from floor of dorsal valve (= brachial loop).

Lophophore. Feeding organ with filiform appendages, symmetrically disposed about mouth; typically suspended from anterior body wall but may be attached to dorsal mantle; occupies mantle or brachial cavity.

Mantle. Prolongation of body wall as fold of ectodermal epithelium; secretes shell tissue.

Mantle canals. Flattened, tube-like extensions of body cavity radiating into the mantle from the body cavity (= pallial sinuses).

Median septum. A vertically disposed shell plate of variable height or length in median plane of either valve, normally present in body cavity only.

Pallial sinuses. See mantle canals.

Pedicle. Cuticle-covered stalk, commonly protruding from ventral valve; attaches animal to substratum; controlled by muscles.

Pedicle aperture. See foramen.

Pedicle valve. See ventral valve.

Periostracum. The thin organic layer on exterior of the shell.

Protegulum. The first-formed valves secreted by the juvenile brachiopod; commonly distinguished from later shell by absence of ornamentation.

Punctate. Used to describe a shell perforated by minute holes or canals known as endopunctae.

Ribs. A form of external ornamentation in which the shell surface is radially ridged; very fine radial ridges termed striations.

Septum. Relatively long, narrow elevation of secondary shell, commonly blade-like.

Setae. Chitinous bristle arising from invagination of muscle groove (singular, seta).

Sockets. A pair of cavities, near posterior margin of dorsal valve, into which the teeth fit (= dental sockets).

Socket ridges. Ridges of shell, extending anterolaterally from cardinal process, bordering the inner side of tooth sockets on dorsal valve.

Spicules. Small, irregular bodies of calcite secreted within connective tissue of body wall, mantle and lophophore.

Spondylium. Trough-shaped or spoon-like apparatus complosed of dental plates in various stages of coalescence, usually with median septum.

Strophic. Shell with true hinge line parallel to hinge axis.

Sulcate. Form of folding with dorsal valve bearing median sulcus; single sulcus in dorsal valve, opposed by fold in ventral valve (reverse of uniplicate).

Sulciplicate. Type of fold involving a raised uniplicate fold with median sulcation (= biplicate; reverse of intraplicate)

Sulcus. Depression of valve surface, externally concave in transverse profile and radial from umbo.

Teeth. Two principal articulatory processes, situated on ventral valve at anterolateral margins of delthyrium (= hinge tooth; singular, tooth).

Tubercles. Large nodose protuberances on shell surface.

Umbo. Posterior median, apical region of either valve, containing the beak.

Uniplicate. Single fold in dorsal valve opposing a sulcus in ventral valve (reverse of sulcate).

Ventral valve. Valve through which pedicle commonly emerges; usually larger than dorsal valve (= pedicle valve).

List of Species

Class Inarticulata Huxley, 1869

- Order Lingulida Waagen, 1885
  - Superfamily Linguloidea Menke, 1828
    - Family Lingulidae Menke, 1828
      - *Glottidia albida* (Hinds, 1844)

- Order Acrotretida Kuhn, 1949
  - Suborder Craniidina Waagen, 1885
  - Superfamily Cranioidea Menke, 1828
    - Family Craniidae Menke, 1828
      - *Neocrania californica* (Berry, 1921)

Class Articulata Huxley, 1869

- Order Rhynchonellida Kuhn, 1949
  - Superfamily Rhynchonelloidea Gray, 1848
    - Family Frieleiidae Cooper, 1959
      - *Frieleia halli* Dall, 1895

- Order Terebratulida Waagen, 1883
  - Suborder Terebratulidina Waagen, 1883
  - Superfamily Cancellothyridoidea Cooper, 1973
    - Family Cancellothyrididae Thompson, 1926
      - *Terebratulina crossei* Davidson, 1882
      - *Terebratulina unguicula* (Carpenter, 1865)

  - Suborder Terebratellidina Muir-Woods, 1955
  - Superfamily Terebratelloidea King, 1850
    - Family Laqueidae Hatai, 1965
      - *Laqueus californianus (Koch, 1848)*
    - Family Dallinidae Beecher, 1893
      - *Terebratalia occidentalis (Dall, 1871)*
      - *Terebratalia transversa (Sowerby, 1846)*
    - Family Platidiidae Thompson, 1927
      - *Platidia hornii (Gabb, 1861)*

Key to Genera of West Coast Brachiopods

1A.	Shell flattened dorsal ventrally (depth less than one-half width)	2
1B.	Shell deep, not flattened (depth greater than one-half width)	4
2A.	Pedicle absent; lower valve cemented directly to substrate	*Neocrania*
2B.	Pedicle present	3
3A.	Shell large, elongate, lateral margins subparallel; pedicle very long; infaunal, in soft substrates	*Glottidia*
3B.	Shell small, round in outline; pedicle very short; foramen extending to brachial valve; epifaunal, or attached to hard substrates	*Platidia*
4A.	Shell thin, translucent	5
4B.	Shell thick, solid, not translucent	6
5A.	Shell inflated, shape globular to elongate, longer than wide; live in depths less than 500 m	*Laqueus*
5B.	Shell flattened, shape triangular, as wide as long; live in depths greater than 500 m	*Frieleia*
6A.	Shell usually longer than wide; anterior valve margin straight (without undulations) or very slightly sulcate; beak large	*Terebratulina*
6B.	Shell usually wider than long; anterior valve margin with pronounced undulations; beak small	*Terebratalia*

Descriptions of Species

Class Inarticulata Huxley, 1869

Diagnosis. Valves not locked together posteriorly; hinge teeth and sockets absent; valves held together by muscles and body tissues. Lophophore spirolophous or zygolophous; never supported by brachidium. Pedicle absent or moderately long; originating embryologically from ventral mantle. Embryological development of mantle direct without reversal. Functional anus present. Two groups of muscles present — adductors and obliques. Spicules absent in soft parts of body. Shell chitionophosphatic or calcareous.

Order Lingulida Waagen, 1885

Diagnosis. Valves thin, shape elongate, narrow; partly chitinous with calcium phosphate as principal inorganic constituent. Pedicle long, flexible; containing coelomic lumen.

Superfamily Linguloidea Menke, 1828

Family Lingulidae Menke, 1828

Diagnosis. With characters of the order.

Type Genus. *Lingula* Bruguière, 1797

Genus *Glottidia* Dall, 1870

Diagnosis. Shell elongate, lateral margins gently convex to subparallel; thin, slightly thickened in areas of muscle attachment. Pedicle valve with two low septa internally, diverging from beak and extending forward about 1/3 length of valve; brachial valve with low median septum of similar length. Gill ampullae project into mantle cavity from mantle.

Type Species. *Lingula albida* Hinds, 1845; by original designation.

Remarks. Externally similar to *Lingula* but characterized by the presence of internal septa.

Glottidia albida (Hinds, 1844)

Figure 1.4 A-C

Lingula albida Hinds, 1844: 71, pl. 19, fig. 4. —Sowerby, 1847: 339, pl. 67, fig. 6. —Davidson, 1852: 377. —Reeve, 1859: pl. 1, fig. 4. —Carpenter, 1864: 636. —Cooper, 1867: 3; 1888: 246. —Yates, 1890: 39. —Thompson, 1927: 128.

Glottidia albida: Dall, 1870: 157, pl. 8, figs. 1-6; 1873: 204; 1874: 296; 1877: 160-161; 1878: 28; 1889: 232; 1920: 267.—Davidson, 1888: 221, pl. 28, figs. 2-4. —Beecher, 1892: pl. 1, figs. 1-3. —Arnold, 1903: 94. —Kelsey, 1907: 40. —Berry, 1907: 18.—Oldroyd, 1924b: 221, pl. 49, fig. 3. Johnson and Snook, 1927: 153-154, fig. 127. —Hatai, 1936: 78. —Burch, 1942: 1. Hertlein and Grant, 1944: 12-16, text-figs. 1a-c, pl. 1, figs. 5-7. —Smith and Gordon, 1948: 209. —Mattox, 1956: 76-77, 80, 83. —Hertlein and Grant, 1960: 89-90, pl. 19, figs. 17, 18, 23-25. —Jones and Barnard, 1963: 27-52, fig. 1. —Ricketts and Calvin, 1968: 319, fig. 236. —MacGinitie and MacGinitie, 1968: 177-178, fig. 55. —Zimmer and Haderlie, 1980: 110.

Glottidea [sic] *albida*: Keep, 1904: 14, text-fig. 7; 1911: 19, text-fig. 9. —Keep and Baily, 1935: 19, text-fig. 1.

Glottidia palmeri: Dall, 1920: 267-268 [in part]. —Burch, 1942:1-2. (**Not** Dall).

Material Examined. *California*: Santa Maria Basin, Station 21, 1 specimen, (24.2 mm TL), USNM; 4 specimens,(2.7-15.9 mm TL); Station 64, 59m; SBMNH.

Additional material examined: 13 lots (see List of Additional Specimens Examined).

Description. *Shell* smooth, thin; shape narrow and elongate. *Valves* similar in size, sides parallel to subparallel. *Pedicle* long (longer than shell); fleshy. *Color* of shell - brownish white when alive or freshly dead, often with red-brown or brownish markings.

Shell size medium; total lengths to 35 mm; widths, 11-13 mm; depths about one-half width.

Type Specimens and Type Locality. Holotype, BMNH (Paleontology) ZB.1. MEXICO, Magdalena Bay, 7 fm [13 m]. Not seen.

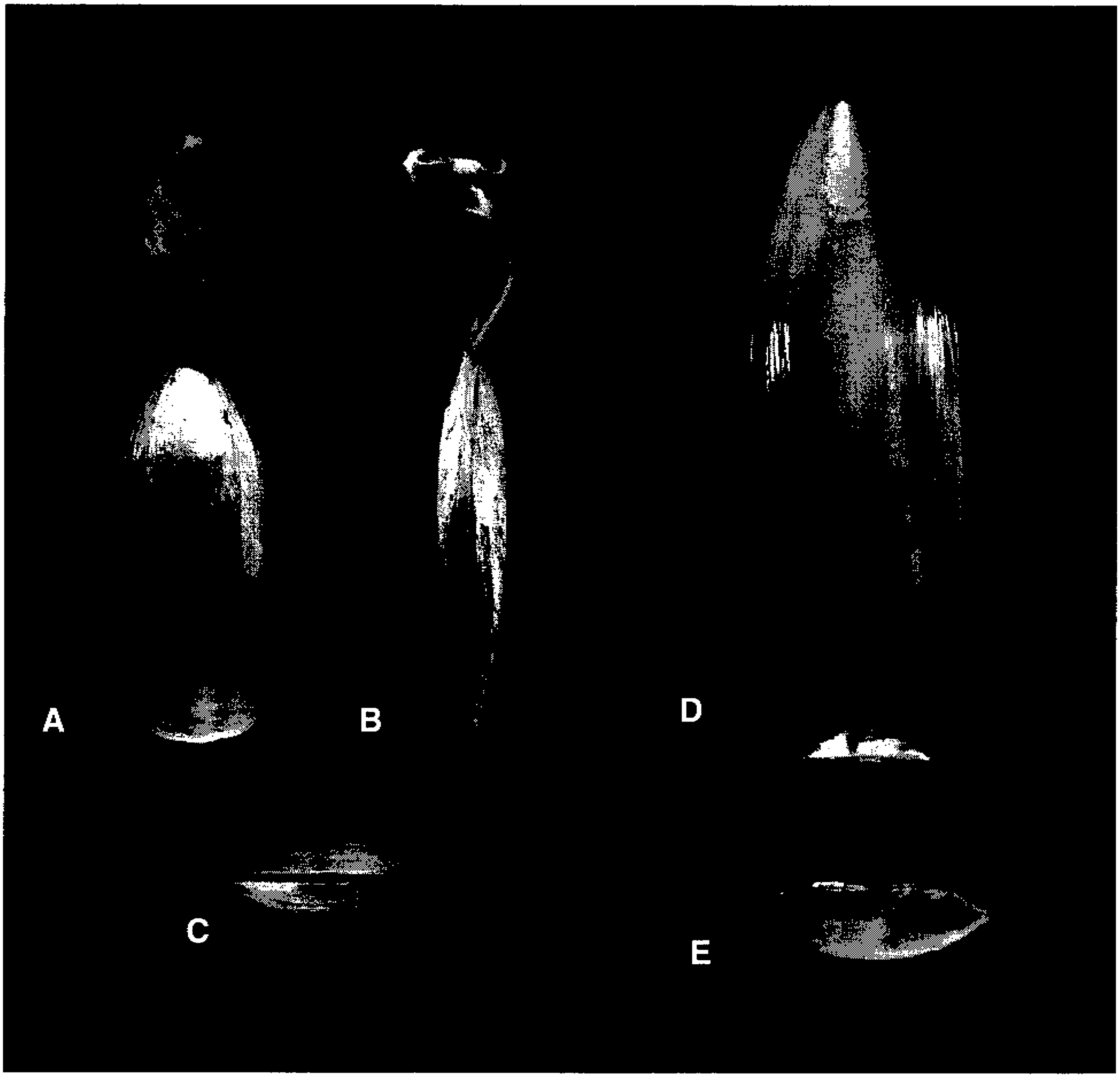

Figure 1.4. A-C, *Glottidia albida* (Hinds, 1844); depth unknown, San Pedro Bay, California (SBMNH [SSB 155]); 24.4 mm TL. A, dorsal view; B, lateral view; C, end view, anterior margin. D, E, *Glottidia palmeri* Dall 1871; depth unknown, San Felipe, Baja California, Mexico (SBMNH 46125); 42.2 mm TL. D, dorsal view, pedicle not visible; E, end view, anterior margin.

Distribution. Late Eocene to Recent. Eastern North Pacific, known to range from Tomales Bay, California (38°N) to Todos Santos Estero, Baja California, Mexico (26°N). Common in soft sediments at depths ranging from the low intertidal zone to 150 m.

Etymology. Name derived from the Latin *albidus*, meaning "white" denoting the characteristic color of the shell.

Common Name. White tongue shell. Erroneously called a "tongue clam."

Biology. *Glottidia albida* live in vertical burrows in mud or soft sediments. The long fleshy pedicle anchor the animal in its burrows. The anatomy of the mantle has been studied by Williams (1977) and aspects of the reproductive biology, especially oogenesis, are reviewed in Chuang (1983).

A small crepidulid snail, *Crepidula glottidiarum* Dall, 1905, is found on some valves of this brachiopod (Dall, 1905; Hertlein and Grant, 1944; MacGinitie and MacGinitie, 1968; see also McLean, 1996, Taxonomic Atlas, Vol. 9). The sipunculid, *Golfingia hespera* (Chamberlain, 1919), is reported to live in the burrows in close association with *Glottidia albida* (MacGinitie and MacGinitie, 1968). Neither the specificity nor the biological aspects of these two relationships are known.

Remarks. For the purposes of this paper the southern limits of the range of *Glottidia albida* are considered to be close to the tip of Baja California on the Pacific side. In the Gulf of California and south to Panama *G. albida* is replaced by *G. palmeri* Dall, 1871 (see Figure 1.4 D, E). In the southern part of its range *G. albida* may be confused with *G. palmeri* from which it is distinguished by: 1) smaller maximum shell size; 2) very much smaller pedicle; 3) anterior margin of shell rounded not truncate; 4) anterior commissure smooth without gaps between shell valves; 5) internal septa more divergent; and 6) whiter shell color (not brown). The records of *G. albida* from the states of Jalisco, Oaxaca and Guerrero along the mainland coast of Mexico can not be confirmed. The records of *Glottidia palmeri* and *G. audebarti* Broderip, 1835 from southern California most likely represent *G. albida* but locality-specific specimens need to be reexamined.

Order Acrotretida Kuhn, 1949

Diagnosis. Shell chitinophosphatic or calcareous; absent in embryo. Dorsal valve distinctly larger and more convex than ventral valve; apex marginal to subcentral; outline shape circular to subcircular. Mantle lobe with or without setae. Pedicle absent or very short; if present it emerges through foramen on ventral valve; without muscle layer, but muscles fill coelomic lumen. Lophophore schizolophous or spirolophous. Statocysts absent.

Suborder Craniidina Waagen, 1885

Diagnosis. Shell calcareous; densely punctate; bristles absent on shell margin; shell not present until postlarval stage. Dorsal valve conical; ventral valve relatively flat; conforms to shape of substrate to which it is entirely cemented; no gap between valves. Setae absent on mantle edge. Pedicle absent. Lophophore spirolophous. Muscles - 2 pairs adductors + 2 pairs obliques.

Superfamily Cranioidea Menke, 1828

Family Craniidae Menke, 1828

Diagnosis. Shell calcareous; punctate, puncta in dorsal valve branching in some recent genera. Dorsal valve usually conical, ventral valve subconical or convex when free, conforming to shape of attachment surface when fixed. Pedicle absent. Marginal sinus absent. Marginal setae absent.

Type Genus. *Crania* Retzius, 1781

Genus *Neocrania* Lee and Brunton 1986

Diagnosis. Shell of medium size, subcircular to quadrangular in outline. Ventral valve cemented to substrate by entire surface; valve varying from thin, uncalcified organic film to wholly calcified and thickened with anterolateral rim. Valve interior with sometime sunken posterior muscles scars with anterior scars united medially. Dorsal valve smooth, slightly pustulose or finely ribbed, umbo centrally to posteriorly placed. Valve interior with large, widely separated pad-like posterior muscle scars and smaller diverging V-shaped anterior scars. Weak posterior submarginal rim, internal surfaces strongly endopunctate.

Type Species. *Patella anomala* Müller, 1776; by subsequent designation.

Neocrania californica (Berry, 1921)

Figure 1.5

Crania californica Berry, 1921:210-212, pl. 11, figs. 1-3. —Thompson, 1927: 136. —Keep and Baily, 1935: 20. —Hatai, 1936: 80. —Burch, 1942: 3. —Hertlein and Grant, 1944: 40, pl. 3, figs. 3, 5, 6. —Bernard, 1972:75, fig. 2. —Kozloff, 1987: 419-420, fig. 20.1.

Neocrania californica: Lee and Brunton, 1986: 151.

Material Examined. *Holotype* - California, Los Angeles Co., Santa Monica, from rock at base of siliceous sponge, 100 fm [183 m]; coll. fishermen, summer 1918; SBMNH 34501 [SSB 4530].

Additional material examined: 2 lots (see List of Additional Specimens Examined).

Description. *Shell* shape subrectangular to rounded-oval, strongly depressed. *Ventral valve* thick, flat; entirely cemented to substrate, margins free, flared outward; interior with strong submarginal thickenings. *Dorsal valve* smooth, small apex situated subposteriorly. *Interior of shell* microscopically granulose. *Adductor attachment scars* prominent; 4 in number, diamond-shaped. *Color* of shell - exterior whitish brown; interior brownish white.

Shell size relatively large; total lengths to 20.0 mm; widths to 23.0 mm; depths less than one-fifth width.

Type Specimens and Type Locality. Holotype, SBMNH 34501. USA, California, Santa Monica, 100 fm [183 m].

Distribution. Recent. Eastern North Pacific known from type locality and off shore banks (32°N; CASIZ collections) to British Columbia, Canada (51°N; Bernard, 1972). Lives attached to hard substrates at depths ranging from 120-200 m.

Etymology. Named after the State of California.

Common Name. None.

Biology. Attached to hard substrate.

Remarks. This is the only locally occurring brachiopod in which the ventral valve is cemented directly to the substrate. It is most similar to *Crania patagonica* Dall, 1902 from the coast of Chile and the Straits of Magellan in South America but lacks the short spines on the dorsal valve.

The species rarely has been reported in the literature and is very uncommon in west coast museum collections. Kozloff (1983) reported the species to be abundant in the subtidal off the open coast in the northern part of its range. It appears to be either sporadic in occurrence or lives in rock or large cobble habitats which are seldom sampled.

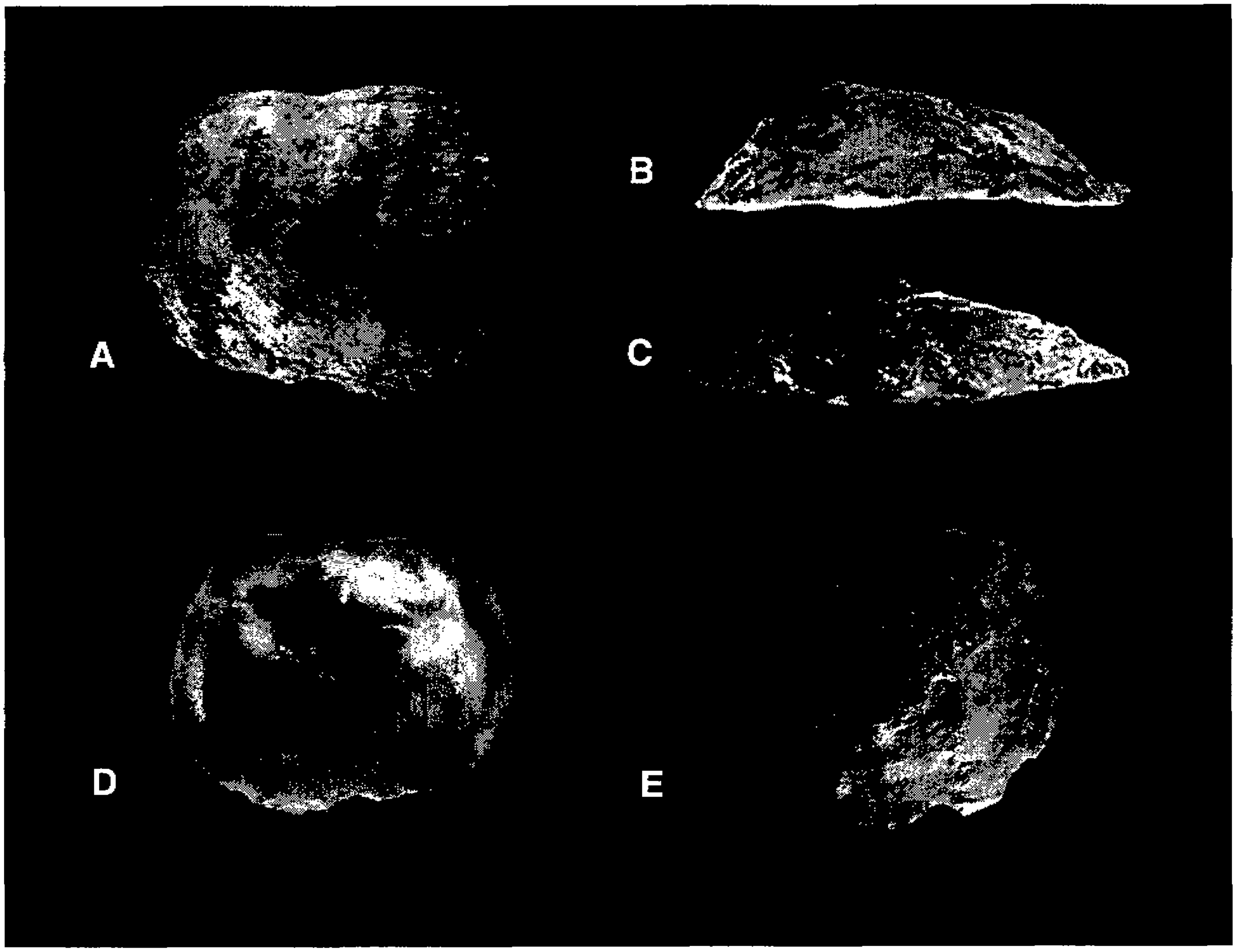

Figure 1.5. *Neocrania californica* (Berry, 1921). A-D, Holotype, 180 m, off Santa Monica, California (SBMNH 34501); 13.0 mm TL. A, dorsal view; B. lateral view; C. end view, anterior margin; D, interior view of dorsal valve. E, 124 m, Cordell Bank, California (CAS 105948); 20.0 mm TL. E, dorsal view.

Class Articulata Huxley, 1869

Diagnosis. Shell composed of scleroproteins and calcite; shell absent until postlarval stage. Valves locked together posteriorly with articulated hinge; hinge teeth and sockets present. Lophophore supported by skeletal structure (brachidium). Pedicle present; originates from foramen in ventral valve; distal end may be branched; internal muscles in pedicle absent; coelomic lumen in pedicle absent. Adductor muscles present; oblique muscles absent. Functional anus absent; intestine ends blindly. Spicules absent or present in soft parts of body. Coelom formation enterocoelous; mantle reversal occurs after settlement. Epifaunal.

Order Rhynchonellida Kuhn, 1949

Diagnosis. Shell small to moderate size; typically impunctate. Pedicle not used in locomotion. Lophophore spirolophous, with dorsally directed cones; partly supported by crura. Mantle canals with 2 main trunks in each mantle lobe. Dental plates typically present. Spicules absent. Metanephridia present, 1 or 2 pairs.

Superfamily Rhynchonelloidea Gray, 1848

Family Frieleiidae Cooper, 1959

Diagnosis. Shell small to medium size. Pedicle relatively short; as broad as foramen. Intestine straight without terminal enlargement. Dorsal median septum present as low thick ridge or absent. Crura short, straight, spinuliferous, supported by short plates.

Type Genus. *Frieleia* Dall, 1895.

Genus *Frieleia* Dall, 1895

Diagnosis. Shell thin; outline elongate oval to subtriangular; greatest width at or anterior to middle; both valves may be somewhat sulcate; surface smooth to minutely costellate. Ventral valve with greater depth and convexity; beak short, nearly straight to suberect; foramen incomplete, elongate oval; deltidial plates thick, disjunct but nearly united; apex marked by small triangular plate elevated above valve floor. Ventral valve interior with long, curved corrugated teeth buttressed by prominent dental plates; muscle and pallial marks lightly impressed. Dorsal valve interior with deep corrugated sockets marginate by thick socket ridges; crura of spinulifer type, long, thin, divergent, attached directly to socket ridges; inner hinge plates small, rounded, disjunct; media septum long, slender, elevating posteriorly and united to inner hinge plates forming small V-shaped chamber. Median septum rising to crest just anterior to apex; cardinal process small, triangular, transversely striated pit at apex; adductor scars long, narrow, posteriorly situated.

Type Species. *Frieleia halli* Dall, 1895; by original designation.

***Frieleia halli* Dall, 1895**

Figure 1.6

Frieleia halli Dall, 1895:714, pl. 24, figs. 6, 9-13; Dall, 1920: 292-293.—Kelesy, 1907: 40. —Jackson, 1918: 192, pl. 1, fig. 8.—Oldroyd, 1924a: 224. —Thompson, 1927: 157-158, text-fig. 48. Nomura and Hatai, 1934: 16. —Keep and Baily, 1935: 23-24, text-fig. 7. —Hatai, 1936: 225, fig. 24; Hatai, 1940: 219, text-fig. 21. —Burch, 1942: 4. —Hertlein and Grant, 1944: 58-59, text-fig. 11, pl. 4, figs. 6, 7. —Smith and Gordon, 1948: 209. —Cooper, 1959: 54; Cooper, 1969: pl. 2, fig. 19, pl. 5, figs. 18, 19. —Bernard, 1972:77, fig. 7.

Hemithryris psittacea: Keep, 1904, fig. 6. —Keep and Baily, 1935: 23 [in part]. (**not** Gmelin).

Material Examined. 14 lots (see List of Additional Specimens Examined).

Description. *Shell* shape subtrigonal, smoothly rounded or with medial depression; anterior margin bilobed. *Valves* extremely thin; smooth; translucent to transparent. *Color* of shell light yellow, yellowish-gray or colorless.

Shell size medium; total lengths, 18-20 mm; widths, 16-18 mm.

Type Specimens and Type Locality. Holotype, USNM 123148. USA, California, Cortez Bank.

Distribution. Miocene to Recent. Eastern North Pacific, known from Aleutians and Gulf of Alaska (58°N; Dall, 1920) to San Diego, California (32°N; SBMNH collections). Western North Pacific, reported from Japan and Kamchatka. Collected from 40-2200 m, typically occurring between 500-1000 m.

Etymology. Named in honor of James Hall, a noted brachiopod expert.

Common Name. Hall's lamp shell.

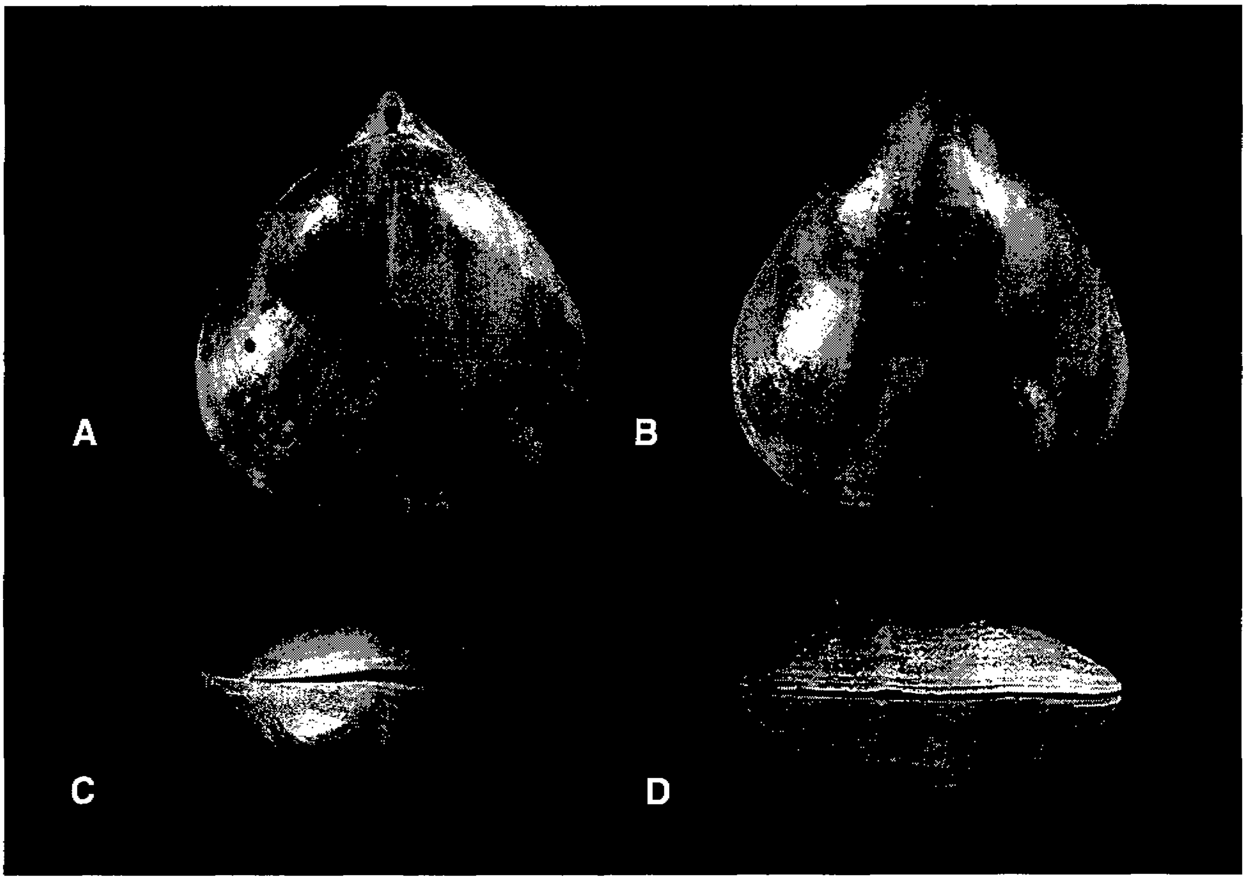

Figure 1.6. *Frieleia halli* Dall, 1895: 1150-1170 m, off San Diego, California (SBMNH [SSB 3038]); 17.7 mm TL. A, dorsal view; B, ventral view; C, lateral view; D, end view, anterior margin; E, end view, posterior margin.

Biology. Exclusively attached to organic substrates, i.e., dead bivalve shells, living sponges, polychaete tubes and pogonophoran tubes. Valentine and Ayala (1975) documented genetic variation and Rokop (1977) discussed seasonal reproduction of *Frieleia halli* in the deep sea. A number of dead specimens examined for the latter paper had tiny holes in the shell, and probably had been drilled by a predator such as an octopus (see fig. 1.6A). Nothing additional has been reported on the biology of this species.

Remarks. *Frieleia halli* is a northern boreal species that was formerly considered to be the young of *Hemithrys psittacea* (Chemnitz, 1785) from which it differs principally in its lighter color. Records of *H. psittacea* from south of Oregon are probably *Frieleia halli*. In addition, young *F. halli* have been confused with *Cryptophora hesperis* Cooper 1982, a cryptoporid known only from the type locality off southern Oregon in 170 m. *Cryptophora*, in contrast to *Freilia*, has unmodified marginal deltidial plates, a gently sulcate anterior commissure and the outline shape is rounded. Fossil brachiopods from the Tertiary of California and Oregon, presently referred to *Hemithrys* may belong in the genus *Freilia*.

Order Terebratulida Waagen, 1883

Diagnosis. Shell small to large; punctate; light colored often with bright colors. Pedicle normal and functional, vestigal and non-functional, or absent. Mantle canals with 2 or 4 main trunks in each mantle lobe. Dental plates present or absent. Metanephridia present, 1 pair. Lophophore in call configurations, supported by calcareous loop. Spicules present or absent.

Suborder Terebratulidina Waagen, 1883

Diagnosis. Shell small to large. Dorsal valve lacks median septum. Lophophore supported by short skeletal loop; developed directly from cardinal process. Pedicle distal end often split into large rootlets. Spicules commonly present. Gonads reticulate, located in pair of pillared spaces in each mantle lobe.

Remarks. There are no representatives of the Superfamily Terebratuloidea off California. The Superfamily Cancellothyridoidea is represented by two species of *Terebratulina.*

Superfamily Cancellothyridoidea Cooper, 1973

Diagnosis. Shell size small to moderately large; costellate to costate or secondarily smooth; color drab to bright. Dorsal pedicel adjustor muscles attached to dorsal valve floor. Lophophore spirolophorous through pletophorous. Dental plates rarely developed. Cardinal process weak to moderately developed. Hinge plate absent; socket ridges present. Dorsal median septum absent. Crura united to form ring or open.

Family Cancellothyrididae Thompson, 1926

Diagnosis. Shell size medium to moderately large; costellate or capillate; punctate with externally branching pores. Dental lamellae absent. Hinge plates absent; socket ridges fused with crural bases; cardinal process developed. Deltidial plates disjunct. Pedicle very short to moderately long, muscles attached to floor valve. Loop short, crural processes united to form ring with transverse band. Lophophore typically plectolophous, may be spirolophous or subplectolophous. Spicules present.

Type Genus. *Terebratulina* d'Orbigny, 1847

Genus *Terebratulina* d'Orbigny, 1847

Diagnosis. Shell outline oval or elongate, inflated; finely striated; auriculate; deltidium usually rudimental; foramen incomplete. Loop short, appears annular in adult through union of oral processes; crura forming wide ring; lophophore plectolophous.

Type Species. *Anomia caputserpentis* Linné, 1767; by original designation.

Key to Species of the Genus *Terebratulina*

1A. Shell smooth or with faint riblets; anterior valve margin smooth; shape round to elongate; umbo orbicular .... *Terebratulina crossei*

1B. Shell with conspicuous ribs; anterior valve margin crenulated; shape distinctly triangular; umbo narrow .... *Terebratulina unguicula*

Terebratulina crossei Davidson, 1882

Figure 1.7

Terebratulina crossei Davidson, 1882:106, pl. H-7, fig. 1.—Dall, 1910: 96; Dall, 1920: 303. —Burch, 1942: 5-6. —Bernard, 1972:77, 79, fig. 9. —Roth, 1972: 5.

Terebratulina crossii [sic] Davidson, 1886: 33, pl. 3, figs. 4-6.

Terebratulina crossei **not** Davidson. —Fischer and Oehlert, 1892: 5, pl. 8, figs. 1-8.

Terebratulina kiiensis **not** Dall and Pilsbry. —Dall and Pilsbry, 1891b: 152, pl. 11, figs. 9, 10; 1895: 720, pl. 32, figs. 8, 9.—Dall, 1894: 720, pl. 32, figs. 8, 9; 1920: 307. —Oldroyd, 1924a: 203, pl. 29, figs. 13-14.—Keep and Baily, 1935: 23, fig. 6. —Hatai, 1936: 100-101; 1938: 112, 128, pl. 19, figs. 5, 6, 8, 9.Nomura and Hatai, 1937: 141, pl. 21, fig. 17.—Burch, 1942: 5. —Hertlein and Grant, 1944: 68-71, text-fig. 16, pl. 6, figs. 11, 12, pl. 17, figs. 3, 6, 10. —Smith and Gordon, 1948: 209. —Roth, 1972: 8.

Terebratulina (*unquicula* var.) *Kiiensis* Dall and Pilsbry, 1891a: 18, pl. 1, figs. 4, 5, 1894: 720, pl. 32, figs. 8, 9.

Terebratulina kiiensis Dall and Pilsbry. —Dall, 1910: 96, 1920: 307. —Oldroyd, 1924a: 203, pl. 29, figs. 13-14, 1924b: 226, pl. 16, figs. 13, 14. Keep and Baily, 1935: 23, text-fig. 6. —Hatai, 1940: 235, pl. 7, figs. 18-21.—Hertlein and Grant, 1944: 71-73, text-fig. 18a-c, pl. 6, figs. 10, 13 [in part]. —Nomura and Hatai, 1983: 63. —Zezina, 1970: 443, pl. 1, fig. 3. —Roth, 1972: 8. —Cooper, 1982: 6-8, pl. 1, figs. 8-18.

Type Specimens and Type Locality: Holotype - USNM 128463. JAPAN, coast of Kii Province. Not seen.

Terebratulina species. —Cooper, 1982: 8, pl. 1, figs. 5-7.

Material Examined. *California*: Santa Maria Basin, Station BRA-16, 591m; 17 specimens, 4.3-37.5 mm TL; USNM.—3 specimens., 12.7-30.3 mm TL; SBMNH.

Additional material examined: 28 lots (see List of Additional Specimens Examined).

Description. *Shell* thin; shape elongate to nearly circular; rostrum inflated, very short; smooth or with sculpture of fine radial riblets; anterior valve margins smooth. *Color* of shell waxen white, often with brownish stains.

Shell size medium; total lengths, reported to 44 mm, observed to 37 mm; widths, reported to 40 mm, observed to 33 mm.

Type Specimens and Type Locality. Types in BMNH; not searched. JAPAN, Sagami Bay.

Distribution. Miocene to Recent. A boreal species known to range from Japan to southern California and possibly as far south as Peru and Chile. Eastern North Pacific, from Vancouver Island, British Columbia, Canada, (51°N; Bernard, 1972) to La Jolla, California (32°N; SBMNH) and the California Islands.—Western North Pacific, Japan. Depth off California reported to range from 100-450 m.

Etymology. Named in honor of T. Crosse, a noted brachiopod expert.

Common Name. Cross's lamp shell.

Biology. The species appears to be solitary and is considered rare in its occurrence. Nothing is reported in the literature about the biology of this species.

Remarks. Under the synonymy for *Terebratulina crossei* I also reviewed references to California records of *T. kiiensis*. *Terebratulina crossei* appears almost identical to *T. kiiensis* Dall and Pilsbry, 1891 (see Figure 1.7F). When comparing the two species *T. kiiensis* has: 1) a larger shell size; 2) a flatter and more discoid shell shape; 3); a coarser shell sculpture with larger, more conspicuous longitudinal ribs; 4) a darker, more brownish color when fresh; and 5) lives in deeper water.

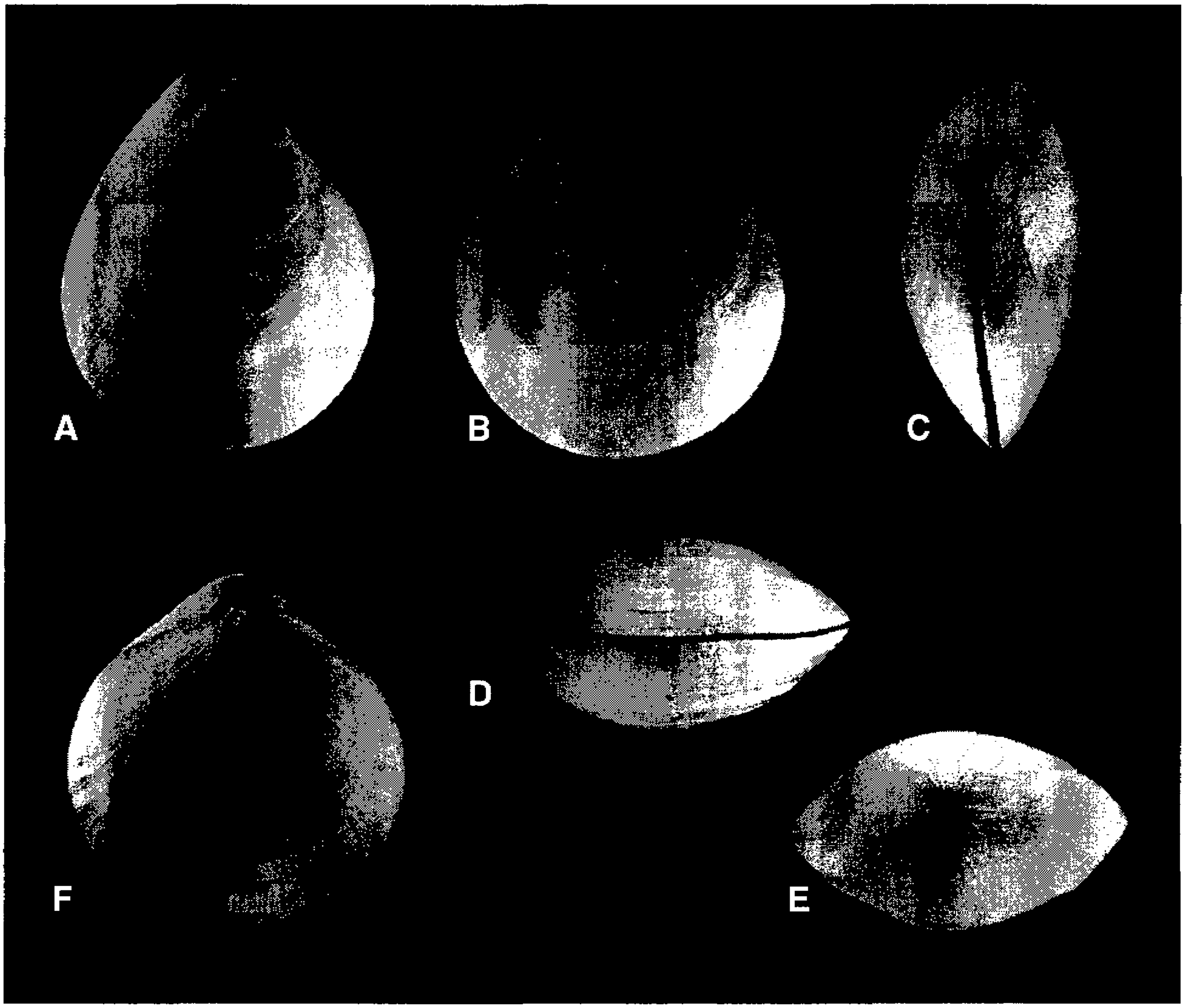

Figure 1.7. A-E, *Terebratulina crossei* Davidson, 1882; 88 m, off Santa Monica, California (SBMNH); 30.7 mm TL. A, dorsal view; B, ventral view; C, lateral view; D, end view, anterior margin; E, end view, posterior margin. F, *Terebratulina kiiensis* Dall and Pilsbry, 1891; 183 m, off La Jolla, California (SBMNH [SSB 3265]); 31.8 mm TL. F, dorsal view.

After examining a large number of lots from California I cannot reliably separate the two species. Both species are widely distributed in the Eastern North Pacific Ocean, reportedly ranging from Alaska to California (Dall and Pilsbry, 1891; Dall, 1920; present study). Cooper (1982) additionally noted the presence of *T. kiiensis* in South America. Cooper (1982: pl. 1, figs. 5-7) illustrated a single specimen from 439 m off Santa Barbara which he identified as intermediate between *Terebratulina crossei* and *T. kiiensis*. In the next sentence he indicated that the specimen "seems to be a new species." In light of the morphological variations seen in other brachiopod species (principally shell shape and sculpture) it would appear that the validity of the closely related *crossei-kiiensis* complex should be critically reevaluated. For the purposes of this Atlas I have chosen to use the name *T. crossei* for all California specimens in this complex because it is the first described of the two species.

In comparison with *Terebratulina unquicula* the shells of *T. crossei* are: 1) considerably larger, and proportionally wider and deeper; 2) smoother; and 3) the beak proportionally shorter.

Terebratulina unguicula (Carpenter, 1864)

Figure 1.8

Terebratula unguiculus Carpenter 1864: 607.

Terebratula unguicula Carpenter. Carpenter, 1865: 201, text-figs. 1-4. —Cooper, 1867: 3. —Dall, 1870: 102.

Terebratulina unguicula (Carpenter). —Dall, 1873: 180; 1877a: 155; 1920: 300-301. —Whiteaves, 1878: 468. —Dall and Pilsbry, 1891: 19, pl. 1, figs. 6, 7. —Du Bois, 1916: 178.—Oldroyd, 1924a: 203, pl. 27, figs. 2-5; 1924b: 226, pl. 38, figs. 2-5. —Johnson and Snook, 1927: 156, text-fig. 130. —Hatai, 1936: 83. —Burch, 1942: 5. —Hertlein and Grant, 1944: 79-81, pl. 5, figs. 9, 10, pl. 6, figs. 1, 6, 7, pl. 17, figs. 9, 13, 14, 18, 19. —Smith and Gordon, 1948: 210. —Mattox, 1956: —Bernard, 1972: 79, fig. 8. —Roth, 1972: 14-15.

Terebratulina unguiculata [sic] (Carpenter): Davidson, 1880: 14.

Terebratulina caput-serpentis var. *unguiculata* (Carpenter): Davidson, 1886: 25-26, pl. 5, figs. 38, 40. —Kelsey, 1907: 50.

Terebratulina caput-serpentis **not** Linnaeus: Cooper, 1894: (pages not numbered). —Dall, 1895: 719, pl. 32(figs. 2, 5). —Kelsey, 1907: 50. —Willett, 1918: 66. —Keep and Baily, 1935: 22-23, fig. 5.

Material Examined. *California*: Santa Maria Basin, Station BRA-21, 75-90m, 27 spec., 2.4-18.5 mm TL, USNM; 54-63m,ca. 25 spec., 2.3-18.8 mm TL, SBMNH.

Additional material examined: 25 lots (see List of Additional Specimens Examined).

Description. *Shell* thick; shape ovate to triangular, longer than wide; valves almost equally convex, rounded laterally and anteriorly; lateral sides of umbo strongly auricular, especially in young and medium-size specimens. Anterior commissure straight, regularly crenulated; lateral commissure straight or slightly sinuous, crenulated. *Beaks* short; obliquely truncated by relatively large, incomplete foramen; margined anteriorly by umbo of dorsal valve and by 2 small lateral deltidia. *Pedicle* short. *Valve surface* marked by numerous prominent radiating ribs, simple and stronger at their origin, some dichotomously branched; number rapidly increases from bifurcations and by interpolation with shorter riblets between larger ones; valves crossed with delicate concentric raised striae. *Ventral valve* evenly convex, occasionally slightly depressed anteriorly. *Loop* short and simple; crura disunited in young, annelidiform in larger specimens. *Color* of shell light yellowish-white to greyish-ash.

Shell size small; maximum total lengths, reported to 25 mm, majority observed measure less than 15 mm; widths, reported to 22 mm, observed to 10 mm.

Type Specimens and Type Locality. Types reported to be in the Cumings Museum; not searched. USA, California, Monterey.

Bernard (1972) erroneously reported the type locality to be off Vancouver Island, British Columbia, Canada.

Distribution. Miocene to Recent. Eastern North Pacific, Priblof Islands, Alaska (57°N; Dall, 1920) to Cabo San Lucas, Baja California Sur, Mexico (23°N; Dall, 1920).—Western North Pacific, reported from the Kamchatka Peninsula.

Depths typically range from 10-850 m; in the northern part of the range the species may be locally abundant intertidally in areas of broken rock and coralline algae.

Etymology. From the Latin word *unguicula* meaning having "claws" in reference to the characteristic radiating ribs.

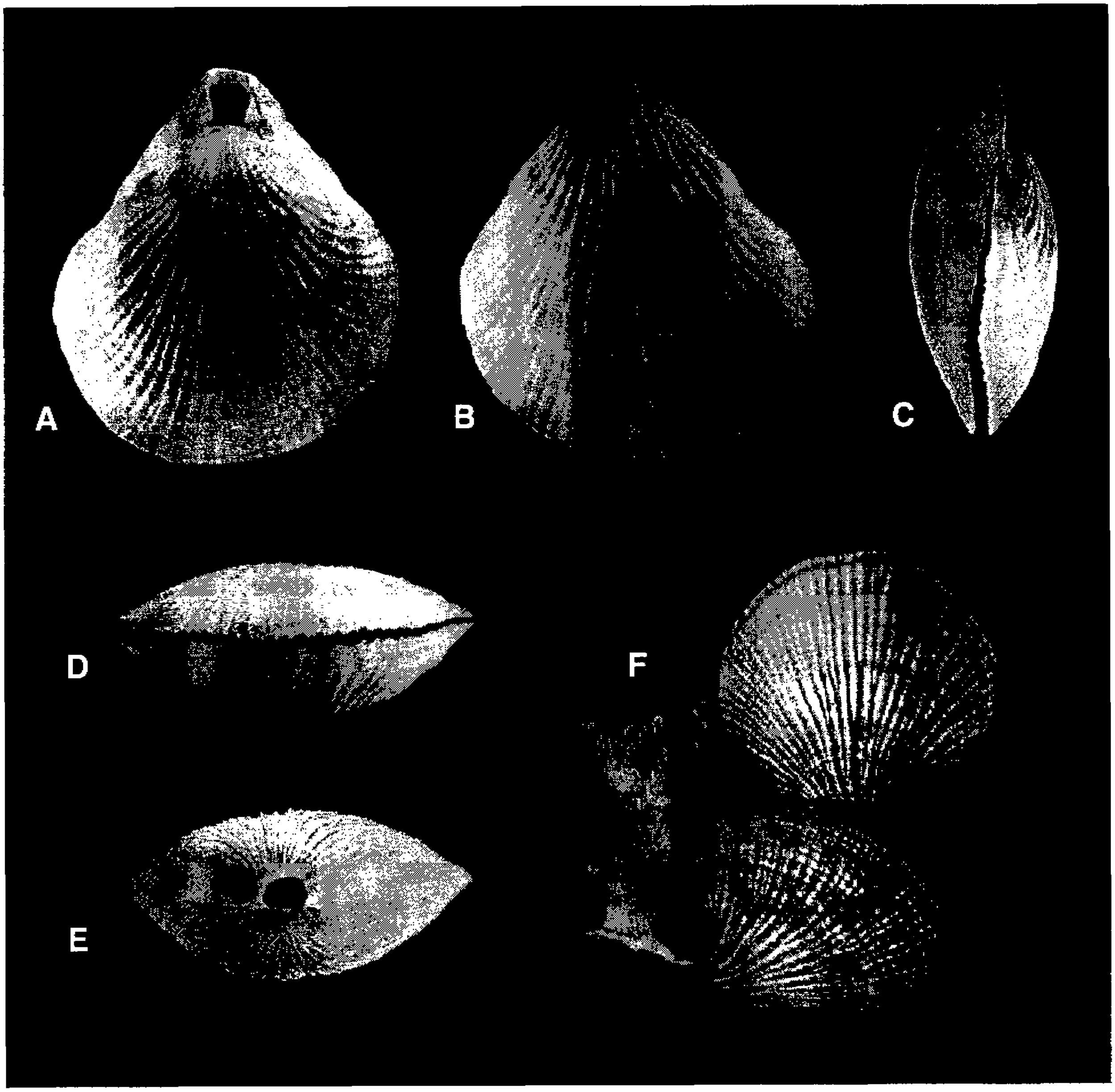

Figure 1.8. *Terebratulina unguicula* (Carpenter, 1865). A-E, 132 m, off Gaviota, California (SBMNH), 18.3 mm TL. A, dorsal view; B, ventral view; C, lateral view; D, end view, anterior margin; E, end view, posterior margin. F, depth unknown, off La Jolla, California (SBMNH [SSB 13507]); 17.0 mm TL. F, two specimens attached to solitary coral.

Common Name. None.

Biology. This species typically nestles inside dead bivalve and gastropod shells or in the hollow spaces in dead hexactinellid sponges. It also has been found attached to the hairy periostracum of the large gastropod *Fusitriton oregonensis* and to the corallum of solitary corals such as *Paracyathus stearnsii* (see Figure 1.8F).

Various aspects of the biology of *Terebratulina unguicula* have been extensively studied, especially in Washington and Canada where live specimens are easily obtained. Reproduction and development have been reviewed by Reed (1987). Details of embryology are treated by Long (1964). Wilkens (1978a, b, 1987) investigated the physiology of muscle activation and contraction. The orientation of this brachiopod to water currents and functional aspects of the lophophore were examined by LaBarbera (1978, 1981, 1986). Fouke (1986) documented the functional significance of spicule-reinforced connective tissues. A number of papers have examined details of distribution and ecology, especially in populations living in British Columbian fjords which have low ocygen concentrations and high turbidity flows (see Thayer, 1981; Farrow *et al.*, 1983; Tunnicliffe and Wilson, 1988).

Remarks. According to Bernard (1972) the records of *Terebratulina unguicula* from the Western North Pacific probably represent *T. crossei*. This shells of this species are distinguished from *T. crossei* by: 1) their smaller maximum size; 2) narrower umbo; 3) distinct sculpture of large, coarse ribs; and 4) crenulated valve margins.

The close resemblance of *Terebratulina unguicula* to fossils specimens of *T. tejonensis* Stanton from the Eocene of California warrents additional study.

Family Laqueidae Hatai, 1965

Diagnosis. Shell size medium to moderately large; shape biconvex; smooth to costate; posterior margin non-strophic. Dental plates present. Brachidia with cross union between discending and recurved parts of loop. Hinge plates present. Spicules typically absent (present only in *Laqueus*). Lophophore plectolophous. Cardinal process small or absent.

Type Genus. *Laqueus* Dall, 1870.

Genus *Laqueus* Dall, 1870

Diagnosis. Shell thin, large, inflated; hinge line curved, beak prominent; pedicle foramen small, complete. Brachidium long.

Type Species. *Terebratula californiana* Koch, 1848; by original designation.

***Laqueus californianus* (Koch, 1848)**

Figure 1.9

Terebratula californiana Koch, 1848: 38 + 1844: pl. 2b, figs. 21-23. —Davidson, 1852: 364. —Carpenter, 1864: 568, 574.

Terebratula californica: Sowerby, 1847: 352, pl. 70, figs. 50, 51.

Waldheimia californica: Gray, 1853: 60. —Carpenter, 1856: 298; 1864: 636.

Laqueus californica: Hatai, 1936: 90.

Laqueus californicus: Dall, 1870: 123, pl. 7, fig. f, pl. 8, figs. 9, 10; 1894: 725; 1920: 344 [in part]. —Davidson, 1887: 112, pl. 18, figs. 6-9. —Beecher, 1893b: 383, pl. 1, figs. F4, G4. —Lowe, 1904: 19. —Berry, 1907: 18. —Arnold and Anderson, 1907: 153. —Kelsey, 1907: 41. —Oldroyd, 1924a: 205, pl. 28, figs. 1-4, 1924b: 230, pl. 17, figs. 1-4. —Thompson, 1927: 258, fig. 85. —Johnson and Snook, 1927: 157, fig. 129. —Keep and Baily, 1935: 20-21, fig. 2 [sic *Laqueas*]. —Nomura and Hatai, 1937: 187-188, pl. 25, figs. 5-10. —Burch, 1942: 8. —Smith and Gordon, 1948: 210. —MacGinitie and MacGinitie, 1968: 178, fig. 56.

Laqueus californianus: Hertlein and Grant, 1944: 144-147, text-fig. 31, pl. 13, figs. 5, 8, 14, pl. 21, figs. 1-7; 1960: 96-97, pl. 20, figs. 1-3, 5-7. —Mattox, 1956: 75, fig. 2. —Bernard, 1972: 81, fig. 1. —Kozloff, 1987: 419-420, fig. 20.2.

Terebratula kochii Küster in Martini-Chemnitz, 1848: 39, pl. 2d, figs. 1-3. —Dall, 1920: 348.

Type Specimens and Type Locality: Not searched.

Laqueus erythraeus Dall, 1920: 350. —Oldroyd, 1924b: 231-232. —Thompson, 1927: 259. —Hatai, 1936: 90. —Cooper, 1969: pl. 1, fig. 2.

Type Specimens and Type Locality: Holotype,—USNM 19395. California, off Santa Catalina Island, 80 fm [146 m]. Not seen.

Megerlia Jeffreysi Dall, 1877: 187. —Whiteaves, 1878: 468. —Beecher, 1893: 383.

Type Specimens and Type Locality: Types not searched. British Columbia, Vancouver.

Frenula Jeffreysi: Dall, 1871a: 55 [in part]. (**not** Dall).

Ismenia Jeffreysi: Dall, 1871d: 65-66, pl. 11, figs. 7-10, 1887: 65, pl. 11, figs. 7-10 [in part]. (**not** Dall).

Laqueus jeffreysi (Dall). —Dall, 1894: 725. —Lowe, 1904: 19. —Arnold, 1907: 425. —Du Bois, 1916: 178. —Willett, 1918: 66. —Keep and Baily, 1935: 21.

Laqueus californicus jeffreysi (Dall). —Oldroyd, 1924a: 205-206.

Terebratula californianus forma *vancouveriensis* Davidson, 1877: 113, pl. 18, figs. 10-13, 13a, 13b.

Type Specimens and Type Locality: Types not searched. British Columbia, off Vancouver Island.

Laqueus californicus vancouverensis [sic] (Davidson). —Oldroyd, 1924a: 206, pl. 28, figs. 5-10. —Oldroyd, 1924b: 231, pl. 17, figs. 5-10. —Thompson, 1927: 259.

Laqueus vancouverensis [sic] (Davidson). —Hatai, 1936: 90. —Burch, 1942: 8.

Laqueus vancouveriensis (Davidson). —Hertlein and Grant, 1944: 147-151, text-fig. 32, pl. 13, (figs. 6, 7, 9, 10, pl. 17, figs. 15-17, pl. 18, figs. 15-17, 19-21. —Bernard, 1972:81, fig. 5. —Roth, 1972: 15.

Laqueus vancouveriensis diegensis Hertlein and Grant, 1960: 97-98, pl. 20, figs. 4, 8, 21. —Roth, 1972: 5.

Type Specimens and Type Locality: Holotype,—CASIP 7355. California, San Diego, Pacific Beach [Pliocene].

Material Examined. 21 lots (see List of Additional Specimens Examined).

Description. *Shell* thin; inflated; shape ovoid to nearly circular, length slightly to much greater than width. *Dorsal valve* uniformly convex, with slight tendency to depression close to frontal margin. *Ventral valve* slightly deeper than dorsal valve, sometimes with slight indication of masial longitudial elevation or flattened fold. *Beaks* curved; truncated by small circular foramen; margined anteriorly by 2 wide delthidial plates; beak-ridges sharply defined, a distinct flattened space present between ridges and hinge-line. *Pedicle* elongate, long and narrow. *Valve surfaces* smooth, with faint concentric growth lines. *Crura* short, curved. *Color* yellowish-brown to light reddish-brown to almost white; often with darker markings where mantle canals show through thin shell.

Shell size large; maximum total lengths to 53 mm; widths to 42 mm; depths to 25 mm.

Type Specimens and Type Locality. Types not searched. California.

Distribution. Pliocene to Recent. Eastern North Pacific, reported from the Cook Inlet, Alaska (59°N) to La Jolla, California and the offshore islands (32°N; SBMNH). Western North Pacific, from Sea of Japan. Depths reported from the intertidal to 1500m; abundant intertidally in northern part of range.

Etymology. Named for the State of California where the species was first found.

Common Name. California lamp shell

Biology. One of the most abundant mid-depth species in southern California. It occurs in dense populations often with individuals attached to each other forming large clusters. Found on clean rock or gravel bottoms. Many shells examined appear to have been drilled by *Octopus* or other molluscan predators.

The biology of *Laqueus californicus* has been extensively studied throughout its range. The functional morphology of the lophophore, especially in relation to food collection and waste rejection, have been documented by Strathman (1973), Reynolds and McCammon (1977), Gilmour (1978), and LaBarbera (1986). The orientation of *Laqueus* to water movements and the dynamics of inhalent and exhalent currents was elucidated in LaBarbera (1978, 1981). Clarke and Wheeler (1915) analyzed the chemical components of the shell and Mackay and Hewitt (1978) examined the ultrastructure of the pedicle. Physiological studies include those of Wilkens (1978a, b, 1987) who investigated the activation and contraction of adductor and diductor muscles and Scheid and Awapara (1972) who investigated metabolism.

The presence of *Laqueus* populations living in fjords in British Columbia which are known to have low oxygen concentrations and high turbidity flows has been documented by Thayer (1981), Farrow *et al.* (1983) and Tunnicliffe and Wilson (1988). The relationship of these ecological conditions to the *vancouveriensis* ecomorph is discussed.

Remarks. There is some confusion as to the status of the rounder and smaller *Laqueus vancouveriensis* (Davidson, 1877) which typically is found in quiet waters on rocks mixed with mud. Hertlein and Grant (1944) considered the differences sufficient to warrant separation at the species level, whereas, Bernard (1972) considered *L. vancouveriensis* to represent a quiet water ecomorph. In comparison with *L. californianus*, the *vancouveriensis* morph is characterized by: 1) a larger foramen; 2) a smaller shell size; 3) valves which are flatter and thicker; 4) an olive drab or yellowish-white color vs pinkish-white. In addition, the animals are reported to live singly or in small clumps *versus* large, dense colonies. Reports in the earlier literature of *L. vancouveriensis* in California should be refered to *L. californianus*. *Laqueus jeffreysi* is a senior synonym of this species but this name has not been commonly used in the literature. Dall considered this the young of the former species (see Oldroyd, 1924b).

Suborder Terebratellidina Muir-Woods, 1955

Diagnosis. Shell small to large. Dorsal valve with median septum. Lophophore suppported by long skeletal loop; developed with both cardinal process and median septum. Pedicle distal ends seldom split into rootlets. Spicules rarely present. Gonads not located in pilleard mantle.

Superfamily Terebratelloidea King, 1850

Family Dallinidae Beecher, 1893

Diagnosis. Loop passing through all or part of pre-campagiform, campagiform, frenuliniform, terebrataliiform, and dalliniform growth stages, or modifications of these. Spicules present in some forms but never abundant. Dental plates typically present.

Type Genus. *Dallina* Beecher, 1893

Genus *Terebratalia* Beecher, 1893

Diagnosis. Shell large, smooth or ribbed, anterior margin sulcate; deltidium incomplete; foramen large. Punctae developed. Beak short, suberect. Hinge teeth with poorly developed dental plates. Brachidium highly developed and complex; attached to septum.

Type Species. *Terebratula transversa* Sowerby, 1846; by original designation.

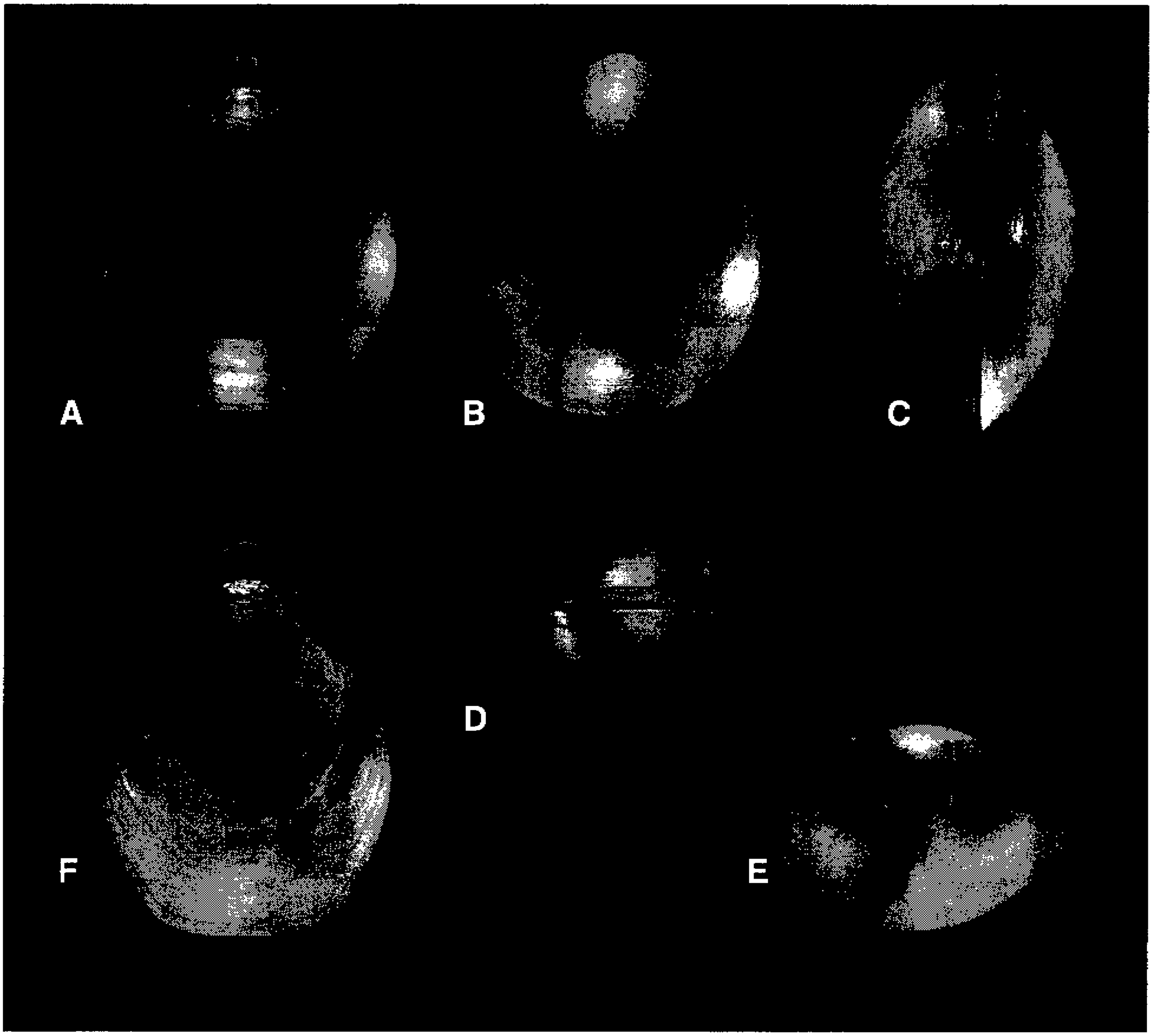

Figure 1.9. *Laqueus californianus* (Koch, 1848): A-E, 90 m, off Santa Catalina Island, California, (SBMNH); 45.7 mm TL. A, dorsal view; B, ventral view; C, lateral view; D, end view, anterior margin; E, end view, posterior margin. F, 155 m, off Morro Bay, California (SBMNH [SSB 18432]); 42.5 mm TL. F, dorsal view.

Key to Species of *Terebratalia*

1A. Anterior commissure uniplicate, medial flexure of dorsal valve convex; shell typically slightly longer than wide; with few, broad, low-relief ribs .... *Terebratalia occidentalis*

1B. Anterior commissure sulcate, medial flexure of dorsal valve concave; shell wider than long; smooth or with numerous, distinct, narrow ribs .... *Terebratalia transversa*

Terebratalia occidentalis (Dall, 1871)

Figure 1.10

Terebratella occidentalis: Dall, 1871a: 182, pl. 1, fig. 7, 1891: 172-173, pl. 4, figs. 8, 9 only.—Davidson, 1887: 79-81 [in part], pl. 16, fig. 13 only. —Lowe, 1904: 20.

Terebratalia occidentalis: Dall, 1894 [1895]: 729, pl. 31, figs. 7, 8; 1920: 341.—Kelsey, 1907: 50. Eldridge and Arnold, 1907: pl. 39, figs. 6-9. —Arnold, 1907: 534, pl. 49, figs. 6-9a. —Arnold and Anderson, 1907: pl. 22, figs. 4a, b.—Oldroyd, 1924a: 229. —Hertlein and Crickman, 1925: 267, 272. —Keep and Baily, 1935: 21, fig. 3. —Burch, 1942: 7. —Hertlein and Grant, 1944: 127-131, text-fig. 27, pl. 10, fig. e, pl. 17, figs. 2, 5, 8, 11, 12; 1960: 94-95, pl. 19, figs. 16, 22, 31.—Smith and Gordon, 1948: 210.—Mattox, 1956: 75-76, figs 4A-M. —Roth, 1972: 9.

Dallinella occidentalis: Thompson, 1927: 246. —Woodring, 1930: 60. —Hatai, 1936: 89; 1940: pl. 9. igs. 22-24, 26, 27).—Nomura and Hatai, 1937: 185-187, pl. 25, figs. 15-19.

Terebratella occidentalis var. *obsoleta* Dall, 1891: 186.

Type Specimens and Type Locality: Syntype, USNM 123142. MEXICO, Baja California, NW of Cerros [Cedros] Island, 113 fm [207 m]; USBCF *Albatross*, station 2984. Not seen.

Terebratalia occidentalis obsoleta: Hertlein and Grant, 1944: 131-133, text-fig. 28, pl. 12, figs. 5, 9-11. —Roth, 1972: 9.

Terebratalia obsoleta: Dall, 1893: 382, pl. 2, figs. 4-12, pl. 3, figs. 1-15. —Beecher, 1893a: 382. —Beecher, 1893b: 392-394, pl. 2, figs. 4-12, pl. 3, figs. 1-15. —Dall, 1894 [1895]: 726, pl. 30, fig. 70. —Dall, 1920: 341-343. —Oldroyd, 1924b: 229-230. —Burch, 1942: 7. —Roth, 1972: 9.

Terebratella obsoleta: Lowe, 1904: 20.

Terebratula obsoleta: Dall, 1910: 96.

Dallinella obsoleta: Thompson, 1915: 75. —Thompson, 1927: 246. —Hatai, 1936: 90.

Terebratulia obsoleta: Etherington, 1931: 49.

Terebratalia arnoldi Hertlein and Grant, 1944: 119, pl. 11, figs. 1-3, 10-15, 1960: 92-93, pl. 19, fig. 30. —Roth, 1972: 3.

Type Specimens and Type Locality: Holotype, CASIP 7313. USA, California, Ventura Co., Tapo Canyon, center of southwest one-fourth of Section 23, T. 3 N., R. 18 W., S.B.B. and M. [Middle Pliocene]. Not seen.

Waldheimia Kennedyi Dall, 1874: 299; 1903: 1540.

Type Specimens and Type Locality: Syntype, USNM, 370827. Mexico, Baja California, Cerros [Cedros] Island [Miocene].

Terebratalia kennedyi: Dall, 1907: 33, pl. 17, figs. 4a-d.—Thompson, 1927: 246. —Hatai, 1938: 717; —1940: pl. 9, figs. 39-42. —Hertlein and Grant, 1944: 125-126, pl. 13, figs. 1-4.—Roth, 1972: 8.

Miogryphus willetti Hertlein and Grant, 1944: 95-96, pl. 11(figs. 4-9). —Mattox, 1956: 76. —Roth, 1972: 16.

Type Specimens and Type Locality: Holotype CASIP 7361. USA, California, Santa Barbara Co., 6.4 km S of Lompoc, west side of San Miguelito Creek [Miocene, Temblor Formation]. Not seen.

Material Examined. 19 lots (see List of Additional Specimens Examined).

Description. *Shell* deep; ribs wide undulations of shell. *Pedicle* short. *Color* of shell whitish, ribs often carmine.

Shell size large; total lengths to 42 mm; widths to 46 mm; depths to 28 mm.

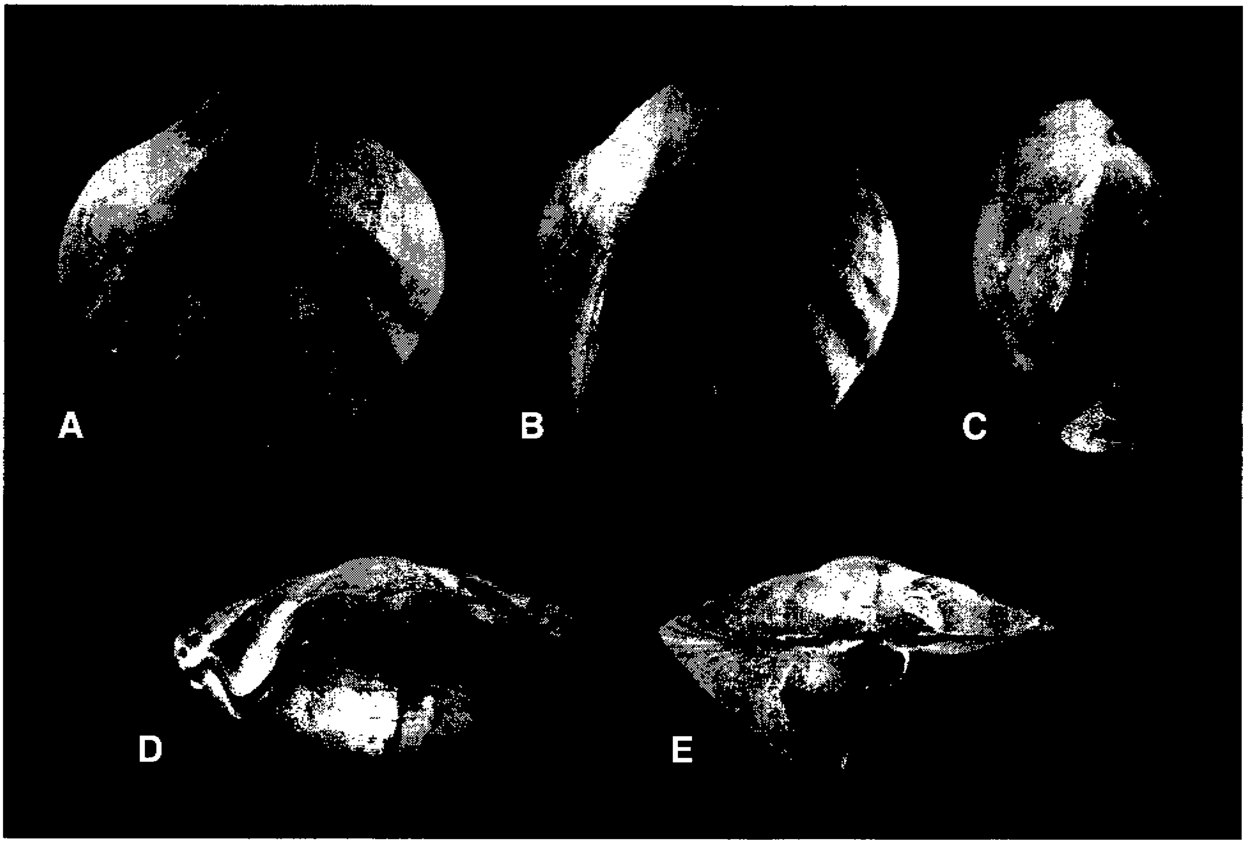

Figure 1.10. *Terebratalia occidentalis* (Dall, 1871): off Santa Catalina Island, California (SBMNH 32400); 38.5 mm TL. A, dorsal view; B, ventral view; C, lateral view; D, end view, anterior margin; E, end view, posterior margin.

Type Specimens and Type Locality. Holotype, — USNM 95850. California, off San Clemente Island, 45 fm [82 m], *Albatross* station 2981.

Distribution. Oligocene to Recent. Monterey, California (36°N) southward to Cabo San Lucas, Baja California, Mexico (23°N, SBMNH) and out to Cedros Island. Ranges in depth of collection from 50-250 m.

Etymology. Specific name derived from the Latin word *occidentalis*, meaning "western or westerly."

Common Name. Western lamp shell.

Biology. Nothing is known about the biology of this species. In southern California the species is abundant in collections that also include *Laqueus californianus*. The species typically occurs attached to rocks or other brachiopod shells either singly or in small clusters (Mattox, 1956).

Remarks. Woodring (1950) and later Mattox (1956) questioned the distinctness of *Terebratalia arnoldi* Hertlein and Grant, 1944, a Pliocene fossil which is very similar to *T. occidentalis* in general shape and ornamentation. It is considered here to represent a junior synonym. Other fossil taxa, such as *T. smithi* Arnold, 1917, need to be reevaluated and their taxonomic placement critically assessed. The smooth subspecies *Terebratalia occidentalis obsoleta* Dall, 1891 currently is considered to represent an ecomorph of *occidentalis*.

Terebratalia transversa (Sowerby, 1846)

Figure 1.11

Terebratula transversa Sowerby, 1846: 94; 1847: 361, pl. 72, figs. 114, 115. —Gould, 1860: 120.

Terebratella transversal: Gray, 1853: 89. —Reeve, 1860: pl. 5, fig. 22. —Dall, 1873: 185. —Whiteaves, 1878: 468. —Davidson, 1887: 79 [in part], pl. 16, figs. 6-9 only.

Terebratalia transversa: Dall, 1891: 172, 526, pl. 4, figs. 6, 7; 1894 [1895]: 727 [in part]; 1920: 339.—Beecher, 1893a: 382. —Beecher, 1893b: 377.—Kelsey, 1907: 50. —Willett, 1918: 66. —Oldroyd, 1924a: 204, pl. 29, figs. 1-3; 1924b: 227, pl. 16, figs. 1-3. —Hertlein and Crickman, 1925: 256. —Thompson, 1927: 245, text-fig. 79. —Johnson and Snook, 1927: 157, figs. 128, 131. —Keep and Baily, 1935: 21-22, fig. 4. —Hatai, 1936: 89. —Nomura and Hatai, 1937: 180-181, pl. 25, fig. 20 —Burch, 1942: 6-7. —Hertlein and Grant, 1944: 135-138, text-figs 8, 9, pl. 8, figs. 10, 15, 16, pl. 9, figs. 1, 2, 5-7, pl. 21, figs. 8, 9. —Smith and Gordon, 1948: 210. —Mattox, 1956: 76, figs. 5A-J . —Rickets and Calvin, 1968: 262-264, fig. 195. —MacGinitie and MacGinitie, 1968: 178. —Bernard, 1972:81, figs. 11-14. —Roth, 1972: 14. —Kozloff, 1973: 177. —Zimmer and Haderlie, 1980: 109-110, pl. 39, figs. 7.1a, b.

Terebratulina transversa: Dall, 1907: 18.

Magasella radiata Dall, 1877a: 159; 1877b: 49.—Davidson, 1887: 101, pl. 18, fig. 1.

Type Specimens and Type Locality: Holotype, USNM 110913. Alaska, Popoff Strait, Shumagin Islands, low tide.

Terebratula transversa caurina Gould, 1850: 347; 1857: 468, pl. 44, fig. 582. 1862: 97.

Type Specimens and Type Locality: Holotype,—USNM 5964. Washington, Puget Sound. Not seen.

Terebratula caurina: Gould, 1852: 468. —Carpenter, 1856 [1857]: 210, 298 [*canrena,* sic]

Terebratella caurina: Gould, 1862: 97. —Dall, 1870: 119, pl. 6, figs. 1-3. —Thompson, 1927: 246.

Terebratella transversa var. *caurina*: Davidson, 1887: 80, pl. 16, figs. 10-12, 14, 14a only.

Terebratalia transversa caurina: Dall, 1894[1895]: 733, pl. 31, figs. 12, 13; 1920: 340. —Oldroyd, 1924a: 204, pl. 29, figs. 4-7; 1924b: 228, pl. 16, figs. 4-7. —Fenton, 1932: 53-54, figs. 1-3. —Hatai, 1936: 89. —Nomura and Hatai, 1937: 181, pl. 25, figs. 1-4. —Burch, 1942: 1. —Hertlein and Grant, 1944: 138-143, text-figs. 29, 30, pl. 8, figs. 11-14, pl. 9, figs. 9, 10, 12, pl. 12, figs. 2, 8, pl. 15, figs. 7, 12, 13, 15, 16, pl. 21, figs. 12, 14. —Smith and Gordon, 1948: 210. —Mattox, 1956: 76, figs. 5A-D.

Terebratalia caurina: Thompson, 1927: 246. —Hatai, 1936: 89.

Terebratella coreanica: Carpenter, 1864: 636. [see Dall, 1920: 345]. (**not** Adams and Reeve, 1850).

Terebratalia transversa var. *rubescens* Dall, 1910: 96.

Type Specimens and Type Locality: Holotype, —USNM, 253820. California, San Pedro. Not seen

Terebratalia caurina rubescens: Dall, 1920: 341. —Burch, 1942: 7.

Terebratalia rubescens: Hatai, 1936: 89.

Waldheimia grayi: Carpenter, 1864: 636 [see Dall, 1920: footnote 350, 360]. (**not** Davidson, 1852).

Terebratalia hemphilli Dall 1902: 561, pl. 40, figs. 8, 10. —Arnold, 1903: 92, pl. 17, figs. 1-3. —Arnold, 1907: 425, pl. 58, figs. 4a, b. —Smith 1919: 150-151. —Hertlein and Grant, 1944: 123-125, pl. 9, figs. 3, 4, pl. 10, figs. 1, 2; 1960: 93-94, pl. 19, figs. 26, 27. —Roth, 1972: 7.

Type Specimens and Type Locality: Holotype, —USNM 108495. California, west of Santa Barbara, Arroyo Buero [Burro], in Hope Ranch 1/2-1 mi inland from sea [Pliocene]. Not seen.

Terebratalia hemphillii [sic]: Carson, 1925: 268.

Terebratalia obsoleta: DuBois, 1916: 178, pl. 32, figs. 1-8. (**not** Sowerby).

Material Examined. *California*: Santa Maria Basin, Station BRC-1, 73.5-78m, 2 specimens, 11.8, 19.5 mm TL; USNM (w). Station BRA-13, 92-100m, 1 specimen, 5.5 mm TL; SBMNH (w).

Additional material examined: 22 lots (see List of Additional Specimens Examined).

Description. *Shell* shape subovate to transversely produced, wider than long. *Anterior commissure* sulcate, sometime sinuated; valve margin smooth to crenulated. *Valves* smooth, wrinkles with growth lines toward margin; valves surface of *carina* morph ornamented with 12 or more obtusely angular, radiating ribs, gradually enlarging and sometimes bifurcating; interspaces and elevations about equal; valves punctate. *Beaks* short, concavely flattened beneath each side; foramen very large; deltidium small, widely divided. *Color* typically red, occasionally pale yellow to white or light gray.

Shell size large; total lengths to 45 mm; widths to 55 mm; depths to 37 mm.

Type Specimens and **Type Locality.** BMNH, not searched. Washington, Puget Sound. Bernard (1972) indicated that a type locality was not designated by Sowerby.

Distribution. Miocene to Recent. Eastern Pacific Ocean, Kodiak Islands, Alaska (58°N; Dall, 1920) to Ensenada, Baja California, Mexico (32°N; Burch, 1942). Reported from the lower intertidal zone in the northern part of its distribution to 1800 m in the south.

Etymology. Specific name derived from the Latin *transvers* meaning "situated or lying across" in obvious reference to the distinct ribs seen in some morphs of this species.

Common Name. Transverse lamp shell.

Biology. A voluminous literature documents the biology of *Terebratalia transversa.* The species has been studied extensively in Puget Sound and other areas in Washington. Ecological studies by Paine (1969, 1974) and Thayer (1975) have documented growth, size distribution, and the role and structure of *T. transversa* populations in intertidal communities. This species is often extremely abundant intertidally in the northern part of its range, generally on underside of large boulders.

Details of the ontogeny of shell secretion, such as development of the mantle and formation of the juvenile shell and the development of the pedicle are elucidated in several papers by Stricker and Reed (1985a-d). Details of metabolism and shell growth are discussed by Williams (1971), Hughes *et al.* (1988), Rosenberg *et al.* (1988) and Tkachuck *et al.* (1989).

Reed (1987) and later Long and Stuckey (1994) reviewed reproduction and development in *Terebratalia transversa* and several other west coast brachiopod species. In part they review the earlier embryology studies in the dissertation of Long (1964).

The ultrastructure and physiology of muscles, especially slow and rapid contraction mechanisms are treated in papers by Wilkens (1978a, b, 1987), Eshleman and Wilkens (1979), Eshelman *et al.* (1982), and Ackerly (1991a-c).

The ultrastructure of a variety of organs are treated in papers by Gustus and Cloney (1972; setae), Reed and Cloney (1977; tentacles), and Cavey and Wilkens (1982; statocysts). Aspects of the functional morphology of the lophophore, including oxygen consumption, feeding and nutrient assimilation, are discussed by Strathman (1973), McCammon and Reynolds (1976), Reynolds and McCammon (1977) and LaBarbera (1986). The orientation of animals in relation to currents and the dynamics of ventilation are included in LaBarbera (1978b, 1981). Thayer (1986) and later Rhodes and Thayer (1991) investigated the effects of turbidity on suspension feeding in *Terebratalia transversa* and compared the efficiency of feeding in bivalves and articulate brachiopods.

Bradbury (1970) described *Urceolaria kozloffi*, a mobile ciliophoran from the tentacles of the lophophore of two brachiopods from Puget Sound, *Terebratalia transversa* and *Hemithyris psittacea*. The protozoan is thought to feed at the expense of the host's food supply.

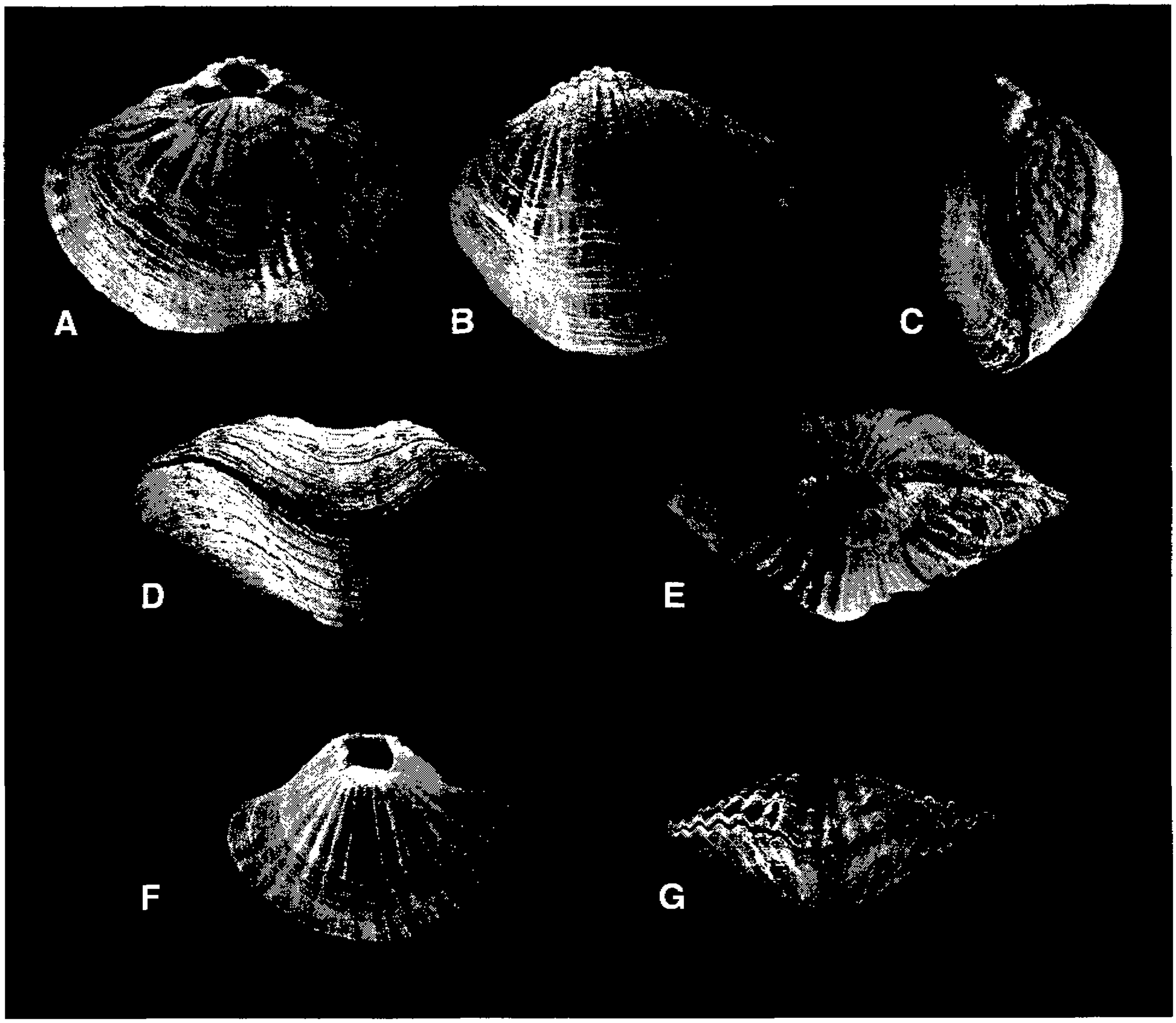

Figure 1.11. *Terebratalia transversa* (Sowerby, 1846). A-E, depth unknown, off Point Conception, California (SBMNH 46074); 34.4 mm TL. A, dorsal view; B, ventral view; C, lateral view; D, end view, anterior margin; E, end view, posterior margin. F, G, 0.5 m, Mission Bay, San Diego, California (SBMNH); 22.5 mm TL. F, dorsal view; G, end view, anterior margin.

Remarks. The environmental variation of this highly plastic species has been discussed by Shimer (1905) and Du Bois (1916). Bernard (1972) stated that the subspecies *Terebratalia transversa caurina* (Gould) is not valid but is simply a southern heavily ribbed, gibbous form with a tendency to a reddish hue.

Terebratalia hemphilli, a widely distributed Pliocene fossil in Central California, is similar to the large smooth form of *T. transversa*, but generally is longer and broader (length 64mm, width 58mm and depth 40 mm). It should be regarded as a synonym.

Family Platidiidae Thomson, 1927

Diagnosis. Shell size small, plain colored; plano-convex, amphithyridid. Hinge plates absent; socket ridges present. Pedicle short. Foramen large, occupies posterior area of both valves (= amphithyridid). Loop rudimentary or absent. Spicules conspicuously present. Dental plates absent or low and heavy. Lophophore shizolophous or plectolophous. Cardinal process absent.

Type Genus. *Platidia* Costa, 1852.

Genus *Platidia* Costa, 1852

Diagnosis. Shell minute, thin; penetrated by numerous microscopic punctae. Hinge teeth weak, crura long and curved; septum a triangular plate.

Type Species. *Orthis anomioides* Sacchi and Philippi, 1844; by monotypy.

***Platidia hornii* (Gabb, 1861)**

Figure 1.12

Morrisia hornii Gabb, 1861:371. —Carpenter, 1864: 632. —Gabb, 1869: 36, pl. 12, fig. 63. —Cooper, 1871: 4. —Hertlein and Grant, 1944: 110-112, text-figs. 24, 25, pl. 7, fig. 30, pl. 19, figs. 14-18. —Smith and Gordon, 1948: 210, 233.

Platidia hornii: Thompson, 1927: 219. —Hatai, 1938: 715. —Bernard, 1972:79, fig. 4. —Zimmer and Haderlie, 1980: 110.

Platidia anomioides var. *radiata* Dall (in Orcutt), 1885: 552. —Dall, 1886: 204. —Thompson, 1927: 219.

Type Specimens and Type Locality: Syntypes, —USNM 860930. California, San Diego, beach drift. Not seen.

Platidia seminula var. *radiata*: Dall, 1889: 28.

Platidia seminula radiata Dall, 1885: 551; 1920: 332-333. —Oldroyd, 1924b: 226, pl. 49, figs. 2, 7. —Burch, 1942: 6.

Platidia radiata: Hatai, 1936: 87; 1938: 715.

Not *Platidea aneminoides* [sic]: Berry, 1907: 39. —Gripp, 1909: 137. —Oldroyd, 1914: 81. —Keep and Baily, 1935: 22.

Not *Platidia anomioides*: Kelsey, 1907: 47. —Dall, 1907: 86.

Not *Platidea anomioides*: Berry, 1908: 39. —Gripp, 1909: 137. —Oldroyd, 1914: 81.

Material Examined. *California*: Santa Maria Basin, Station BRA-13, 92-100m, 44 specimens, 1.1-2.8 mm TL; USNM(w). Station BRA-25, 64.5-72m, ca. 30 spec., 1.3-2.7 mm TL; SBMNH(w).

Additional material examined: 16 lots (see List of Additional Specimens Examined).

Description. *Shell* flattened; shape uniformly circular; valves thick; inner surface with numerous small punctae; outer surface without distinct sculpture, either smooth or with concentric growth lines. *Pedicle* short; foramen large, occupies posterior area of both valves. *Color* of shell light brown.

Shell size minute; maximum diameter observed to 4.6 mm.

Type Specimens and Type Locality. Holotype, presumed to be in ANSP collection. California, Santa Barbara [Miocene]. See remarks below.

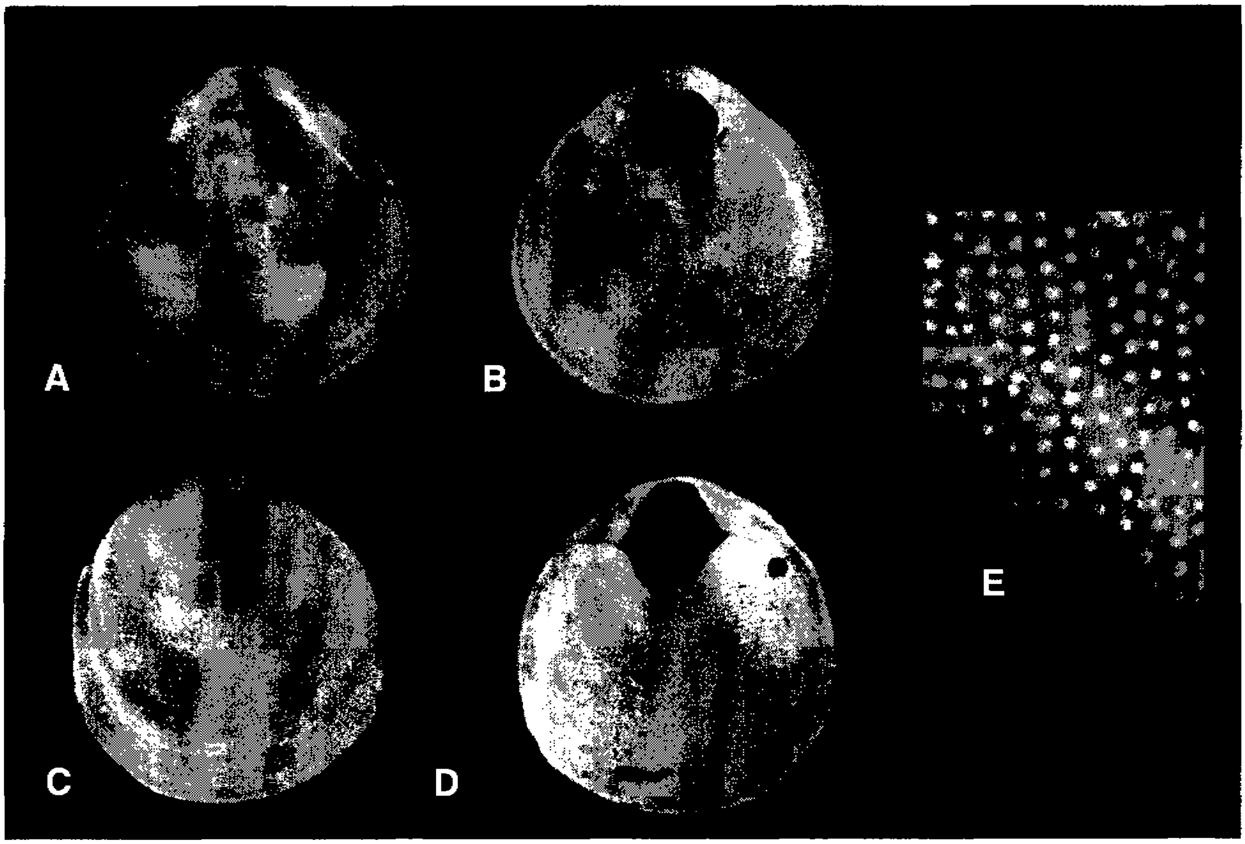

Figure 1.12. *Platidia hornii* (Gabb, 1861). A, B, 97 m, off Point La Jolla, California (SBMNH [SSB 30052]); 3.6 mm TL. A, dorsal view; B, ventral view. C-E, 45 m, off Monterey, California (CASIZ 105953); 4.6 mm TL. C, ventral view; D, ventral view; E, detail of punctae at edge of shell.

Distribution. Upper Pliocene to Recent. Eastern North Pacific, British Columbia, (51°N; Bernard, 1972) to Todos Santos Bay, Baja California, Mexico (23°N; Dall, 1885). Depths range from low intertidal to 500 m.

Biology. Attached to stones or dead shells in the low intertidal zone along semiprotected rocky shores and in subtital waters. Additional information on the biology of this species is not not known. Tiny, young or immature specimens appear very similar to foraminiferans and often are confused as such.

Remarks. A lot (ANSP 4495) labeled in Gabb's hand as the type of *Morrisia horni* was obtained on loan from Philadelphia. Unfortunately the specimen does not correspond to *Platidia*. It is presumed that the type is not extant. Cooper considered the species to belong in the genus *Amphithyris* (see Hertlein and Grant, 1944: 112).

Reports of this species from Santa Cruz Island in the West Indies are presumed to instead refer to Santa Cruz Island off the south central coast of California (see Dall, 1889). This apparent mistake has been perpetuated in all subsequent papers which discuss distribution of this species.

Acknowledgments

The following individuals provided valuable assistance in completing this publication: Andrea Moe cataloged brachiopod material in the SBMNH collection; Elizabeth Kool and Terry Gosliner facilitated access to the brachiopod collections at CASIZ; Mike Sweeney helped locate literature and provided assistance with collections at the NMNH; Joann Rounds prepared illustrations for the introductory sections of this paper; Paul Scott and Marie Murphy helped to prepare plates of digitized images of brachiopod shells.

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List of Additional Specimens Examined

Additional brachiopod specimens examined. Specimens preserved in alcohol are indicated by (w) following the catalog number, all other specimen lots are dry. Abbreviations: Co. = county; coll. = collector (s); spec. = specimen(s); TL = total length.

Glottidia albida

California: 1 specimen, 12.0 mm TL; Ventura Co., Point Mugu, USNMC Base, 1/2 mi N of Mugu Pier, 3/8 mi offshore, 40-50 ft [12-15 m]; coll. M. Conboy and G.E. MacGinitie, 13 August 1963; SBMNH 44477M. —2 spec., 16.4, 16.6 mm TL; Ventura Co., Point Mugu USNMC Base, 3/4 mi off Mugu Pier, 50-60 ft [15-18 m]; coll. B. Spronce and party, 06-07 October 1963; SBMNH 46150 (w). —2 spec., 23.4 mm TL; Ventura Co., off Ventura, 20 fm [36 m]; coll. P. Brophy, June 1967; SBMNH. —2 spec., 5.0, 11.5 mm TL; Santa Barbara Co., Santa Barbara Channel, bearing 187°T, 2.5 mi from Platform *Hilda*; coll. R/V *Velero*, station 12747, 06 March 1969; SBMNH 43528. —2 spec., 5.2 mm TL; Santa Barbara Co., Santa Barbara Channel, bearing 123°T, 2.7 mi from Stearns Wharf; coll. R/V *Velero*, station 12861, 03 April 1969; SBMNH 43604. —1 spec., 15.7 mm TL; Santa Barbara Co., Santa Barbara Channel, bearing 119°T, 2.8 mi from Stearns Wharf; coll. R/V *Velero*, station 12857, 04 April 1969; SBMNH 43566. —4 spec., 3.9-6.6 mm TL; Santa Barbara Co., Santa Barbara Channel, bearing 117°T, 3 mi from Stearns Wharf; coll. R/V *Velero*, station 12858, 03 April 1969; SBMNH 43558. Ventura Co., bearing 150°T, 4 mi off Port Hueneme Lighthouse, 20 fm [36 m]; coll. R/V *Velero*, station 12792, 20 March 1969; SBMNH 43786. —9 spec., 22.1-31.7 mm TL; Los Angeles Co., off San Pedro; coll. and date unknown; SBMNH 28265 [*ex* F.S. VanDenBergh]. —10 spec., 14.5-19.9 mm TL; Los Angeles Co., Santa Catalina Island, off Avalon, 50 fm [91 m]; coll. and date unknown; SBMNH [SSB 686]. —1 spec., 33.3 mm TL; Orange Co., Newport Harbor, depth unknown; coll. W.S. Smith, — 1967; SBMNH 47644 (w). —4 spec., 12.7-22.2 mm TL; Orange Co., Newport Bay, depth unknown; coll. and date unknown; SBMNH. —2 spec.; San Diego Co., off La Jolla Cove, 32°52'N, 117°17.4'W, 73 m; coll. F. Rokop and S. Luke, R/V *Oconostota*, station 1, Van Veen grab, 04 November 1969; BIM/SIO B22.

Neocrania californica

California: 1 specimen + 9 valves, 11.4-14.4 mm TL; Coronado Bank, 32°32.8'N, 117°21.1'W, 60 fm [110 m]; coll. H.V. Hamilton, U.S. Bureau of Mines, station 58, date unknown; CASIZ 105949. —1 spec., 20.0 mm TL; Cordell Bank, bearing 347°T, 6.2 mi from distant rocks, 37°55'N, 123°24'W, 68 fm [124 m]; coll. USS *Mulberry*, station 19, 28 September 1950; CASIZ 105948.

Frieleia halli

California: 13 specimens, 12.8-19.0 mm TL; San Diego Co., off San Diego, 628-640 fm [1149-1170 m]; coll. USBCF *Albatross*, station 4353 date unknown; SBMNH [SSB 3038]. —17 spec., 9.5-17.2 mm TL; San Diego Co., S of San Diego, "depth 1 mi"; coll. C. Snell, December 1969; SBMNH 25850. —24 spec., 6.1-20.0 mm TL; San Diego Co., San Diego Trough, 32°37'N, 117°32.6'W, 1171-1217 m; coll. F. Rokop, R. McConnaughey and S. Luke, R/V *Agassiz*, station Rokop 70-I-12, 25 ft otter trawl, 29 October 1970, attached to sponges; SBMNH [*ex* SIO] (w). —2 spec., 15.3-16.3 mm TL, Monterey Bay, 700 fm [1280 m]; coll. and date unknown; SBMNH [SSB 1183 or 1883?]. —1 spec., 18.0 mm TL; San Diego Co., San Diego Bay; coll. F.W. Kelsey, date unknown; CASIZ 029804 [*ex* Hemphill 19206; voucher, Hertlein and Grant, 1944, text-fig. 11, pl. 4, figs. 6, 7]. —4 spec., 13.0-15.5 mm TL; Monterey Bay; coll. USBCF *Albatross*; CASIZ 106304. —3 spec., 15.7-18.0 mm TL; San Diego Co., off San Diego, 32°40'N, 117°31'W, 822 fm [1503 m]; coll. USBCF *Albatross*, station 2923, 19 January 1889; CASIZ 106306. —4 spec., 14.4-

18.0 mm TL; San Diego Co., San Clemente Island, bearing 74°W, 5.8 mi from E point of Northwest Harbor, 542-599 fm [991-1096 m]; coll. USBCF *Albatross*, station D4402, 08 April 1904; CASIZ 106305. —1 spec., 16.7 mm TL; San Diego Co., off San Diego, 32°24.7'N, 117°27.7'W, 658-680 fm [1243-1203 m]; coll. T. Matsui, SIO71-29, 25 ft otter trawl, 18-19 January 1971; BIM/SIO B42 (w). —200+ spec., 6.8-18.6 mm TL; San Diego Trough, 32°35'N, 117°28'W, 1097-1180 m; coll. F. Rokop and S. Luke, R/V *Oconostota*, station 4, 07 November 1969; BIM/SIO B27 (w). —200+ spec., 5.0-18.0 mm TL; San Diego Trough, 32°37.0'N, 117°32.6'W, 1170-1216 m; coll. F. Rokop and S. Luke, R/V *Agassiz*, station Rokop 70-I-12, 25 ft otter trawl, 29 October 1970; BIM/SIO B53 (w). —140 spec., 7.2-18.2 mm TL; San Diego Trough, 32°35.0'N, 117°33.6'W, 1183-1216 m; coll. F. Rokop and S. Luke, R/V *Agassiz*, station Rokop 71-II-28, 25 ft otter trawl, 21 January 1971; BIM/SIO B55 (d). —2 spec., 14.0, 16.4 mm TL; off La Jolla, 32°55.5'N, 117°37.4'W, 896 m; coll. J. F. Siebenaller, R/V *Oconostota*, station 10, 16 ft otter trawl, 06 September 1974; BIM/SIO B116 (w). —27 spec., 7.8-19.9 mm TL; San Diego Trough, 32°52.1'N, 117°42.1'W, 1057 m; coll. J.F. Siebenaller, R/V *Agassiz*, station A-24 Afterthot II, 25 ft otter trawl, 08 May 1975; BIM/SIO B117 (w).

Terebratulina crossei (also included here are specimens previously identified as *T. kiiensis*)

California: 1 specimen (broken), 27.4 mm TL; bearing WSW 3.5 mi off La Jolla Point, 53 fm [97 m]; coll. H. Barrington, F/V *Christine*, 10 April 1962; SBMNH [SSB 30049]. —2 spec., 18.1, 24.0 mm TL; off Monterey, "deep water"; coll. H.R. Turner (from fishermen), 02 April 1943; SBMNH [SSB 16908]. —2 spec., 21.9, 27.2 mm TL; San Diego Co., off Tijuana River, 70-80 fm [128-146 m]; coll. R. McAllister, October 1953; SBMNH [SSB 25547 and 24789]. —3 spec., 5.6-31.4 mm TL; off La Jolla, 100 fm [183 m]; coll. San Diego Marine Biological Association, 1901; SBMNH [SSB 3265]. —1 spec., 27.4 mm TL; San Diego Co., bearing SW, 9.7 mi off Point Loma, 34°34.2'N, 117° 24'W, 120 fm [220 m]; coll. W. Dahlstrom, prawn trap, 29 March 1969; SBMNH [SSB 36310]. —35 spec., 6.6-25.0 mm TL; Cortez Bank, 125 fm [229 m]; coll. L. Zermatten, hook and line, April 1965; SBMNH [SSB 33321]. —1 spec., 4.0 mm TL; Cortez Bank, 100 fm; coll. L. Zermatten, December 1962; SBMNH [SSB 30019]. —1 spec., 30.6 mm TL; bearing S, 9 mi off Santa Monica, 48 fm [88 m]; coll. P. Brophy, ballon trawl, August 1971; SBMNH. —2 spec., 11.9, 15.2 mm TL; Santa Barbara Channel, off Gaviota, 73 fm [133 m]; coll. P. Brophy, June 1966; SBMNH. —8 spec., 10.2-12.8 mm TL; Santa Barbara Channel, off Gaviota, 72 fm [132 m]; coll. P. Brophy, June 1968; SBMNH. —2 spec., 11.0, 18.0 mm TL; Santa Catalina Island, off Isthmus, 50 fm [91 m]; coll. P. Brophy, 2 m beam trawl, June 1972; SBMNH (w). —1 spec., 31.3 mm TL; Venture Co., Sycamore Bank (between Point Mugu and Point Dume), 50 fm [91 m]; coll. H. Barrington, F/V *Christine*, 24 March 1962; SBMNH [SSB 30069]. —1 spec., 27.0 mm TL; San Francisco Co., Farallon Islands, W of Middle Farallon Island, bearing 101°T, 9.2 mi from Farallon Light, 37°43.8'N, 126°04.6'W, 70-126 fm [128-230 m]; coll. USS *Mulberry*, 26 August 1944; CASIZ 105951 [GE 32934]. —1 spec., 30.0 mm TL; San Diego Co., San Diego region, 32°32'N, 117°19.0'W, 104-250 m; coll. San Diego Marine Biological Association, 27 July 1901; CASIZ 106307. —3 spec., 18.1-28.0 mm TL; Santa Barbara Co., bearing 233°T, 3 mi off Coal Oil Point, 64-80 fm [117-146 m]; coll. G.D. Hanna, R/V *N.B. Scofield*, 6 June 1953; CASIZ 106308. —4 spec., 17.3-28.5 mm TL; San Diego Co., San Diego region, 32°52'N, 117°17'W, 100-195 m; coll. San Diego Marine Biological Association, 23 July 1901; CASIZ 106309. —1 spec., 31.4 mm TL; Los Angeles Co., off Redondo Beach, deep water; coll. and date unknown; CASIZ 106336. —1 spec., 35.0 mm TL; Los Angeles Co., off Redondo Beach, deep water; coll. H. Hill, pre 1938; CASIZ 029801 [voucher, Hertlein and Grant, 1944, pl. 17(figs. 3, 6 10)]. —2 spec., 34.9, 37.2 mm TL; Monterey Co., Lopez Point, 70 fm [128 m]; coll. A. Sorensen, date unknown, attached to solitary coral, *Paracyathus stearnsii*; CASIZ 105950 [GE 37188]. —2 spec., 28.8, 35.5 mm TL; Monterey Co., off Point Sur, 36°20.45'N, 122°06.15'W, 208 fm [380 m]; coll. R. Bolin and Budd, 12 November 1935; CASIZ 016592. —1 spec. 29.5 mm TL; San Diego Co., off San Diego, 50 fm [91 m]; coll. and date unknown; CASIZ 029806 [voucher for *T. kiiensis*, Hertlein and Grant, 1944, text-fig. 18]. —3 spec., 32.0-34.1 mm TL; Monterey Bay, 50-60 fm [91-110 m]; coll. unknown, 28 June 1932; CASIZ 106335. —3 spec., 21.8-34.0 mm TL; Los Angeles Co., off San Pedro, deepwater; coll.

T.S. Oldroyd, date unknown; CASIZ 106334. —3 spec., 20.0-21.0 mm TL; San Diego Co., La Jolla, 100 fm [183 m]; coll. University of California, pre 1912; CASIZ 105952. —2 spec., 28.2, 29.1 mm TL; off San Diego, 137 m; coll. and date unknown; BIM/SIO B65 [*ex* Baker-Kelsey collection]. —3 spec., 21.5-29.6 mm TL; Forty-mile Bank, 32°N, 117°56.2'W, 183 m; coll. F.P. Shepard, R/V *E.W. Scripps*, station Shepard 69, dredge, 10 June 1938; BIM/SIO B118. —5 spec., 25.0-31.0 mm TL; Forty-mile Bank, 32°40'N, 118°12'W, 60 fm [110 m]; coll. F.P. Shepard, R/V *E.W. Scripps*, dredge, 22 March 1938; BIM/SIO B119. —2 spec., 33.0, 34.2 mm TL; San Diego Co., Nine-mile Bank, 9 mi W by SW off Point Loma, 32°40'N, 117°28'W, depth unknown; coll. Capt. J. LaGrange, F/V *Cloud Nine*, spring 1990; SBMNH.

Terebratulina unguicula

California: 7 specimens, 2.8-17.7 mm TL; Monterey Co., off Point Piños, 46-56 fm [84-102 m]; coll. USBCF *Albatross*, station 4551, date unknown; SBMNH [SSB 3034]. —10 spec., 5.4-13.9 mm TL; Santa Barbara Co, Anacapa passage, 26-27 fm [47-49 m]; coll. C.L. Hubbs and party, R/V *Orca*, station H51-252, 02 July 1951, on coral colony; SBMNH [SSB 23577]. —17 spec., 3.9-14.7 mm TL; Santa Rosa Island, off E point, 80 fm [146 m]; coll. F. Fricia, 15 May 1953; SBMNH [SSB 18889]. —10 spec., 5.2-11.2 mm TL; San Diego Co., off Oceanside; coll. H.G. Eaton, ca. 1906, from kelp holdfasts; SBMNH [SSB 9096]. —9 spec., 5.9-11.7 mm TL; San Diego Co., off La Jolla, La Jolla Canyon; coll. Scripps Institution of Oceanography, 22 March 1938, on solitary corals; SBMNH [SSB 13507]. —6 spec., 3.8-8.9 mm TL; Ventura Co., Sycamore Bank (between Point Mugu and Point Dume), 34°00'N, 119°02'W, 50 fm [91 m]; coll. H. Barrington, F/V *Christine*, 24 March 1962; SBMNH [SSB ??]. —6 spec., 3.0-14.9 mm TL; San Diego Co., bearing WSW, 3.5 mi off La Jolla Point, 53 fm [97 m]; coll. H. Barrington, F/V *Christine*, 10 April 1962; SBMNH [SSB 30050]. —41 spec., 3.3-15.8 mm TL; Monterey Bay, 15-30 fm [27-55 m]; coll. and date unknown, station 3-18, attached to solitary coral; SBMNH 28272. —1 spec., 9.8 mm TL; 195°T 10 mi from Marina del Rey Harbor, 59-62 fm [108-113 m]; coll. P. Brophy, shrimp trawl, 9 September 1974, on coral head; SBMNH (w). —1 spec., 12.5 mm TL; Humboldt Co., off Trinidad, 180 fm [329 m]; coll. unknown, September 1975; SBMNH. —1 spec., 10.0 mm TL; San Diego Co., off San Diego; coll. and date unknown; CASIZ 29820 [ex Hemphill 6073; voucher, Hertlein and Grant, 1944, pl. 5(figs. 9, 10)]. —14 spec., 11.5-14.0 mm TL; Monterey Bay, Monterey Co., off Del Monte, 35-40 fm [64-73 m]; coll. J.Q. Burch and A.G. Smith, 20 August 1937, attached to solitary corals; CASIZ 106319. —6 spec., 13.5-23.0 mm TL; Humboldt Co., off Eureka, 67 fm [122 m]; coll. Capt. J. Riley, M/V *Inez*, March 1969; CASIZ 106333. —6 spec., 4.2-13.4 mm TL; Ventura Co., off San Nicolas Island; coll. and date unknown; CASIZ 27603. —8 spec., 9.0-18.5 mm TL; Humboldt Co., Eel River Canyon, 40°28'N, 200 fm [366 m]; coll. Capt. K. Einhern, F/V *Stephanie*, 19 September 1975, attached to calcitic rock; CASIZ 106321. —1 spec. + 1 valve, 6.0-6.8 mm TL; Monterey Bay, Monterey Co., off Mussel Point, 10 fm [18 m]; coll. A.G. Smith and M. Gordon, station 4, 27 September 1932; CASIZ 106320. —18 spec., 8.5-13.2 mm TL; Monterey Bay, Monterey Co., off Monterey, ca. 2-1/2 mi offshore, 35-40 fm [64-73 m]; coll. A.G. Smith and J. Burch, 20 August 1937; CASIZ 28916. —22 spec., 3.3-13.0 mm TL; Monterey Bay, Monterey Co., 1/2 mi off Hopkins Marine Station, between Pacific Grove bell bouy and Del Monte wharf, 20-30 fm [37-55 m]; coll. G.D. Hanna, A.G. Smith and J.L. Nicholson, July 1930; CASIZ 106318. —102 spec., 2.0-10.5 mm TL; Monterey Bay; coll. and date unknown, attached to solitary corals, *Paracyathus stearnsii*; CASIZ 106322. —2 spec., 24.0, 25.0 mm TL; Monterey Bay; coll. J. Strohbeen, March 1956; CASIZ 106338. —7 spec. + 3 valves; Monterey Bay, Monterey Co., Pacific Grove, 20 ft [6m]; coll. Harrington; CASIZ 106316 [ex SU 53167]. —2 spec., 5.4-7.5 mm TL; off Point Loma, 64 m; coll. USBCF *Albatross*, 12 August 1916, attached to solitary coral, *Paracyathus stearnsii*; BIM/SIO B102. —1 spec., 15.6 mm TL; off La Jolla, in Scripps Canyon, 1/2 mi off SIO pier, 32°52.12'N, 117°15.58'W, 600 ft [183 m]; coll. R. McConnaughey, trap, 03 February 1984; BIM/SIO B156 (w).

Washington: 4 specimens, 8.3-25.0 TL; Clallam Co., 50 mi W of Umatilla Rocks, 72 fm [132 m]; coll. Capt. E. Anderson, F/V *Marie II*, March 1960; CASIZ 106315. —1 spec., 21.0 mm TL; Puget Sound, 25 fm [46 m]; coll. and date unknown; CASIZ 106314.

Laqueus californianus

California: 7 specimens, 23.2-40.0 mm TL; Los Angeles County, off San Pedro, 62-79 m; coll. W.E. Ritter and W.J. Raymond, San Diego Marine Biological Association, station 23, 22 June 1901; SBMNH 28267 and 46052. —1 spec., 41.5 mm TL; Santa Barbara Co., Santa Barbara Channel, 70 fm [128 m]; coll. V. Stevens, 01 August 1930; SBMNH 28273. —1 spec., 32.2 mm TL; Santa Barbara Co., Santa Barbara Channel, off Gaviota, 130 fm [238 m]; coll. Capt.R. Hazard, F/V *Kildee*, March 1974; SBMNH. —26 spec., 14.3-50.5 mm TL; Los Angeles Co., Santa Catalina Island, off White's Landing, 30 fm [55 m]; coll. G.Willett, 1927; SBMNH [SSB 6331]. —15 spec., 11.1-45.5 mm TL; Los Angeles Co., off Santa Catalina Island; coll. S/S *Anton Dohrn*, 31 March 1915; SBMNH 46050. —9 spec., 12.7-45.9 mm TL; Los Angeles Co., Santa Catalina Island, off Isthmus, 30 fm [55 m]; coll. P. Brophy, beam trawl, May 1969; SBMNH. —5 spec., 41.1-49.0 mm TL; San Luis Opispo Co., SSE of San Simeon Point, 35°29.4'N, 121°08.8'W, 116-118 fm [212-216 m]; coll. W. Dahlstrom, 19 October 1960; SBMNH [SSB 30077]. —1 spec., 40.5 mm TL; San Luis Opispo Co., off San Simeon, 90 fm [165 m]; coll. P. Brophy, shrimp trawl, November 1969; SBMNH. —21 spec., 10.0-49.3 mm TL; San Luis Obispo Co., off Morro Bay, 85 fm [155 m]; coll. J. Squire, R/V *Alama II*, 02 February 1953; SBMNH. —24 spec., 4.9-51.6 mm TL; Monterey Co., Monterey Bay, 36°40.3'N, 122°07.1'W, 75 fm [320 m]; coll. R.L. Bolin, 22 December 1937; SBMNH [SSB 8948]. —16 spec., 3.8-47.4 mm TL; Los Angeles Co., Santa Catalina Island, off Avalon, 50 fm [91 m]; coll. J.H. Paine, 1903; SBMNH [SSB 93]. —ca. 10 spec., 3.2-6.1 mm TL; Los Angeles Co., Santa Catalina Island, off Isthmus, 42 fm [77 m]; coll. P. Brophy, beam trawl, September 1974; SBMNH. —3 spec., 8.0-38.2 mm TL; San Francisco Co., off Moritero Point, 180 fm [329 m]; coll. P. Gregory, July 1968; SBMNH (w). —10 spec., 13.8-45.0 mm TL; Monterey Co., Monterey Bay, 36°40'30"N, 122°07'15"W, 75 fm [137 m]; coll. R. Bolin, 22 December 1937; SBMNH (w). —28 spec., 12.0-49.5 mm TL; Los Angeles Co., Santa Catalina Island, 2.8 mi E of Long Point, 33°26'00"N, 118°24'40"W, 68-88 fm [124-161 m]; coll. R/V *Velero III*, station 1307-41, 03 April 1941; SBMNH (w). —108 spec., 4.5-31.8 mm TL; coll. R/V *Velero III*, station 2953-54; SBMNH [*ex* AHF] (w). —1 spec., 32.3 mm TL; San Luis Obispo Co., Morro Bay, mud flats, depth unknown; coll. unknown, 29 June 1957; SBMNH. —1 spec., 46.0 mm TL; San Luis Obispo Co., Morro Bay, depth unknown; coll. M. Smith, 1969; SBMNH. —3 spec., 13.3-37.8 mm TL; Los Angeles Co., San Pedro, off Point Vicente, 40 fm [73 m]; coll. unknown, 1924; SBMNH. —13 spec., 5.0-29.6 mm TL; Monterey Co., Monterey Bay, 2-3 mi SW of Soberanes Point, 85-110 fm [155-201 m]; coll. R/V *Searcher*, station C-71-59, 22 July 1971; CASIZ 106313. —9 spec., 6.4-29.6 mm TL; Mendocino Co., bearing W by S 1/4 W, 3 mi from Fort Bragg bouy, 60-65 fm [110-119 m]; coll. G.D. Hanna, R/V. *N.B. Scofield*, station NBS 277, 02 August 1940; CASIZ 106312. —3 spec., 22.4-44.3 mm TL; Los Angeles Co., W of Santa Catalina Island, 33°23.0'N, 118°30.9'W, 165-230 m; coll. C.A. Kofoid and W.J. Raymond, San Diego Marine Biological Association, station 34, 28 June 1901; CASIZ 106328.

Terebratalia occidentalis

California: 3 specimens, 37.4-39.9 mm TL; southern California, "deep water"; coll. and date unknown; SBMNH 46068. —2 spec., 38.1, 39.9 mm TL; Los Angeles Co., off Santa Catalina Island; coll. unknown, ca. 1933; SBMNH 32400. —3 spec., 12.3-39.5 mm TL; Los Angeles Co., San Pedro Bay; coll. and date unknown; SBMNH 32380. —1 spec., 33.2 mm TL; Los Angeles Co., Santa Catalina Island, off SE end, 33°26'N, 118°25'W, 33-43 fm [60-79 m]; coll. unknown, 09 February 1949; SBMNH 46064. —1 spec., 42.8 mm TL; Los Angeles Co., Santa Catalina Island, off Avalon, 50 fm [91 m]; coll. J.H. Paine, 1903; SBMNH [SSB 394]. —1 spec., 32.4 mm TL; Los Angeles Co., off San Pedro; coll. W.H. Golisch (from fishermen), date unknown; SBMNH [SSB 458]. —19 spec., 13.3-37.6 mm TL; Los Angeles Co., off Santa Catalina Island, 40 fm [73 m]; coll. USC, station D103, 19 July 1924; SBMNH. —1 spec., 32.7 mm TL; Los Angeles Co., Santa Catalina Island, off Isthmus Cove; coll. USC, date unknown; SBMNH. —18 spec., 14.4-42.3 mm TL; Los Angeles Co., Santa Catalina Island, off White's Landing, 30 fm [55 m]; coll. G. Willett, 1927; SBMNH [SSB 63332, 6333, 6334, 6335]. —7 spec., 9.9-28.6 mm TL; Los Angeles Co., off San Pedro, 62-79 m; coll. W.E. Ritter and W.J. Raymond, San Diego Marine Biological Association, 22 June 1901; SBMNH 46079. —3 spec., 11.0-20.4 mm TL; Los Angeles Co., off Santa Catalina Island; coll. S/S *Anton Dohrn*, dredge, 31 March 1915; SBMNH 46078. —2 spec., 31.6, 41.0 mm TL; Los Angeles Co., Santa Catalina Island, off Isthmus, 30 fm [55 m]; coll. P. Brophy, May 1969; SBMNH. —3 spec., 18.5-23.9 mm TL; Los Angeles Co., off San Pedro; coll. T.S. Oldroyd, date unknown; SBMNH 46060. —6 spec., 8.8-32.0 mm TL; San Diego Co., Nine-mile Bank, 9 mi W by SW of Point Loma, depth unknown; coll. Capt. J. LaGrange, F/V *Cloud Nine*, spring 1990; SBMNH. —1 spec., 28.5 mm TL; Los Angeles Co., off Santa Catalina Island, 30 fm [55 m]; coll. G. Willett, pre 1934; CASIZ 29805 [voucher for *T. o. obsoleta*, Hertlein and Grant, text-fig. 28]. —4 spec., 23.0-41.4 mm TL; Los Angeles Co., off San Pedro; coll. Mrs. M. Baldridge, date unknown; CASIZ 106311 [ex A.G. Smith 6352]. —14 spec., 23.0-41.4 mm TL; Los Angeles Co., off Santa Catalina Island, 30 fm [55 m]; coll. G. Willett, date unknown; CASIZ 106310. —1 spec., 34.0 mm TL; Los Angeles Co., Santa Monica Bay, bearing W, 6.25 mi off Playa del Rey, 300-378 ft [91-115 m]; coll. W. Donnelly, F/V *Prowler*, 14 March 1962; CASIZ 106337.

Mexico: 6 specimens, 15.8-29.5 mm TL; Baja California (outer coast), Bahia Asuncion, 27°02.1'N, 114°21.1'W, 57-62 fm [104-113 m]; coll. C. Hubbs and R. Wisner, R/V *Horizon*, station MV-65-I-29 [SIO 65-212]; 45 ft otter trawl; 21 June 1965; SBMNH [*ex* BIM/SIO B21] (w).

Terebratalia transversa

California: 1 specimen, 29.2 mm TL; Los Angeles Co., off El Segundo, 31 fm [57 m]; coll. P. Brophy, beam trawl, February 1974; SBMNH. —11 spec., 11.8-28.1 mm TL; southern California, deep water; coll. and date unknown; SBMNH 28263. —3 spec., 36.1-42.5 mm TL; Orange Co., Newport, 600 ft [183 m]; coll. fishermen, date unknown; SBMNH. —8 spec., 24.9-30.6 mm TL; Los Angeles Co., San Pedro; coll. W.H. Eshmaur, date unknown; SBMNH [SSB 154]. —15 spec., 6.7-27.0 mm TL; Los Angeles Co., San Pedro, Government Breakwater, low intertidal; coll. E.P. Chace, November 1914; SBMNH [SSB 3409]. —3 spec., 12.4-24.7 mm TL; San Clemente Island, off SW side, 70 ft [21 m]; coll. R. Fay, September 1972; SBMNH. —10 spec., 12.8-34.9 mm TL; ca. 10-3/4 mi W of Point Dume, 34°00.20'N, 119°01.20'W, 47-48 fm [86-88 m]; coll. R/V *Velero III*, station 1276-41, 23 March 1941; SBMNH [*ex* AHF] (w). —12 spec., 15.5-25.7 mm TL; Santa Barbara Co., Santa Barbara; coll. and date unknown; SBMNH 28261 [*ex* F.S. VanDenBergh]. —1 spec., 40.2 mm TL; Santa Barbara Co., Santa Cruz Island, off Gull Island, 5 fm [9 m]; coll. C. Snell, November 1967; SBMNH. —1 spec., 19.6 mm TL; Los Angeles Co., Santa Catalina Island, off Avalon, 30 fm [55 m]; coll. and date unknown; SBMNH [SSB 293]. —7 spec., 28.0-42.1 mm TL; Santa Barbara Co., off Point Conception; coll. B. McMillen, December 1965; SBMNH 46074. —1 spec., 13.2 mm TL; Santa Barbara Co., off Point Conception; coll. B. McMillen, 09 June 1965; SBMNH 46075. —1 spec., 24.6 mm TL; Santa Barbara Co., off Rincon, 45 fm [82 m]; coll. P. Brophy, July 1965; SBMNH. —2 spec., 21.7, 27.4 mm TL; 9 mi S of Santa Monica, 48 fm [88 m]; coll. P. Brophy, balloon trawl, August 1971; SBMNH. —1 spec., 22.5 mm TL; Monterey Co., Monterey Bay, 15 fm [27 m]; coll. Stanford University marine lab, 1908; SBMNH [SSB 2999]. —3 spec., 20.5-35.0 mm TL; Los Angeles Co., off San Pedro; coll. and date unknown; CASIZ 29798 [voucher for *T. t. caurina*, Hertlein and Grant, 1944, pl. 15 (figs. 7, 12, 13, 15)]. —1 spec., 25.0 mm TL; Los Angeles Co., San Pedro Bay; coll. and date unknown; CASIZ 29799 [*ex* H. Hemphill; voucher for *T. t. caurina*, Hertlein and Grant, 1944, pl. 15 (fig. 16)]. —10 spec., 12.0-34.4 mm TL; Los Angeles Co., San Pedro, Government Breakwater; coll. E.P. Chace, 19 June

1916; CASIZ 106329 + 106330 [*ex* A.G. Smith 1318 + 1462]. —2 spec.; Monterey Bay, Monterey Co., off Del Monte, 12 fm [22 m]; coll. A.G. Smith, 05 June 1992 [*ex* A.G. Smith 2439]. —3 spec., 17.0-36.7 mm TL; Cortez Bank, 32°30.2'N, 119°13.7'W, 282 ft [86 m]; coll. F.H. Berry, 16 May 1963; BIM/SIO B47 (d). —1 spec., 39.8 mm TL; Quast Rock, off La Jolla, depth unknown; coll. W.A. Newman, spring 1968; BIM/SIO B96.

Washington: 2 specimens, 36.5, 47.0 mm TL; Puget Sound; coll. T.S. Oldroyd, date unknown; CASIZ 29816 [ex H. Hemphill 13951; voucher, Hertlein and Grant, 1944, pl. 8(figs. 10, 15, 16), pl. 9 (figs. 1, 2)].

Platidia hornii

California: 25 specimens, 2.1-4.4 mm TL; Santa Barbara Co., S of San Miguel Island, 65 fm [119 m]; coll. L. Zermatten, hook and line, 05 December 1966; SBMNH [SSB 33309]. —10+ spec., 2.3-2.7 mm TL; Los Angeles Co., San Pedro Bay; coll. E.P. Chace, date unknown, on empty *Mytilus californiensis* shell; SBMNH 19853. —1 spec., 3.5 mm TL; San Diego Co., off La Jolla, Scripps Canyon, 30 fm [55 m]; coll. R/V *E.W. Scripps*, 23 January 1948; SBMNH [SSB 15351]. —20+ spec., 2.2-4.8 mm TL; San Diego Co., bearing WSW, 3.5 mi off La Jolla Point, 53 fm [97 m]; coll. H. Barrington, F/V *Christine*, 10 April 1962; SBMNH [SSB 30052]. —20+ spec., 1.9-4.4 mm TL; Ventura Co., Sycamore Bank (between Point Mugu and Point Dume), 34°00'N, 119°02'W, 50 fm [91 m]; coll. H. Barrington, F/V *Christine*; 24 March 1962; SBMNH [SSB 30068]. —3 spec., 3.5-4.2 mm TL; Ventura Co., midway between Ventura and Anacapa Island, 125 fm [229 m]; coll. H. Barrington, F/V *Christine*, — 1962; SBMNH [SSB 30021]. —5 spec., 3.8-4.4 mm TL; San Luis Obispo Co., off Avila, 35°00.7'N, 121°21.5'W, 220-240 fm [402-439 m]; coll. G. Bickford, station 63-A-2, 23 March 1963; SBMNH [SSB 30086]. —3 spec., 2.5-4.1 mm TL; Los Angeles Co., off Redondo Beach, depth unknown; coll. G. Willett, date unknown; CASIZ 106322. —4 spec., 3.0-4.6 mm TL; Monterey Co., off Carmel, 25 fm [46 m]; coll. M. Gordon, date unknown; CASIZ 105953. —5 spec., 3.2-3.6 mm TL; Monterey Co., Carmel Bay, 25 fm [46 m]; coll. H. Heath, R/V *W.L. Scofield*, pre March 1930; CASIZ 106327. —1 spec., 4.0 mm TL; San Francisco Co., NW of Middle Farallon Island, 70 fm [128 m]; coll. and date unknown; CASIZ 33150. —1 spec., 3.9 mm TL; NW of Cordell Bank, 38°03.0'N, 123°33.0'W, 200-400 fm [366-732 m]; coll. USS *Mulberry*, station 56, 29 March 1950; CASIZ 106326. — 32 spec., 1.7-3.2 mm TL; Los Angeles Co., off San Diego, 32°40'N, 117°18'W, 110-240 m; coll. W.J. Raymond, San Diego Marine Biological Association, station 83, 05 August 1901; CASIZ 106325. —2 spec., 3.0, 4.0 mm TL; Los Angeles Co., off San Pedro, 200 fm [366 m]; coll. and date unknown; CASIZ 106324. —29 spec., 1.8-3.0 mm TL; San Diego Co., off San Diego, depth unknown; coll. T.S. Oldroyd, date unknown; CASIZ 106323. —2 spec., 2.6, 3.2 mm TL; off San Diego, 50 fm [91 m]; coll. and date unknown; BIM/SIO B82 [*ex* Baker-Kelsey collection].

2. PHYLUM SIPUNCULA

by

Paula S. Winchell[1]

Introduction

The Sipuncula, commonly referred to as the "peanut worms," include roughly 250 species in 17 genera. They are benthic marine animals, burrowing in sediments, hiding under stones and in some cases in mollusc shells or granular tubes.

Sipuncula are coelomate, bilateral, and similar to annelids although they are not segmented. The body is spherical or cylindrical, and can be separated into two distinct areas: the trunk and a retractable introvert region. The intestines are coiled and U-shaped, meaning that the anus is not found on the posterior end of the animal but anteriorly, in the region where the trunk and introvert meet.

During the Phase I reconnaissance only three species were found, each from a different genus, a fourth genus and species was found in the Phase II monitoring program. It is likely that additional species occur in the general area as well. In the last two decades the phylum as a whole has undergone major taxonomic revisions, and it is important to have the recent literature on hand in order to identify the animals correctly.

Taxonomic History

In 1767 Linnaeus included illustrations of Sipuncula in the twelfth edition of his *Systema Naturae* under the heading Vermes. In 1828, DeBlainville introduced the name Sipunculida, and grouped the animals with parasitic helminths. Quatrefages grouped the sipunculans, echiurans and priapulans together under the heading Gephyrea in 1847. *Gephyra* is a greek root meaning "bridge". Quatrefages thought the animals in these three groups were the intermediary between the annelids and echinoderms. Although he based his ideas on superficial characteristics, the notion persisted well into the twentieth century despite attempts by several authors to raise the groups to separate phyla. The first suggestion of elevating the Sipuncula to phylum was made by Sedgwick (1898). The Sipunculida was finally elevated to phylum rank by Hyman (1959). Stephen (1964) proposed the currently accepted spelling of the phylum. Stephen and Edmonds (1972) established four families and 17 genera. Cutler and Gibbs (1985) further classified the phylum into two classes, four orders, six families and 17 genera. A key to the families and genera is presented by Gibbs and Cutler (1987), as well as discussions of subgenera. The keys to subgenera and species can be found in a series of papers by Cutler (1979, 1986); Cutler and Cutler (1982, 1983, 1985a, 1985b, 1986, 1987, 1988, 1989, 1990); Cutler *et al.* (1983); Cutler and Jurczak (1975); Cutler and Murina (1977) and Gibbs *et al.* (1983). An overview of sipunculan systematics and synoptic keys to all known genera and species is presented in the recent treatise by Cutler (1994)[2].

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[1] 948 Head of the Bay Road, Plymouth, Massachusetts 02360.

[2] Cutler's (1994) book was received too late to be fully incorporated into this chapter. This work provides a thorough review of the systematics, biology, and phylogeny of the Sipuncula.

Chamberlin (1920) produced a list of the sipunculans of Laguna Beach. There were six species, four of which were new to science. Ricketts and Calvin (1952) included several species of Sipuncula in their discussions of findings on the Californian shore, but it is a listing by habitat and is therefore difficult to use as a taxonomic guide. Fisher (1952) was the first to present a guide to the Sipuncula of California complete with keys and species descriptions. In this study he reports the species identifiable from the deep-sea collections of the *Albatross* in 1904, adding that the majority of this collection was not usable by the time he attempted identifications. Although both are good references for the intertidal region, they have little or no information on the deep-sea animals. Rice (1975) is a guide to the sipunculans of the central Californian coast, but is virtually lacking in information on the deeper water species as well. Hartman and Barnard (1958 and 1960) characterized the fauna of the deep-sea basins off Southern California, but the majority of the sipunculans were not named to species, and were not described sufficiently to allow for a reasonable identification. Frank (1983) gives a listing of the Sipuncula from Canadian waters, and some of his species have distributions that extend as far south as Baja California and can be a helpful reference.

Systematics

- Class Phascolosomida Cutler and Gibbs, 1985
  - Order Aspidosiphoniformes Cutler and Gibbs, 1985
    - Family Aspidosiphonidae Baird, 1868
      - *Aspidosiphon* Diesing, 1851
      - *Cloeosiphon* Grube, 1868
      - *Lithacrosiphon* Shipley, 1902
  - Order Phascolosomaformes Cutler and Gibbs, 1985
    - Family Phascolosomatidae Stephen and Edmonds, 1972
      - *Antillesoma* Stephen and Edmonds, 1972
      - *Apionsoma* Sluiter, 1902
      - *Phascolosoma* Leuckart, 1828
- Class Sipunculida Cutler and Gibbs, 1985
  - Order Golfingiaformes Cutler and Gibbs, 1985
    - Family Golfingiidae Stephen and Edmonds, 1972
      - *Golfingia* Lankester, 1885
      - *Nephasoma* Pergament, 1946
      - *Thysanocardia* Fisher, 1950
    - Family Phascolionidae Cutler and Gibbs, 1985
      - *Onchnesoma* Koren and Danielssen, 1875
      - *Phascolion* Théel, 1875
    - Family Themistidae Cutler and Gibbs, 1985
      - *Themiste* Gray, 1828

Order Sipunculiformes Cutler and Gibbs, 1985
Family Sipunculidae Baird, 1868
Phascolopsis Fisher, 1950
Siphonomecus Fisher, 1947
Siphonosoma Spengel, 1912
Sipunculus Linnaeus, 1766
Xenosiphon Fisher, 1947

Morphology

The Sipunculan body can be broken down into two distinct regions: the **trunk** and the retractable **introvert** (Fig. 2.1A). The introvert is extended by an increase in coelomic pressure when the **circular muscles** of the body wall are contracted (Fig. 2.1A). At the anterior end of the introvert is the mouth and feeding **tentacles** (Fig. 2.1A). The tentacles may be highly elaborate, as in *Thysanocardia* and *Themiste*, or greatly reduced as in *Nephasoma* and *Onchnesoma.* The tentacles are part of the **compensation system.** This fluid filled system is separate from the coelom of the body, and when the introvert is extended, the circular muscles apply pressure to the **contractile vessels** or **compensation sacs** (Fig. 2.1B). This pressure forces the fluid out of the sacs and up into the tentacles, thereby extending them. Posterior to the tentacular region of the introvert there may be an area of chitinous **hooks** (Fig. 2.1A). These hooks may be arranged in a pattern or scattered. The introvert is not always extended in preserved specimens, thus hindering the efforts of taxonomists in the use of the tentacles as taxonomic characters. The introvert is withdrawn by the **retractor muscles**, which number from one to four, and can be seen through the body wall of the smaller abyssal specimens, or by dissection of the larger opaque animals (Fig. 2.1B). The body of the animal is covered completely, but to varying degrees, by a **cuticle.** The cuticle of the trunk may have distinctive **papillae** and/or holdfasts, and may appear striated due to a constriction of the **longitudinal muscles** (Fig. 2.1B). The anterior and/or posterior regions of the trunk can also have a **"shield"** made of chitin, another important taxonomic characteristic (Fig. 2.1A). The shape of the trunk is usually not of taxonomic importance due to the constriction of soft-bodied animals when they are preserved. Because of pressure changes, the bodies of one species can look very different from animal to animal. For taxonomic purposes it is best to use internal structures along with any exterior characteristics which are unique.

The **nephridia** are paired in most animals, occasionally numbering only one (Fig. 2.1B), and are located ventrally on the anterior portion of the trunk. In close proximity to the nephridiopores is the **anus** (except in the genus *Onchnesoma* where it can be found on the introvert) (Fig. 2.1A). In the area of the anus a strand of muscle attached to the body wall extends down the center of the intestinal coil adding to its stability. This **spindle muscle** may end along the length of the gut, or continue on towards the posterior end of the trunk (Fig. 2.1B). There may also be **fastening** or **fixing muscles** present to attach the **oesophagus** or the posterior region of the intestine to the body wall (Fig. 2.1B). The **nerve cord** runs ventrally down the entire length of the trunk, and off this cord branch the lateral nerves which extend to the body wall muscles as well as to sensory receptors in the epidermis (Fig. 2.1B).

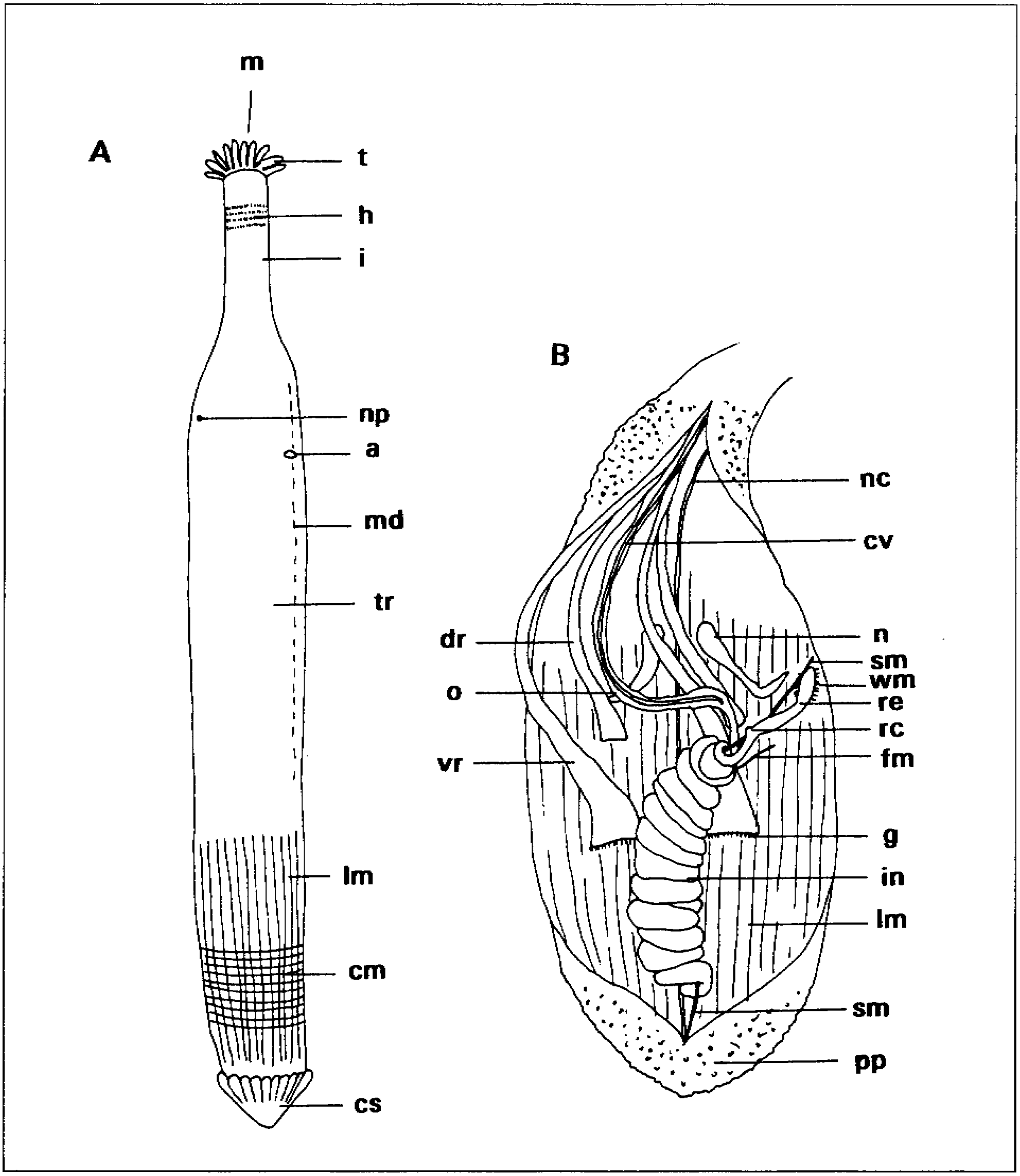

Figure 2.1. Morphology of a generalized sipunculan: A, external morphology; B, internal anatomy of dissected specimen. (modified from Frank, 1983).

Biology

Sipunculans regenerate tentacles, as well as introvert, trunk and digestive tract parts. They can reproduce asexually through transverse fission of the body, although this is not common. Most sipunculans are dioecious. The gametes arise from the coelomic lining and are released into the coelom for maturation. Once mature they are picked up selectively by the nephridia where they are stored until released from the body. The males spawn first. The sperm in the water prompts the female to spawn. After fertilization the zygotes generally follow a prostomous development. Cleavage is spiral and holoblastic. Some species develop a free-living lecithotrophic **trochophore larva** which develops into a juvenile worm. Others develop a second larval stage, a planktonic **pelagosphera larva**, which elongates and settles to become a juvenile sipunculan. After fertilization of the egg, a few species undergo direct development. These fertilized eggs attach to the substratum, and the embryo develops into a vermiform individual which hatches as a juvenile sipunculan.

Glossary

Anus. The opening in the cuticle where the intestine ends through which solid waste is excreted. It is located anteriorly on the trunk, and in some cases on the introvert. In most animals it will be in close proximity to the nephridiopores.

Circular muscles. The outer muscle of the body wall used to contract the body to evert the introvert and tentacles as well as to move the animal. The muscle may be grouped into bands, or form a continuous sheet.

Compensation system. A separate fluid filled coelomic system of the body which regulates the extension of the tentacles. See also **contractile vessels.**

Contractile vessels or **Compensation sacs.** The balloon-like structures which the circulatory muscles squeeze when the introvert is extended, forcing fluid through a closed system into the tentacles, extending them for aid in feeding.

Cuticle. The outer layer of the body wall, usually thicker around the trunk and tapering towards the mouth region of the introvert.

Introvert. The area of the body which is retractable, used for feeding and touching.

Longitudinal muscles. The inner muscles of the body wall which is a continuous sheet in most animals, but can be bundled or banded together in some genera. It is this banding that causes the cuticle of some animals to appear striated.

Nephridia. Saclike organs located in the anterior portion of the trunk used in excretion and as gonoducts.

Nerve cord. The single cord from which lateral nerves arise and extend to the body wall muscles as well as to sensory receptors in the epidermis.

Oesophagus. Region of the intestine between the pharynx and the descending loop.

Papillae. Projections of the epidermal glands into the cuticle forming raised bumps on the external body wall. They are used for cuticle production, mucus secretion and as sensory organs. They may also have a chitinous outline ridge and can be used as holdfasts.

Pelagosphera larva. Second larval stage of some sipunculans. Swims by means of a ciliated metatroch and is often found in plankton samples.

Retractor muscles. Muscles connected to the body wall as well as to the introvert used to withdraw the introvert into the trunk region.

Shield. Thickened cuticular areas or calcareous deposits on the anterior and sometimes posterior trunk regions of the Aspidosiphonidae, used for protection and burrowing.

Spindle muscle. The strand of muscle attached to the inner body wall in the area of the anus which runs through the intestinal coil and reattaches to the inner wall at varying points in different animals, giving stability to the gut coil.

Tentacles. The hollow extensions of the introvert used in feeding, the arrangement of which may be an important taxonomic character.

Trochophore larva. First larval stage of those animals not undergoing direct development. Free-living larva which will develop into a juvenile worm or metamorphose into a pelagosphera larva.

Trunk. The region of the body of the animal which is not retractable.

List of Abbreviations on Figures

a, anus
cm, circular muscle
cv, contractile vessel (compensation sac)
cs, caudal shield
dr, dorsal retractor
fm, fastening muscle
g, gonad
h, hooks
i, introvert
in, intestine
lm, longitudinal muscle
m, mouth
md, mid-dorsal line
n, nephridium
no, nuchal organ
nc, nerve cord
np, nephridiopore
o, oesophagus
pp, papillae
rc, rectal caecum
re, rectum
rm, retractor muscle
sm, spindle muscle
t, tentacle
tr, trunk
vr, ventral retractor
wm, wing muscle

List of Species from the MMS Surveys

Nephasoma diaphanes (Gerould, 1913)
Phascolion lutense Selenka, 1885
Thysanocardia nigra (Ikeda, 1904)
Siphonosoma (Siphonosoma) ingens (Fisher, 1947)

Key to the Sipuncula of the Santa Maria Basin

1A. Longitudinal muscles of the body wall gathered into separate or anastomosing bands .... Family Sipunculidae .... *Siphonosoma ingens*

1B. Longitudinal muscle of body wall in a uniform continuous layer 2

2A. A single nephridium present .... Family Phascolionidae .... *Phascolion lutense*

2B. Two nephridia present .... Family Golfingiidae ... 3

3A. Numerous tentacles present; hooks absent .... *Thysanocardia nigra*

3B. Tentacular crown reduced to short lobes; small, scattered hooks present .... *Nephasoma diaphanes*

Descriptions of Species

Nephasoma diaphanes (Gerould, 1913)

Figure 2.2

Phascolosoma diaphanes Gerould, 1913:395.

Golfingia diaphanes: Cutler and Cutler, 1980a:425-453; 1980b:201-202.—Frank, 1983:15-16.—Cutler *et al.*, 1984:269-270.

Phascolosoma improvisum Gerould, 1913:395-396.—Wesenberg-Lund, 1930:32-34; 1939:22-23.

Golfingia improvisa: Wesenberg-Lund, 1955:11; 1963:110-111.—Murina, 1958:1625-1628; 1968:197; 1971:42; 1972:300; 1973:69; 1978:123.—Stephen and Edmonds, 1972:145.—Amor, 1975:113-115.—Edmonds, 1976:222-224.

Phascolosoma minutum Théel, 1911:31.—Sluiter, 1912:10-11.—Fischer, 1922a:34; 1922b:237; 1929:464-467 (*partim*).—Wesenberg-Lund, 1930:30; 1932:9-10; 1937:12-13.

Golfingia minuta: Wesenberg-Lund, 1955:11; 1963:110-111.—Murina, 1957a:994-995; 1958:1628-1634; 1968:197; 1971:42; 1972:300; 1973:69; 1974:235; 1976:65; 1978:124.—Stephen and Edmonds, 1972:149-150.—Cutler, 1973:155-159; 1977a:143.—Cutler and Cutler, 1979:957-958.—Saiz-Salinas, 1984:183.

Golfingia sectile Murina, 1974:228-230.

Phascolosoma anceps Sluiter, 1912:10.—Wesenberg-Lund, 1925:90.

Phascolosoma cinctum Gerould, 1913:398-400, pl. 59, fig 6, text-fig. 8.

Golfingia cincta: Stephen and Edmonds, 1972:137-138.

Phascolosoma sabellariae Gerould, 1913:392-395.

Material Examined. California: Santa Maria Basin, off Point Buchon, Sta. 12 (3); off Point San Luis, Sta. R-1 (77); off Point Sal, Sta. PJ-6 (1); off Purisima Point, Sta. 42 (1), Sta. 52 (80); off Point Arguello, Sta. 65 (71).

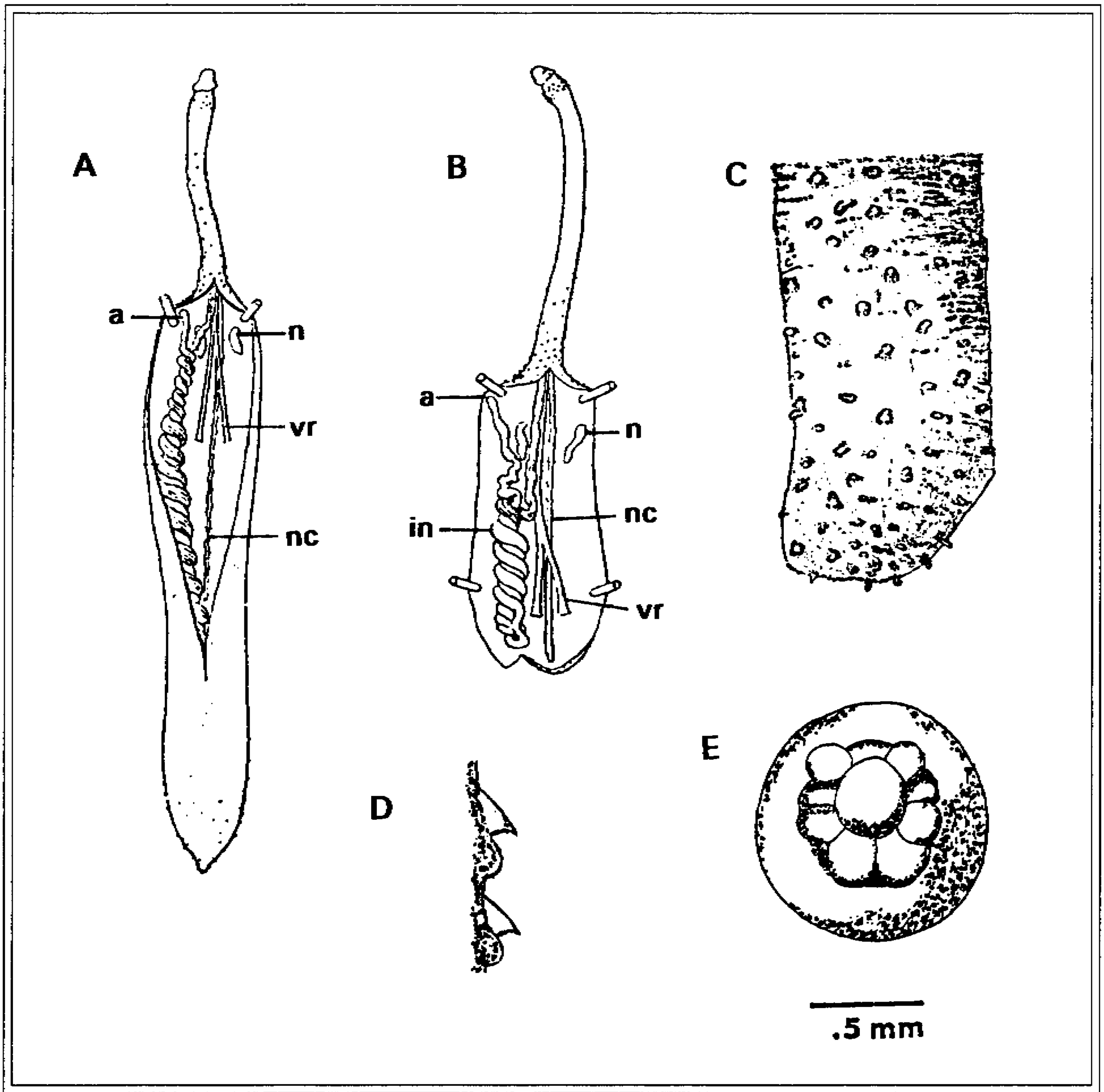

Figure 2.2 *Nephasoma diaphanes*: A, internal, dissection of extreme anterior end; B, internal, dissection of posterior end showing origin of retractor muscles; C, portion of posterior end showing papillae; D, hooks; E, reduced tentacles. (A-D after Cutler, 1973; E after Cutler *et al.*, 1984).

Description. Small pear-shaped to cylindrical animals, trunks occasionally reaching length of 30 mm, usually 10 mm or less. Introvert approximately equal in length to trunk, but can vary from 50-150% of trunk length. Skin translucent to opaque, may exhibit longitudinal wrinkles or folds on base of introvert and anterior part of trunk. Some animals with papillae on posterior end (Fig. 2.2C). Tentacular crown reduced to 6-8 short lobes and 2 longer dorsal tentacles (Fig. 2.2E). Small, scattered, pale triangular hooks present (Fig. 2.2D). Two nephridia short, free at level of, or just posterior to, anus (Fig. 2.2A and B). Pair of ventral retractor muscles originating near posterior end in small animals, in mid-trunk in larger ones. Intestines in double helix and with weakly developed spindle muscle within coil, not extending onto rectum.

Remarks. There are two subspecies of *Nephasoma diaphanes*, of which *N. diaphanes corrugatum* differs from *N. diaphanes diaphanes* in the nature of the epidermis. *Nephasoma diaphanes diaphanes* has smooth, translucent to transparent skin, occasionally with raised pigmented papillae. *Nephasoma diaphanes* is often confused taxonomically with *N. minutum*. Prior to the revision of *Nephasoma* by Cutler and Cutler (1986), *N. diaphanes* was often called *Golfingia minuta*. That paper accepts the change of status proposed by Gibbs (1975) to redefine the species *Golfingia minuta* to include only those hermaphroditic populations from the shallow northeastern Atlantic. All other populations of dioecious animals are therefore referred to the species *Nephasoma diaphanes*.

Distribution. Cosmopolitan, cold water, most from bathyal and abyssal depths. The subspecies *Nephasoma diaphanes corrugatum* is found in the Atlantic and Pacific oceans and the Mediterranean and Red Seas from 80-5900 m.

***Phascolion lutense* Selenka, 1885**

Figure 2.3

Phascolion lutense Selenka, 1885:16-17, pl.4, figs 22-23.—Fischer, 1928:484.—Murina, 1957b:1781-1790, figs. 4a-b, 5a-d; 1961:140-142, fig. 1; 1971:43; 1972:305-306; 1974:235; 1978:124.—Stephen and Edmonds, 1972:180-181.—Cutler, 1977:145-146; Cutler and Cutler, 1985a:829-830, fig. 7b.

Phascolion canum Cutler and Cutler, 1980a:454-456, fig. 2.—Gibbs, 1985:321.

Phascolion species Cutler and Cutler, 1980b:197.

Material Examined. California: Santa Maria Basin, off Point Estero, Sta 2 (1); off Point Sal, Sta. PJ-1 (3). Western Santa Barbara Channel, Sta. 86 (3).

Description. External body surface smooth, with small papillae at anterior end and inconspicuous skin bodies in mid-trunk of some animals (Fig. 2.3B, D). Holdfast papillae absent. Tentacular crown reduced to lobes (Fig. 2.3E). Most specimens bearing pale hooks, 40-150 m long (Fig. 2.3C). One nephridium present. Retractor muscles fused for most of length, with 3 or 4 distinct origins (Fig. 2.3A).

Biology. This species is commonly found residing in gastropod shells.

Remarks. All material examined was originally named *Onchnesoma* sp. A.

Type Location. South Pacific 53°55'S, 108°35'E at 3658m. Holotype: BMNH, no. 1885.12.3.22.

Distribution. Eastern Pacific; a deep-water species, in southern hemisphere (36-66°S) in Pacific Ocean off Argentina, southeastern Indian Ocean, northwestern Pacific and Bay of Biscay.

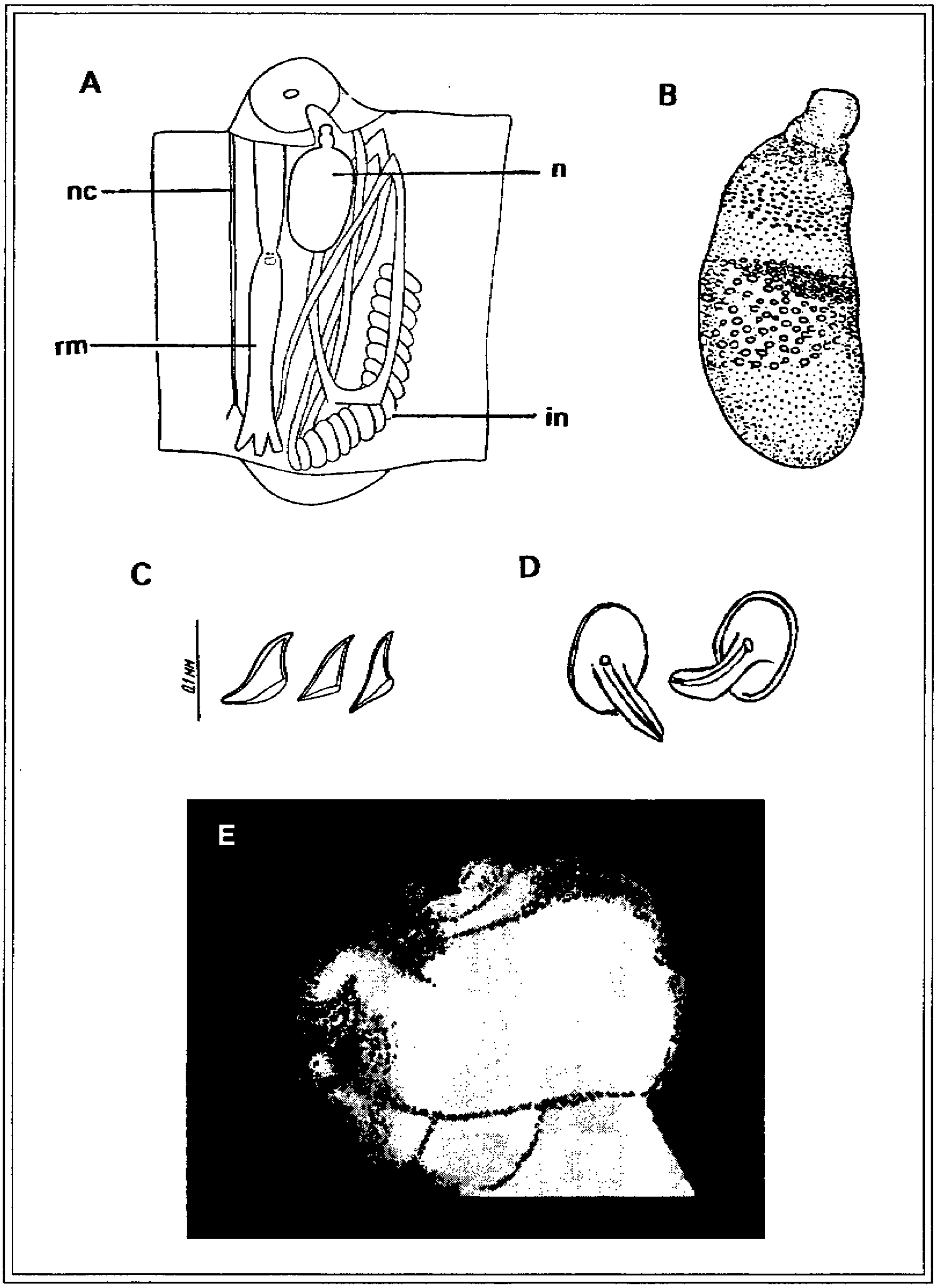

Figure 2.3 *Phascolion lutense*: A, dissection showing internal anatomy; B, external view; C, hooks; D, glands with papillae; E, tentacular lobes (A-C after Murina, 1975b; D, after Selenka, 1885; E, after Cutler and Cutler, 1985a).

Siphonosoma (Siphonosoma) ingens (Fisher, 1947)

Figure 2.4

Siphonomecus ingens Fisher, 1947:365-368, pl. 15, fig. 15.
Siphonosoma ingens: Fisher, 1952:382-385, pl. 20, fig. 21.

Material Examined. California: Santa Maria Basin, off Point Sal, Sta. R-8 (1).

Description. Body long and slender; introvert much shorter than trunk; introvert with papillae but without hooks. Body wall with coelomic extensions, longitudinal muscle gathered into bands (Fig. 2.4A). Four retractor muscles and 2 nephridia present (Fig. 2.4B). Nuchal tentacles lacking, but oral disk with 12 double rows of tentacles around mouth (Fig. 2.4C). Spindle muscle attached near anus and at posterior end of body. Villi present on contractile vessel. Posterior end of trunk with tubular, fusiform glandular bodies (Fig. 2.4D).

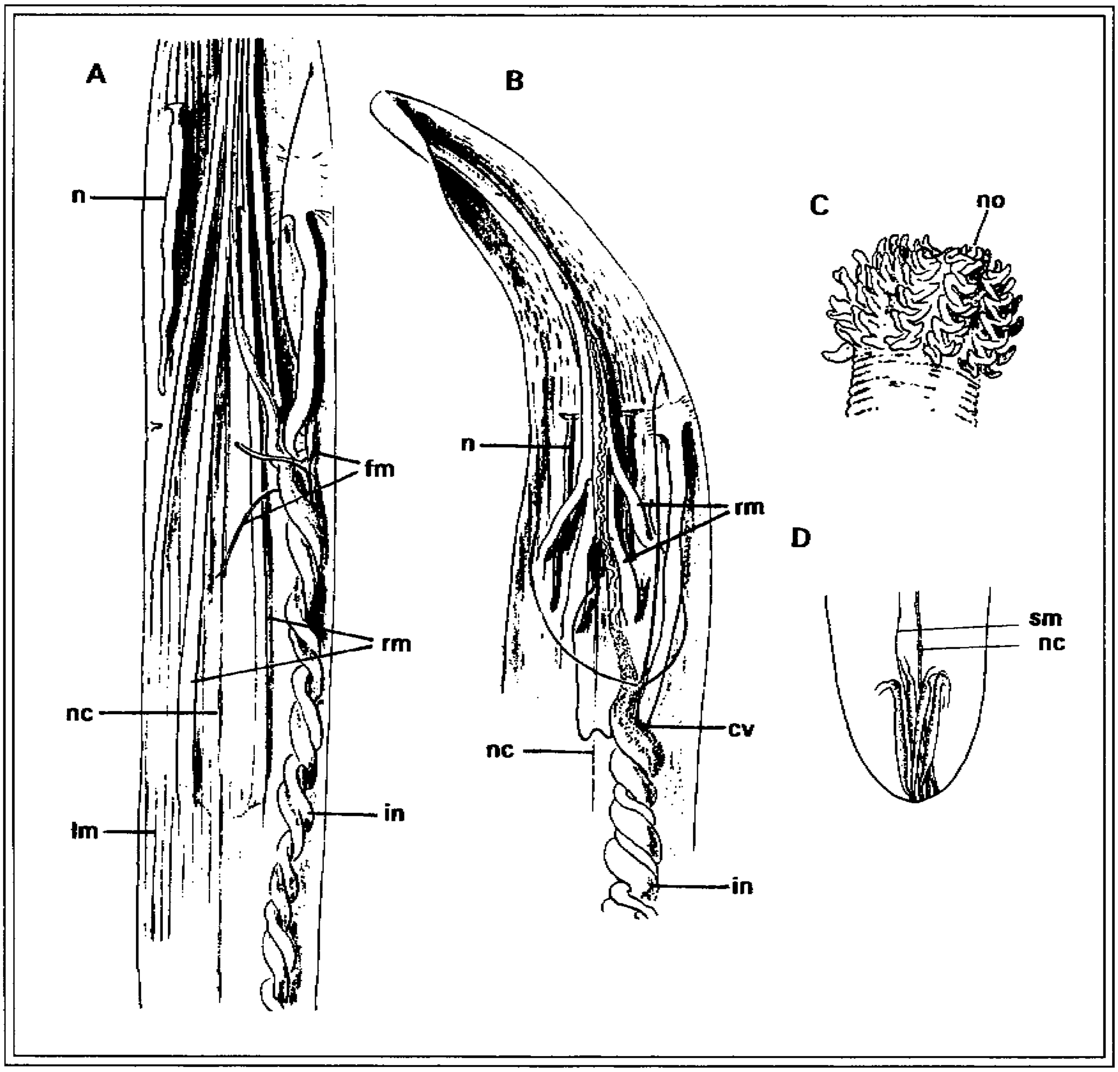

Figure 2.4 *Siphonosoma ingens*: A, internal, dissection of anterior portion of trunk; B, internal, dissection of anterior end of paratype showing contracted retractor muscles, partly invaginated introvert; C, tentacles; D, internal, posterior trunk showing tubular, fusiform glandular bodies. (A-C after Fisher, 1947; D after Cutler and Cutler, 1982).

Remarks. This species is very similar to *Siphonosoma mourense* except that it has posterior fusiform bodies on the posterior end of the trunk. Both species occur in the North Pacific.

Type Locality. Morro Bay, San Luis Obispo County, California; intertidal. Holotype: USNM 20910.

Distribution. Southern California.

Thysanocardia nigra (Ikeda, 1904)

Figure 2.5

Phascolosoma nigrum Ikeda, 1904:3, text figs. 1, 25-27.—Satô, 1934:247; 1939:409.—Chin, 1947:101.

Golfingia (Thysanocardia) nigra: Cutler and Cutler, 1981:68.

Phascolosoma catherinae Satô, 1937:154; 1939:406.

Golfingia (thysanocardia) catherinae: Cutler, 1977b:152.

?*Golfingia procera* Fisher, 1952:402.

Phascolosoma zenibakense Ikeda, 1924:29-30, fig. I.—Satô, 1930:17-20, pl. 3 figs. 11-12, text-figs. 5; 1937:153-157; 1939:410.—Okuda, 1946:223.

Phascolosoma hyugensis Satô, 1934:12-14, pl. 1, fig. 6, text-figs. 15-16.

Phascolosoma hozawai Satô, 1937:158-160, pl. 4, fig. 15, text-figs. 5-8.

Phascolosoma onagawa Satô, 1937:156-158, pl. 4, fig. 14, text-figs. 3-4.

Golfingia macginitiei Fisher, 1952:402-404, pl. 26.

Golfingia pugettensis Fisher, 1952:401.—Rice, 1967:144-170.

Material Examined. California: Santa Maria Basin, off Point Arguello, Sta. 66 (3), Sta. 74 (3).

Description. A fairly large species with trunk up to 70 mm long. Introvert approximately twice as long as trunk, ranging from 1.5-2.5 times as long, difficult to measure when trunk constricted. Numerous tentacles present, hooks absent (Fig. 2.5B). Number of tentacles varying with size of animal, but in large specimens up to 24 festoons of 60 tentacles each, with another 30 tentacles surrounding nuchal organ. Tentacles darkly pigmented violet-mauve in life, fading to dark brown in preservative, sometimes fading completely after long preservation. Skin rough, often with wavy wrinkles, usually colored grey or rarely black. Posterior end of trunk constricted, resembling a tail or a point.

Internally a pair of retractor muscles present originating between 55-75% of the distance to posterior of trunk. Two nephridia unattached, 25-70% of the trunk length, opening anteriorly to anus. Rectal caecum usually present. Contractile vessel villi present along oesophagus, increasing in size and complexity, and becoming long and branched posteriorly (Fig. 2.5A).

Remarks. The pigmentation of the tentacles differentiates *T. nigra* from *T. catherinae*, though as stated above, the use of pigmentation is not an ideal taxonomic character because it tends to fade in alcohol and may be lacking entirely in smaller specimens.

Type Location. According to Cutler and Cutler (1981) a lectotype had been deposited at the University of Tokyo Zoological Museum, paralectotypes at the National Science Museum, Tokyo, and reference material at the National Museum of Natural History, Washington, D.C.

Distribution. North Pacific: Philippines and Japan to California; Singapore.

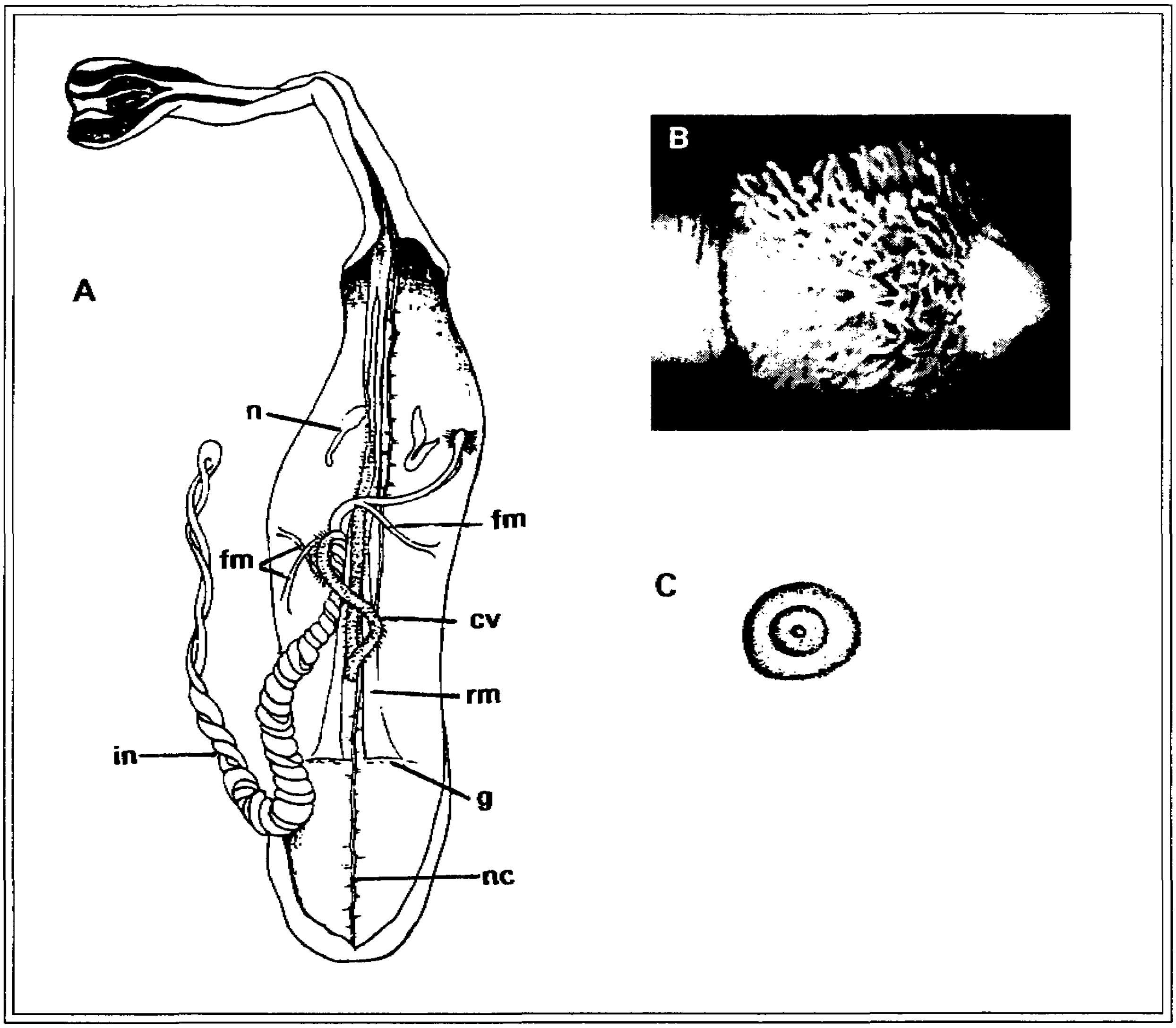

Figure 2.5 *Thysanocardia nigra*: A, internal view of dissected specimen; B, tentacles; C, papilla from posterior of trunk. (A after Ikeda, 1924; B after Cutler and Cutler, 1981; C after Ikeda, 1904).

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3. ECHIURA

by

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Introduction

The Echiura are small group of unsegmented, coelomate marine organisms. Although their distribution is cosmopolitan, they are uncommon and only a few species are known well through basic research.

Morphology

The echiuran body is ovoid or sausage-shaped and typically has an extensible **proboscis** (homologous with the annelid prostomium). The proboscis is deciduous in many species and must be treated with care when found attached to the trunk. The mouth is anterior on the trunk at the base of the proboscis. Few external characters are available for use in identification save the presence of **setae** and **nephridiopores** adjacent to the mid-ventral line near the anterior end. **Longitudinal muscle bands** may be present and visible in the body wall of the trunk.

The spacious fluid-filled coelom contains the loosely-suspended, elongated digestive tract, usually filled with sediment pellets. A small collateral tube, the intestinal **siphon**, is present in most species. The posterior end of the intestine may bear an enlarged bump called the **intestinal caecum**. Thin-walled, paired hind-gut sacs, **anal vesicles**, are present in all species. The vesicles may be simple or branched and frequently bear **ciliated funnels**. The proximal ends of the ventral setae project into the coelom and are equipped with muscle bands that connect to the body wall and aid in manipulation. A strong **interbasal muscle** typically connects the proximal ends of the two setae. Nephridia are modified for use as gamete collection, storage and spawning organs, **metanephridia**. They are attached to the body wall on the anterior ventral region adjacent to the ventral nerve cord. The **nephrostome** frequently is modified into a characteristic form such as elongated, coiled strands or as fimbriae. Presumably these features aid in the selection of developed gametes from the coelomic fluid so that they may be stored prior to spawning. Nephridia filled with gametes have been called **storage organs** and may be quite large relative to the length of the trunk.

A blood vascular system is present in all echiurans except members of the Order Xenopneusta (genus *Urechis*). The proboscis has a median vessel that carries blood anteriorly to the tip. At the tip the median vessel splits to form paired **lateral vessels** and these return blood to the trunk. These vessels emerge in the trunk as a single **ventral vessel** and follow the ventral nerve cord to the posterior end of the body. Just anterior to the setae, the **neuro-intestinal vessel** branches from the ventral vessel and extends to the esophagus. On the way it may form a loop around the interbasal muscle. At the esophagus the vessel may surround the gut as a **ring vessel**. The **dorsal vessel** extends from here along the anterior gut and enters the base of the proboscis as the median vessel.

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The location of the gonad is not always known in echiurans but where it is, it is unpaired and on the posterior region of the ventral vessel. Gametogenesis begins here but shortly the gametes become free within the coelomic fluid where gametogenesis continues. The most mature gametes are removed selectively from the coelom by the nephrostome and stored in the modified nephridia until spawning. Fertilization is external and a trochophore larva is produced.

Taxonomic History

Quatrefages (1865) classified echiurans with sipunculans and priapulids as the phylum Gephyrea because collectively they represented a "bridge" between the echinoderms and annelids. Later, echiurans were considered as a class of the annelids (Sedgwick, 1898). Based on the detailed embryological studies and the suggestion of Newby (1940), Fisher (1946) erected the phylum Echiuroidea. Stephen (1964) renamed the phylum Echiura.

The most recent classification system is that of Stephen and Edmonds (1972). It is modified from Fisher (1946, 1949) and based on characteristics such as body wall musculature, proboscis morphology, vascular system anatomy, anal vesicle morphology, and the number, position, and morphology of setae and nephridia. They recognized 3 orders, 4 families, 34 genera, and 129 species. Additional species have been described.

Biology

The presence of an elongate proboscis is an indication that the species is a deposit feeding member of benthic communities. In all species of this form, a burrow is formed in soft mud, coral, or rock, depending on the species and habitat. U-shaped burrows are most common and may extend 10-20 cm into the sediment and 10 to 40 cm horizontally. When feeding the proboscis is extended from the burrow aperture onto surrounding sediment where it explores the deposit and picks up particles for transport posteriorly to the mouth. Discrimination and sorting of food by the proboscis has been documented in *Bonellia* (Jaccarini and Schembri, 1977). Organic matter is extracted from this material in the digestive tract before being released as compacted fecal pellets.

Members of the genus *Urechis* have a short, stubby proboscis and are not deposit feeders. Instead, they produce mucus nets within the burrow and pump water and suspended particulates through it by peristalsis. Intermittently, the net becomes clogged with trapped food, is consumed, and a new net is constructed.

Commensals are common in the burrows of echiurans. Typically, these include polychaetes, small crustaceans, small mollusks, and hydroids. Endoparasitic protozoa, platyhelminths, nematodes, and annelids have been described (see Stephen and Edmonds, 1972 for a list).

Echiurans may represent ecologically significant members of benthic communities. *Listriolobus pelodes* formed dense accumulations in areas offshore from Santa Barbara, California and at the White's Point sewer outfall, Palos Verdes, California.

Glossary

Anal vesicle - A pair of thin-walled hindgut sacs lying in the posterior coelom and connecting to the posterior digestive tract. They may be simple or branched and usually bear small ciliated cups or funnels. The function of the vesicles is unclear but may be involved in respiration by "inhaling and exhaling" the surrounding seawater.

Ciliated funnel - A small ciliated cup-like structure present on the coelomic epithelium of anal vesicles.

Caecum - A small pouch on the precloacal region of the intestine in some echiurans. Its function is unknown.

Dorsal vessel - That portion of the vascular system lying on the dorsal side of the posterior foregut and carrying blood anteriorly to the median vessel.

Interbasal muscle - A prominent muscle band connecting the proximal ends of the setae. Absent in some species.

Longitudinal muscle bands - Thickening of the longitudinal muscle layer of the body wall into bands. The bands usually are visible externally and are important taxonomic characters.

Lateral setal muscles - Muscles located at the body wall where the setae emerge into the coelom. They extend laterally and may serve to separate the setae. An uncommon character.

Lateral vessels - The paired blood vessels that return blood from the anterior tip of the proboscis to the trunk.

Median vessel - That vessel carrying blood from the dorsal vessel and the trunk to the tip of the proboscis.

Metanephridium - The modified excretory organ that sorts and stores gametes prior to spawning. Usually present as one or a few pairs but, in some species, they may be unpaired or numerous (as many as 400).

Nephridiopore - The external opening to the nephridium. Gametes are released through the pore during spawning.

Nephrostome - The coelomic opening to the nephridium. The position of this structure and the modification of the lips of the nephrostome are important taxonomic characters. The nephrostome may be basal (near the nephridiopore) or distal (away from the nephridiopore and towards the coelom). The lips are ciliated and may be modified as fimbriae or elongated threads. They function to collect the most differentiated gametes from the coelom for storage in the nephridium prior to spawning.

Neuro-intestinal vessel - The blood vessel that branches from the anterior ventral vessel and carries blood to the dorsal vessel. It may form a loop around the interbasal muscle.

Papillae - Prominent tubercles present on the exterior of the body of most echiurans. Larger ones usually are present at the anterior and posterior ends of the trunk. Papillae may be glandular.

Proboscis - The muscular and highly extensible structure that projects anteriorly from the area dorsal to the mouth. In some literature it may be referred to as the "prostomium". The organ is used for feeding, burrowing, and perhaps for respiration. The ventral surface has mucus glands, is ciliated and functions to carry sediment particles to the mouth in mucous strings.

Although adult echiurans probably do not leave their burrows intentionally, specimens requiring new burrows will use the proboscis in the burrowing process first to scoop out a shallow depression and later as a wedge and terminal anchor.

Proboscides are morphologically variable and deciduous in some species. In the genus *Urechis* the proboscis is reduced to a stubby upper lip. In many bonellids, the proboscis is bifid at the tip while in other bonellids and in the echiurids it is elongated and unbranched.

Ring vessel - The point where the neuro-intestinal vessel surrounds the posterior foregut and connects to the dorsal vessel. The structure is present in varying degrees of development and is absent in some species.

Setae - Hooked or bristle-like structures present in the ventral body wall posterior to the mouth. Typically paired. Setae encircle the anus in the genera *Echiurus* (two rings of setae) and *Urechis* (one ring of setae).

Siphon - A small collateral tube associated with much of the midgut. The anterior and posterior ends join with the alimentary tract as a ciliated groove.

Storage organ - A term used in the literature to describe the portion of the metanephridium used to store gametes prior to spawning. It has been referred to as a "segmental organ" because it is variable in diameter when it is filled with gametes.

Ventral vessel - The blood vessel that is attached to the dorsal surface of the ventral nerve cord and runs posteriorly to the end of the trunk.

Abbreviations Used in the Figures

a, anus
av, anal vesicle
cg, ciliated groove
dv, dorsal vessel
g, gonad
gi, gizzard
i, intestine
ic, intestinal caecum
im, interbasal muscle
lm, longitudinal muscle
m, mouth
n, nephridium
niv, neuro-intestinal vessel
nl, anterior nerve loop
np, nephridiopore
p, proboscis
pap, papillae
ph, pharynx
s, setae
ss, secondary seta
vbv, ventral blood vessel
vnc, ventral nerve cord

Key to the Orders, Families, Genera, and Species of Echiura from the Santa Maria Basin and Western Santa Barbara Channel

1A. Open vascular system, coelom with hemoglobin-containing corpuscles; posterior intestine thin-walled and functioning in respiration, anal vesicles present; proboscis present as a stubby upper lip. .... Order Xenopneusta

1B. Closed vascular system; anal vesicles present but posterior intestine not otherwise modified for respiration; proboscis elongate but may be deciduous. .... Order Echiuroinea 2

2A. Species with sexual dimorphism, males very small and commensal on or in female; proboscis bifid, cylindrical or triangular (may be deciduous or absent); anal vesicles usually branched; 1 or 2 nephridia present. .... Family Bonellidae: *Nellobia eusoma*

2B. Species without sexual dimorphism; proboscis not bifid; anal vesicles saclike; 2 or 4 nephridia present; longitudinal muscle bands may be present .... Family Echiuridae 3

3A. Longitudinal muscles grouped into bands; nephrostomal lips elongate 4

3B. Longitudinal muscles not in bands; nephrostome broad funnel with frilled rim .... *Arhynchite californicus*

4A. Six longitudinal muscle bands present; with 2 nephridia .... *Listriolobus hexamyotus*

4B. Eight longitudinal muscle bands present; with 4 nephridia .... *Listriolobus pelodes*

Description of Species

Listriolobus pelodes Fisher, 1946

Figure 3.1

Listriolobus pelodes Fisher, 1946:234-240.—Barnard and Hartman, 1959:1-16.—Pilger, 1980:129-142.

Material Examined. California, off Point San Luis, MMS Phase I Sta. 21, 49 m, 1 specimen (USNM); 1 specimen (SBMNH).

Description. Trunk 40-60 mm long, 12-25 mm in diameter (Figure 3.1A). Body wall translucent with 8 longitudinal muscle bands; bands may be less distinct in small specimens. Small papillae present in small circular folds at anterior and posterior ends. Proboscis unbranched and highly extensible. Two hooked ventral setae with interbasal muscle (Figure 3.1B). Two pairs of nephridia each with paired, elongated, and coiled nephrostomal lips. Two anal vesicles capable of great extension and bearing small, scattered ciliated funnels (Figure 3.1C). Intestinal caecum present near anus. Vascular system with interbasal muscle loop and ring vessels. Gonad on posterior-most portion of ventral blood vessel at junction with intestinal caecum. Small coelomic oocytes present in clusters, large oocytes single.

Biology. *Listriolobus pelodes* is a deposit feeding echiuran common in fine-grained sediments at depths from 18-155 m. Particularly dense though temporally variable populations have been described from the shelf off Santa Barbara, California (Barnard and Hartman, 1959) and Palos Verdes, California (Pilger, 1980; Stull, Haydock, and Montagne, 1986). The reproductive biology of specimens from southern California has been described (Pilger, 1980).

Remarks. *Listriolobus pelodes* is distinct from *L. hexamyotus* in having eight longitudinal muscle bands instead of six. "Small phase" specimens 7-15 mm long and sexually mature were described by Fisher and also found by Hartman (Fisher, 1946). Although Fisher (1946) did not indicate anatomical differences sufficient to warrant taxonomic distinction, Pilger (1980) noted that their reproductive biology may be different from larger specimens.

Type Locality and Type Specimens. Monterey Bay, California, moderate depth, fine sand, from the stomach of flounders. Type specimen deposited in National Museum of Natural History (USNM 20608).

Distribution. West coast of North America from northern California to Baja California, Mexico.

Listriolobus hexamyotus Fisher, 1949

Figure 3.2

Listriolobus hexamyotus Fisher, 1949:484-485, pl. 29.

Material Examined. California, Santa Maria Basin, off Point Sal, MMS Phase II Sta. R-7, 565 m, 1 specimen (USNM); off Point Arguello, MMS Phase I Sta. 62, 582m, 1 specimen (SBMNH).W.— Western Santa Barbara Channel, off Point Conception, MMS Phase 1, Sta. 83, 444 m, 1 specimen (USNM).

Description. Trunk elongate, 50 mm x 15 mm (Figure 3.2A). Small papillae present. Six inconspicuous longitudinal muscle bands. Proboscis deciduous, often missing (Figure 3.2B). Lateral edges of proximal portion surround mouth ventrally. Two setae with hooked tips pointing toward midline. Secondary setae forming alongside primaries in some specimens. Strong interbasal muscle and lateral setal muscles present (Figure 3.2C). Pharynx attached to ventral body wall by mesenteric sheet. Foregut shorter than *L. pelodes*. Anal vesicles thin-walled. Ciliated funnels not observed. One pair nephridia, each with 2 elongated but uncoiled nephrostomal lips. Neurointestinal vessel not looping around interbasal muscle. Small, incomplete ring vessel present.

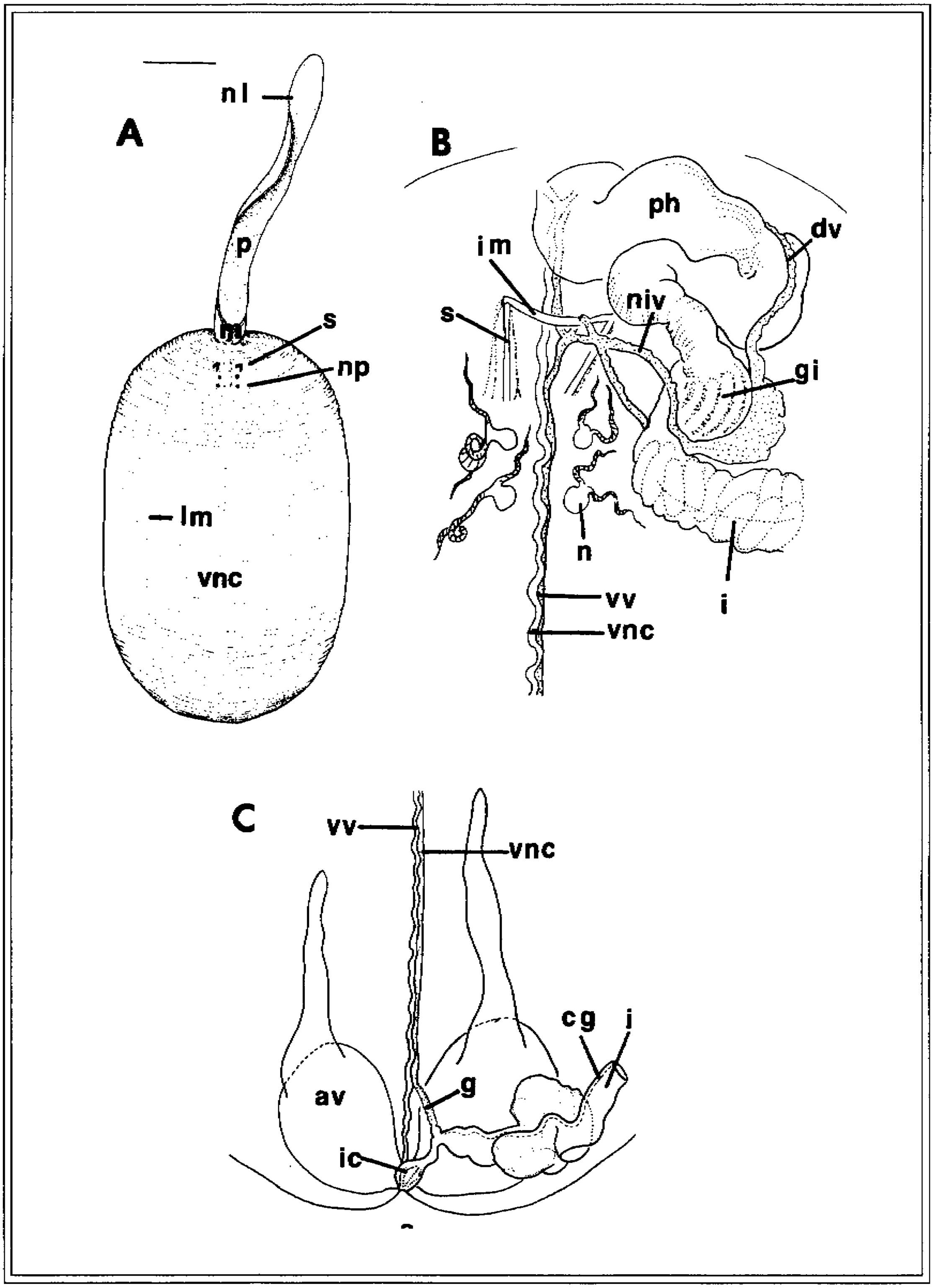

Figure 3.1. *Listriolobus pelodes*: A, external anatomy, ventral view (after Pilger, 1980). B, anterior internal anatomy, dorsal view (after Fisher, 1946); C, posterior internal anatomy, dorsal view (after Pilger, 1980).

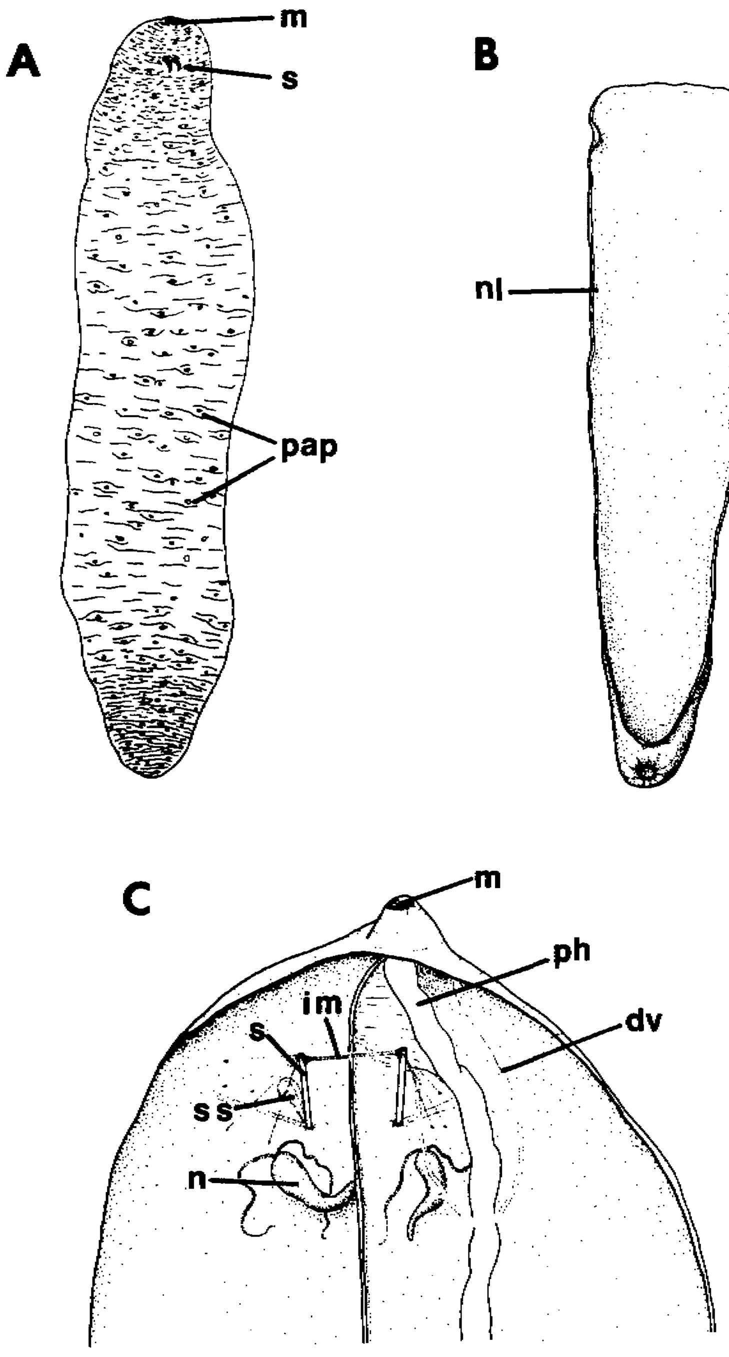

Figure 3.2. *Listriolobus hexamyotus*: A, external anatomy, ventral view; B, proboscis, detached, ventral view; C, anterior internal anatomy, dorsal view.

Biology. While no direct field observations have been made of this species, from its morphology one can infer that it is a deposit-feeding species and probably forms U-shaped burrows in the soft muddy benthos.

Remarks. *Listriolobus hexamyotus* differs from *L. pelodes* in having one pair of nephridia, six longitudinal muscle bands instead of eight, a smaller caecum and shorter foregut. The neuro-intestinal vessel does not form a loop around the interbasal muscle as in *L. pelodes.*

Type Locality and Type Specimens. *Albatross* Sta. 4339, San Diego, California, 574-735 m, green mud. Type specimen deposited in National Museum of Natural History (USNM 21079).

Distribution. Southern California bight mainland shelf, lower slope zone, 400-800 m.

Arhynchite californicus Fisher, 1949

Figure 3.3

Arhynchite californicus Fisher, 1949:486-487

Material Examined. California, off Purisima Point, Sta. R-6, 410 m (USNM); off Point Conception, MMS Phase I Sta. 76, 1 specimen (SBMNH).— Western Santa Barbara Channel, MMS Phase 1, Sta. 86, 197 m, 1 specimen (USNM) .

Description. Trunk elongate with transverse rows of glands present and separated by wrinkles (Figure 3.3A). Body wall thickened, especially at ends. Muscle layers distinguishable in cut sections of body wall. Longitudinal muscle bands absent. Two hooked ventral setae located close to anterior end. Proboscis unbranched, fan-shaped distally, deciduous and often missing. Lateral edges meet ventrally at proximal end (Figure 3.3B). Well-developed interbasal muscle passes through loop of neuro-intestinal vessel. Gut long, attached to body wall by many mesenteric strands. Presiphonal ciliated groove absent. Two nephridia attached to body wall close to setae (Figure 3.3C). Extra nephridia reported in some specimens. Nephrostome within a stalked funnel with frilled rim. Anal vesicles long (up to half body length), anchored proximally by many filaments. Scattered ciliated cups present. Neurointestinal vessel forms loop around interbasal muscle and then attaches to gut. Distinct ring vessel not visible on gut.

Biology. No direct studies of this species have been conducted. It is a deposit feeding form presumed to make U-shaped burrows in soft muds. It is rarely found in water as shallow as 50 m. Typically it lives between 100 and 500 m depth.

Remarks. The genus was erected because of the many specimens were collected without a proboscis before the deciduous nature of this structure was known. It is distinctive in that it is the only species in southern California without longitudinal muscle bands. The presence or absence of the ring vessel may be a variable trait (Thompson, 1979). Differs from *A. pugettensis* Fisher 1949 in this trait and the absence of a ciliated groove in the presiphonal intestine.

Type Locality and Type Specimens. *Albatross* Sta. 4525, Monterey Bay, California, 440 m., soft gray mud. Type specimen deposited in National Museum of Natural History (USNM 21085).

Distribution. Monterey Bay, California south. Typically below shelf depths, 100-500 m.

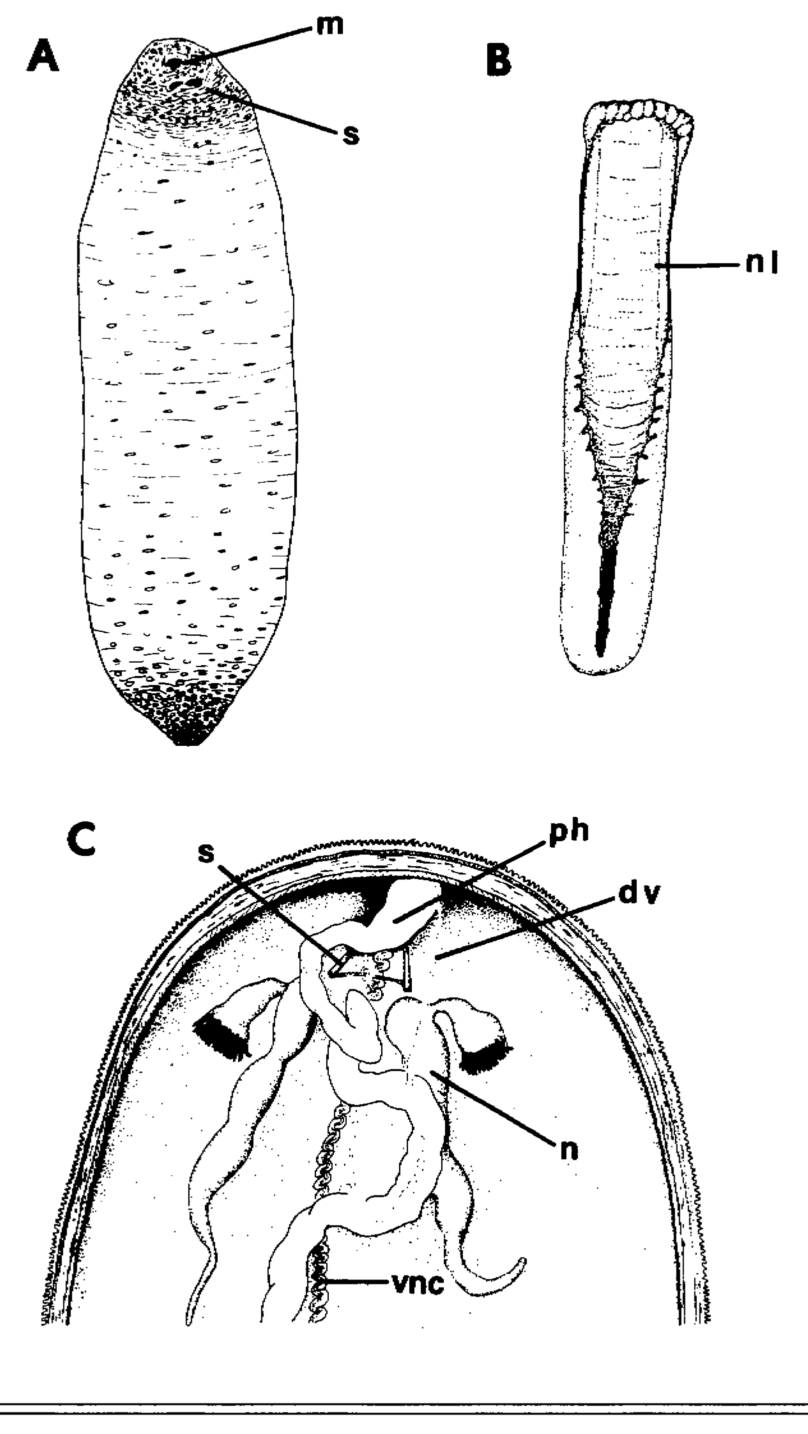

Figure 3.3. *Arhynchite californicus*: A, external anatomy, ventral view; B, proboscis, ventral view; C, anterior internal anatomy, dorsal view.

Nellobia eusoma Fisher, 1946

Figure 3.4

Nellobia eusoma Fisher, 1946:258-259.

Material Examined. California, Santa Maria Basin, off Purisima Point, Sta. R-5, 154 m (1).

Description. *Female.* Trunk 35mm x 19mm. Body wall pigmented, thickest at anterior and posterior ends (Figure 3.4A). Longitudinal muscle bands absent. Single nephridiopore conspicuous, on left of ventral midline. Genital groove and setae absent. Proboscis slightly bifid at tip (Figure 3.4B). Single left nephridium with simple, basal, projected posteriorly nephrostome (Figure 3.4C). Pharynx with many radiating muscle strands to anterior body wall. Cloaca and hind-gut enlarged. Anal vesicles crescent-shaped sacs on each side of cloaca, with unequal dendritic branches on lateral border; smaller branches with numerous small digitiform projections, each capped by ciliated funnel. Vascular system as in other bonellids. Dorsal and neuro-intestinal vessels join through capillary anastomosis on gut rather than through ring vessel. Gonad on ventral vessel, extending as far anterior as junction of neuro-intestinal vessel with ventral nerve cord.

Male. Three found in nephridiopore of type specimen by Thompson (1979). Males possess ventral setae.

Biology. Little has been reported about this species. Stephen and Edmonds (1972) report that it is only known from the holotype but some local knowledge exists within its range and where benthic studies have been regularly conducted. Thompson (1979) reported it from slope areas with *Arhynchite californicus* in the 100-500m depth range. There is no evidence to suggest that it is anything but a deposit feeding species that lives in a U-shaped burrow. The specimen examined was collected in January, 1988 and had its nephridium full of yolky eggs, indicating that spawning was imminent.

Remarks. Fisher (1946) erected this genus to encompass the single specimen collected in Japan. It differed from many other bonellids in that it has a unique anal vesicle morphology and from all other bonellids by the presence of an enlarged muscular cloaca and enlarged terminal hindgut.

Type Locality and Type Specimen. *Albatross* Sta. 5021, (48°32'30'N, 145°08'45'E). Sea of Okhotsk, Japan. 130 m. Type specimen deposited in National Museum of Natural History (USNM 20605).

Distribution. Bering Sea (USNM 29998); Puget Sound, Washington; Monterey Bay and southern California mainland bight.

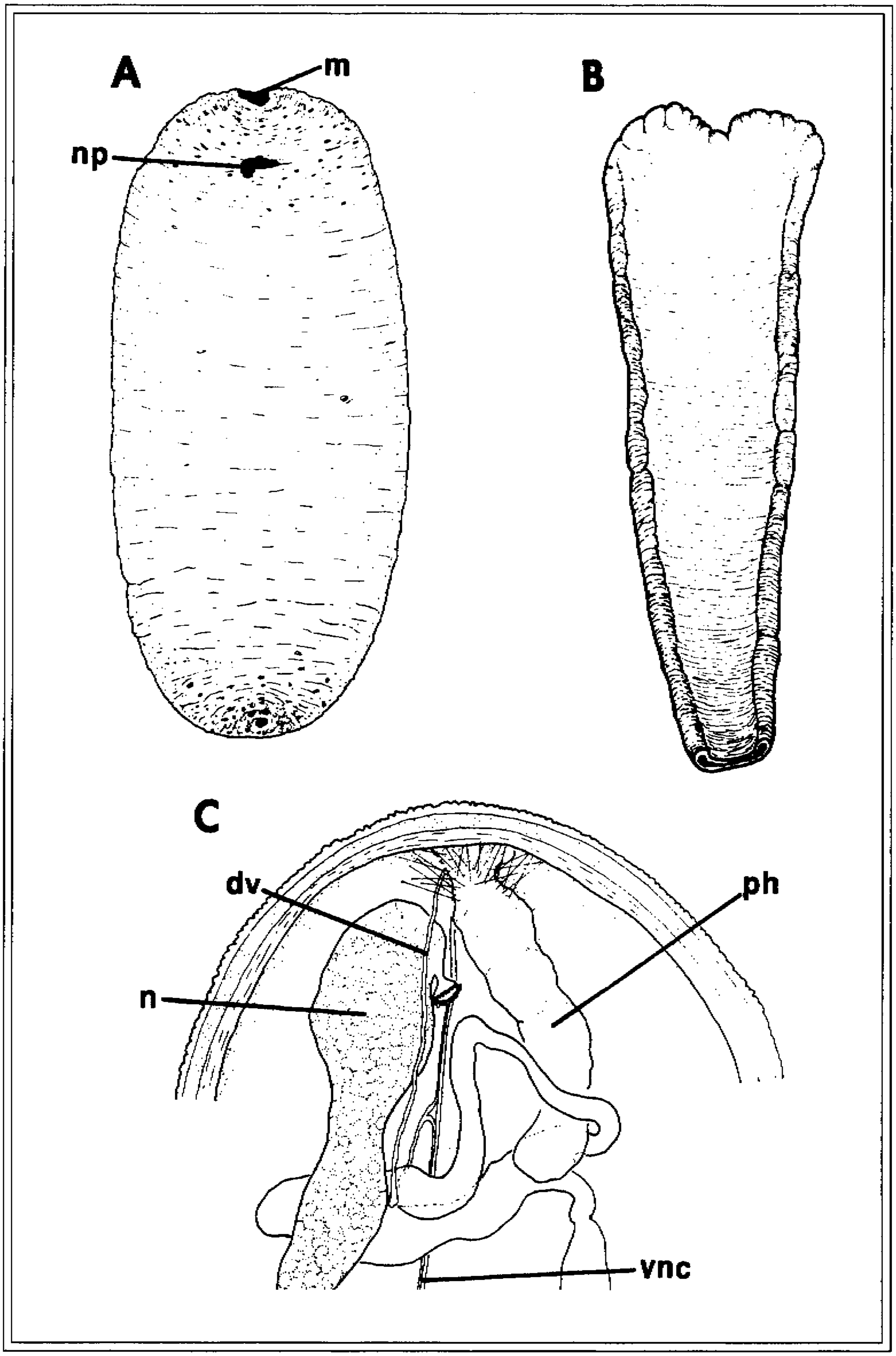

Figure 3.4. *Nellobia eusoma*: A, external anatomy, ventral view; B, proboscis, ventral view; C, anterior internal anatomy, dorsal view.

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4. PHYLUM ECHINODERMATA

by

Andrew Lissner[1] and Debra Hart[2]

Introduction

The phylum Echinodermata contains some of the more familiar marine invertebrates including brittlestars (Class Ophiuroidea); seastars (Class Asteroidea); sea cucumbers (Class Holothuroidea); feather stars and sea lilies (Class Crinoidea); and sea urchins, heart urchins, and sand dollars (Class Echinoidea). Primary references utilized for this section are Ziesenhenne (1941), Hyman (1955), Barnes (1980), Durham *et al.* (1980), Feder (1980), Muscat (1980), Luke (1982), Lawrence (1987), and Maluf (1988). There are approximately 6,700 species of echinoderms, all of which inhabit the marine environment. Of these species, the majority are represented by brittlestars and seastars (approximately 2,000 species each), followed by sea cucumbers (1,200 species), echinoids (800 species), and crinoids (700 species).

Echinoderms occur worldwide in all benthic marine habitats from the intertidal to the deep sea. The general body form of the brittlestars and seastars, comprising the subphylum Asterozoa, consists of arms radiating from a central disc. Compared to seastars, brittlestar arms typically are proportionately longer and set off from the disk, and they lack central arm grooves. Echinoids do not possess arms like seastars and brittlestars. Instead, the body has a spherical to greatly flattened appearance, with a characteristic solid test. Sea cucumbers have elongate, worm-shaped bodies, also without arms, and the body has a less rigid, more leathery texture than other echinoderms. The crinoids are considered the oldest and probably the most primitive echinoderms. Their body structure often consists of an attachment stalk and a crown of arms similar to those of the seastars and brittlestars; however, many species are unstalked and relatively motile.

Most echinoderm species are relatively large (diameters of at least several centimeters) and possess a distinctive, pentamerous radial symmetry in the adult stages. This symmetry is derived secondarily from an initial bilateral symmetry apparent during the larval phase. Thus, echinoderms differ distinctly from other radiate phyla such as sponges, cnidarians, and ctenophores in that they exhibit a more complex life cycle, typically undergoing a radical metamorphosis from a pelagic, bilaterally symmetric larval stage to a sedentary, radially symmetrical adult form. In addition, echinoderms are structurally more complex than these other radiates, and are true coelomates.

All echinoderms retain an internal skeleton composed of calcareous ossicles. Endoskeleton ossicles may be separate articulations, as in seastars and brittlestars, or fused into a rigid theca or test as seen in sea urchins and sand dollars. In most sea cucumber species the ossicles or spicules are reduced to microscopic size within the leathery epidermis. The name echinoderm, or spiny skin, refers to the spines or tubercles projecting from the endoskeleton, giving the body surface a bumpy or spiny appearance.

Echinoderms possess a unique water-vascular or ambulacral system composed of a series of coelomic canals throughout the body. Seawater enters the echinoderm's water-vascular system through a sieve plate (madreporite) and is transported through canals via muscular action and hydraulic pressure to the terminal podia or tube feet. Historically, the podia were believed to function in food collection and transport, although

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this has evolved additionally to a locomotory function in most taxa. Feeding habits of echinoderms are quite diverse. Most species of seastars are carnivorous and many are key predators. Regular urchins are mostly herbivorous, although some function as scavengers or filter their food, while irregular (heart urchins) ingest sediments and associated organic material directly from the substrate. Brittlestars may be scavengers, deposit feeders, filter feeders or, in some cases, may employ all three methods. Sea cucumbers are primarily suspension or deposit feeders, while the crinoids are strictly suspension feeders. Digestion in echinoderms is carried out in a well-developed digestive tract located in the coelom. They have a complete digestive system, although no true excretory system exists. Nitrogenous wastes are diffused through thin surfaces at the body/seawater interface such as the podia.

Most echinoderms are dioecious with fertilization occurring externally in the surrounding seawater. Reproductive strategies include (1) production of large numbers of small eggs that develop into free-swimming, plankton-feeding larvae (most seastars, brittlestars, sea cucumbers and echinoids); (2) free-swimming, yolk-filled larvae that do not require planktonic food (some brittlestars); and (3) production of a few yolky eggs that are brooded to the juvenile stage, thereby eliminating the free-swimming stage (brittlestars and some cold water species of seastars, sea cucumbers, crinoids, and echinoids).

The type and size of ossicles or plates, body shape, the number and length of arms, and, in fresh specimens, color, often are used as key taxonomic features for echinoderms. Class-specific features are presented separately by group in the following chapters.

Sources of Material

Four species of Echinoidea, eight species of Asteroidea, 28 species of Holothuroidea, 19 species of Ophiuroidea, and one species of Crinoidea are treated in this volume. All specimens were collected during the MMS Phase I and Phase II studies of the Santa Maria Basin and western Santa Barbara Channel, predominantly from soft-substrate stations. Exceptions are one species of asteroid, *Henricia leviuscula annectens*, that was collected from both soft and hard substrate, and four ophiuroids (*Gorgonocephalus eucnemis, Ophiopholis, bakeri, Ophiacantha diplasia,* and *Ophiothrix spiculata)* and the crinoid *(Florometra serratissima*) collected from hard substrate.

General accounts of the study areas and descriptions of characteristic communities are presented in Blake (1993), Blake and Lissner (1993), Lissner and Benech (1993), Lissner *et al.* 1991, and SAIC (1986, 1993).

A list of stations, navigational coordinates, and bottom depths from which the specimens were collected are presented in the appendix to this volume. Soft-substrate and hard-substrate specimens were collected using a box corer and a manipulator arm on a manned submersible, respectively.

Individual samples were selected as voucher specimens by the Phase I and Phase II contractors (SAIC and Battelle, respectively). When sufficient material was available, two sets of vouchers were established: (1) a primary collection deposited with the National Museum of Natural History, Smithsonian Institution (designated as USNM on the specimen labels), and (2) a secondary collection deposited with the Santa Barbara Museum of Natural History (SBMNH) or the Natural History Museum of Los Angeles County (designated as LACMNH).

Acknowledgments

This study was funded by the Pacific Outer Continental Shelf Region of the Minerals Management Service, U.S. Department of the Interior, Washington, D.C., under Contract No. 14-35-0001-30484. Michael Hart and Danny Heilprin aided in the literature review for species information and Debra Etchen and Millie Agostino assisted with editing and text entry.

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5. CLASS CRINOIDEA

by

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Introduction

Worldwide there are approximately 700 species of Crinoidea, including 100 species of stalked sea lilies which are limited to the deep sea, and 600 species of unstalked feather stars which are most diverse in tropical reef habitats. In the Central Eastern Pacific Region, from southern California to southern Peru only 12 crinoid species are known. Six are stalked forms, and the 6 feather stars include 1 thalassometrid and 5 antedonid species (Maluf, 1988). All are restricted to deep water, except for *Florometra serratissima*, the only crinoid collected in the Mineral Management Service (MMS) Phase I and Phase II surveys, which can occur near shore at the northern end of its range.

The cornerstones of modern research on crinoids are the monumental Challenger reports (Carpenter, 1884, 1888) and A.H. Clark's invaluable monograph. The latter was published in 5 parts between 1915 and 1967, with the last volume coauthored by A.M. Clark, and brings together information on all aspects of the class. A more up-to-date compendium on the Crinoidea is available in the Treatise on Invertebrate Paleontology (Moore and Teichert, 1978). Messing and Dearborn (1990) and Hendler *et al.* (1995) provide a brief introduction to the crinoids and other echinoderm classes. The nutrition of the group is reviewed by Jangoux and Lawrence (1982), biotic interactions by Meyer and Ausich (1983), reproduction by Holland (1991), and aspects relating to coral reef ecology are covered by Birkeland (1989).

History

A.H. Clark accompanied the *Albatross* on a cruise through the Bering Sea to Japan, and he recalled that "During the 1906 cruise of the *Albatross* I handled tens of thousands of specimens; several times I saw the forward deck of the steamer literally buried under several tons of individuals...everywhere we went we found crinoids; we dredged them at all depths. My ideas of the comparative importance of the recent forms underwent a total change; surely a group so abundant...cannot be considered as decadent or degenerate" (A.H. Clark, 1915:4). In the following years he described the *Albatross* material, and examined nearly every major collection of crinoids from around the world, compiling the results in his monograph.

In the first volume on the Comatulida, A.H. Clark (1915) summarized the history of crinoid studies beginning with the writings of Fabius Columna in 1592. The earliest publication on Eastern Pacific crinoids was written by Hartlaub (1895), but as A.H. Clark (1915:56) claimed, the west coast of the Americas remained "*terra incognita* so far as crinoids were concerned until 1907, in which year many species were described from the region" (by Clark himself). Developments in the taxonomy of Eastern Pacific crinoids can be traced through his first and last papers on the fauna (Clark, 1907; Clark and Clark, 1967).

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Systematics

The classification of Crinoidea perhaps in widest use is the system outlined by Ubaghs (1978), and a history of crinoid systematics is provided by Lane (1978). Simms (1988) offered a contemporary overview of crinoid systematics, in which he reduced the living comatulids to infraordinal status "Comatulidia" within an Order Isocrinida. In the present treatment, Ubagh's scheme is retained, wherein the Class Articulata represents all living crinoids and the Order Comatulida includes all the feather stars. In his organization there are 16 families of Recent comatulids, and over 130 extant genera.

Morphology

Featherstars range in size from 3-50 mm body diameter with arms 50-550 mm in length. Most have 10 arms or more, and depending on the species the number of arms can reach 200.

The soft visceral mass of the crinoid, contained in a naked or weakly calcified tegmen (=disk), rests on supporting rings of ossicles composing a calyx. In the sea lilies the calyx caps a long stalk that supports the animal above the substrate. In the feather stars (Comatulida) only one ring is evident, made up of five radial ossicles, one at the base of each arm. The radials sit on the oral surface of a large discoidal to cylindrical centrodorsal ossicle.

Unbranched cirri articulate with the aboral face of the centrodorsal. The cirri are prehensile, composed of series of ossicles of which the terminal ossicle is usually modified as a claw which can close against an opposing spine on the penultimate cirral. Using its cirri, a feather star can firmly attach to a suitable perch.

The rays are long and flexible, made up of series of small cylindrical ossicles (brachials). The rays generally branch. The row of brachials between branching points is called a division series (=brachitaxis), and terminates in a modified axillary ossicle (=axil) that either bears two unbranched arms or further division series.

Most of the brachials are attached to one another by a ligament below a bony fulcral ridge, and by paired muscle masses above the ridge. The ligaments serve to lock the extended arms in position. Arm movements are powered by the contraction of the muscle masses pulling the arms upward, opposing the tension created by the ligaments. Some brachials are connected by rigid syzygies or by synarthries. A syzygy is a ligamentary articulation in which ridges radiating from the center of one brachial are connected to corresponding ridges on the adjacent brachial. In dried specimens, it appears as a perforated line between brachials. A synarthry is a ligamentary connection between two brachials with an aboral/oral fulcral ridge, and is capable of limited side-to-side movement. The brachial proximal to a syzygy or a synarthry lacks a pinnule.

Pinnules are the alternating series of unbranched appendages on the sides of the arms, and they give the arm a feathery appearance. From the base to the tip of the ray there are oral, then genital and finally distal pinnules. Oral pinnules near the mouth are specialized for defense or for cleaning the oral surface. The genital pinnules bear the gonads. The majority of the pinnules are food gathering organs. They are grooved, and the channel (ambulacrum) is bordered by tube feet. The groove of each pinnule unites with an ambulacral furrow that runs down each arm to the mouth. Microscopic tube feet, grouped in threes with a protective lappet, alternate on opposite sides of the food groove.

The tegmen, which encloses the visceral mass, is covered by soft skin. The mouth opens on the tegmen at the meeting point of the ambulacral grooves, and the anus opens at the apex of a small muscular conical papilla (= anal cone). The mouth is central, except in the Comasteridae, the second largest family of feather stars. The tegmen is perforated by hundreds of microscopic pores, probably serving in respiration, which lead into ciliated channels in the central body. The visceral mass is filled with connective tissue that contains numerous microscopic ossicles and surrounds the intestine and axial sinus.

The body plan of crinoids is described in terms of formulae that specify the composition of division series, arrangement of pinnules, number of cirri, and dimensions of ossicles. The formulae are shorthand expressions incorporating abbreviations for the ossicles: Br = brachial, P = pinnule, + = syzygy. Roman numerals specify division series, arabic numerals indicate numbers of ossicles, and subscripts indicate positions of ossicles. For example, IIBr4(3+4) indicates the second division series with 4 brachials, with a syzygy between the 3rd and 4th brachial. Division series are absent in an undivided arm; therefore roman numerals are omitted in its formula; thus Br_{3+4} indicates the third and fourth brachials joined by a syzygy. Interior pinnules (those arising between the arms of a ray) are specified by numerical subscripts, exterior pinnules by subscript letters. For example, P_a is directed medially, and on the next distal brachial P_2 is directed away from the ray. The number of cirri borne on the centrodorsal is specified as a roman numeral.

Ecology and Behavior

Crinoids are "passive suspension feeders" that extend their arms into the water to form a feeding fan. Many crinoids are rheophilic, preferring areas where currents flow between 1-2 knots and carry abundant food. The configuration of the fan varies depending on the species and on environmental conditions, the orientation of the arms and pinnules shifting to increase the effectiveness of particle capture. The pinnules tend to align perpendicular to the flow of water, with the food groove facing down-current, so that reduced velocity and vortices created by the arms slow and direct particles toward the tube feet. Rheophobic species, which occupy low-velocity habitats, hold their arms in haphazard arrays, with the pinnules oriented perpendicular to each other.

Drifting or swimming prey are rapidly flicked by the long outer tube feet toward the food groove, where they are trapped in mucus, then moved along the grooves in the pinnules and arms to the mouth. Crinoids capture zooplankton (forams and actinopods, invertebrate larvae, and small crustaceans), phytoplankton (diatoms and unicellular algae), and particulate matter — most 0.05-0.40 mm in size.

Feather stars can right themselves if overturned, and can pull themselves slowly along the seafloor. Some swim by pulling alternating arms up and down in a coordinated fashion. They are capable of regenerating autotomized and damaged arms and the visceral mass. Crinoids are subject to predation, mostly by fishes. They support a diverse assemblage of parasites and commensals including gastropods, ophiuroids, clingfish, myzostome polychaetes, and crustaceans (including shrimp, copepods, isopods, and cirripedes).

The gonads of crinoids consist of several tissue layers enclosing the gametes, and are borne in specialized basal pinnules. For most feather stars the breeding season is limited to a 1-2 month period in spring or summer. Individuals may spawn *en masse*, and in synchrony, each female feather star releasing thousands or millions of eggs. Spawning events may last an hour or less, or span a period of several days. While spawning, many individuals whip their arms, dispersing gametes, but fertilized eggs often stick to the arms and pinnules. Some species have the capacity to brood their developing young; their eggs adhere to the genital pinnules or enter a brood pouch from which the larvae emerge.

Within a few days after fertilization a uniformly ciliated embryo develops into a doliolaria larva encircled by 3-4 ciliated bands. It lacks a mouth and feeds, if at all, by absorbing dissolved chemicals. The doliolaria swims for several days, before selecting a suitable substrate for settlement where it metamorphoses into a stalked stage called a "cystidean". Since the posterior end of the cystidean becomes the oral surface of the adult, its internal structures must rotate 90° during the transformation to a juvenile "pentacrinoid." At that stage it has the appearance of a miniature stalked crinoid. The pentacrinoid begins feeding when the mouth and anus have formed, and its arms later begin to branch. Species with numerous arms develop from a five-armed juvenile by repeatedly growing back two arms in the place of arm branches that have been shed. After some cirri have developed from the centrodorsal ossicle of the pentacrinoid, the feather star separates from the top of the stalk and attaches directly to the substratum.

Preservation

Details regarding techniques for collecting, anesthetizing, and preserving crinoids and other echinoderms are covered in Messing and Dearborn (1990) and Hendler *et al.* (1995). The most efficient procedure for preservation involves killing individuals with outspread arms by rapid immersion in 95% ethanol. Specimens killed in buffered 10% formalin or in alcohol should be stored in 70-80% ethanol. Often, the details of arm and cirrus structure are best observed on appendages pried from dried specimens using fine forceps. When examination of individual ossicles is required, the structures can be cleaned using dilute sodium hypochlorite (laundry bleach).

Glossary

Terms that are not defined above can be found in the extensive glossaries provided in A.H. Clark (1915), Moore and Teichert (1978), and Messing and Dearborn (1990).

Terminology and Conventions

Body plan formulae are explained above, in the section on morphology. Abbreviations used are: AHF, Allan Hancock Foundation of the University of Southern California; CAMP, California Phase II Monitoring Program; LACM, Natural History Museum of Los Angeles County; SBMNH, Santa Barbara Museum of Natural History; USNM, National Museum of Natural History.

Description of Species

Order Comatulida

Family Antedonidae

Subfamily Heliometrinae

Florometra serratissima (A.H. Clark, 1907)

Figure 5.1

Antedon perplexa A.H. Clark, 1907:70, 74.

Promachocrinus (*Florometra*) *perplexa*, A.H. Clark, 1915:140.

Florometra perplexa, A. H. Clark, 1921: 60, 62, 74,79, 303, 670, 685, 725, 729, 758, 760, figs. 95-96, 131, 590, pl. 5, figs 1009-1014, pl. 13. fig.1053.— Ziesenhenne, 1937: 209, 211.— Hartman and Barnard, 1958:47, 58.— Hartman and Barnard, 1960: 231, 281.— A.H. Clark and A.M. Clark, 1967:299, 313, 317, 318.

Antedon serratissima A.H. Clark, 1907:71, 77.

Promachocrinus (*Florometra*) *serratissima*, A.H. Clark, 1915:140, 142.

Florometra serratissima, Mortensen, 1920:54, 55, 66, 94, pl. 27, figs. 1-7.— A.H. Clark and A.M. Clark, 1967:289, 294, 299-309 [see for additional synonymy], 318, 321, 738, 741.—Breimer, 1978:T36-37, fig. 22.—Gotshall, 1994:77, fig. 185.— Byrne and Fontaine, 1981:11-17, figs. 1-6.

Material Examined. California: Santa Maria Basin, Phase I Sta. BRA-14, 96-105 m (1, USNM primary voucher).—Western Santa Barbara Channel, Phase I Sta. BRA-002, 110-126 m (1, SBMNH secondary voucher).—Off San Miguel Id., R/V *Velero III* Sta. AHF 1396-41, 104-113 m (4, LACM 41-176.3).—Off Santa Rosa Id., R/V *Velero III* Sta. AHF 1392-41, 104 m (2, LACM 41-172.6), R/V *Velero III* Sta. AHF 1395-41, 128-135 m (10, LACM 41-175.1).—Off San Clemente Id., R/V *Velero III* Sta. AHF 1023-39, 101-201 m (1, LACM 39-127.3).—Mexico: Pacific Coast, Baja California, off Islas San Benito, R/V *Velero III* Sta. AHF 1119-40, 159-174 m (67, LACM 40-92.6).

Description. An antedonid with 5 inconspicuous radials, second post-radial ossicle axillary, 10 arms.

Centro-dorsal hemispherical, cirri 40-50 or more, stout, large, 30 mm long, with approximately 36 joints exhibiting tendency to overlap; nearly all cirrals bearing strong dorsal spines.

First radials concealed; second barely visible; IBr_1 short, IBr_2 (axillaries) very broad, prominent synarthrial tubercle between IBr_1 and IBr_2; first brachial very short; second triangular, approximately equilateral; third irregularly oblong; distal brachials to the tenth or twelfth wedge-shaped, then triangular. Syzygies between brachials 3+4, 9+10, 16+17, and distally at intervals of 3 muscular articulations. Radials and lower brachials thickly set with small sharp spines. Brachials short, overlapping, edges bearing numerous small, sharp hyaline teeth; longest proximal brachials broader than long.

Arm length of large individuals 150-280 mm. P_1 17-21 mm long with 45-60 joints, with long comb distally; P_2 longer than first, 18-22 mm in length with 45-60 joints; P_3 20 mm long with 36 joints, bearing comb like the second, or 12 mm long with elongated joints like the fourth; distal pinnules long and slender, their joints overlapping, distal edges set with spines.

Color: Living individuals yellow, brownish yellow, tan, or reddish brown, the cirri whitish to light brown, pinnules may be contrasting dark brown to black. In alcohol pigmentation white, brown, or red (A.H. Clark, 1907; Ziesenhenne, 1937; Gotshall, 1994).

Variation: Abnormal individuals with 9 or 11 arms have been reported. The extent of spine cover varies considerably, with development greatest in specimens from warm water localities (Clark and Clark, 1967).

Remarks. In Clark and Clark (1967) a review of the genus and key to the seven species is provided. *F. perplexa*, originally regarded by A.H. Clark (1907) as a less robust form with smoother, longer arms, is placed in synonymy with *F. serratissima*. In addition, *F. serratissima* is distinguished from *F. mariae* (A.H. Clark), which occurs in Japan, by its relatively short brachials, from *F. tanneri* (Hartlaub), found off Panama, by oral pinnules with stout, carinate, proximal segments, and from *F. asperrima* (A.H. Clark), reported from Monterey Bay to northern Japan, by the position of its 3rd syzygy between brachials 16+17 (sometimes between 15+16) rather than 14+15 and by having more spinose division series and brachials.

The status of *F. serratissima* is unclear, particularly with regard to *F. asperrima*. In their treatment of *F. asperrima*, Clark and Clark (1967:321) state that "the ossicles of the division series and arm bases never show the extreme development of spines frequent in *F. serratissima*, but the least spinous individuals of that species are less spiny than the extreme specimens of *F. asperrima*. From Monterey, California, northward to the Gulf of Alaska *F. asperrima* is more variable than farther northward and westward, and apparently intergrades with *F. serratissima*."

The name *perplexa* has page priority over *serratissima* based on the original publication. A.H. Clark mentioned that his intitial concept of *Antedon perplexa* included what he later regarded as *F. tanneri*, an indication that he was not satisfied with the name *perplexa*. A.M. Clark concluded that "in view of the very brief description of *perplexa* in the form of a comparison with *asperrima*, I do not dispute the use of the name *serratissima* for the species" (Clark and Clark, 1967:309).

Distribution. Natividad Island, Baja California, Mexico to Shumagins and Sannak Island, Alaska, at depths of 11-1252 m (A.H. Clark, 1907; Ziesenhenne, 1937; Clark and Clark, 1967).

Biology. Based on trawled samples it appears that in places "there must be many acres, if not miles, pretty well covered with [*Florometra serratissima*]" (Clark and Clark, 1967:308). Scuba observations reveal that population densities reach at least 30 individuals/m^2 (Byrne and Fontaine, 1981). On soft bottom habitats of the southern California shelf *F. serratissima* is infrequent in occurrence (Barnard and Ziesenhenne, 1960), but on hard bottom habitats it is characterized as an "anchor species" which provides a biogenic refuge for other fauna (Lissner and Benech, 1993). At the southern end of its range it has been collected in association with *Fariometra parvula* (Hartlaub), the young of which it resembles (Clark and Clark, 1967).

Byrne and Fontaine (1981) found that *F. serratissima* occurs where currents are of low velocity, and described how its arms are held in a cone array during slack water, and form a partial fan when flow increases. They studied the feeding process and activities of the triplet groups of podia, noting that each tentacle functions differently in sensing, collecting, and transferring paticles to the food groove. LaBarbera (1982) characterized metabolic rates of individuals in normal current regimes, finding lower values than previously estimated.

The sea star *Pycnopodia helianthoides* (Brandt) and a crab *Oregonia gracilis* (Dana) may prey on *F. serratissima (Mladenov, 1983)*. Its escape behaviors include autotomy and swimming, and the swimming response has been described (Mortensen, 1920; Mladenov, 1983). Breimer (1978) noted that the species has "external obliqueness of radials accompanied by reversion," that is, the pinnules shifting from the low side of proximal brachials to the high side of distal brachials, a characteristic of swimming comatulids. In the field, 80% of the individuals encountered have regenerating arms, probably having escaped from predators;

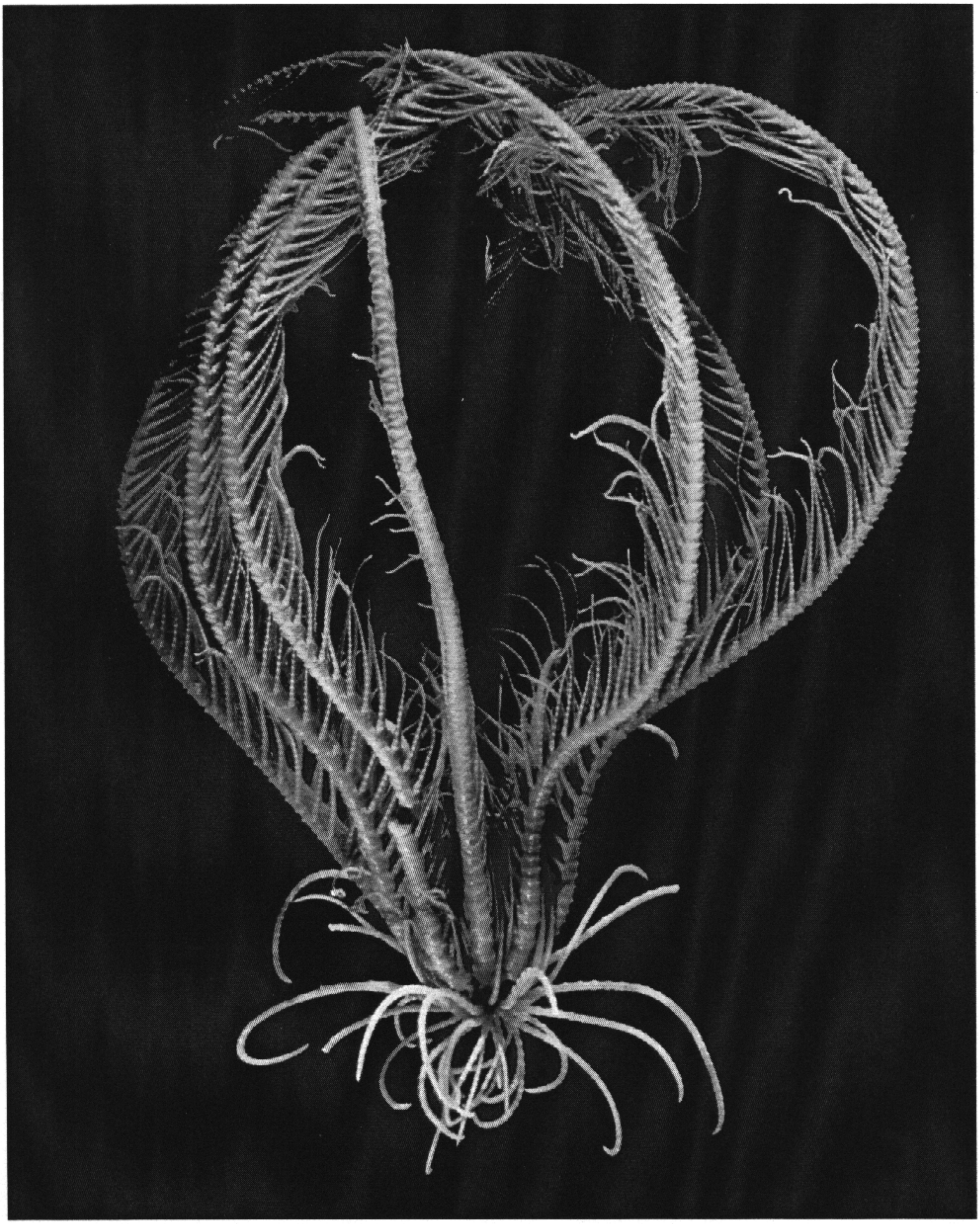

Figure 5.1. *Florometra serratissima* (A.H. Clark): Lateral view (LACM 41-176.3; arm length = 160 mm).

arm regeneration takes approximately 9 months (Mladenov, 1983). An external myzostome parasite, *Myzostomum deani* McClendon is associated with individuals off Washington and northern California (McClendon, 1906; A.H. Clark, 1921).

The reproductive biology and development of *F. serratissima* are described by Mladenov and Chia (1983) and Mladenov (1986), and discussed in a comparative context by Holland (1991) and Nichols (1994). The sexes are separate and the sex ratio of individuals in a population is approximately 1:1. Large specimens (arm length 280 mm) have over 400 genital pinnules with a total of approximately 24,000 eggs. The available data have been interpreted to indicate that reproduction occurs year round, with individuals spawning approximately monthly and the level of activity varying with the season. The gonad structure and process of gametogenesis are clarified by several authors (Bickel *et al.*, 1980; Mladenov, 1986; Holland; 1991).

The eggs are pale pink, 0.21 mm in diameter, and produce a fertilization membrane with a ridged ornamentation. The doliolaria larva is yolky and barrel-shaped, with 4 ciliated bands; formation of the bands and of the larval integument have been described by Chia *et al.* (1986), Lacalli and West (1986, 1987), and Lacalli (1993). The larvae swim up to 9 days before settlement, rapidly metamorphose to a sessile cystidean, and gradually transform to a feeding, stalked pentacrinoid. The feeding response of the pentacrinoid has been studied (Mladenov and Chia, 1983) and the skeletal ontogeny of the pentacrinoid has been depicted (Mortensen, 1920). Between the egg and the prefeeding cystidean stage, 81% of the nutrient in the egg is depleted. As a result, the pentacrinoid has relatively loe energy reserves, possibly making it a vulnerable stage in the crinoid's life history (McEdward *et al.*, 1988).

Mitochondrial DNA has been isolated from *F. serratissima*, but DNA amplification products have not successfully been obtained using echinoid or asteroid primers (Smith *et al.*, 1993).

Acknowledgements

This study was funded by the Pacific Outer Continental Shelf Region of the Minerals Management Service, U. S. Department of the Interior, Washington, DC. J. Blake and A. Lissner offered the MMS collection for study and arranged for its deposition at LACMNH. C. Messing verified specimen identifications. J. Dearborn and D. Pawson reviewed a draft of the manuscript. I am grateful to all those acknowledged, for their assistance with this chapter.

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6. CLASS ASTEROIDEA

by

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Introduction

Asteroids, commonly known as seastars or starfish, are a class of flattened, multli-armed echinoderms containing approximately 2,000 living species, with the highest number of species occurring in the Northeast Pacific. General references utilized for this section are Hyman (1955), Barnes (1980), and Feder (1980). Most seastars possess five arms arranged around and grading into a central disc. However, species with 4 to 24 arms are also common. Additionally, one species (*Heliaster*) from the eastern Pacific can have 40 or more arms. The size of most asteroids ranges from 12 to 24 cm in diameter, although *Pycnopodia* from the northwest coast of the United States may reach a diameter of almost one meter.

Typically, the seastar body is dorsoventrally flattened with the oral surface and tube feet (podia) positioned against the substratum, and the anus and madreporite on the exposed upper (aboral) surface. Furrows (ambulacral grooves) containing the podia extend radially from the mouth into each arm. Podia function primarily as locomotory organs but in many species also are used to attach to hard surfaces, to capture and hold prey, or to burrow into sediments. Attachment of podia is by means of terminal adhesive disks that create suction or through secretion of adhesive mucus.

The seastar endoskeleton is composed of calcareous ossicles embedded in a matrix of connective tissues. Each ossicle is composed of a single crystal of magnesium-rich calcite formed inside a dermal cell. The surface of an asteroid is covered by an epidermis of monociliated columnar epithelium. Sensory nerve cells and mucous gland cells also lie in the epidermis, providing the outer surface with a protective mucous layer.

Diet and feeding methods of seastars can vary considerably. Most species are carnivorous, feeding primarily on molluscs, crustaceans, and other echinoderms. A smaller number are omnivorous scavengers. For other, suspension-feeding species, smaller food items such as plankton and organic particulates in the water column may be trapped by mucus and cilia and moved toward the oral surface for digestion. Seastars may also use their arms to entrap smaller prey, pulling them toward the everted stomach, where digestion begins. Some species such as *Pisaster* can evert their stomachs into openings in mollusc shells and begin digesting prey tissue externally. Other species, including *Luidia* and *Astropecten,* swallow their prey whole, as generally limited by the size of the mouth opening.

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External fertilization is characteristic of most seastars; gametes are shed into the sea by both sexes. Alternately, some Northeast Pacific species such as *Henricia*, *Pteraster*, and *Leptasterias* lay and brood large yolky eggs that develop directly into juvenile seastars. Growth and development are dependent on water temperature and food supply (cooler temperatures and limited food are directly correlated with slower growth). Under natural conditions, growth tends to be slow and life spans are relatively long (e.g., 5-years for *Astropecten* and at least 20 years for *Pisaster ochraceous*). Adult seastars have few natural predators, likely contributing to their longer life spans.

Systematists primarily classify asteroids according to skeletal characteristics, but soft parts such as podia and internal organs may also be used. Seastar size may be used for some taxonomic descriptions, such as the distance between the center of the mouth (or disc) to the tip of the longest arm, and the arm radius.

Taxonomic History

The distinctive morphology, color, and relatively large size of most California asteroids have made them the subject of numerous scholarly and popular presentations on their taxonomy and distinguishing characteristics. Important taxonomic monographs on Pacific Coast Asteroidea include Fisher (1911, 1928, 1930) and Verrill (1914), with a seminal treatise on their worldwide phylogeny presented in Fell (1963). Subsequent papers and reports that provide excellent synopses for many southern California species include Feder (1980), Hopkins and Crozier (1966), and Word and Charwat (1975). A classic reference that summarizes key distinctions among Orders and Families of asteroids, as well as considerable species-specific information on West Coast taxa is Hyman (1955). A particularly useful, popular reference, including color plates of shallow subtidal species, is Gotshall and Laurent (1979). Other relevant summaries of species distributions and their natural history are presented in Ziesenhenne (1941), Hartman (1955), and Hartman and Barnard (1958), Pequegnat (1964), and Lissner and Dorsey (1986). Important synopses of taxonomic collections of asteroids, including those from southern California, are provided in Luke (1982), Muscat (1980), and Maluf (1988).

Morphology

Key features that are useful in identifying asteroids include the number and relative length of the arms compared to the central disc, type and relative size of arm and mouth plates, presence/absence and type of pedicellariae and paxillae, number and type of papulae, and, in fresh specimens, body color. Specifically, important characters that must be recognizable to use the taxonomic key in this section include supramarginal, inframarginal, and ambulacral plates; shape and number of spines on paxillae; type of pedicellariae; and adambulacral (furrow) spines (Figure 6.1 and General Terms below).

The taxonomic key for the asteroids was developed in part, and the identifications were made, with the aid of the monographs of Fisher (1911, 1928, 1930). Many specimens also were compared with the asteroid collection of the Allan Hancock Foundation, University of Southern California.

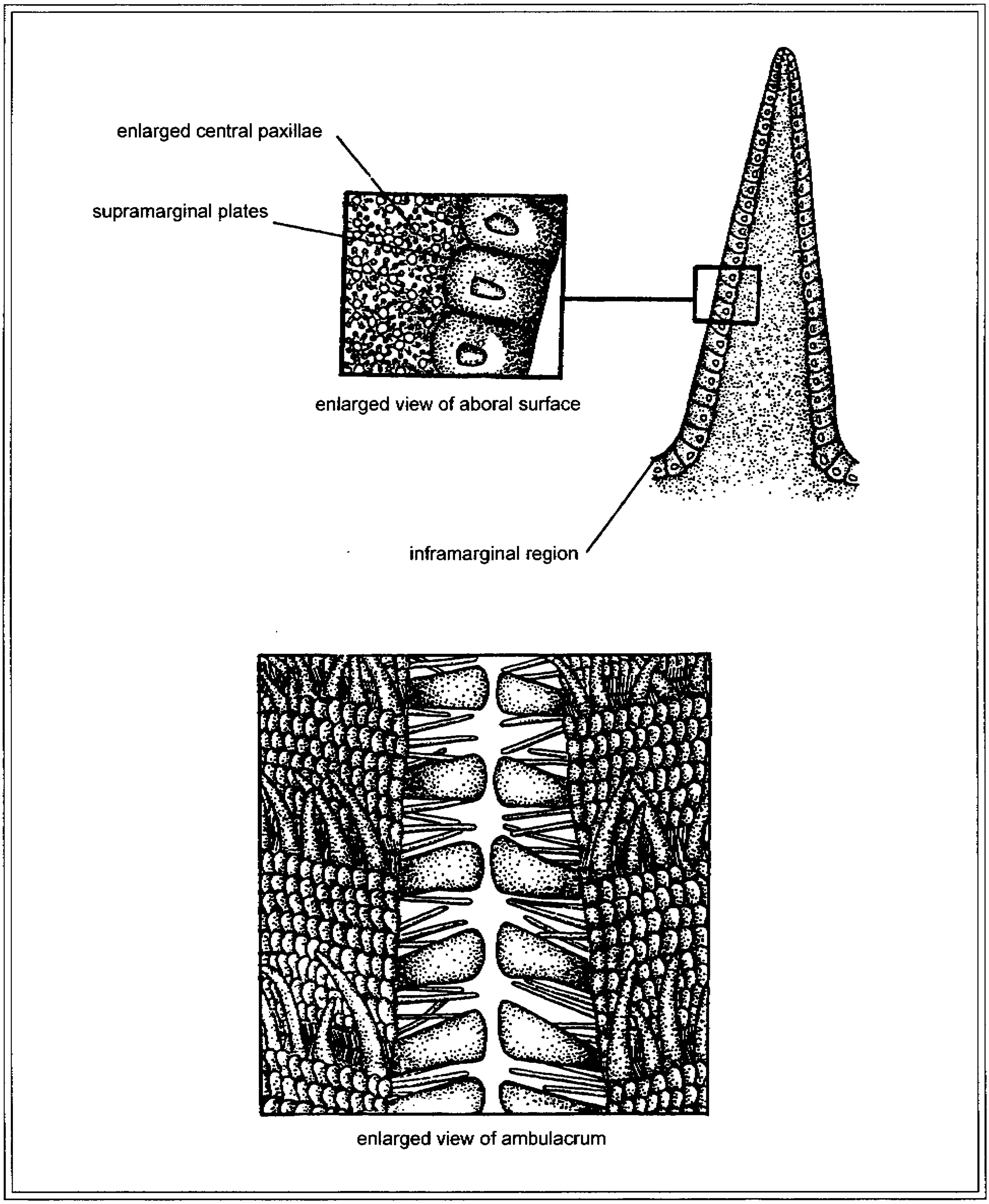

Figure 6.1. Common external features of many seastars (*Astropecten* is depicted). Source: Word and Charwat, 1975.

Glossary

Adambulacral plates. Calcareous plates comprising the ambulacrum and located ventrally along the arm.

Adambulacral spines. Calcareous spines located within the ambulacrum.

Ambulacrum. Central furrow, containing the podia, that extends ventrally along the length of each arm.

Inframarginal plates. Calcareous plates located along the ventral margin of the arm; particularly prominent in Orders such as the Paxillosida.

Paxillae. Small, peg-like, calcareous plates set in the aboral epidermis of most sea stars, particularly the Paxillosida, Valvatida, and Spinulosida.

Pedicellaria. Small, stalked to sessile organs, typically on the aboral surface of most sea stars (except most Spinulosida), comprised of jaw-like valves functioning in defense, cleaning, and scavenging.

Supra-ambulacral plates. Calcareous plates located on the dorsal-extending top of the ambulacrum, particularly in the Order Paxillosida.

Supramarginal plates. Calcareous plates located along the dorsal margin of the arm, particularly prominent in the Order Paxillosida.

Methods of Laboratory Examination

Identification of asteroids was accomplished using the unaided eye to distinguish gross morphological features such as color, number of arms, and general shape. A hand lens or stereomicroscope was used to examine surface features such as paxillae and pedicellariae. Some dissections, aided by the microscope, were performed to verify in cross-section some of the arm plate features, as indicated in the taxonomic key. However, most of the species are very distinct based on external features alone. Specifically, the taxonomic orders can be recognized based on external features such as the size of marginal arm plates, presence and shape of pedicellaria, and presence or absence of suckers on tube feet. Once the order is determined, the type of habitat (soft versus hard substrate), color (in fresh specimens), type of pedicellaria, skin thickness, presence/absence of spinose plates on aboral surface, and presence/absence of a nidamental (brood) chamber (determined by dissection) typically are sufficient to distinguish species from the study area.

List of Species

- Class Asteroidea
  - Order Paxillosida
    - Family Luidiidae
      - *Luidia foliolata* Grube, 1866
    - Family Astropectinidae
      - *Astropecten verrilli* (Fisher, 1906)
  - Order Valvatida
    - Family Goniasteridae
      - *Hippasteria spinosa* Verrill, 1909
  - Order Spinulosida
    - Family Pterasteridae
      - *Pteraster tesselatus arctuatus* (Ives, 1888)
    - Family Poraniidae
      - *Poraniopsis inflata* (Fisher, 1906)
    - Family Echinasteridae
      - *Henricia leviuscula annectens* Fisher, 1910
  - Order Forcipulatida
    - Family Zoroasteridae
      - *Myxoderma platyacanthum* H.L. Clark, 1913
    - Family Asteriidae
      - *Rathbunaster californicus* Fisher, 1906

Key to Orders and Species of Asteroidea Collected from the Santa Maria Basin and Western Santa Barbara Channel

1A. Marginal plates (supramarginals and inframarginals) large and conspicuous 3

1B. Marginal plates not large and conspicuous 2

2A. Pedicellaria absent or rare, not stalked.. .... Order Spinulosida 5

2B. Pedicellaria common, stalked .... Order Forcipulatida ... 7

3A. Supramarginal plates smaller than inframarginals and similar in size to paxillae .... Order Paxillosida, *Luidia foliolata*

3B. Supramarginal and inframarginal plates similar sized and larger than paxillae 4

4A. Suckers present on tube feet; at least one hyaline or unpaired median tooth common to each pair of mouth plates, or supra-ambulacral plates reduced or absent .... Order Valvatida, *Hippasteria spinosa*[3]

4B. Suckers absent on tube feet; hyaline or median teeth absent from mouth plates; supra-ambulacral plates present, not reduced .... Order Paxillosida, *Astropecten verrilli*

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[3] *Hippasteria spinosa* is the only orange-colored (in fresh specimens), five-armed species with extensive aboral spines that occurs in the study area. Other orange to brownish-orange, five-armed taxa can include *Mediaster aequalis* and *Poraniopsis inflata*; however, *Mediaster* has no aboral spines and *Poraniopsis* has only a few, widely spaced spines that typically are white in color.

5A. Mouth plates small, not spade-shaped .... Family Echinasteridae 6

5B. Mouth plates large and spade-shaped .... Family Pterasteridae, *Pteraster tesselatus arctuatus*[4]

6A. Aboral plates covered with thick skin .... *Poraniopsis inflata*

6B. Aboral plates with small spinelets, not covered with thick skin ....*Henricia leviuscula annectens*[5]

7A. Straight and crossed pedicellaria present; no furrow spine ....
.... Family Asteriidae, *Rathbunaster californicus*

7B. Only straight pedicellaria present; prominent furrow spine ....
.... Family Zorasteridae, *Myxoderma platyacanthum*[6]

Descriptions of Species

Order Paxillosida

Family Luidiidae

Luidia foliolata Grube, 1866

Figure 6.2

Luidia foliolata: Fisher, 1911.
Petalaster foliolata: Fell, 1963.

Material Examined. California: Santa Maria Basin, Sta. BRA-26 (USNM), 108-111 m (one specimen, 150 mm arm length); Sta. BRA-22 (SBMNH), 114-115.5 m (one specimen, 130 mm arm length).

Description. Large, long-armed, typically five-armed seastar with dull gray or brown color in fresh specimens (Lambert, 1945). Prominent supramarginal plates absent in the genus (representing a clear distinguishing feature from *Astropecten,* which is the only other common, five-armed seastar co-occurring in most soft substrate areas off California; Figures 6.2 and 6.3). Pedicellariae also absent (Lissner, 1980). Marginal arm spines distinct (Figure 6.2). Arms rectangular in cross-section; podia pointed, without suckers

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[4] *Pteraster tesselatus arctuatus,* representing a "pin cushion" star of the Family Pterasteridae, is the only species in the study area that has a nidamental (brood) chamber; very short and thick arms; and a fleshy, light brown to tan (in fresh specimens) epidermis.

[5] *Henricia leviuscula annectens* is distinguished from *H. leviuscula* by having pseudopaxillae with fewer than 20 spinelets, while the latter species has 20 or more spinelets. *Henricia aspera* is distinguished by having papular areas that are larger than the pseudopaxillae, while in *H. leviuscula* the papular areas are smaller than the pseudopaxillae. *Henricia polyacantha* is distinguished from all these species by having flexible as compared to rigid arms. Additionally, from fresh specimens, *H. leviuscula* is bright orange to, rarely, purple in color while the other species are white.

[6] *Myxoderma platyacanthum* and *M. sacculatum,* representing the two local congeners, are both light tan in color (in fresh specimens) with distinctive, reticulated patterns associated with papulae on the aboral surface. A distinguishing feature is that the terminal arm plate is enlarged (ovoid) in *M. sacculatum* but is tapering (not ovoid) in *M. platyacanthum.*

(Lambert, 1945). Arms autotomize easily when an individual is handled or disturbed, and specimens often fragment during preservation. An important distinguishing feature between *L. foliata* and the sometimes co-occurring *L. armata* is that the former consistently has "only scattered, light-colored individual paxillae on a darker field", as compared to a more mosaic pattern of different colors in the latter (D. Cadien in SCAMIT, 1994).

Biology. The species is found on soft substrates (shell, mud, and sand) and individuals are known to burrow into substratum to capture prey (Lawrence, 1987). *Luidia foliolata* commonly is observed in a "humped" feeding posture, requiring flexion of the rays, and is an active predator on soft substrate organisms including molluscs, crustaceans, and other echinoderms. Feeding is by ingestion of the prey item, and entire, intact heart urchins have been noted within the body cavity of this species (Lissner, pers. obs.). The maximum bivalve that can be swallowed typically cannot exceed the mouth diameter (e.g., 40 mm; Sloan and Robinson, 1983). The escape response elicited from the sea cucumber, *Parastichopus californicus,* probably is an indication of the voracious nature of this seastar (Margolin, 1976).

Remarks. Fell (1963) redefined this species into the Genus *Petalaster,* but most researchers (e.g., Maluf, 1988; SCAMIT, 1994) recognize the original description of *Luidia,* as followed for this atlas.

Distribution. The species ranges from southeast Alaska to the Galapagos Islands, at depths from 0-476 m (Maluf, 1988).

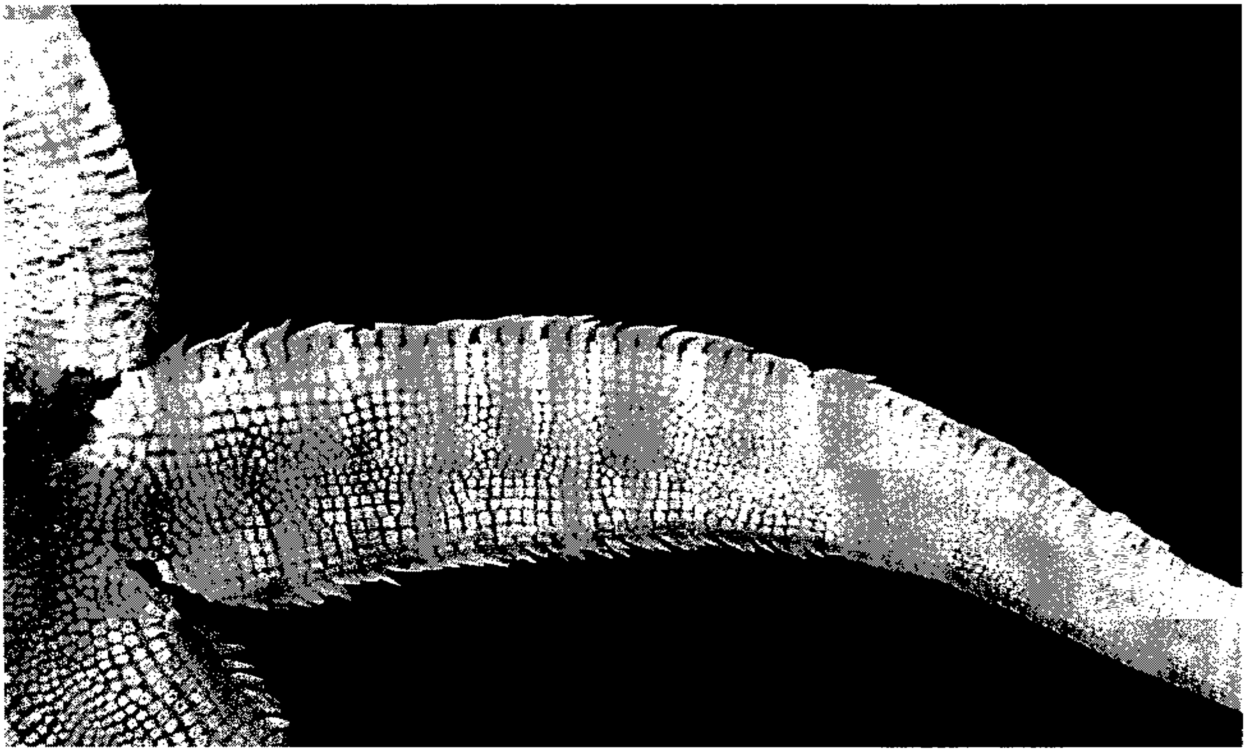

Figure 6.2. Aboral view of arm from *Luidia foliolata* (Station BRA-22), emphasizing lack of prominent supramarginal plates, but distinct arm spines.

Family Astropectinidae

Astropecten verrilli (Fisher, 1906)

Figure 6.3

Astropecten californicus Fisher, 1906.
Astropecten verrilli: de Loriol, 1917.

Material Examined. California: Santa Maria Basin, Sta. BRA-01 (USNM), 69-73.5 m (one specimen, 80 mm arm length); Sta. BSR-21 (SBMNH), 29 m (one specimen, 85 mm arm length); Sta. R-3, Rep. 3 (SBMNH), 409 m (one specimen, 29 mm arm length).

Description. This species typically five-armed, with light tan to grayish color in fresh specimens. Aboral surface covered with small paxillae, of which 4-5 equal in length to 2 supramarginal plates ((Figure 6.3; Lissner, 1980). Prominent, spine-bearing, supramarginal plates present on upper edges of arms (Figure 6.3; Feder, 1980). Podia occur in double rows in ambulacra, and lack suckers, consistent with occurrence of this species on soft substrates. Distinctions between juvenile *A. verrilli* and co-occurring *A. armatus* can be made based on the "relatively longer and more robust lateral spines, and the smaller arm length to disc diameter ratio" for the latter species (D. Cadien in SCAMIT, 1994).

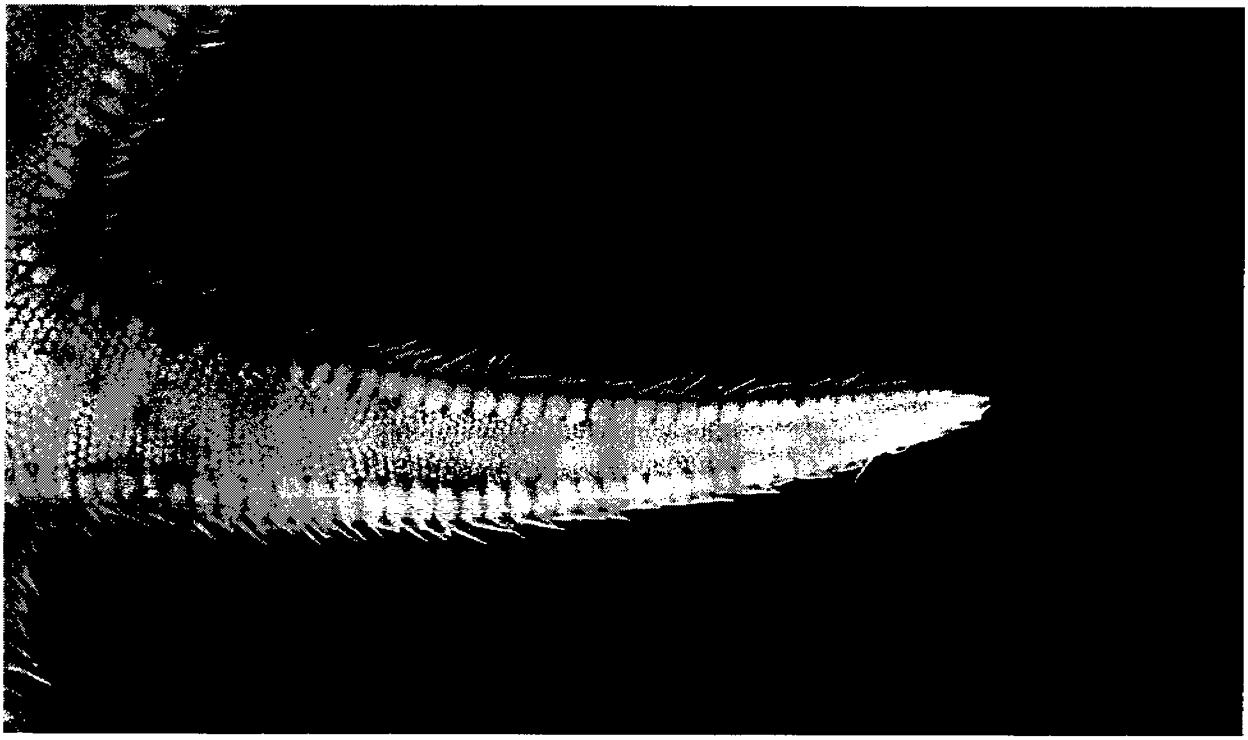

Figure 6.3. Aboral view of arm from *Astropecten verrilli* (Station BRA-01), showing prominent, spinous, supramarginal plates and relatively small paxillae.

Biology. The species is found subtidally on soft substrates such as sand and mud (Feder, 1980). Species in the genus are active predators on a wide variety of organisms, including snails, clams, crustaceans, other echinoderms, and dead fish. Feeding by these seastars is typically accomplished by forcing their arms into the soft substrate around a prey item and then swallowing the organism whole; the stomach is not everted.

Distribution. *Astropecten verrilli* is the only *Astropecten* species known to occur north of San Pedro, California, ranging from Pt. Arena south to Central America at depths from approximately 2-488 m (Maluf, 1988).

Order Valvatida

Family Goniasteridae

Hippasteria spinosa **Verill, 1909**

Figures 6.4A and B

Material Examined. California: Santa Maria Basin, Sta. BRA-20 (USNM), 90-130.5 m (one specimen, 70 mm arm length).

Description. Typically five-armed somewhat stout, with orange to vermillion body in fresh specimens (Lambert, 1945), fading to off white upon preservation. Aboral surface with extensive, thin, sharply-pointed spines, and double row of thicker spines on prominent marginal plates (Figure 6.4A; Lissner, 1980). Oral surface lacks long spines (Figure 6.4B). All plates surrounded by granules producing stellate appearance (Lambert, 1945). Paxillae on oral surface circular to oval in pattern, commonly with central, sessile, clam-like pedicellaria.

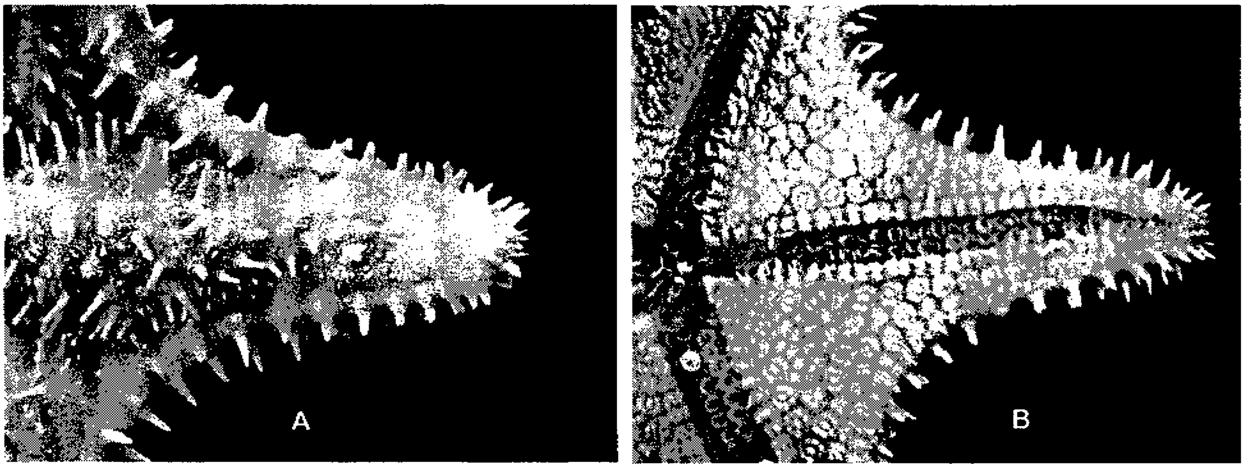

Figure 6.4. A, Aboral view of arm from *Hippasteria spinosa* (Station BRA-20), indicating extensive spination on surface and marginal spines. B, Oral view of arm from *Hippasteria spinosa* (Station BRA-20), depicting lack of prominent surface spines and paxillae surrounding clam-like pedicellariae.

Biology. *Hippasteria spinosa* is typically found on sand and mud, and occasionally rocks (Fisher, 1930). The species is an active predator that is capable of excavating soft substrates up to at least 7.5 cm deep to capture prey (Mauzey *et al.*, 1968). In Puget Sound the species is known to feed primarily on the seapen, *Ptilosarcus gurneyi,* which it consumes by first everting its stomach over the apical tip and progressing down the length (Mauzey *et al.*, 1968). Less common prey items include polychaetes and anemones.

Distribution. This species occurs from Alaska (Kodiak) to southern California (Fisher, 1930), ranging from at least 49-1170 m depth (Maluf, 1988: SAIC and MLML, 1992).

Order Spinulosida

Family Pterasteridae

***Pteraster tesselatus arcuatus* (Ives, 1888)**

Figures 6.5A and B

Material Examined. California: Santa Maria Basin, Sta. BRA-21 (USNM), 75-90 m (one specimen, 60 mm arm length).

Description. This species a five-armed seastar with stubby arms and central, aboral osculum (Figure 6.5A). Color in fresh specimens usually tan, but ranges from cream to yellow to dull gray-purple, with orange or yellow podia (Lambert, 1945). Pedicellariae absent (Lawrence, 1987), with spines separated by membranous fans (Lambert, 1945). Unique nidamental (brood) chamber present (Lissner, 1980). Oral surface with spinous ambulacral grooves and prominent web-like mouth plates (Figure 6.5B).

Biology. The species (as *P. tessalatus*) typically inhabits broken to solid rock substrate (Mauzey *et al.*, 1968), but also is noted from sand and mud (Maluf, 1988). Feeding is accomplished by everting the stomach over sessile prey such as bryozoans, hydroids, and tunicates, although sponges may be the preferred diet (Mauzey *et al.*, 1968). Individuals are capable of producing copious amounts of mucus when handled or disturbed. This mucus is toxic to some snails, hermit crabs, and sea cucumbers. The presence of a supradorsal

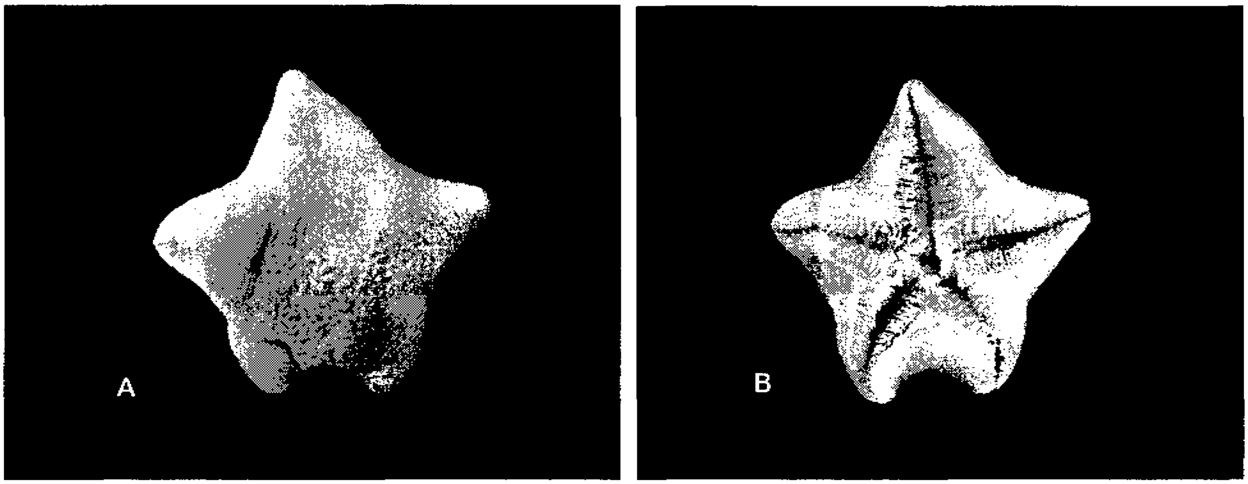

Figure 6.5. A, Aboral view of *Pteraster tesselatus arcuatus* (Station BRA-21), emphasizing stubby body form, smooth surface, and central osculum. B, Oral view of *Pteraster tesselatus arcuatus* (Station BRA-21), showing spinous ambulacral grooves and Prominent mouth plates.

membrane capable of expansion and contraction serves to regulate water flow and thus oxygen uptake (Lambert, 1945). The species is unique in the asteroids in that there is an absence of typical larval body plan features, suggesting direct development from embryos to juveniles (McEdwards, 1994). There appears to be selection for increased development efficiency in brooded offspring such as these.

Distribution. The species (as *P. tesselatus*) is found from the Bering Sea (Fisher, 1930) to at least Santa Monica Bay (Catalina Island), and broadly over the northeast Pacific at depths from 0-435 m (Maluf, 1988).

Family Poraniidae

Poraniopsis inflata (Fisher, 1906)

Figures 6.6A and B

Material Examined. California: Santa Maria Basin, Sta. BRA-21 (USNM), 75-90 , (one specimen, 60 mm arm length); Sta. BRA-20 (SBMNH), 90-130.5 m (one specimen, 14 mm arm length).

Description. *Poraniopsis inflata* is a five-armed seastar with somewhat fat arms (Figure 6.6A). The body color orange to yellow or pink (Anderson and Shimek, 1993), with white, sparse, but evenly distributed spines in fresh specimens (Lambert, 1945). Aboral plates covered with thick skin (Lissner, 1980); pedicellariae sessile (Hyman, 1955). Podia within ambulacra are numerous and small (approximately 3-4 per row; Figure 6.6B).

Biology. Preferred substrates are sand, mud, and rock (Maluf, 1988). Feeding habits are incompletely known, but captive specimens seemed to prefer sponges (Anderson and Shimek, 1993). Other organisms suggested as likely prey include molluscs, cup corals, and sea anemones, potentially as verified by the escape response that this seastar elicits in the anemone *Stomphia didemon*. *Poraniopsis inflata* has a large cardiac stomach, implying a likely capacity for extrusion (Lambert, 1945).

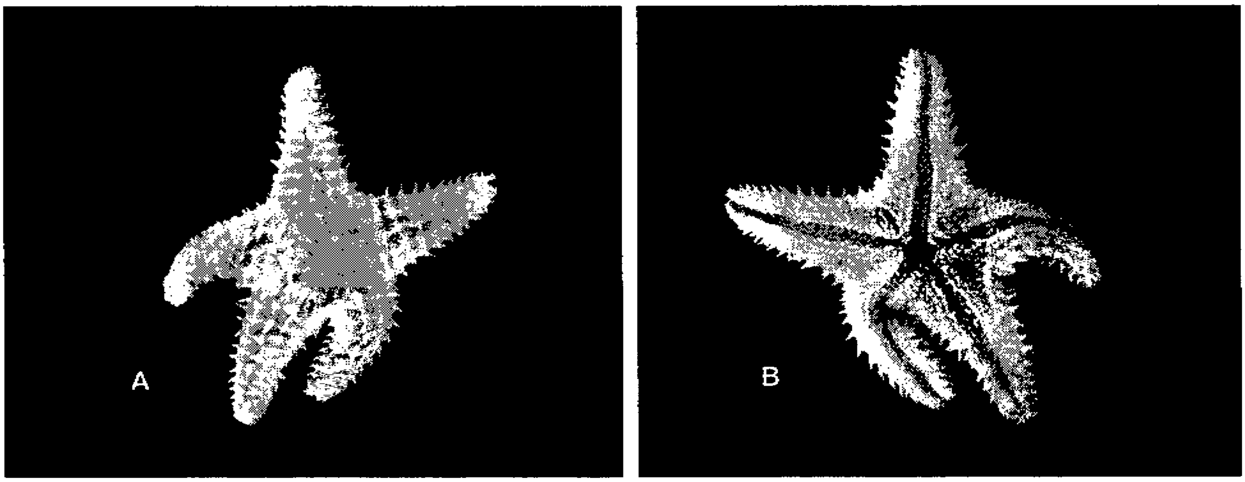

Figure 6.6. A, Aboral view of *Poraniopsis inflata* (Station BRA-21), indicating body form and relatively sparse and evenly distributed surface spines. B, Oral view of *Poraniopsis inflata* (Station BRA-21), emphasizing numerous, small podia per ambulacral row.

Distribution. The species ranges from British Columbia (Hopkins and Crozier, 1966) to South America (Maluf, 1988) at depths from 48-1094 m. A subspecies, *P. inflata flexilis,* is found in deeper water (600-1080 m) within the depth range (Fisher, 1930).

Family Echinasteridae

Henricia leviuscula annectens **(Fisher, 1910)**

Figure 6.7

Material Examined. California: Santa Maria Basin, Sta. BRA-01 (USNM), 69-73.5 m (one specimen, 40 mm arm length); Sta. BRA-14 (SBMNH), 96-105 m (one specimen, 40 mm arm length).

Description. *Henricia leviuscula* exhibits wide variety of size, color, and spine shape, leading to recognition by Fisher (1911) of several subspecies (Feder, 1980), including *H. leviuscula annectens.* This subspecies subtidal only, colored white to off-white in fresh specimens, as compared to more familiar, orange to purplish *H. leviuscula* that common in many intertidal and subtidal areas of California. Species typically with five arms, but four- or six-armed specimens sometimes found. General body form comprises small central disc and proportionately long, sharply tapered arms (Figure 6.7). The aboral surface appears superficially smooth and without prominent spines (Sutton, 1975), although on close inspection (hand lens) pseudopaxillae bearing less than 20 spinelets extensive over the surface, forming a "corral" around papulae (Lissner, 1980). These papulae produce a small-scale, "pock-marked" appearance in preserved specimens (Figure 6.7). Three rows of plates present along lower side of each arm (Lambert, 1945). Pedicellariae absent (Sutton, 1975).

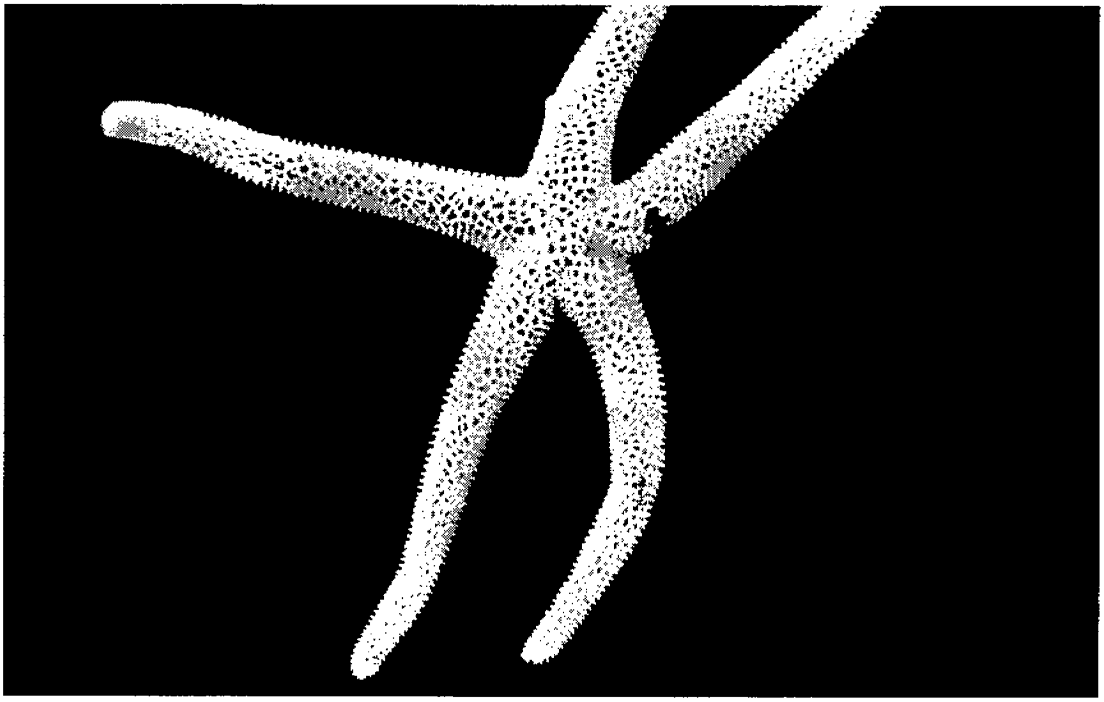

Figure 6.7. Aboral view of arm from *Henricia leviuscula annectens* (Station BRA-01), depicting "pock-marked" appearance of papulae surrounded by pseudopaxillae.

Biology. Little is known about the biology of this subspecies, although the body form and occurrence in hard substrate areas suggests similar habits as *H. leviuscula. Henricia leviuscula* typically occurs under or on the protected sides of rocks (Morris *et al.*, 1980). Typical substrate types are sand, mud, rock, shale, and shelly debris (Maluf, 1988). Two methods of feeding are observed: suspension feeding and eversion of the stomach for direct feeding on sessile organisms, including bryozoans and sponges. The size of the everted stomach is limited to the size of the individual's mouth (Jangoux, 1982).

Distribution. The species (as *H. leviuscula*) ranges from the Aleutian Islands (Alaska) to lower Baja California, at depths from the intertidal to 400 m (Maluf, 1988).

Order Foripulatida

Family Zoroasteridae

Myxoderma platyacanthum H.L Clark, 1913

Figure 6.8

Material Examined. California: Santa Maria Basin, Sta. 092 (USNM), 444 m (one specimen, 31 mm arm length); Sta. 100 (SBMNH), 443 m (three specimens, 25, 27, and 29 mm arm lengths); Sta. R-7, Rep. 2 (SBMNH), 565 m (one fragmented specimen, approximately 32 mm arm length).

Description. Five-armed species, consistently light-tan in color in fresh specimens. Relatively long arms compared to disk diameter, tapering to small, pointed, terminal arm plate (Figure 6.8). Aboral surface with small, reticulate plates, producing a somewhat retangular pattern, with 1-2 papulae per area (Figure 6.8). Plates and spines not covered by membrane (Lissner, 1980).

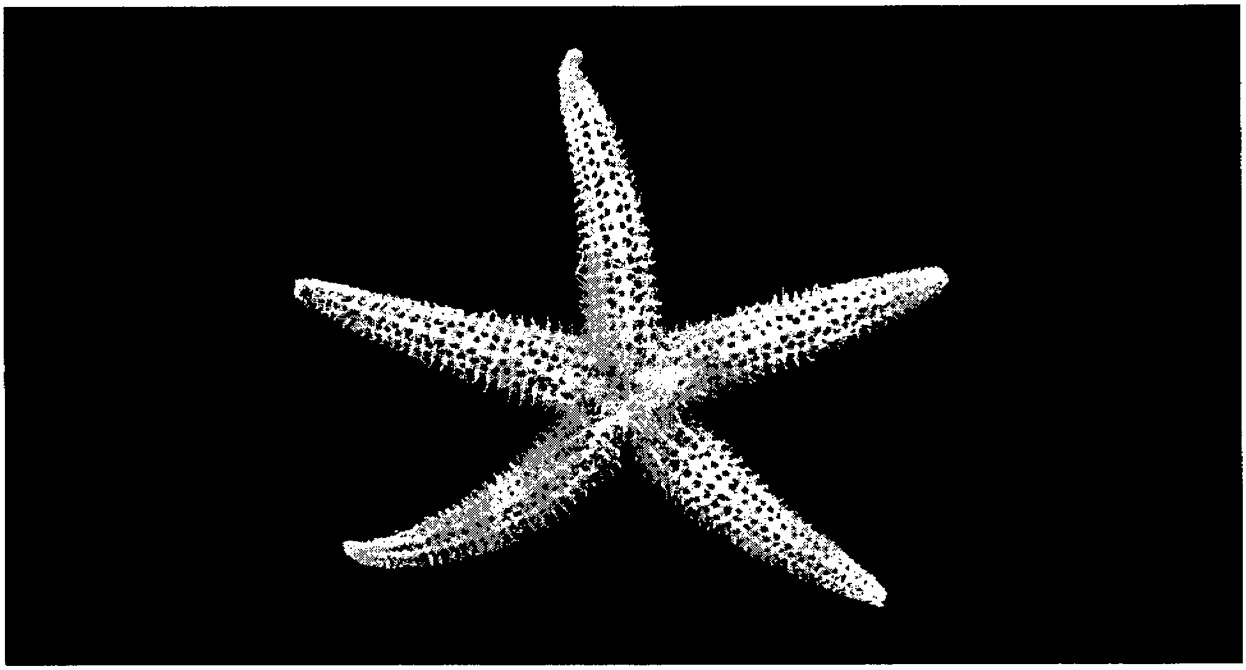

Figure 6.8. Aboral view of *Myxoderma platyacanthum* (Station R-7, Rep. 2), showing body form and reticulate pattern of surface plates.

Biology. Very little is known about the ecology of this species. *Myxoderma platyacanthum* is primarily found on green mud substrates, sometimes occurring in very high densities in trawl samples (SAIC and MLML, 1992). Its occurrence in some oxygen minimum zones may be facilitated by the relatively high density of papulae (functioning in oxygen exchange) on the aboral surface.

Distribution. *Myxoderma platyacanthum* ranges from Pt. Piedras Blancas, California to San Cristobal Bay, Baja California (Fisher, 1930), from depths of 256-768 m (Maluf, 1988).

Family Asteridae

Rathbunaster californicus Fisher, 1906

Figures 6.9A and B

Material Examined. California: Santa Maria Basin, Sta. BRA-26 (USNM), 108-111 m (one specimen, fragmented, approximately 15-arms, 170 mm arm length).

Description. *Rathbunaster californicus* a many-armed (e.g., 12-17) species, with arms proportionately very long and easily detached. Tendency for arm detachment and much longer arm to disc ratio convenient factors helping to distinguish this species from another large, many-armed seastar, *Pycnopodia helianthoides,* co-occurring in the southern California region (D. Cadien in SCAMIT, 1994). Body color typically light orange to light salmon in fresh specimens. Stalked, "pompom-like" pedicellariae are common on the aboral surface (Figure 6.9B), but also easily detached and may be missing on many arm areas of preserved specimens. Papillae long and vermiform (Lawrence, 1987). One inframarginal spine present (Lissner, 1980). Podia in ambulacra numerous, occurring in rows of up to four across (Figure 6.9B).

Biology. The species is usually associated with soft-botttoms of mud and sand, or shale (Maluf, 1988). Little is known of its ecology, although individuals have been observed moving relatively quickly across the bottom, suggesting an active predator (Lissner, pers. obs.). Potential prey that are common in this species habitat include polychaetes, molluscs, anemones, seapens, and other echinoderms (Lissner, pers. obs.).

Distribution. The species ranges from British Columbia (Lawrence, 1987) to San Diego, California, and possibly to Cabo San Lucas, Baja California (Maluf, 1988), at depths from 99-768 m.

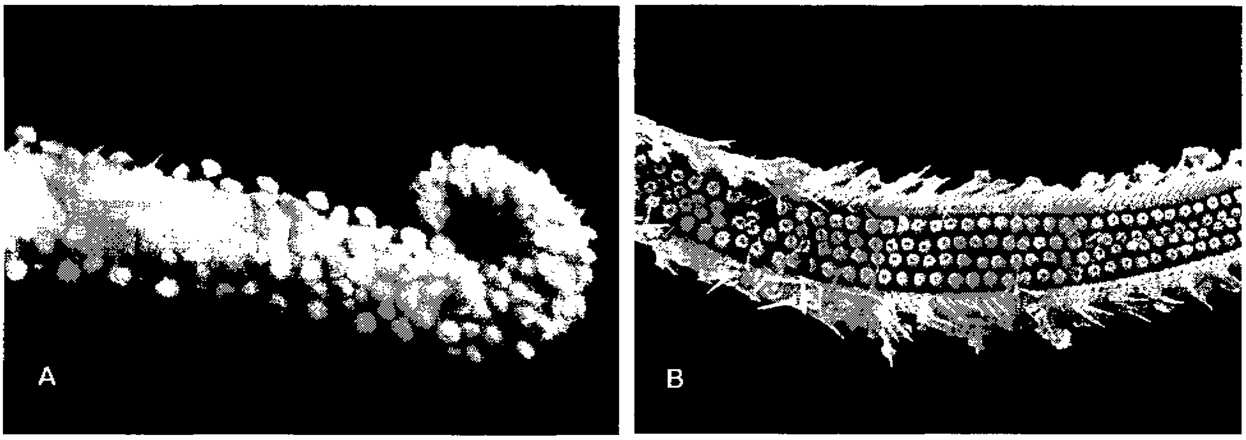

Figure 6.9. A, Aboral view of *Rathbunaster californicus* (Station BRA-26), indicating extensive, stalked pedicellariae on surface. B, Oral view of *Rathbunaster californicus* (Station BRA-26), emphasizing rows of numerous podia and large width of ambulacrum compared to overall arm width.

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7. CLASS OPHIUROIDEA

by

Gordon Hendler[1]

Introduction

Ophiuroids are the most agile and active echinoderms, the most diverse, and often the most abundant. The Class Ophiuroidea, with approximately 2,000 species, 250 genera, and 25 families extant, ranges from arctic to antarctic waters and from intertidal to abyssal and hadal habitats. Ophiuroids are almost exclusively marine; few species are successful in brackish waters.

In the Central Eastern Pacific Region between Pt. Conception, California and Peru, nearly 200 species of ophiuroids have been reported (Maluf, 1988). Representatives of the Southeast Pacific fauna and the less diverse Northeast Pacific fauna (Austin, 1985) occur in the southern Central California region treated in this taxonomic Atlas, but only 19 species are covered in this report.

The Atlas is based on the Minerals Management Service (MMS) Phase I and Phase II surveys of the California outer continental shelf. The surprisingly few species obtained in the surveys probably reflects limitations of the sampling program. Collections were restricted to 50-930 m depths, between Pt. Conception and Pt. Estero, representing localities only 70 miles apart. Coverage was further constrained by the sampling gear employed: small box cores deployed on soft sediments and a modest series of submersible and ROV samples from hard substrates. In a study of ophiuroids on the continental slope off Central California, Summers (1993) demonstrated that box cores undersample ophiuroid species diversity, missing approximately half of the taxa recovered by trawls in the same area.

Despite its limitations, the survey permits a clarification of the taxonomic status of some widespread ophiuroids of the Pacific coast of the United States. The resolution of taxonomic matters provides fresh insight into the ecology of the Eastern Pacific benthos. The synonymy of *Amphioplus hexacanthus* with *Dougaloplus amphacanthus*, is a prime example. As a consequence of uniting the two nominal taxa, the boundaries and composition of the "*Amphioplus hexacanthus* community" (*sensu* Barnard and Ziesenhenne, 1961), a major element on the Southern California continental shelf, can and should be reevaluated.

In this chapter the following species are treated:

Asteronyx longifissus
Gorgonocephalus eucnemis
Amphichondrius granulatus
Amphiodia (Amphispina) digitata
Amphiodia (Amphispina) urtica
Amphioplus (Amphioplus) strongyloplax
Amphipholis pugetana
Amphipholis squamata
Amphiura arcystata
A. diomedeae
Dougaloplus amphacanthus
Amphiuridae sp. juvenile
Ophiacantha diplasia
Ophiopholis bakeri
Ophiuroconis bispinosa
Ophiothrix (Ophiothrix) spiculata
Ophiosphalma jolliense
Ophiura leptoctenia
Ophiura luetkenii

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Thorough descriptions and summaries of biological information are provided for most of these species for the first time. A lectotype is designated for *Amphiura granulata* Lütken and Mortensen, and the species is placed in *Amphichondrius* Nielsen. The photographic figures are intended to improve on the inadequate illustrations previously available. The synonymies furnished are not necessarily exhaustive; they cover major shifts in nomenclature, making the taxonomic literature more accessible. The lists of material examined include: locality, collecting station, depth, number of specimens, repository (or collection); names assigned to specimens in museum collections and by survey taxonomists, if incorrect, are given in brackets.

History

Ophiuroids were among the creatures collected and described by pre-Linnean naturalists. Linnaeus was aware of several species, all of which he placed in the genus *Asterias*. By the early 19th century the considerable diversity of ophiuroids became more apparent. New genera were described, a difference between asteroids and ophiuroids was acknowledged, and two groups of ophiuroids were distinguished: simple armed forms and those with branching arms. The early studies were synthesized and augmented by Müller and Troschel, and by Forbes, and in the latter half of the 19th century the taxonomic treatments of ophiuroids accelerated as specimens from international expeditions became available. During that period, major contributors included Lütken, Ljungman, Lyman, and Verrill. Taxonomists of the early 20th century who studied the wealth of new material from major oceanographic explorations left an enduring mark on ophiuroid systematics; among the most prolific were Koehler, Döderlein, Matsumoto, and Mortensen, and later H. L. Clark and A. M. Clark. Brief historical reviews of these developments appear in Fell (1960) and Hyman (1955).

Surprisingly little effort was ever directed toward the study of the Eastern Pacific ophiuroid fauna. Early workers including Lütken, Ljungman, Lyman, Verrill and others, helped to delineate the shallow-water fauna. Major contributions on the offshore fauna by Lütken and Mortensen (1899) and H. L. Clark (1911, 1917, 1923), were based on explorations of the fisheries research vessel *Albatross*. Supplemental studies made by H. L. Clark (1901, 1902, 1910, 1913, 1915), McClendon (1909), and May (1924) were incorporated in Nielsen's (1932) overview of the fauna between Southern California and British Columbia. Later publications by Ziesenhenne (1937, 1940) also augmented knowledge of region's fauna.

A contemporary, worldwide, monographic treatment of the Ophiuroidea is unavailable, Lyman's (1882) *Challenger* report being long out of date. There are no monographic works on the ophiuroids of the Eastern Pacific. Fortunately, Fell's (1960) synoptic key to the genera of ophiuroids and H. L. Clark's (1915) catalog of Recent species are applicable to the region.

Systematics

Early taxonomic works assigned ophiuroid species to genera and families, and segregated the families into two or three major divisions. After the turn of the century, the divisions Euryalae and Ophiurae generally were used, the former including animals with branching arms (basket stars), and the latter consisting of most simple-armed species (brittle stars). The basis for the separation was the nature of the arm-joint articulation, a poorly defined characteristic. Then and now there were ambiguously defined genera and families, and species whose placement was in question.

Matsumoto's (1917) iconoclastic monograph proposed a phylogeny of the Ophiuroidea based on morphology of the genital plate, genital scale, radial shields, and other internal and external ossicles. Murakami's (1963) analysis of the oral and dental plates supported Matsumoto's arrangement to a great extent. Their contributions underlie Fell's (1962) synoptic key to the genera of ophiuroids. In turn, his arrangement was the basis for Spencer and Wright's (1966) widely used classification.

Spencer and Wright recognized three orders of living Ophiuroidea: the Oegophiurida (with one species extant), the Phrynophiurida, and the Ophiurida. The Phrynophiurida is composed of the Suborder Ophiomyxina (consisting of one family) and the Suborder Euryalina, both groups characterized by a thick, dense integument. The Euryalina includes four families of basket stars and related taxa, which together were formerly classified as Euryalae. The Ophiurida is composed of taxa with reduced integument and relatively robust disk and arm plates. Within the Ophiurida, Spencer and Wright recognize the Suborders Chilophiurina, Laemophiurina, and Gnathophiurina, the distinctions between the suborders based on internal skeletal morphology.

Smith *et al.* (1995) have published a cladistic analysis of the class based on the type genera of 26 Recent families, and using data for 43 morphological characters, largely drawn from published sources. They conclude, since only parts of the most parsimonious cladogram seem securely founded, that a complete revision of the higher taxonomy of ophiuroids is still required. However, they feel there is sufficient support to justify a classificatory scheme of two subclasses: Oegophiuridea for the Ophiocanopidae, and Ophiuridea for all other taxa. Within the Ophiuridea they recognize the Orders Euryalida with four families (equivalent to the Euryalina mentioned above), and the Ophiuridea. The latter is equivalent to the Ophiurida, except that it includes the Suborder Ophiomyxina, excluding the subfamily Ophiobyrsinae as *incertae sedis*. The Suborder Ophiurina constitutes the remainder of the Subclass Ophiuridea, and includes the infraorders Hemieuryalina, Chilophiurina, Gnathophiurina, Ophiodermatina, and Ophiolepidina. It is likely that a number of these recommendations will be adopted in the future. However, a more comprehensive analysis is needed considering additional taxa and a revised set of characters.

Morphology

Despite a deceptive similarity in form, ophiuroids show a considerable range of size and body plans. At one extreme are commensal species several millimeters in diameter, and at the other are basketstars with intricately branched arms spanning a meter. The general anatomy of ophiuroids is covered in Hyman (1955) and Spencer and Wright (1966), and their microscopic anatomy is reviewed by Byrne (1994). Information on ophiuroid reproduction and development is summarized by Hendler (1991).

Major anatomical structures of ophiuroids are depicted in Figure 7.1. The disk and arms are well demarcated, and protected by series of integument-covered ossicles called shields, plates, scales, spines, and granules. Minute, finger-like, fluid-filled tube feet emerge from each arm joint. Some species employ the tube feet for locomotion, but most move by flexing and extending the arms to push the disk ahead; several species can swim. The adhesive properties of the tube feet enable some ophiuroids to scale smooth vertical surfaces and many to catch and manipulate particles of food.

Within the disk are a capacious stomach, a series of gonads, and sac-shaped bursae. The latter structures, which are invaginations of the body wall functioning in respiration and reproduction, open through bursal slits beside the base of the arms. The stomach is a blind sac; an anus is absent. The stomach and gonads are situated within a fluid-filled perivisceral coelom. Ophiuroids, like other echinoderms, have additional coelomic structures including the hemal and the water-vascular systems.

In many species, pairs of radial shields are evident on the dorsal surface of the disk near the base of the arm. Near its distal tip, the radial shield articulates with a genital plate which is attached to a part of the arm within the disk, and a genital scale which supports the outer adradial edge of the bursal slit. Conspicuous structures below the disk include five oral shields, at least one of which (incorporating the madreporite) typically is enlarged and perforate. Beside each oral shield is a pair of adoral shields, homologous with lateral arm plates.

According to many accounts, ophiuroids move their arms only in a horizontal plane. However, the arms are composed of a series of moveable joints, and in most species are capable of a degree of vertical bending or coiling. At the core of the arm are the vertebrae, ossicles resembling bones of the human spine, which are connected in series by muscles and connective tissues. Modified arm ossicles are joined in a ring beneath the disk, forming the five triangular jaws that frame a centrally placed mouth. Attached to the jaws are ossicles called oral papillae and/or dental papillae, and teeth. The ring of jaws, oral shields, adoral shields, and associated ossicles is referred to as the oral frame.

The arm joints beneath and beyond the edge of the disk have protective lateral arm plates bearing arm spines; the joints are capped above and below by dorsal and ventral arm plates. The arm spines may be well-developed or inconspicuous, and they and the arm hooks and tentacle scales serve in feeding and defense. At the tip of the arm is a cylindrical ossicle, the terminal plate, through which the distal-most tube foot protrudes. New arm joints arise at the inner edge of the terminal plate. Therefore, the youngest joints are those nearest the arm tip. As the disk grows, new plates arise between older ones, and the disk overgrows the oldest, most proximal arm joints as it enlarges.

The reproductive organs (testes and ovaries) of ophiuroids consist of clusters of gamete-lined tubules that typically are housed within the disk; they occur inside the arms in only two families. Spawning ophiuroids assume a "push-up" posture, raising their disks off the substrate while releasing gametes from gonoduct openings near the edge of the bursal slits. Fertilization is external.

Ophiuroid larvae develop for a few days to over a month before metamorphosing to juvenile ophiuroids. Some species have large, yolky eggs and abbreviated development. Their non-feeding, barrel-shaped vitellaria larvae swim using rings of cilia, and metamorphose in less than a week. In contrast, many species produce hundreds of thousands of tiny eggs, which develop into multi-armed, long-lived larvae. The larva is a transluscent, microscopic ophiopluteus, with an intricate crystalline supporting skeleton, and with sinuous ciliary bands that are used for food gathering and locomotion.

A minority of ophiuroid species are hermaphroditic, either sequentially (transforming from one sex to another), or simultaneously. There is a correlation between hermaphroditism and mode of development, all hermaphroditic ophiuroids (and a few species with separate sexes) brooding their young. Their embryos are retained in a bursa of the parent where they develop into miniature "crawl-away" young. Relatively few ophiuroids are capable of asexual reproduction by a process called fission, whereby autotomy across the disk produces a pair of half-ophiuroids. The halves heal, regenerate missing structures, grow, and can split again.

Ecology and Behavior

Ophiuroids are members of many benthic communities, from tide pools to the deep sea (Gage and Tyler, 1991; Hendler *et al.*, 1995). As Barnard and Ziesenhenne (1961: 136) point out, "ophiuroid communities cover a relatively large share of southern California coastal shelf bottoms: roughly 26% of the 916 nautical square miles (3,125 square km) between Pt. Conception and the Mexican border...in depths of 0-50 fathoms (0-91.5 meters)." Their conclusion was substantiated by data from surveys of the shelf, island, and basin faunas of the southern California borderland (Hartman, 1955, 1966; Hartman and Barnard, 1958, 1960; Jones 1969).

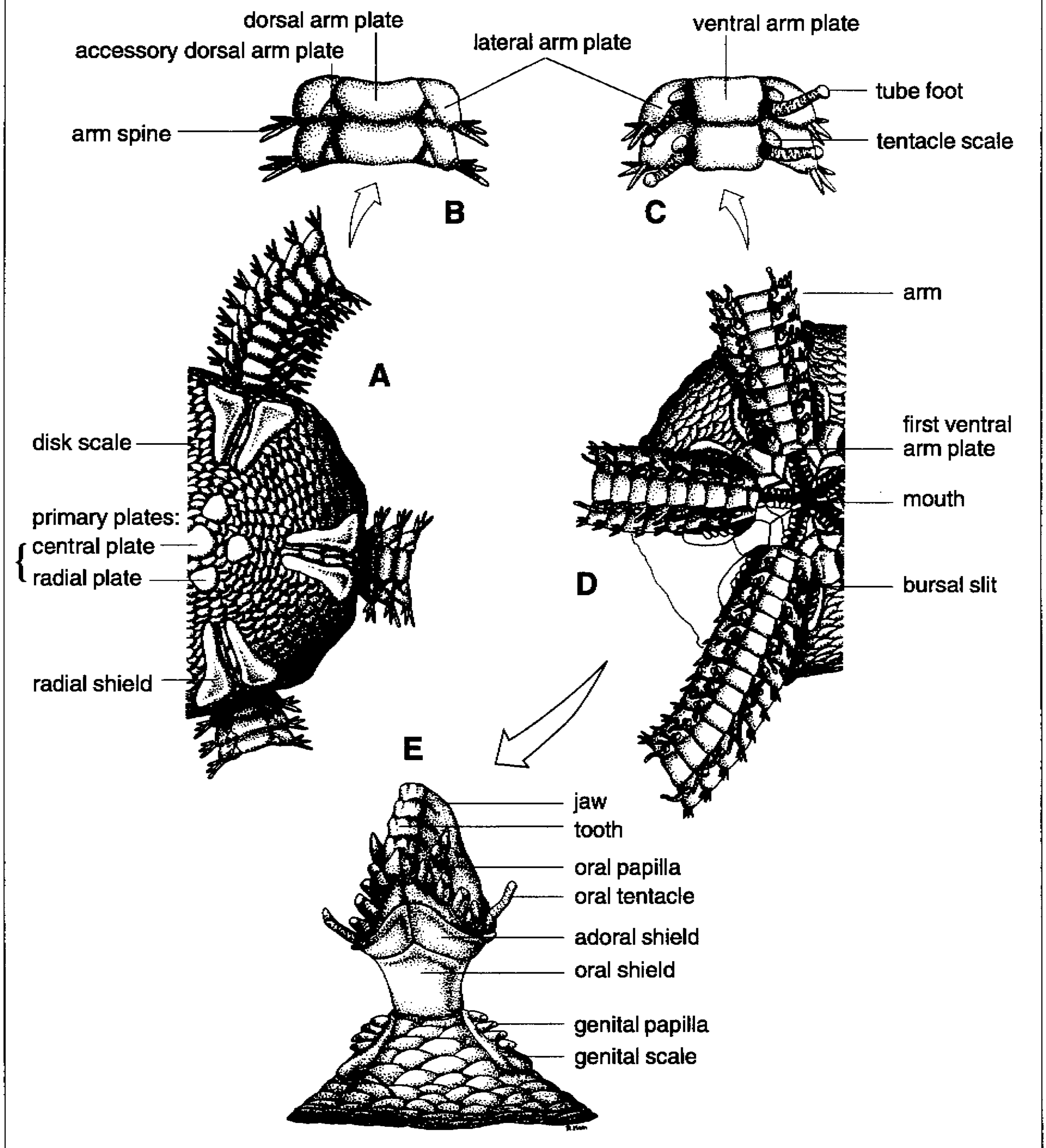

Figure 7.1. Major anatomical features of an ophiuroid: A, the dorsal surface of the disk; B, the dorsal surface of an arm; C, the ventral surface of an arm; D, the ventral surface of the disk; E, a ventral interradius and the jaw structures that project into the mouth. (After Hendler *et al.*, 1995.)

The significance of ophiuroids in benthic communities is reflected in their abundance and distribution. Burrowing amphiurids frequently number in the thousands per square meter, and epifaunal species such as ophiurids can literally carpet the seafloor. Despite their seemingly refractory skeleton, ophiuroids figure in the diets of commercially important crabs, shrimp, and fish, and they are consumed by sea stars and other ophiuroids. Surprisingly, the extent of their ecological role is largely untested, and their interactions with other organisms are poorly documented. Unfortunately, the natural history of not a single endemic Eastern Pacific ophiuroid species has been well and thoroughly described.

The feeding behaviors of ophiuroids are flexible and remarkably diverse. They can take up dissolved compounds through their integument, and they convey particulate food to their mouths with tube feet and in loops of the arms. Some ophiuroids quickly coil their arms, particularly the slender tips of the arms, and capture small active organisms including fishes. The tube feet are capable of sensing extremely dilute concentrations of chemicals such as amino acids and vitamins, enabling individuals to detect food. Coordinated movements of the hundreds of feet under the arm can collect and relay minute particles with great dexterity. The characterization of all ophiuroids as detritivores is inaccurate. Macroparticulate feeders may be carnivores or scavengers with either restricted or relatively indiscriminate diets. Specialized deposit feeders and suspension feeders harvest microparticulate material. The subject of ophiuroid feeding is reviewed by Warner (1982).

Most species remain concealed during the day, perhaps avoiding diurnal predators. Ophiuroids lack eyes, but it is thought that nerves beneath microscopic transparent nodules (expanded peripheral trabeculae = EPT) in the skeletal plates are photosensitive. Furthermore, the discovery that some ophiuroids can change color suggests how the amount of light striking the nerves is controlled. Pigment-containing cells shield the transparent nodules during the day and uncover them at night. The adjustment enables ophiuroids to detect crevices in sunlight or moonlight, an ability that is essential for their escape from predators and competitors in shallow water. The colors of most species are fixed, although pigmentation patterns may transform dramatically as individuals grow. Color patterns of an individual are as specific as a fingerprint, and in some species intraspecific variations can be striking.

Ophiuroids owe their common name "brittle stars" to a remarkable capability for autotomy, the ability to voluntarily break their arms. This behavior is potentially advantageous when an individual is attacked by a predator. Some species (probably most Amphiuridae) can also autotomize the disk, and with it the stomach, gonads, and other tissues. That process is all the more remarkable because these individuals can completely regenerate the broken arms or regrow the disk and associated viscera, in several weeks or months. Autotomy in ophiuroids is effected by nervously-controlled mutable collagenous tissue, the same tissue permitting the arms to flex and stiffen. Other ophiuroid defenses include distastefulness and luminescence, speedy escape, and the shadow-response, which is a stop-motion reflex triggered by passing predators.

Major ecological and morphological differences among groups of ophiuroids are most readily recognized at the family level. Ophiuroids may show greater fidelity in body plan to the substratum they occupy than to phylogenetic affinity or distribution. For example, species in the family Amphiuridae living in soft sediments have adaptations for burrowing, such as soft disks and long delicate arms, which would jeopardize their survival in an exposed habitat. Burrowing *Ophiopsila* species, in the family Ophiocomidae, are remarkably similar in appearance to amphiurids. The burrowing ophiuroids maintain semi-permanent burrows composed of a mucous coated chamber that surrounds several upraised arms and the disk. The arms undulate to pump water through the burrow, and they can be extended to the surface to convey waste material and tailings from the burrow, and carry food particles towards the disk. Species in several families, which are epizoic on soft coral and sponges, have hooked spines used to cling to their host and similar structural and behavioral defenses against predation.

Collection and Preservation

Ophiuroids occur on, within, and under many benthic substrates in the marine environment, and some even live on pelagic scyphozoans. Their delicate construction, and the tendency of ophiuroids to autotomize makes it advantageous to isolate them from samples before more resistant taxa are processed. It is sometimes helpful to allow material, such as rubble, to rest in a bucket of water it in order to permit delicate cryptic fauna to emerge, before fragmenting the substrate.

A full and up-to-date account of techniques for the preservation of ophiuroids and other echinoderms is presented in Hendler *et al.* (1995). When possible, freshly collected ophiuroids should be anesthetized by placing them in a solution of magnesium chloride that is isosmotic with seawater, or by gradually adding magnesium sulfate (epsom salts) to the seawater in which ophiuroids are held. Other invertebrate anesthetics may be effective to a degree, but gradually adding alcohol to seawater is not a reliable means to relax ophiuroids. In contrast, basketstars, which do not respond to magnesium salts, are best preserved by holding individuals with extended arms in a tray of concentrated alcohol so that they quickly die with the branches extended.

Anesthetized specimens, with their arms disentangled, can be briefly fixed in buffered 10% formalin or placed directly in 70-80% ethanol. In either case, specimens should be washed in distilled water to remove formalin and excess salts before their permanent storage in ethanol. Museum specimens of ophiuroids are sometimes dried because microscopic details are most clearly seen using desiccated material, and because maintaining alcohol levels requires additional resources. However, it is preferable to maintain specimens in alcohol for long-term storage, partially or completely drying them only when required for examination. That approach permits the conservation of soft tissue and lessens the potential for damage by fungi and other pests.

Glossary

Accessory dorsal arm plate. In some ophiuroids, one or several small, symmetrically arranged plates that are inserted between the dorsal arm plate and the lateral arm plate.

Aboral. In a direction away from the mouth; the part of the body opposite the mouth.

Adoral shields. A pair of plates, one of which is found at each side of the oral shield.

Arm. A moveable, jointed ambulacral projection, distal to the disk, that carries a radial branch of the water vascular system and the nervous system.

Arm joint. One of a series of articulating units comprising the arm, consisting of an internal vertebral ossicle, the dorsal, lateral and ventral arm plates, and associated structures.

Arm length. A body dimension of an ophiuroid measured from the edge of the disk to the tip of an arm.

Arm spines. Spines attached to the lateral arm plate.

Asexual reproduction. Reproduction that occurs without the fusion of male and female gametes, by splitting of the body into two parts that regenerate. The genetically identical offspring of asexual parents are a clone.

Autotomy. A defensive process initiated in response to adverse stimuli, involving the loss of portions of the arms or disk.

Brooding. Reproductive mode in which the embryos are protected on, in, or beneath the parent, and emerge as tiny, crawl-away juveniles.

Bursa. An organ within the disk formed by an inpouching of epidermis (see **bursal slit**). Bursae function as respiratory structures and are associated with the gonoducts. They house the developing embryos of brooding species.

Bursal slit. The opening of a bursa, located on the ventral interradius of the disk at the base of the arm. Typically, there is one bursal slit on each side of an arm.

Calcite. The mineral form of calcium carbonate that makes up the echinoderm skeleton.

dd. See **disk diameter**.

Dental papillae. See **papillae**.

Dermis. The stratum of cells beneath the epidermal covering of the body wall. In echinoderms, the skeleton develops in the dermis and is filled with dermal tissue.

Disk. The round or pentagonal central body region of an ophiuroid.

Disk diameter. A body dimension of an ophiuroid measured from the distal edge of a pair of radial shields to the disk edge in the opposite interradius. Abbreviated dd.

Distal. In a direction away from the center of the body; for example, towards the tip of the arm.

Dorsal. In echinoderms, this term is variously applied, but in ophiuroids it refers to the surface of the body that is opposite the mouth.

Dosal arm plate. A plate on the aboral surface of an ophiuroid arm joint.

Echinulate. Referring to a roughened texture composed of tiny spines.

Embryo. An early developmental stage that is enclosed in a fertilization membrane or protected by the body of the parent. It transforms into a juvenile through metamorphosis.

EPT (= expanded peripheral trabeculae). Microscopic, transparent nodules on the surface of skeletal plates. In some ophiuroids they are a component of a photoreceptor system.

Fission. Asexual reproduction by splitting of the body into two parts, each of which regenerates into a complete animal.

Genital papilla. Granules or spinules attached to the edge of the bursal slit. The term is also used (perhaps more appropriately) for the fleshy outlets of the gonoducts in ophiuroids that lack bursae.

Genital plate. A bar-like ossicle connecting the radial shield to the arm and supporting the radial edge of the bursal slit.

Genital scale. An ossicle connected to the genital plate, which supports the adradial edge of the bursal slit.

Granules. See **skeletal elements**.

Hooks. Minute, moveable, crescentic ossicles that articulate with arm ossicles in gorgonocephalid ophiuroids (other ophiuroids may have hook-shaped *arm spines* attached to the lateral arm plates).

Infradental papillae. See **papillae**.

Interradial. (interradii). Referring to interambulacral sectors of the body, dorsal or ventral regions between two arms.

Jaw. A moveable triangular structure that extends into the mouth.

Joint. See **arm joint**.

Larva. An early developmental stage that is independent of the fertilization membrane and the parent (pl. **larvae**). Through metamorphosis it transforms into a juvenile.

Lateral arm plates. Paired plates covering the sides of each arm joint and bearing the arm spines.

Lecithotrophy. A mode of reproduction in which free-swimming larvae develop using nutrients laid down in the egg. Lecithotrophic larvae do not feed on particulate matter, but they may supplement yolk reserves by the uptake of nutrients dissolved in seawater.

Madreporite. A perforated plate that is connected to the water-vascular ring by a so-called stone canal. In ophiuroids it is a modified oral shield.

OFL. See **oral frame length**.

Ophiopluteus. The free-swimming larval stage of an ophiuroid. Ophioplutei have appendages that are supported by skeletal rods and bear ciliary bands. During metamorphosis, the juvenile ophiuroid develops from a rudiment on the ventral surface of the larva; the process may involve resorption or loss of parts of larval structures.

Oral. In a direction towards the mouth; a part of the body on the same surface as the mouth.

Oral Frame. The series of ossicles encircling the mouth, including the oral, dental, and peristomial plates, the first ventral arm plates, the oral and adoral shields, and associated structures.

Oral frame length. An index of ophiuroid body size measured from the distal edge of an oral shield to the distal edge of the first ventral arm plate in the oral slit of the opposite interradius. Abbreviated **ofl.**

Oral papillae. See **papillae**.

Oral shield. A relatively large plate at the distal end of the jaw. At least one of the oral shields is modified as a madreporite.

Oral tentacles. Tube feet inside the mouth, arising from the jaws. Also referred to as **oral tube feet**.

Ossicle. A small, usually microscopic skeletal element, embedded in integument; the term is sometimes used to refer to all skeletal elements.

Papillae. In ophiuroids, certain skeletal elements of the jaws or disk: **dental papillae** - a cluster of small, blunt, spinelike structures on the dental plate, near the ventral tip of the jaw. **Fence papillae** - peg-shaped spinelets fringing the edge of the disk of *Ophiophragmus* species. **Infradental papillae** - in amphiurid ophiuroids, a pair of small, blocklike plates attached at the ventral tip of the jaw, below the teeth. **Oral papillae** - small plates at the edge of the mouth, attached to the edges of the jaw plate and/or the to adoral shield. Oral papillae can be variously shaped, from spinelike to scalelike. Also see **genital papillae.**

Planktotrophy. The mode of development of free-swimming larvae that feed on particulate matter obtained from the plankton.

Plates. See **skeletal elements**.

Primary plates. The first-formed plates on the dorsal side of the disk. In ophiuroids these are the **central** and five **radial plates**. In adults, they may form a rosette of scales near the center of the disk, or they may be separated by numerous secondarily developed scales.

Proximal. Towards the center of the body.

Radial. In a direction towards the central axis of an arm or ambulacrum; a part of the body near an arm or ambulacrum.

Radial shields. Pairs of plates on the dorsal surface of the ophiuroid disk, which lie near the base of each arm. They are usually relatively large and conspicuous, but may be hidden by granules or superficial scales.

Rheophilic. Literally, "current-loving." Rheophilic organisms prefer habitats with significant water movement. **Rheophobic** organisms avoid currents, and occupy sheltered positions or are restricted to low-energy habitats.

Scales. See **skeletal elements**.

Skeletal elements. Supporting and protective dermal structures consisting of a calcite meshwork (stereom) and invested with a thin layer of tissue (stroma). Various skeletal elements are distinguished as follows: **plates** are tabular structures with a characteristic shape and a fixed position; **scales** are flat, thin structures that are overlapping, tesselate, or haphazardly arrayed; **spines** are *moveable*, articulating structures that are long, slender, and attenuated. Small structures *fixed* to the surface of scales or plates include: **granules** that are minute and nearly equidimensional; **spinelets** that are enlarged, elongate cylindrical or angular granules (this term is sometimes applied to small spines); **spinules** that have various numbers of pointed apical projections (e.g., bifid, trifid, multifid). Also fixed, and relatively larger than granules, are small structures referred to as **stumps**, which are usually prickly, and **tubercles** which are smooth and more massive. In addition, **tubercles** (see below) can refer to outgrowths of plates, rather than to separate elements. Also see **papillae**.

Spines. See **skeletal elements**.

Spinelets. See **skeletal elements**.

Stone canal. A tube, usually reinforced with ossicles, leading from the madreporite to the water-vascular ring canal.

Teeth. Small plates or spines attached to the dental plate on the inner edge of the jaw, a series extending into the mouth.

Tentacle pore. An opening between the ventral arm plate and the lateral arm plate, through which a tube foot projects. Each arm joint has two tentacle pores.

Tentacle scales. Small, moveable spines or scales, associated with ophiuroid tube feet, which are attached to the ventral arm plate and/or lateral arm plate. Tentacle scales may cover the tentacle pores and protect the retracted tube feet.

Trifid. Divided into three parts. Regarding "trifid spinule" see **skeletal elements.**

Tube feet. Fluid-filled, fingerlike extensions of the water vascular system, which protrude through openings in the skeleton or between skeletal elements. Specialized tube feet are used for locomotion, feeding, burrowing, respiration, and a combination of functions (see **papillae**, **tentacles**).

Tubercle. See **skeletal elements**.

Ventral. In echinoderms, this term is variously applied, but in ophiuroids it is the surface of the body that carries the mouth.

Ventral arm plate. A plate on the oral surface of each arm joint.

Vertebra. An internal ossicle within an arm joint, connected by ligament and muscle to the vertebrae of adjacent joints. It is so named because of a resemblance to bones in the human spinal column.

Vitellaria. A type of free-swimming lecithotrophic echinoderm larva. It is barrel-shaped, has several transverse rings of locomotory cilia, and lacks a mouth.

Terminology and Conventions

The colors noted in the species accounts pertain to living ophiuroids, unless otherwise noted; pigmentation and color patterns are altered or removed by preservatives. Arm structures are described for the proximal third of the arm, unless otherwise noted. Towards the tip of the arm the relative dimensions of the ossicles change; the arm spines and tentacle papillae diminish in number. The numbers of arm spines and tentacle scales refer to the number on each *side* of an arm joint on a portion of the arm near the disk. For example, "this species has 3 arm spines" means that near the disk there are 6 arm spines on each joint, and 3 on each lateral arm plate. Similarly, the number of oral papillae cited for a species refers to the number on one side of a jaw.

Disk diameter (abbreviated dd) is measured from the distal edge of a pair of radial shields to a point on the opposite edge of the disk. Oral frame length (abbreviated ofl) is measured from the outer edge of an oral shield to the outer edge of the opposite first ventral arm plate. Arm length is the distance from the disk edge (the base of an arm) to the tip of the longest arm.

The abbreviations used are: AHF, Allan Hancock Foundation of the University of Southern California; CAMP, California Phase II Monitoring Program; LACM, Natural History Museum of Los Angeles County; SBMNH, Santa Barbara Museum of Natural History; USNM, National Museum of Natural History; ZUUC, Zoological Museum, University of Copenhagen.

Description of Species

Order Phrynophiurida

Family Asteronychidae

Asteronyx longifissus Döderlein, 1927

Figure 7.2

Asteronyx longifissus Döderlein, 1927:58, 59, 65-68, 97, pl. 7, figs.1-3.—A. M. Clark, 1965:68.—Thompson *et al.*, 1993:30, 38.

Material Examined. California: Santa Maria Basin, Phase I Sta. BSR-025, 390 m (1, SBMNH secondary voucher [as *Asteronyx loveni*]); Phase I Sta. BSR-036, 492 m (1, USNM primary voucher [as *Asteronyx loveni*]).—Off Huntington Beach, R/V *Thomas G. Thompson* Sta. BLM 821, 687-698 m (1, LACM 77-204.1).—Off Newport Beach, R/V *Velero IV* Sta. AHF 22631-75, 533 m (1, LACM 75-148.1).—Off Dana Point, R/V *Velero IV* Sta. AHF 22723-75, 611 m (3, LACM 75-226.1).

Description. Moderately large ophiuroid with disk diameter reaching 31 mm, arm length generally 5-9 times, and up to 13 times diameter of disk. Disk and slender, markedly tapering arms smooth, apparently naked. Scales in integument only conspicuous in small specimens.

Disk five lobed, indented interradially, appearing naked but for dense layer of small thin scales covering radial shields. Radial shields thin, riblike; proximal end nearly reaching center of disk, distal end expanded, hoof-shaped, articulating with similarly shaped projection of genital plate.

Jaws elongate, ventrally projecting. Oral shields inconspicous, frequently overgrown by adoral shields. Adoral shields large, curved, bridging first lateral arm plates of adjacent arms.

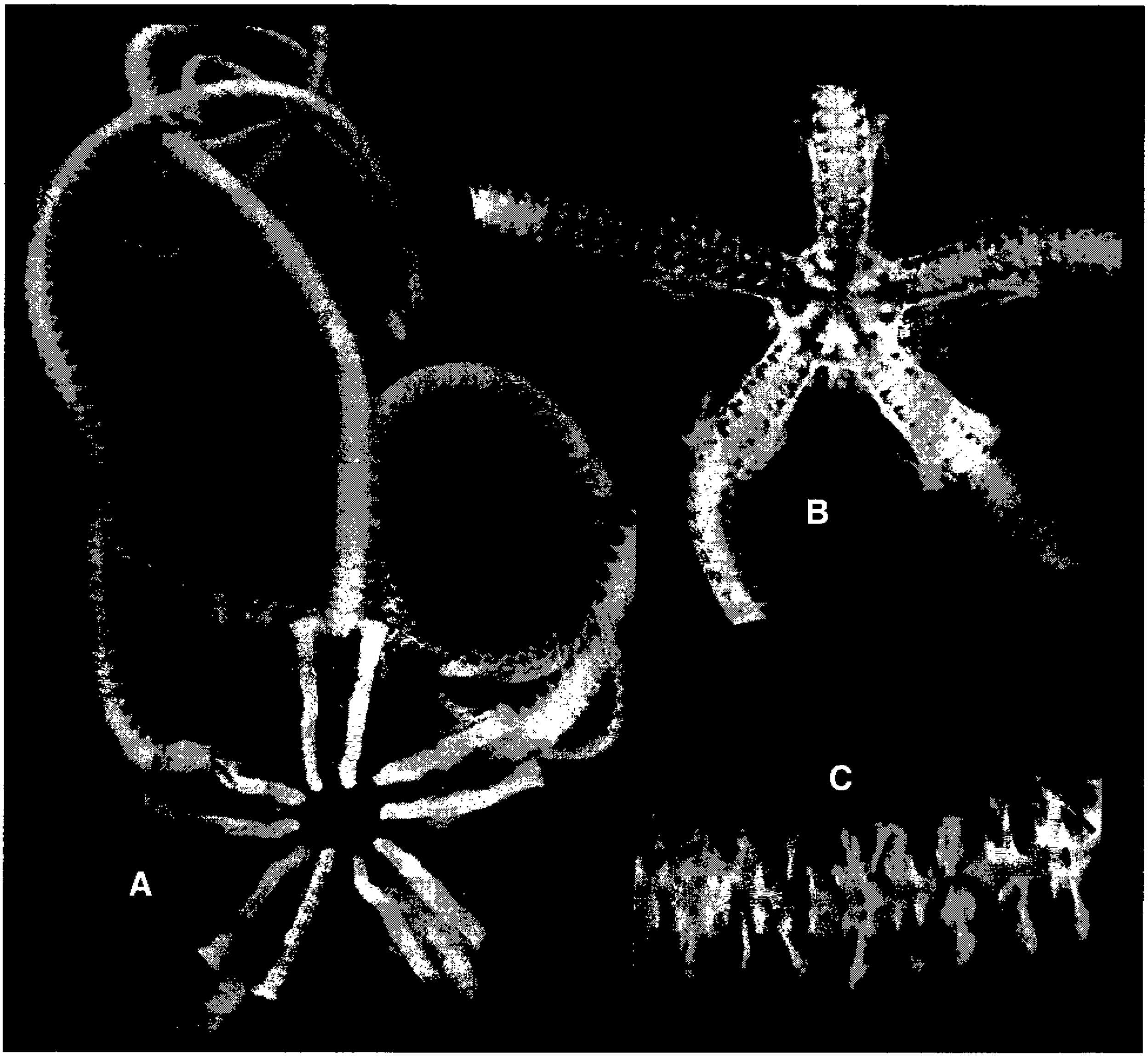

Figure 7.2. *Asteronyx longifissus* Döderlein: A, dorsal view; B, disk, ventral view; C, distal portion of an arm, ventral view, showing elongate, club-tipped ventral-most spine and hooked dorsal arm spines (LACM 77-204.1; dd = 25.0 mm).

Genital slit large, extending from first or second arm joint to edge of disk. Ventral interradius nearly naked, with scattered, embedded scales; minute scales at edge of bursal slit.

Arms all of equal length in juveniles; arms of uneven length in adults. Arms covered with thick, translucent integument, markedly arched dorsally, flattened ventrally, narrowing abruptly beyond edge of disk. Ventral surface of arm beneath disk markedly concave and broad.

Dorsal and ventral arm plates reduced to microscopic, thin, perforated scales, numerous, irregularly arranged, embedded in integument. Arm vertebrae visible through integument, appearing W-shaped dorsally, V-shaped ventrally.

Lateral arm plates situated ventrally on arm. Arm spines 5 or more, hooklike; base bulbous, opaque; distal portion with multiple, hyaline teeth. First several arm joints lacking spines; on distal arm joints ventralmost spine elongate, club-tipped. Lateral arm plates and spine-groups forming paw-shaped structures on distal arm joints.

Remarks. The range of the species overlaps that of *Asteronyx loveni* Müller and Troschel. The latter species is distinguished by its relatively short bursal slits, which are restricted to the inner half of the ventral interradius. Döderlein (1927) provides a key to *Asteronyx* species and related taxa.

Distribution. Point Conception to San Diego, 266-1800 m (Döderlein, 1927).

Biology. The autecology of *A. longifissus* is probably similar to that described (Fujita and Ohta, 1988) for the suspension-feeding *A. loveni*, which clings to stalked cnidaria. Thompson at al. (1993) indicated that it is one of the most abundant megabenthic invertebrates trawled at mid and lower slope depths (300-780 m) of the San Pedro and Santa Monica basins in Southern California. They suggested that its population density may have increased by an order of magnitude following an El Niño event.

Family Gorgonocephalidae

Gorgonocephalus eucnemis (Müller and Troschel, 1842)

Figure 7.3

Astrophyton eucnemis Müller and Troschel, 1842:123.—Ljungman, 1867:335.—Lyman, 1882:263.

Gorgonocephalus eucnemis, Lyman, 1880:42.—Döderlein 1900:226, pl. 10, fig. 1-4.—Koehler, 1907: 349.—1911:31, 33, 103-104.—H.L. Clark, 1911:185.—Campbell, 1921a:4.—1921b:49.—May, 1924:270-271.—Boolootian and Leighton, 1966:4, 8, fig. 3.—Austin and Hadfield, 1980:154-155, pl. 51, fig. 10.12.—Irimura (in Imaoka *et al.*), 1990:72-73, figs. A-D.

Astrophyton Caryi Lyman, 1860:424-425.—1882:264.—Ljungman, 1867:335.—Verrill, 1867:326.

Gorgonocephalus caryi, Verrill, 1867:253.—Lyman, 1882:264.—Döderlein 1911:31, 104.—H.L. Clark, 1911:5, 9, 17-18, 20-21, 287-292.—Matsumoto, 1917: 61, 64, 70, 71, 354.—Campbell, 1921b:49.—D'yakonov, 1954:18-19.—Astrahantseff and Alton, 1965:1414-1415, 1419, 1422.—Kyte, 1969:1729, 1730, 1735-1737.—Smirnov, 1882:113, 116.

Gorgonocephalus Caryi, Lyman, 1880:42.

Astrophyton stimpsonii Verrill, 1869: 12:388.—Lyman, 1882:264.

Gorgonocephalus stimpsoni, Döderlein, 1911:104.

Gorgonocephalus japonicus Döderlein, 1902:321.—1911:30-33, 104, pl. 1, figs. 1-3, pl. 7, figs. 1-2c.

Gorgonocephalus sagaminus Doflein, 1906:204, fig.

Material Examined. Oregon: Off Newport, R/V *Waseca* Sta. AHF 1481-42, 84-132 m (1, LACM 42-39.4).—California: Western Santa Barbara Channel, Phase I Sta. BRA-002, 110-126 m (1, USNM primary voucher).—Off Santa Catalina Id., R/V *Velero IV* Sta. AHF 10698-65, 265-290 m (1, LACM 65-333.1).

Description. A large basket star with numerous arm branches. Disk diameter reaching 140 mm, extended arms 4-5 times as long; total diameter exceeding 0.5 m with arms outstretched.

Disk massive, conspicuously indented between the radial shields, covered with thick integument. Radial shields tapering, nearly meeting at center of disk; thick, truncate distally, thin, narrowing proximally. Radial shields densely covered with scales bearing roughened granules, similar scales concentrated at disk margin; dorsal interradial region of disk nearly naked, scattered with small granules. Expanded hoof-shaped distal tip of radial shield articulating with similarly shaped projection on genital plate.

Jaws broad, ventrally directed. Teeth and oral papillae spinelike. Oral frame ossicles obscured by thick integument.

Ventral interradius nearly naked, with small scattered granules and scales. Bursal slit beginning near first arm branching, restricted to outer half of interradius. Edge of genital scale bearing large granules or spinelets.

Arms complexly branching, coiling; terminal portion of arm with fine, coiling branches. First arm branching beneath disk, second branching at or beyond disk edge; 6 joints before first branching, 9 joints to second branching. Arms higher than wide in cross section; covered with thick integument; edges of lateral arm plates forming thick ridges below disk.

Conspicuous dorsal and ventral arm plates lacking; embedded scales and granules covering dorsal and lateral arm surfaces; microscopic, thin, perforated plates covering ventral surface. Microscopic, flesh-covered, crescentic, hyaline arm hooks, borne on embedded ossicles; hooks present after 2nd arm branching, becoming more numerous on distal joints; 1-2 hooks on proximal joints; by 6th branching, arms annulated with bands of hooks on ridges girdling the sides and top of each joint.

Lateral arm plates positioned sublaterally, bearing up to 5 echinulate spines on 1st and 2nd arm branches; 4 or fewer spines on distal branches, hooked, usually with 3 hyaline teeth. Articulated tentacle scales absent; granules embedded in walls of some tube feet.

Color: Pigmentation ranging from maroon, reddish, brown, tan, beige, orange, salmon, pink, to almost white; the disk usually darker than the arms. The dorsal surface is more intensely colored than the ventral surface. Frequently, coloration is not uniform. According to Patent (1970b), in a collection of 100 animals 34 were brown, 45 pink or coral, 18 orange, and 3 yellowish.

Remarks. Extensive collections of *Gorgonocephalus* from Atlantic and Pacific localities must be compared for the taxonomy of Californian basket stars to be resolved. In the present report, *G. eucnemis* is regarded as a senior synonym of *G. caryi* because none of the characteristics cited in the literature reliably distinguish the two nominal taxa.

Lyman (1960: 425) separated the small, unique type-specimen of *A. caryi* from *A. eucnemis* by "...more regular granulation of the disk, by having blunter tentacle-scales, and by close rows of grains along the edge of the genital slits." On the basis of extensive northern Pacific collections, H. L. Clark (1911) synonymized *G. japonicus* and *G. stimpsonii* with *G. caryi*, but he reserved judgement on the distinction between *G. caryi* and *G. eucnemis* pending study of the latter species. Moreover, he suspected that "...*agassizii*, *eucnemis*, and *caryi* may prove to be three names for a single species. Material from the west coast of Greenland and the regions north of America would be very desirable in settling the question" (H.L. Clark, 1911:292). Without further explanation, H. L. Clark (1915) synonymized *G. caryi* and *eucnemis*, as did Downey (1969) and Irimura (in Imaoka *et al.*, 1990). Döderlein (1927), D'yakonov (1954), and Kyte (1969) recognized both nominal taxa.

Gorgonocephalus diomedeae Lütken and Mortensen is the only eastern Pacific congener of *G. eucnemis*. Described from off Panama at 1270 m, it is distinguished from *G. eucnemis* by the short spines covering its disk.

Distribution. California to Alaska, Sea of Japan, and Korea Strait to Bering Sea, Okhotsk Sea and Laptev Sea, Finmark, Spitzbergen, and across the Arctic Circle to Cape Cod and Greenland; at depths from 15-1850 m.

Biology. The species is rheophilic, clinging to various cnidaria and sponges in high current areas (May, 1924; Astrahantseff and Alton, 1965; Austin and Hadfield, 1980). Photographs taken in situ, off Point Conception, California (Lissner and Benech, 1993:figs. 4.2, 4.10) show *G. eucnemis* in typical array with some arm branches gripping the substratum and other branches upraised. The extended arms are used to suspension feed, presumably in the same manner as other basket stars (Kyte, 1969; Patent, 1970b; Austin and Hadfield, 1980; Hendler, 1982). The species is not a predator on sea pens as once claimed (MacGinitie, 1949). Its metabolic rate has proved to be similar to simple-armed, suspension feeding ophiuroids (LaBarbera, 1982).

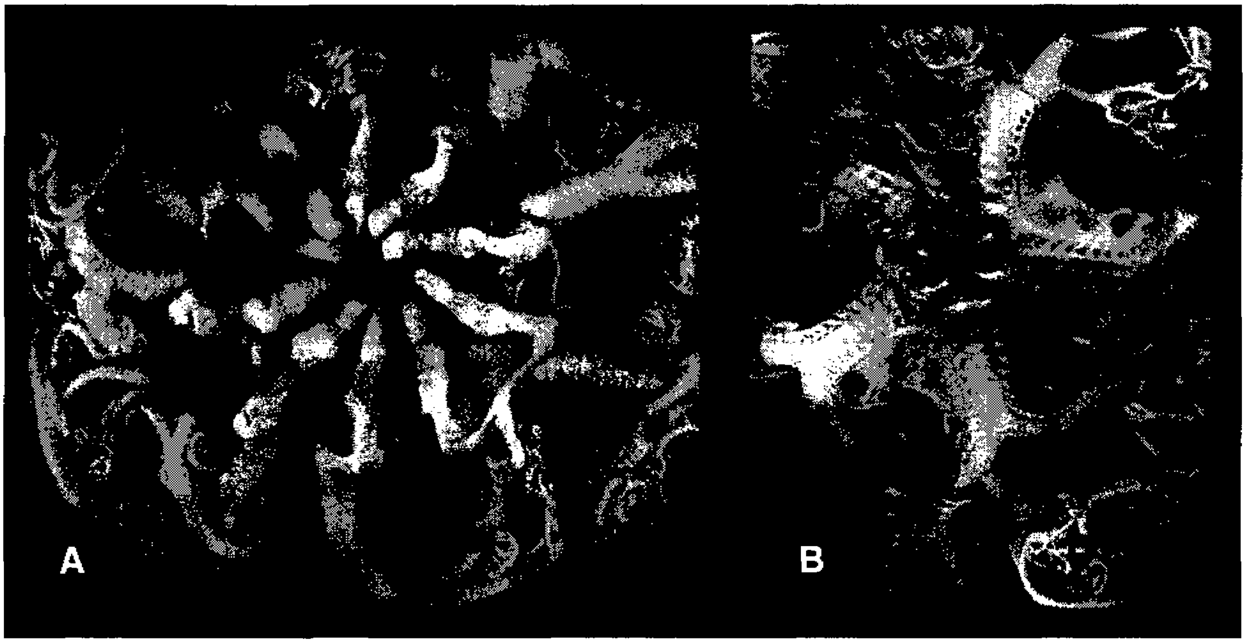

Figure 7.3. *Gorgonocephalus eucnemis* (Müller and Troschel): A, dorsal view (LACM 42-39.4; dd = 35.0 mm); B, ventral view (LACM 65-331.1; dd = 56.0 mm).

Patent (1969, 1970a,b, 1976) treats the gonadal morphology, reproductive cycle, and development of the species. She interpreted the spawning season to last the 6 months of summer and fall in the San Juan Islands, Washington, but her data suggest that gonadal growth occurring in the summer precedes spawning between October and February. The egg is moderately large (0.22 mm diameter) and gives rise to a yolky, non-feeding larva of unusual morphology, which metamorphoses in about a week. Early developmental stages are associated with the alcyonacean *Gersemia* sp., and the larger juvenile cling to the soft coral and adult basket stars.

Individuals are occasionally snagged by fishermen using hook and line (Campbell 1921a). Given that large basket stars can have a relatively long life-span of over 7 years (Wolfe, 1982), curio-hunting scuba divers could pose a threat to the survival of shallow water populations (Austin and Hadfield, 1980). The populations could be slow to recover, depending on the age at reproduction and the frequency of successful settlement.

Order Ophiurida

Family Amphiuridae

Amphichondrius granulatus (Lütken and Mortensen, 1899) new combination

Figure 7.4

Amphiura granulata Lütken and Mortensen, 1899:155-156, pl. 10, figs. 1-4.

Amphipholis granulata, H.L. Clark, 1917:437.—Fell, 1962:13, 21.

Amphipholis puntarenae McClendon, 1909:44, figs. 20-21 (not *Amphipholis puntarenae* Lütken).

Amphichondrius granulosus Nielsen, 1932:304-6, fig. 21 a,b.—H.L. Clark, 1940:335, 337.—Barnard and Ziesenhenne, 1961:143.—Hartman, 1963:85, 217.—Boolootian and Leighton, 1966:4, 10, fig. 8.—A. M. Clark, 1970:31.

Amenichondrius granulosus, Fisher (in Parker, 1964:357).

Amphichondrius unamexici, Caso, 1983:209-212, pls.1-17.

Material Examined. California: Santa Maria Basin, Phase I Sta. BSV-042, 100 m, (2, USNM primary voucher); Phase II Sta. R-1, 91 m (2, CAMP voucher; 2 juvenile LACM 89-411.1).—Western Santa Barbara Channel, Phase I Sta. BSS-094, 96 m (4, SBMNH secondary voucher).—Mexico: Gulf of California, off Isla Espiritu Santo, R/V *Velero III* Sta. AHF 634-37, shallow water (1, LACM 37-35.2) — Panama: Gulf of Panama, R/V *Albatross* Sta. 3355, 333 m, lectotype (1, USNM 19539 [as *Amphiura granulata*, syntype]; herein designated lectotype).—North Pacific Ocean, R/V *Albatross* Sta.?, (3, USNM 19540 [as *Amphiura granulata*, syntypes]).—Colombia: Off Isla Gorgona, R/V *Velero III* Sta. AHF 854-38, 73-110 m (4, LACM 38-122.4).—Ecuador: Off Cabo San Francisco, R/V *Velero III* Sta. AHF 850-38, 27 m (1, LACM 38-118.24).

Description. A moderate sized amphiurid ophiuroid. Disk diameter up to 9 mm; a specimen 6.5 mm dd has arms approximately 34 mm long.

Disk round, flat, covered with moderately sized imbricating scales. Scales somewhat angular, regularly arranged, thickened at disk margin. Sharp transition between dorsal and ventral disk surfaces. Radial shields prominent, somewhat less than one-fouth disk diameter, distal halves in contact, proximal halves separated by wedge of one or several scales. Radial shields D-shaped in small specimens, quadrilateral in large specimens, tapering to a point proximally, to a short straight edge distally.

Jaws broad, oral gaps nearly sealed by oral papillae and teeth. Infradental papillae separated, small, narrow, rectangular. Middle papilla flattened, ovoidal to subquadrangular. Distal papilla largest, ovoidal to subquadrangular, with protruding, pointed, proximal adradial edge. Teeth wedge-shaped, with proximal edge of imperforate stereom. Oral shields roughly diamond-shaped, proximal end pointed, distal end rounded; paired proximal edges longer and more concave than distal edges. Madreporite larger than oral shields, rounded, inflated, multiperforate. Adoral shields large, maximum length equals oral shield; proximal lobes narrow, in contact proximal to oral shield; radial lobes larger, touching first ventral arm plate; adradial lobe nearly right angled.

Arms broad near disk, markedly narrowing near tip; in cross-section, dorsal surface gently curved, ventral surface flattened.

Ventral interradius flattened or inflated, appearing wrinkled in living individual, covered with minute, angular granules. Genital plate and genital scales bare at edge of bursal slit. Parallel "furrows" on genital scale (noted in Nielsen, 1932) actually demarcate edges of overlapping series of scales. Bursal slit narrow, concealed beneath arm, nearly reaching edge of disk.

Dorsal arm plates ovoidal, 2 times wider than long, in contact at base of arm; at tip of arm separated by lateral arm plates, fan-shaped; proximal edge slightly concave, or with medial lobe, or convex; distal edge convex.

Lateral arm plates prominent, with wedge-shaped extension separating successive dorsal arm plates and ventral arm plates, spine articulation ridge on distal edge. Three arm spines, with thick, hollow base, abruptly narrowing to blunt tip, slightly curving distally, rounded, smooth. Spines approximately equal to length of joint on proximal joints. Dorsal-most spine relatively longer at base of arm than at tip. Two rounded tentacles scales, nearly covering tentacle pore, appear to be aligned with edge of ventral arm plate; smaller proximal scale attached to lateral arm plate, larger distal scale attached to ventral arm plate.

Ventral arm plate in mouth angle bearing blunt conical protrusion extending into mouth; more distal arm plates pentagonal, broader than wide, with slightly concave edges; outer edge medially indented, thickened. Plates nearly in contact at base of arm, separated distally.

Variation: The ventral interradial granules and bare dorsal scales that characterize the genus are present in juvenile specimens of *A. granulatus*, only 1.0 - 1.2 mm dd. Individuals of that size have only a few disk plates and just three arm joints.

Color: Disk very dark brown or brownish-gray, larger scales surrounded by pale (connective?) tissue; radial shields darker than other scales, marginal scales more pale; granules of ventral interradius pale gray or whitish; jaw structures dark gray, madreporite contrasting cream or yellowish. Arms salmon, salmon-brown, or reddish brown; dorsal arm plates with indistinct medial salmon or whitish stripe and pale gray edges; lateral arm plates brown, arm spines gray or brown, tentacle scales gray. Boolootian and Leighton (1966) note arms white with gray or blackish mottling.

Pigmentation fades in alcohol preserved specimens.

Remarks. Lütken and Mortensen's (1899) description of *Amphiura granulata*, despite their rather poor illustration, unmistakably characterizes the unique disk armament of the species. They discussed the possible placement of *A. granulata* in *Ophiocnida*, a genus that is distinguished by short disk spines. Nielsen (1932) overlooked their work when erecting *Amphichondrius granulosus*, new genus and species. The correspondence of these species was verified by comparison of Nielsen's definitive illustrations with specimens identified by Lütken and Mortensen. Its oral formula and disk granulation exclude the species from *Amphiura* as currently defined (see A. M. Clark, 1970), and its placement in Nielsen's genus *Amphichondrius* is appropriate. Therefore, *Amphichondrius granulosus* Nielsen is regarded as a junior synonym of *Amphiura granulata* Lütken and Mortensen, and a new combination is proposed, *Amphichondrius granulatus* (Lütken and Mortensen).

The specimen upon which Lütken and Mortensen based their description, which lacks primary plates, matches the syntype catalogued as USNM 19539, *Albatross* Sta. 3355, Gulf of Panama, 182 fathoms (later labelled: Panama, Azuero Peninsula, 7° 12' 20"N 80° 55' 00"W, 333 ms, 23 Feb 1891). Therefore, I propose USNM 19539 as the lectotype of *Amphiura granulata* Lütken and Mortensen. Another lot, with three specimens catalogued as USNM 19540, *Albatross* 1891 (later labelled: Type, between Mexico and Galapagos) may correspond to the second lot examined by Lütken and Mortensen, which was originally numbered 8158.

Ziesenhenne (1940) described a second species in the genus, *Amphichondrius laevis*, also from Eastern Pacific waters. He distinguished it from *A. granulatus* based on several ambiguous characteristics including the primary plates, lateral arm plates, and oral shields. Reexamination of Ziesenhenne's material in the Allan Hancock collection of LACM, including the types, shows that *A. laevis* is a small species, generally less than 4 mm dd; its disk is pentagonal with pointed extensions jutting between the arms and capped by a large mid-marginal scale approximately twice as wide as long (rather than thrice as in *A. granulatus*). The dorsal arm plates of *A. laevis* are narrower and more triangular than those of *A. granulatus*.

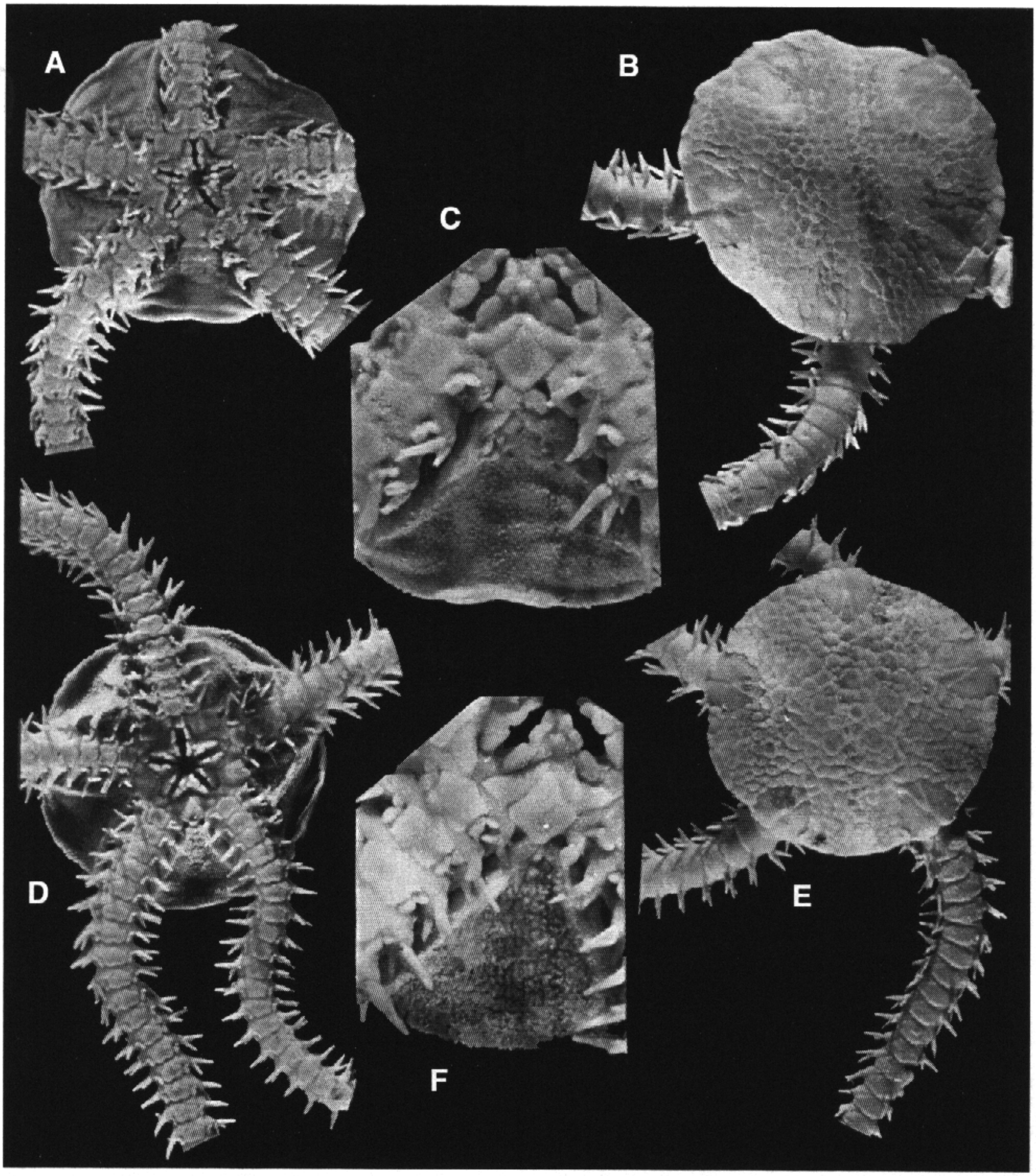

Figure 7.4. *Amphichondrius granulatus* (Lütken and Mortensen): A, disk, ventral view; B, disk, dorsal view; C, ventral interradius, showing granule covering (USNM 19539, lectotype, *Amphiura granulata*; dd = 6.4 mm); D, disk, ventral view; E, disk, dorsal view; F, ventral interradius, showing granule covering (LACM 38-122.4; dd = 6.1 mm).

A. laevis has minute pointed granules covering the edges of the bursal slits; granules are confined to the interradii in *A. granulatus*.

A third nominal Eastern Pacific congener, *Amphichondrius unamexi* Caso, is regarded as a synonym of *A. granulata*. A paratype of *A. unamexi* (UNAM, Mexico City, Acc. No. 2368), provided by F.A. Solis-Marin, was not distinguishable from typical specimens of *A. granulatus*.

Distribution. Pt. Conception, California, to Mexico, and Panama, at depths of 18-384 m (Lütken and Mortensen, 1899; H.L. Clark, 1917, 1940; Barnard and Ziesenhenne, 1961; Hartman, 1963).

Biology. Barnard and Ziesenhenne (1961) estimated fewer than 0.4 specimens/m^2 for 176 stations between Pt. Conception and the Mexican border at 9-183 m. A few living individuals that I have examined behaved sluggishly, and their tube feet lacked microscopic papillae. These traits suggest that the species is a relatively inactive deposit feeder. Specimens are gonochoric, and those as small as 4.5 mm dd have recognizable gonads.

Amphiodia (Amphispina) digitata Nielsen, 1932

Figure 7.5

Amphiodia (Amphispina) digitata Nielsen, 1932:275, 277-279, fig. 12a-c.—A. M. Clark, 1970:25.—Sutton, 1976:347, 350-352.

Amphiodia digitata, Barnard and Ziesenhenne, 1961:143.—Parker, 1964:359.—Boolootian and Leighton, 1966:5, 8, fig. 11.—Hartman, 1965:85, 154, 200, 217, 237, 251, 285.

Amphiodia barbarae (Lyman), McClendon, 1909:45, figs. 22, 23 (in part).

Material Examined. California: Santa Maria Basin, Phase I Sta. BSR-073, 98 m (1, USNM primary voucher [as *Amphiodia occidentalis*]); Phase II Sta. R-1, 91 m (1, CAMP voucher [as *Amphiodia urtica*]); Phase II Sta. R-1 (1, CAMP voucher).—Off Santa Cruz Id., R/V *Velero III* Sta. AHF 1005-39, 59-62 m (1, LACM 39-109.11).—Off Santa Barbara Id., R/V *Velero III* Sta. AHF 978-39, 38-51 m (1, LACM 39-82.7). —Off San Nicolas Id., R/V *Velero III* Sta. AHF 1219-40, 27-40 m (2, LACM 40-194.7).—Off La Jolla, Dr. Th. Mortensen's Pacific Expedition, 165-183 m, syntypes (ca. 60, Zoological Museum, University of Copenhagen); 110 m, syntype (1, ZUUC).

Description. A small amphiurid growing to 7 mm dd, with long, slender arms.

Disk round, slightly inflated, with coarse scaling; less than 10-12 columns of scales in dorsal interradius; disk surface uneven, raised along edge of radial shields. Radial shields in contact most of length, separated by 1-2 scales proximally; shields more than twice as long as wide, approximately one-fourth disk diameter in length. Uppermost row of ventral disk scales with free edge expanded into into 2-3 (up to 6) hyaline points, toothed scales forming continuous series between radial shields.

Jaws moderately wide. Oral gap narrow, oral papillae covering most of slit. Infradental papillae close; two lateral papillae flattened, with expanded free edge, distal papillae largest. Oral shields pentagonal; madreporite larger, inflated, generally possessing 1 pore. Adoral shields in contact, or nearly so, proximal to oral shield; radial lobe adjoining first lateral arm plate, inserting between first two ventral arm plates.

Scales covering ventral interradius smaller than those on dorsal disk surface. Bursal slit spanning oral shield, reaching nearly to disk margin; some scales at edge of slit with free edge produced into pointed projection.

Arms slender, distal portion of arm gradually tapering; in cross-section rounded dorsally, flattened ventrally.

Lateral arm plates with prominent spine-articulation ridge on distal edge, bearing 3 spines, sharply pointed, of about equal length, 1-1.5 times length of arm joint. Spines, most markedly middle spine, distinctly wider at base than at tip, curving slightly towards arm tip; dorsal and ventral spines laterally compressed, middle spine dorso-ventrally compressed. Two uppermost arm spines on joints below disk with sharp, proximally curving, hyaline tip.

Dorsal arm plates subrectangular, somewhat wider distally, generally with slightly concave distal margin. Soft tissue between joints not readily visible in dorsal aspect.

Ventral arm plates pentagonal, nearly in contact, long as wide, widest across proximal edge, distal edge with medial notch. First ventral arm plate U-shaped, set at distal angle of oral slit. Two tentacle scales at right angles, in contact; scale on ventral arm plate markedly larger, with broad free edge.

Color of living individuals: Disk gray to dark grayish brown tinged with purple; scales grayish-brown edged with gray or blackish; radial shields brown with yellowish-brown distal edge; ventral interradii pale gray. Arms reddish with irregular gray blotches or irregularly banded with gray and pale gray or cream, with indistinct, discontinuous, medial, orange-red stripe; ventral surface gray or brown. Eggs and ovaries orange, orange-red, or salmon colored.

Specimens in alcohol fade; Nielsen (1932) described them as whitish-yellow.

Remarks. *A. digitata* and its sympatric congener, *A. urtica*, are similar but distinct species. Their identification has been clouded by the appearance of seemingly "intermediate" individuals, generally with regenerating disks and arms, lacking the characteristics of perfect specimens. In addition, consistent differences between the juvenile stages of the two species have not been determined. The misidentification of specimens made during preliminary taxonomic analysis in the present survey is typical. An examination of earlier Allan Hancock Foundation material in LACMNH indicates the two species were confused in previous surveys of Southern California waters. (Bergen, 1995; pers. obs.). Characteristics distinguishing *A. digitata* are:

1) relatively few, large, dorsal disk scales on specimens with primary plates

2) uppermost row of ventral disk scales with some free edges expanded into into 2-3 (up to 6) prominent, widely diverging, hyaline points. The modified scales form a prominent, nearly continuous series between the arms. They are aligned with smaller hyaline-toothed scales that border the bursal slits. *A. urtica* has ventral interradii with roughened spiny scales, generally with a single hyaline point, which are most evident along the genital slit and at the base of the arms

3) relatively rectangular dorsal arm plates with lateral edges that conceal the tissue-filled gaps between successive joints. *A. urtica* has more ovoidal dorsal arm plates, between which wedges of soft tissue are apparent.

4) disk coloration grayish in *A. digitata*, reddish in *A. urtica*.

Sutton's (1976) contention that *Amphiodia digitata* is a junior synonym of *Amphiodia* (*Amphispina*) *periercta* H.L. Clark, 1911 is rejected based on a study of Eastern Pacific *Amphiodia* (*Amphispina*) species (Hendler and Wang, in prep.).

Distribution. Point Conception, California to Mexico, at depths 18-280 m (Nielsen, 1932; Barnard and Ziesenhenne, 1961; Hartman, 1963; Parker, 1964).

Biology. Barnard and Ziesenhenne (1961) reported the species from 6% of 176 stations at 9-183 m depths between Pt. Conception and the Mexican border, with an overall average density of 7.5 individuals/m^2. Specimens collected in Santa Monica Bay, California in October, 1991 and December, 1992 had eggs that appeared to be ripe, with maximum diameters of 0.16 mm. This is a somewhat larger gamete than typical for species with ophiopluteus larvae (Hendler, 1991), perhaps an indication that the larva has an abbreviated mode of development.

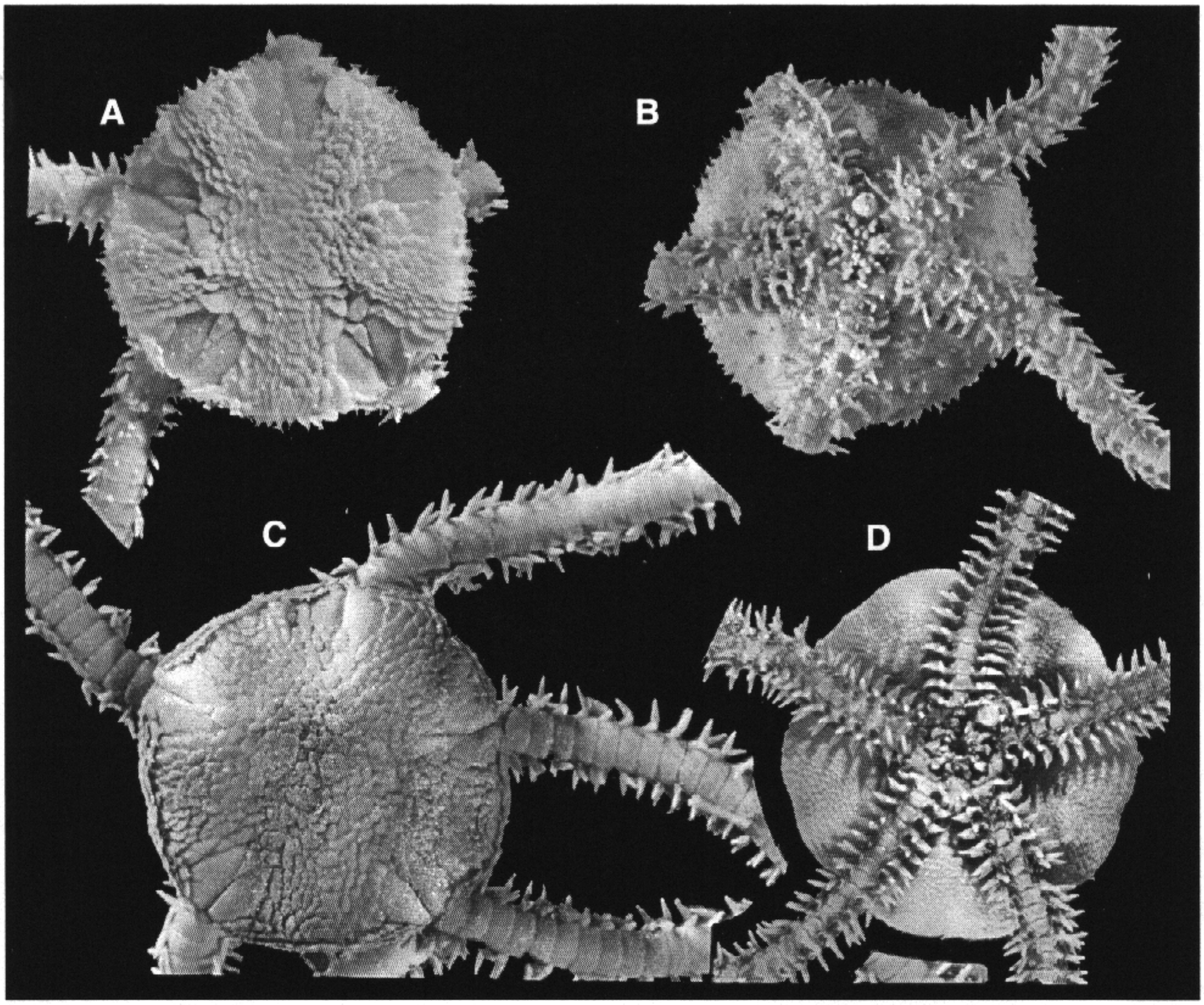

Figure 7.5. *Amphiodia* (*Amphispina*) *digitata* Nielsen: A, disk, dorsal view; B, disk, ventral view (syntype, ZM; dd = 4.9 mm); C, disk, dorsal view (LACM 39-82.7; dd = 4.9 mm); D, disk ventral view (LACM 39-109.11; dd = 7.4 mm).

Amphiodia (*Amphispina*) *urtica* (Lyman, 1860)

Figure 7.6

Amphiura urtica Lyman, 1860:195-196.—1865:12, 115, 128-129.—1880:21.—1882:125, 147, 311.

? *Amphiura urtica*, H.L. Clark, 1901:330 (not *A. urtica* Lyman).

Amphipholis urtica, Ljungman, 1867:315.

Amphiodia urtica, Verrill, 1867:325.—1899:313.—H.L. Clark, 1911:11, 154, fig. 64a-c.—1915:249.—Campbell 1921b:47.—May, 1924:288-89, fig. 11a-e.—Berkeley, 1927:4-5.—Ziesenhenne, 1937:224.—1940:331, 338.—Barnard and Ziesenhenne, 1961:133-151.—Hartman, 1963: 85, 137, 153, 170, 185, 201, 217, 237, 251, 285, 305, 334, 349, 365, 382, 400.—Boolootian and Leighton, 1966:5, 8, fig. 12.—Kyte, 1969:1729, 1734-1736, 1738.—A. M. Clark, 1970:26.—Austin and Hadfield 1980:150-151, pl. 49, fig. 10.5.

? *Ophiophragmus urtica*, Fell, 1962:14, 26.

Amphiura barbarae Lyman, 1875:5, 17, pl. 3, figs. 32-34.—McClendon, 1909:45, figs. 22-23 (in part).—H.L. Clark, 1915:245. Campbell, 1921a:3, fig. 4..—1922b:47.—1922:38, pl. 3, figs. a-f (in part?).

Amphiodia Barbarae, Lyman, 1880:21.—Verrill, 1899:313.

Amphiura (Section *Amphiodia*) *barbarae*, Koehler, 1907:306.

Diamphiodia barbarae, Fell 1962:14, 19.

Material Examined. California: Santa Maria Basin Phase I Sta. BSR-023, 195 m (1, SBMNH secondary voucher); Phase I Sta. BSR-073, 98 m (20, USNM primary voucher; 35, SBMNH secondary voucher [as *Amphiodia occidentalis*]); Phase II Sta. R-1, 91 m (78, CAMP voucher); Phase II Sta. R-1, 91 m (52+, CAMP voucher [as *Amphiodia* sp.]).—Western Santa Barbara Channel, Phase I Sta. BSR-085, 113 m (92, USNM primary voucher).—Off Pt. Loma Lt., R/V *Velero IV* Sta. AHF 5200-57, 72 m (numerous, LACM 57-240.3).

Description. A small amphiurid, reaching 9 mm dd, with arms 12 times as long. Disk rounded to pentagonal, inflated, covered with delicate, minute, imbricating scales. Primary plates and scales surrounding radial shields larger than other disk scales. Radial shields approximately 3 times longer than broad, length approximately one-fifth disk diameter, in contact most of length, proximal tips separated by small wedge of scales.

Jaws narrow, oral gap wide. Three oral papillae; infradentals blocklike, separated, middle papilla smallest, outer papillae largest; both lateral papillae flattened, rounded triangular shape, with point of attachment narrow, free edge expanded.

Oral shields pentagonal to rhombic, about as long as wide; proximal end pointed, distal end broadly rounded. Madreporite almost twice size of oral shield, thick, inflated, with 1 or more pores. Adoral shields with rounded lobes in contact proximal to oral shield; pointed radial lobes in contact with first lateral arm plate, inserting between first two ventral arm plates. Ventral interradius finely scaled; scales generally quite small and sparse near oral shield. Bursal slit conspicuous, extending to edge of disk. Scales near genital slit enlarged, generally bearing single, minute, hyaline teeth. Series of spinose scales commonly extending to distal corner of radial shield, sometimes sparsely distributed across the lower lateral edge of the disk between the arms.

Arms slender, broader than high; dorsal and ventral surfaces gently rounded. Characteristic gaps between arm joints filled by wedge of soft tissue; dorsal edge of the vertebra visible within.

Dorsal arm plates ovoidal, with convex proximal edge, lateral edges lobed, distal edge with broad medial covexity; successive dorsal arm plates barely in contact or slightly overlapping.

Lateral arm plates thin, with distally protruding spine-bearing ridge. Three arm spines of about equal length, rounded in cross section, with thick base, tapering to acute point; dorsal and ventral spines slightly laterally compressed, middle spines slightly dorso-ventrally compressed. Dorsal spines on first several arm joints beneath disk with proximally curved, sharply pointed, hyaline tip. Two tentacle scales, thin, ovoidal; scales covering little of tentacle pore; scale on ventral arm plate larger, longer, often bi-lobed.

Ventral arm plates pentagonal with concave edges, forming 2 postero-lateral lobes and indented medio-distal edges, slightly separated by interdigitating lateral arm plates. Proximal ventral arm plates about as long as wide, distal plates longer than wide. First ventral arm plate U-shaped, set at distal angle of oral slit.

Color: Disk reddish to grayish-brown, primary plates contrastingly dark, radial shields gray with pale tips. Arms reddish gray, with irregular gray or brownish blotches, reddish medial stripe; dorsal arm plates gray with pinkish gray border, ventral arm plates yellowish brown, arm spines pinkish gray. Ovaries and eggs pink, testes whitish.

In alcohol disk and arms fade to pale yellowish brown.

Remarks. The subgenus *Amphispina* Nielsen is characterized by the presence of scales with spiny margins among the uppermost row of ventral disk scales. Although mention was omitted from the original description, there are commonly spinose scales along the bursal slits of the type species, *Amphiodia (Amphispina) digitata*. *A. urtica* has spinose scales on the disk margin, mostly occuring near the arms, and as noted by A.M. Clark, individuals exhibit varying densities of spinose scales on the ventral interradius and along the bursal slit. Therefore, I do not concur with A. M. Clark's (1970) exclusion of *A. urtica* from *Amphispina*, and have retained the species in the subgenus as originally proposed by Nielsen (1932), together with *A. digitata*, *A. duplicatus* (Koehler), and *A. microplax* Burfield.

Distribution. Mexico and Southern California to British Columbia and Alaska, at depths of 9-198 m, and possibly as deep as 708 m (H.L. Clark, 1911, 1915, 1940; Berkeley, 1927; Nielsen, 1932; Ziesenhenne, 1937; May, 1924; Barnard and Ziesenhenne, 1961; Hartman, 1963).

Biology. The species has proved to be the most numerous ophiuroid of Southern California mainland shelf and offshore basins (Hartman, 1955, 1966; Hartman and Barnard 1958, 1960; Jones, 1969). Based on 176 stations at 9-243 m depths between Pt. Conception and the Mexican border, Barnard and Ziesenhenne (1961:133) characterized *A. urtica* as "...the most abundant and widespread animal in any phylum on the coastal shelves, occurring in 86% of all samples and having a frequency for all depths of 422 animals per square meter. It forms the dominant in the two most widely distributed communities of the coastal shelf." They found that it is most numerous in sandy silts that feel sticky to the touch, and that it frequently occurs with *Amphiura arcystata* and in a community dominated by *Amphioplus hexacanthus* (=*Dougaloplus amphacanthus*). Bergen (1995) concluded that *A. urtica* is most abundant in sediments with a median grain size of 0.035-0.093 mm (coarse silt to very fine sand) at depths 15-85 m. The species is similarly abundant in Puget Sound, Washington, where it appears to have a life span of at least five years (Lie, 1968).

Juvenile individuals commonly comprise a major component of the population, as they did in the collection under study. The many small specimens examined can be identified with certainty only to genus, because they lack the features of taxonomic importance used to characterize the adults. Therefore, many specimens from the Atlas survey that are probably immature *A. urtica* are not listed above with other material examined.

In southern California, *A. urtica* is routinely collected in studies assessing the impact of wastewater pollution on benthic communities. It is considered an indicator species, and is frequently cited in the extensive gray literature of governmental agencies dealing with wastewater management. Some of that literature is covered in a recent symposium proceedings (see: Diener and Fuller (1995), Dorsey *et al.* (1995), Scanland (1995)). It is generally thought that populations of *A. urtica* are diminished near wastewater outfalls, and recover when pollution is abated (Dorsey *et al.*, 1995; Scanland, 1995). However, it has also been suggested that population density may be held in check by predatory fish which congregate near outfalls (Diener and Fuller, 1995).

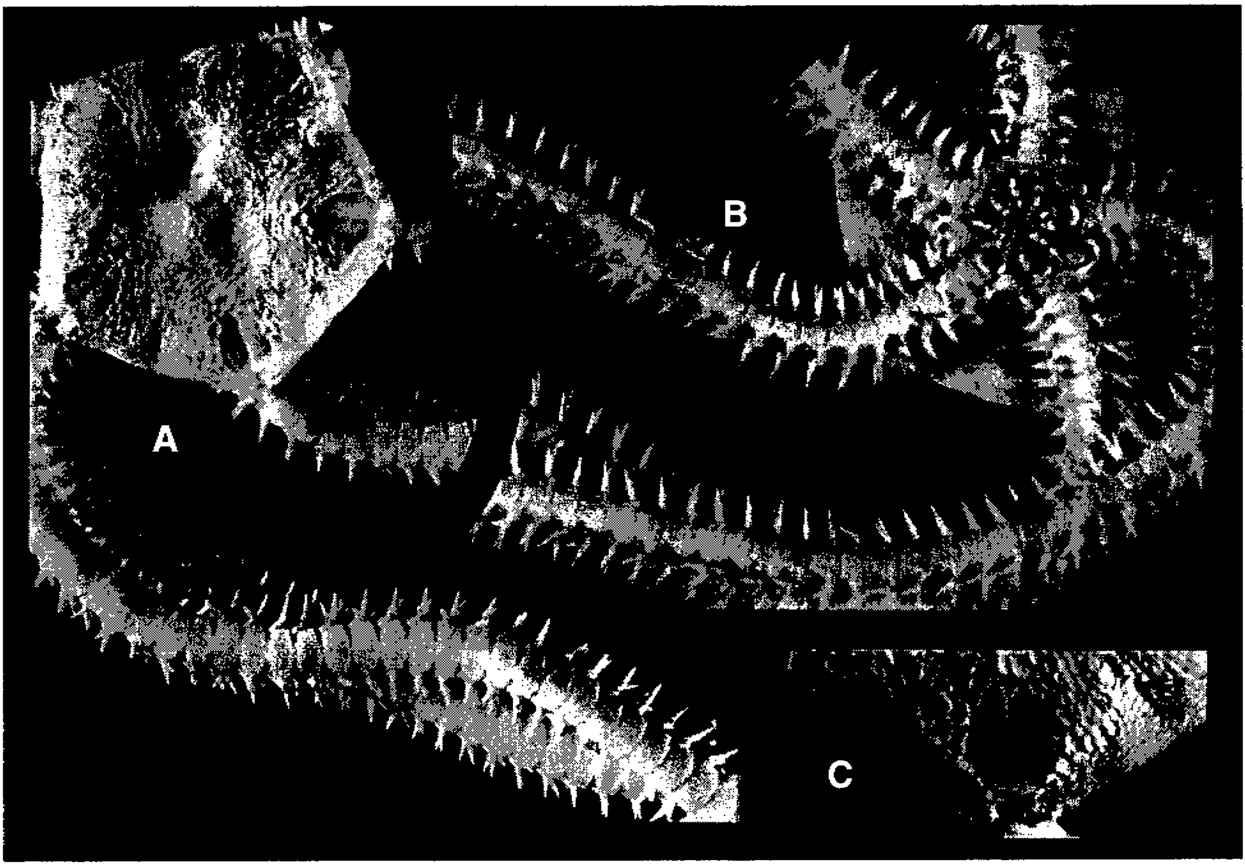

Figure 7.6. *Amphiodia (Amphispina) urtica* (Lyman): A, disk, dorsal view; B, disk, ventral view; C, disk edge, showing spinose scales on disk margin (LACM 56-66.7; dd = 4.9 mm).

The available literature treats the density and distribution of the species and its response to polluted sediment. However, its life history, behavior, and ecology are poorly known. Austin and Hadfield (1980) summarize the limited information on its biology, estimating densities up to 1,500 individuals/m^2, pointing out that it burrows, suspension and deposit feeds, and is capable of arm and disk autotomy and regeneration. The species is gonochoric. Its eggs are approximately 0.12 mm diameter, the size indicating development as a feeding, ophiopluteus larva (Hendler, 1991). Kyte (1969) reports the young of *A. urtica* occur under loose gravel and coarse sand. In British Columbia, its predators include lemon sole, flathead sole, sand sole, and the sea star, *Luidia foliolata*. Nielsen (1932) notes that individuals are frequently infested with a copepod which he identified as a *Cancerilla* species.

Amphioplus (*Amphioplus*) *strongyloplax* (H. L. Clark, 1911)

Figures 7.7

Amphiodia strongyloplax H. L. Clark, 1911: 10, 164-165, fig. 71a-c.—1915:249.—Campbell, 1921b:47.—Sutton, 1976:349.

Amphioplus strongyloplax, Nielsen, 1931:295-296, fig. 18a-b.—Barnard and Ziesenhenne, 1961:143.—Hartman, 1963:85, 125, 154, 170, 185, 217, 251, 285, 305, 334, 350, 365, 382.—Astrahantseff and Alton, 1965:1414, 1416, 1420.—Boolootian and Leighton, 1966:5, 9, fig. 16.—Alton, 1972:507, 510.

Unioplus strongyloplax, Fell 1962:16, 25.—Kyte, 1969:1729, 1733, 1735, 1737.

Amphioplus (*Amphioplus*) *strongyloplax*, A.M. Clark, 1970:20, 44, 57, 77, fig. 9b.

Material Examined. Washington, Cape Flattery, R/V *Albatross* Sta. 2866, 313 m, holotype (USNM 25615 [as *Amphiodia strongyloplax*]).—Oregon: Off Columbia River mouth, R/V *Commando* Sta. ?, 400 m (1+, LACM 64-242.1).—California: Santa Maria Basin, Phase I Sta. BSV-042, 100 m (1, SBMNH secondary voucher); Phase II Sta. R-5, 154 m (1, CAMP voucher [as *Amphiolpus macraspis*]); Phase II Sta. R-1, 91 m (3, CAMP voucher); Phase II Sta. PJ-4, 150 m (1, CAMP voucher [as *Amphioplus hexacanthus*]); Phase II Sta. PJ-11, 136 m (2, LACM 86-492.9).—Western Santa Barbara Channel, Phase I Sta. BSS-084, 394 m (1, USNM primary voucher).—Off San Miguel Id., R/V *Velero IV* Sta. AHF 23165-75, 96 m (1, LACM 75-409.4).—Off Santa Rosa Id., R/V *Velero III* Sta. AHF 993-39, 229-238 m (1, LACM 39-97.4). - Los Angeles, off El Segundo, R/V *Velero IV* Sta. AHF 3400-55, 400 m (4, LACM 55-110.1).—Off San Pedro, R/V *Velero III* Sta. AHF 1228-41, 230-252 m (2, LACM 41-8.3).

Description. An amphiurid of moderate size, the maximum disk diameter exceeding 10 mm; a specimen of 5.5 mm disk diameter estimated to have arms 50 mm long (H. L. Clark, 1911), one 8 mm disk diameter has arms over 95 mm long; judging from the fragmented specimens of the present survey, arm length probably exceeds 12 times disk diameter.

Disk soft, flat, indented interradially. Disk covering variable, ranging from scales restricted to region surrounding the radial shields, to completely coating entire disk. Scales irregularly arranged, sometimes multi-layered, smallest at center of disk, largest near radial shields, those below disk drastically reduced in size and number. Primary plates discernible on all but regenerating disks. Radial shields diverging and tapering proximally, nearly in contact distally, with radial edge straight, abradial edge convex; length approximately 4-5 times width, approximately one-fourth disk diameter, relatively larger or smaller on regenerating disks.

Jaws narrow, ventrally projecting, with deep indentation distal to apex; oral gap pronounced, widening distally. Generally 5 oral papillae; infradental papillae touching or nearly so, small, blocklike, with protruding proximo-radial corner; buccal scale sometimes equal in size to lateral papilla, high in jaw, triangular or spinelike; two lateral papillae flattened, triangular to blunt spinelike, outermost usually largest; distal-most minute, set between first ventral arm plate and adoral shield. Teeth chisel shaped; proximal tip irregular or straight, composed of imperforate stereom.

Oral shields variable, subpentagonal, diamond-shaped to irregularly ovoidal; somewhat longer than wide; madreporite thicker, larger, more rounded, usually with single perforation. Oral shield overlapping little of adoral shield. Adoral shields L-shaped; proximal lobes of adjacent plates touching or nearly so; distal lobes larger, inserting between first and second ventral arm plates. Ventral interradii with extremely small thin scales and irregular granules separated by integument; larger flat scales on abradial edge of bursal slit. Bursal slit extending from oral shield to disk edge.

Arms long, slender, narrowing near disk, wider at midlength, tapering distally, gently rounded dorsally, flat ventrally.

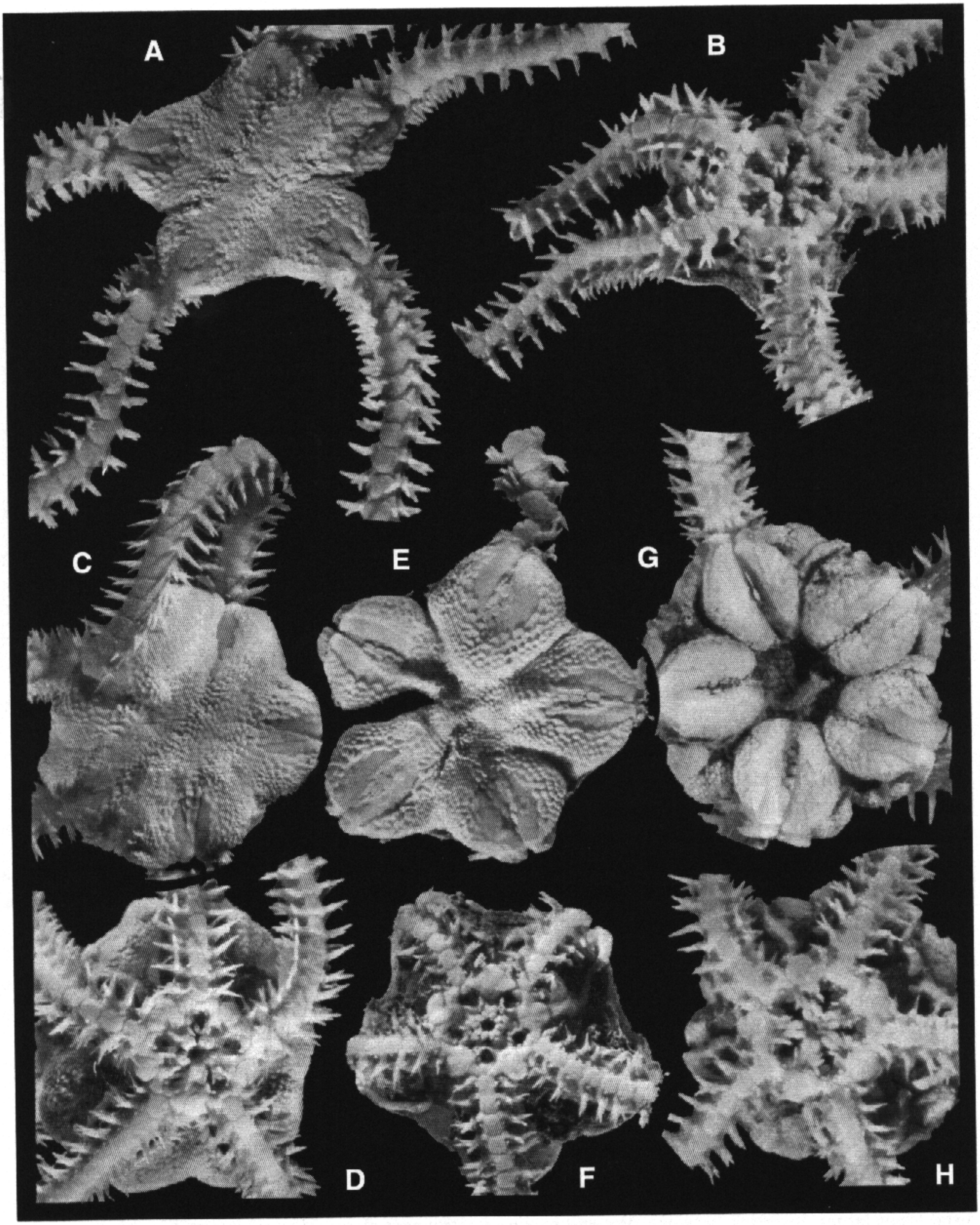

Figure 7.7. *Amphioplus* (*Amphioplus*) *strongyloplax* (H.L. Clark): A, disk, dorsal view; B, disk, ventral view (USNM 25615, holotype, *Amphiodia strongyloplax*; dd = 4.9 mm); C, disk, dorsal view; D, disk, ventral view (LACM 64-242.1; dd = 7.2 mm); E, disk, dorsal view; F, disk, ventral view (LACM 55-110.1; dd = 9.3 mm); G, disk, dorsal view; H, disk, ventral view (LACM 75-409.4; dd = 6.6 mm). Note variability in disk scalation; all the disks shown are regenerating.

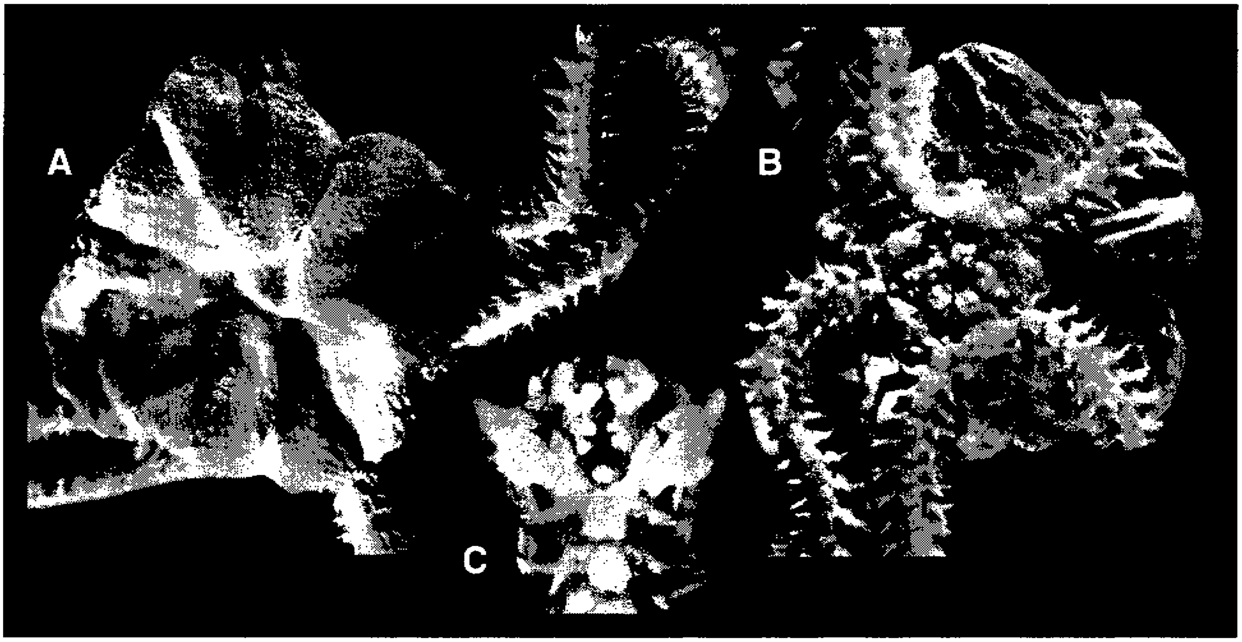

Figure 7.8. *Amphioplus (Amphioplus) macraspis* (H.L. Clark): A, disk, dorsal view (USNM 25584, syntype, *Amphiodia macraspis*; dd = 11.5 mm); B, disk, ventral view; C, oral frame, showing broad oral shields (USNM 25584, syntype, *Amphiodia macraspis*; dd = 8.5 mm).

Dorsal arm plates thin, little broader than long, ovoidal to hexagonal with short lateral edges, smaller than joint, separated by lateral arm plates and wedges of soft tissue between joints. First few basal plates reduced in size.

Lateral arm plates with prominent spine-bearing ridge. Five arm spines, occasionally 6 on basal joints, gradually tapering, acutely pointed, smooth, delicate, hollow with wall of spine much thinner than internal cavity. Spines beneath disk equal or slightly exceeding length of ventral arm plate. On joints with 5 spines dorsal-most and ventral-most spines longest, middle spine shortest, all slightly compressed, gradually tapering, pointed. On joints with 4 and 3 spines near middle of arm, spines increasing in length ventrally, second spine from bottom noticeably broadened at base, dorso-ventrally compressed; spines near arm tip very slender, acute.

First ventral arm plate set in oral slit, with distal edge broadened; second ventral arm plate hexagonal. Those plates on proximal joints slightly longer than broad, with rounded posterolateral lobes, generally with distal medial indentation. Several basal plates in contact or nearly so; distal ventral arm plates separated by lateral arm plates. Tentacle scales 1-2, minute, embedded in soft tissue, covering little of large tentacle pore.

Variation: Number of arm spines is size related: at 2.0 mm dd (ofl 1.8) there are 3 arm spines, at 2.3 mm dd (ofl 2.0) 4 arm spines, at 7.6 mm dd (ofl 3.2 mm) 5 arm spines. Likewise, number of tentacle scales size is related: some joints of small specimens lack tentacle scales; a few joints of large specimens have 2 tentacle scales.

Color: Alcohol preserved specimen with regenerated disk has pale scales and blotches of yellow and brown; radial shields gray, yellow, and white; dorsal and ventral arm plates marked with orange to yellow-brown pigmentation, forming discontinuous medial stripe. Orange-yellow pigmentation present on some arm spines, oral and adoral shields, jaws, and radial shields. According to H. L. Clark (1911), specimens dried from alcohol with "disk grayish, arms very light brownish; radial shields and arm plates with orange-brown tint."

Remarks. H. L. Clark (1911) noted the similarity of *A. strongyloplax* to *Amphioplus (Amphioplus) macraspis* (compare Figures 7.7 and 7.8). Comparison of type material indicates *A. macraspis* (USNM 25584, syntype) differs in having the ventral arm plates broadly in contact, broad oral shields, and relatively wide dorsal arm plates. *A. strongyloplax* has been described as resembling *Amphioplus hexacanthus*. The latter is discussed below, and synonymized with *Dougaloplus amphacanthus*.

Distribution. Mexican border and Southern California to British Columbia; depth range 91-623 m; a doubtful record from 4 m (H.L. Clark, 1911, 1915; Nielsen, 1932; Barnard and Ziesenhenne, 1961; Astrahantseff and Alton, 1965; Alton, 1972; Kyte, 1969).

Biology. Barnard and Ziesenhenne (1961) reported this species from 23% of 176 stations taken between 9-243 m depths from Pt. Conception, California to the Mexican border. They calculated an overall population density of 4.3 individuals/m^2, but Astrahantseff and Alton (1965) provide a more realistic estimate of 60 individuals/m^2 off the Oregon coast. The species occurs in mud with varying amounts of sand and gravel (Kyte, 1969). It certainly burrows in soft sediment, presumably the reason that Alton (1972) found it is taken with infaunal sampling gear, never with trawls. A specimen examined in the present survey (Phase I Sta. PJ-11) was a female with eggs of 0.18 mm diameter, an oocyte size indicative of an ophiopluteus larval form or an abbreviated mode of development (Hendler, 1991).

Amphipholis pugetana (Lyman, 1860)

Figure 7.9

Amphiura pugetana Lyman, 1860:193-194.—1865:12, 15, 115, 125-126.—1880:19.—1882:125, 145, 311.—Koehler, 1907:305.

Amphipholis Pugetana, Verrill, 1865:325.—1899:312.

Amphipholis pugetana, Ljungman, 1867:312.—McClendon, 1909:43-44, figs. 12, 13 (in part?).—H.L. Clark, 1910:323, 340-341, pl. 9, fig. 2.—H.L. Clark, 1911:166-67, fig. 73a-c.—1915:242.—Matsumoto, 1917:185, 191, 358, 365, fig. 51.—Campbell, 1921b:48.—May 1924:289-290, fig.12a-c.—Berkeley, 1927:5, fig. 12.—Nielsen, 1932:281, 288-90.—D'yakonov, 1954:58.—Barnard and Ziesenhenne, 1961:143.—Fell, 1962:13, 24.—Hartman, 1963: 85, 137, 154, 201, 217, 286, 320, 335, 365, 383, 391, 401.—Boolootian and Leighton, 1966: 5, 9, fig. 9.—Austin and Hadfield 1980:148-149.—Smirnov, 1982:113.

Amphiopholis pugetana, Bush, 1921:72.

Axiognathus pugetana, Kyte, 1969:1728, 1729, 1735-1737.

Material Examined. Oregon: Off Columbia River mouth, R/V *Commando*, 900 m (1, LACM 64-241.2). - California: Santa Maria Basin, Phase I Sta. BRA-013, 92-100 m (58, USNM primary voucher [as *Amphipholis squamata*]); Phase I Sta. BRA-016, 91.5-123 m (36, USNM primary voucher [as *Amphipholis squamata*]); Phase II Sta. R-4, 92 m (3, CAMP voucher [as *Ophiura luetkeni*]).—Off Santa Catalina Id., R/V *Velero IV* Sta. AHF 1989-50, 604 m (1, LACM 50-45.2); R/V *Velero IV* Sta. AHF 2425-53, 64-70 m (8, LACM 53-159.1).—Off San Clemente Id., R/V *Velero IV* Sta. AHF 22943-75, 319 m (9, LACM 75-297.2).

Description. A small amphiurid, with maximum disk diameter 5 mm; an individual 3.5 mm dd has arms 25 mm long.

Disk round to rounded pentagonal, inflated, with radial shields appearing slightly sunken; disk margin sharply demarcated by broad ventral scales overlapping elongated dorsal scales. Disk scales conspicuous, rounded, imbricating, with opaque, thickened outer edge. Primary plates forming rosette occupying central one-third of disk. Radial shields three times longer than wide, length approximately one-fifth diameter of disk; radial edges straight, adradial edges curved; proximal end pointed, distal end short, straight. Paired shields in contact, except proximal ends separated by 1-2 small scales.

Jaws broad. Oral gap narrowed by oral papillae. Infradental papillae rounded, blocklike, separated. Middle papilla rounded, quadrangular, breadth increasing from attachment point to free edge. Distal papilla largest, quadrangular, elongate, narrowing distally, overlapping first ventral arm plate.

Oral shields diamond to spade-shaped, corners rounded, about as long as wide; proximal portion elongated and pointed, edges concave; distal corner abutting genital scale. Madreporite larger than oral shields, inflated, bearing one pore. Adoral shields quadilateral, usually larger than and extending above oral shields; paired plates in contact. Ventral interradii inflated, covered with small imbricating scales. Genital scales frequently with proximal ends touching or nearly so, short axis aligned dorso-ventrally. Bursal slit partly hidden by arms, nearly reaching edge of disk.

Arms generally 6 times disk diameter, slightly increasing in width to a distance of approximately 10 joints from disk, then gradually tapering. In cross-section dorsal surface somewhat rounded, ventral surface nearly flat. Joints with lateral edges diverging gradually, distal segments not sharply knotted in appearance. Terminal plate gradually tapering, with truncate distal tip.

Dorsal arm plates barely in contact, or separated by lateral arm plates; proximal edge convex, widely diverging lateral edges, lateral corners rounded, posterior edge slightly convex.

Lateral arm plates prominent, broad, with pronounced spine attachment ridge. Lateral plates forming tight wedge between dorsal arm plates, meeting conspicuously between ventral arm plates. Arm spines slender, tapering gradually, smooth, lacking microscopic grooves. Spines equalling or exceeding length of arm joint, gradually tapering to blunt tip, dorsal and ventral spines slightly laterally compressed and curved distally, middle spine slightly dorso-ventrally compressed. Spines frequently 4 in number for one to several joints beyond disk. When 4 in number, increasing in length ventrally; when 3 in number middle spine generally largest and longest. Beginning 5 to 15 joints from edge of disk, on widest portion of arm, middle arm spine markedly enlarged, length at least equalling width of the dorsal arm plate on that joint. Enlarged spines 1.5 times length of joint, somewhat 8-pin shaped, with bulbous base and inflated tip. Tentacle scales paired, covering tentacle pore; scale on lateral arm plate with pointed tip; scale on ventral arm plate similar or larger, elongate or teardrop-shaped.

First ventral arm plate flat, pentagonal, overlapped by adoral shield and distal oral papillae; proximal few ventral arm plates in contact, equilateral, with lateral edges narrowing adjacent to tentacle pore, width across distal lobes no greater than across proximal lobes; distal plates longer than wide, regularly pentagonal, separated by lateral arm plates.

Color: Disk gray or orange-red and gray, darker than arms. Arms dorsally blotched with orange and reddish-orange, with greenish and gray, or pale brown. Arm spines pale, oral frame and ventral surface of arms orange colored, pale brown, or gray. Austin and Hadfield (1980) describe the species as "gray or banded gray and white." Nielsen (1932) notes alcohol preserved specimens are "colorless" with the disk reddish in a few specimens.

Remarks. In the region covered by this report only two *Amphipholis* species occur, *A. pugetana* and the cospmopolitan *A. squamata.* D'yakonov (1954:58) regarded *A. pugetana* as "probably identical with the ubiquitous *A. squamata*" finding "no tangible differences between the two." His data are unconvincing, as are the accounts of most authors cited in the partial synonymy above. My reexamination of specimens from this and previous coastal surveys represented in the LACMNH indicated that many existing identifications and records for the two species are incorrect.

H.L. Clark (1911: 167) claimed that "characteristic mouth parts" easily distinguish *A. pugetana* - the only *Amphipholis* species represented in the *Albatross* collection. He provided the first illustration of the species, showing spade-shaped oral plates and the middle arm spine longer than others. Nielsen (1932) separated *A. pugetana* from *Amphipholis* species of the tropical Eastern Pacific by its number of arm spines and rectangular distal mouth papilla. He distinguished it from *Amphipholis squamata* by the presence of arm spines as long as 1.5 arm joints (noting that spine length equal to that of the joint in *A. squamata*), and

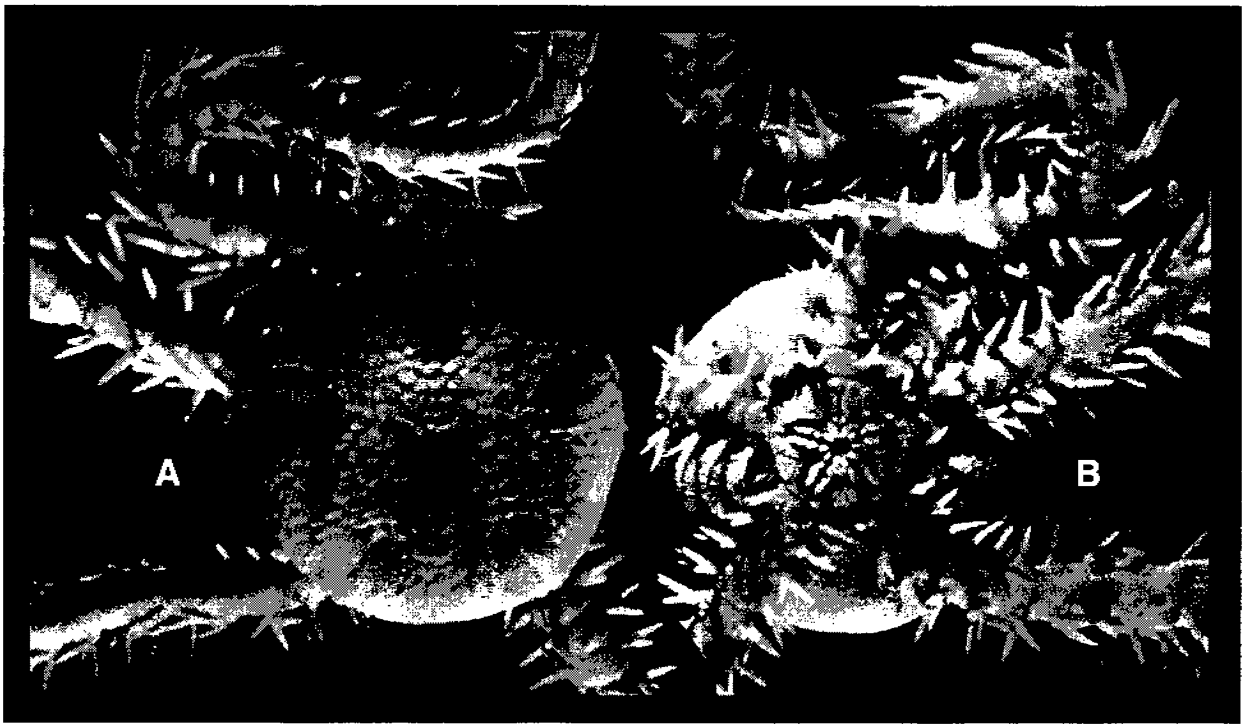

Figure 7.9. *Amphipholis pugetana* (Lyman): A, disk, dorsal view; B, disk, ventral view (LACM 75-297.2; dd = 4.1 mm).

pointed out the middle arm spine exceeds the dorsal and ventral spines on some part of arm, and in large specimens usually becomes thickened at the proximal and distal ends on 10-15 arm joints near middle of arm. Furthermore, the arm length is 7-8 times the disk diameter (compared to 4 times in *A. squamata*), and the oral shield is narrower than long (while in *A. squamata* the length equals width). Nielsen recognized that *A. squamata* broods its young internally, unlike *A. pugetana*. Later authors have not improved on the distinctions drawn by Nielsen, and we still are unable to distinguish small and sexually immature specimens of the two species.

Distribution. Peru (record highly doubtful) and Southern California to Washington, British Columbia, and Alaska, at depths from 15-604 m (H. L. Clark, 1910, 1911, 1915; Berkeley, 1927; this report), and possibly to 1,620 m (Hartman, 1963). Published records suggest it is amphi-Pacific (Matsumoto, 1917; Smirnov, 1982; Irimura *et al.* 1995). See distribution for *A. squamata* below.

Biology. Barnard and Ziesenhenne (1961) recognized this species at 1.7% of 176 stations taken between 9-243 m depths from Pt. Conception, California to the Mexican border. They calculated an overall population density of 2.2 individuals/m^2. However, my examination of samples still at LACMNH from their survey indicated that specimens of *A. pugetana* and *A. squamata* were frequently confused. Thompson and Jones (1987) reported both species from the lower slopes of Southern California offshore basins, with densities of *A. pugetana* up to 45 individuals/m^2.

Amphipholis squamata (Delle Chiaje, 1828)

Figure 7.10

Asterias squamata Delle Chiaje, 1828:74, 77, 79, pl. 34, figs. 1-4.

Ophiolepis squamata, Müller and Troschel, 1842:92.

Amphiura squamata, Lütken 1859:226-227.—Lyman, 1865:12, 14, 115, 121-123.—1875:5, 16.—Lyman, 1880:19.—1882:125, 136, 291, 296, 309-310, 314, 321-322, 324.—Ives, 1889: 177.—Koehler, 1907:305.

Amphipholis squamata, Verrill, 1899:312.—H.L. Clark, 1910:323, 340-341.—Clark, 1915:242.—1923:154-155.—1940:331, 337.—Mortensen, 1927:221, fig. 125.—Nielsen, 1932:281, 290.—Ziesenhenne, 1937: 223-224.—A.H. Clark, 1939:2.—D'yakonov, 1954:57.—Barnard and Ziesenhenne, 1961:143.—Fell, 1962: 13, 25.—Hartman, 1963: 85, 137, 154, 185, 200, 218, 237, 251, 285, 305, 334, 349, 366, 382, 401.—Boolootian and Leighton, 1966: 5, 9, fig. 10.—A. M. Clark, 1970: 7, 30-31, fig. 1g.—Austin and Hadfield 1980:148-149, pl. 49, fig. 10.3.

Axiognathus squamata, Thomas, 1966:831-832.—Kyte, 1969: 1729, 1733, 1735-1737.

Material Examined. California: Santa Maria Basin, Phase II Sta. R-4, 92 m (11, CAMP voucher); (1 juvenile ?, CAMP voucher [as *Amphiodia* sp.]); Phase II Sta. R-4, 92 m (6, CAMP voucher [as *Ophiura luetkeni*]).—Los Angeles, off Portuguese Bend, R/V *Velero III* Sta. AHF-39, intertidal (31, LACM 39-117.13).—Off Newport Beach, R/V *Velero III* Sta. AHF 1225-41, intertidal (4, LACM 41-5.12). - Off Laguna Beach, intertidal (14, LACM 57-278.1).

Description. In many respects the description *A. pugetana* applies to *A. squamata*. The structure of the arm spines is the most reliable differential character in adult specimens. Other features distinguishing *A. squamata* are the following:

Dorsal disk scales smooth, flat, edges not thickened.

Distal oral papillae with flaring, rounded outer edges meeting to seal oral gap.

Oral shields more pentagonal than diamond-shaped; distal edge broad or lobate. Oral shield larger than adoral shield, greatest width of oral shields exceeding greatest width of adoral shield. Distal end of oral shield overlapping and separating proximal end of genital scales.

Arms short, up to 4 times disk diameter. Distal-most arm segments appearing knotted due to proximal constriction of lateral arm plates.

Basal dorsal arm plates of equal length and width.

Lateral arm plates with expanded, rounded, spine attachment ridge.

Ventral arm plates pentagonal, width across distal lobes generally exceeding that across proximal lobes.

Terminal arm plate with bulbous base, abruptly narrowing distally.

Arm spine length equal or less than length of arm joint. Spines with broad base, abruptly tapering near tip, somewhat compressed, surface echinulate with microscopic grooves. Tentacle scale on ventral arm plate generally smaller than scale on lateral arm plate.

Remarks. Since its discovery, *A. squamata* has been assigned at least 25 different scientific binominals; a partial synonymy is provided by Fell (1946). A.M. Clark (1970) points out that the name *Ophiura elegans* Leach, 1815, probably has priority. However, following her application to the International Commission on Zoological Nomenclature the name *squamata* was placed on the Official List of Specific Names in Zoology (Opinion 1560, 1989).

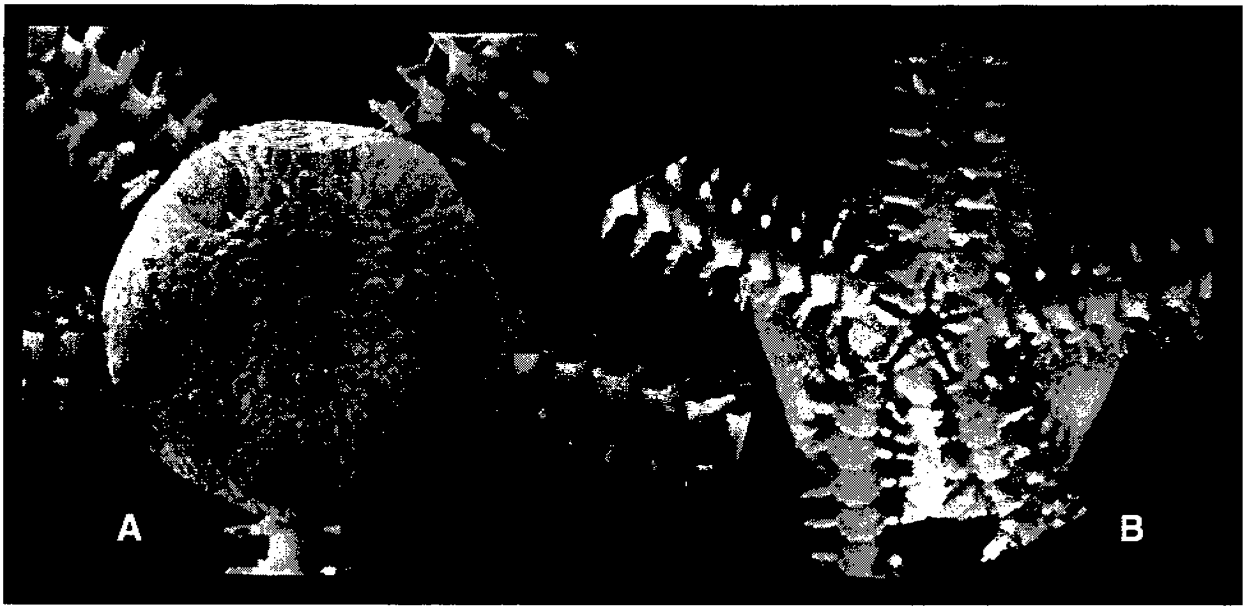

Figure 7.10. *Amphipholis squamata* (Delle Chiaje): A, disk, dorsal view (LACM 41-5.12; dd = 3.6 mm); B, disk, ventral view (LACM 41-5.12; dd = 3.3 mm).

It should be noted that the species, as currently recognized, may actually comprise more than one taxon (Hendler *et al.*, 1995). See remarks under *A. pugetana.*

Distribution. Reputedly cosmopolitan, reported for all but extreme polar regions, and at depths from the intertidal to 1,330 m (Hendler *et al.*, 1995). Preliminary examination of material at LACMNH suggests that in Southern California this species typically occurs in littoral habitats; *A. pugetana* may be relatively more numerous offshore.

Biology. Aspects of the species' biology summarized in Austin and Hadfield (1980) and Hendler *et al.* (1995), include its specializations for viviparous reproduction, hermaphroditism, and luminescence and fluorescence. *A. squamata* is a browser and detritus feeder (Kyte, 1969). Despite its small size, it is the host of a number of unusual parasites. Nielsen (1932) notes that elsewhere the species is parasitized by copepods in the genus *Cancerilla*, but none of 500 Eastern Pacific specimens in his collection were infested.

The importance of this species in California waters is evidenced in the survey reports of Hartman (1955, 1966), Hartman and Barnard (1958, 1960), and Jones (1969), but some occurrences of the species noted in these and similar studies probably are based on records of misidentified *A. pugetana*. Barnard and Ziesenhenne (1961) recognized *A. squamata* at 25% of 176 stations taken between 9-243 m depths from Pt. Conception, California to the Mexican border. They calculated an overall population density of 44 individuals/m^2. My examination of samples still at LACMNH from that survey indicate that identification of *A. pugetana* and *A. squamata* were frequently confused, casting doubt on the survey data. Thompson and Jones (1987) report both species from the lower slopes of Southern California offshore basins, with densities of *A. squamata* up to 70 individuals/m^2.

Amphiura arcystata H.L. Clark, 1911

Figure 7.11

Amphiura acrystata (*lapsus* for *arcystata*) H.L.Clark, 1911:10, 145-148, fig. 58a-i.—Matsumoto, 1917:194, 196, 203, 359.—Downey, 1969:20.

Amphiura arcystata, Clark, 1915:224.—1940:331, 336.—May, 1924:283.—Nielsen, 1932:264.—Ziesenhenne, 1937:223.—D'yakonov, 1954:64-65.—Barnard and Ziesenhenne, 1961:140, 143.—Hartman, 1963: 85, 125, 154, 185, 218, 251, 285, 320, 335, 349, 382.—A. M. Clark, 1965:44-45.—Boolootian and Leighton, 1966: 4, 8, fig. 7.—A.M. Clark, 1970: 10-11.

Amphiura (*Amphiura*) *arcystata*, Irimura (in Imaoka *et al.*), 1991:142, text fig.

Hemilepis arcystata, Fell, 1962:10, 19.

Material Examined. California: Santa Maria Basin, Phase I Sta. BSV-042, 100 m (1, USNM primary voucher); Phase I Sta. BSS-064, 59 m (3 juvenile, SBMNH secondary voucher [as Amphiuridae sp. A, *Amphiura acrystata*]); Phase II Sta. R-1, 91 m (3 juvenile, CAMP voucher).—Off Santa Cruz Id., R/V *Velero III* Sta. AHF 996-39, 64-82 m (26, LACM 39-100.7).—Off Santa Barbara Id., R/V *Velero III* Sta. AHF 975-39, 46-49 m (60, LACM 39-79.11).

Description. A large amphiurid, attaining over 16 mm dd with arms 10 to 20 times the disk diameter. A 7 mm dd individual has arms 80 mm long, a 10 mm dd individual has arms 150 mm long, a 15 mm dd individual has arms over 195 mm in length.

Disk lobate, indented interradially, covering ranging from full coating of small, imbricating scales to nearly naked (see Clark, 1911: fig. 58). Disk central and radial regions generally covered with soft tissue and relatively few minute scales, largest scales surrounding radial shields. Radial shields slender, blunt tipped, distinctly curved, diverging proximally; shields shaped like paired parentheses ( ), not in contact.

Jaws projecting ventrally, framing tissue-covered cavity proximal to oral shield. Oral gap conspicuous, widening distally. Infradentals large, blocklike, generally in contact, extending high in mouth. Buccal scale high on jaw, small, flattened, pointed or spinelike; distal papilla large, bluntly pointed, erect, projecting ventrally, originating near proximal tip of adoral shield. Tooth chisel-shaped with broad convex or straight free edge of imperforate stereom.

Oral shields diamond-shaped to spade-shaped, sides slightly concave, corners lobate, lateral lobes largest. Madreporite twice as large as oral shields, inflated, with pores in lateral series. Adoral shields with 3 rounded corners, proximal lobes separated, radial lobes abutting first ventral arm plates. Ventral interradii fleshy, scales small, scattered; conspicuous imbricating scales bordering adradial edge of bursal slit. Bursal slits capacious.

Arms constricted near disk, widening, then tapering distally; in cross section broader than tall, dorsal surface very slightly rounded, ventral surface nearly flat.

Dorsal arm plates twice as wide as long, generally overlapping, ovoidal to subrectangular, lateral edges short, sometimes angular. Several basal plates reduced in size, surrounded by integument. In dorsal aspect, wedge of soft tissue and part of lateral arm plate visible between successive dorsal arm plates. In alcohol plates appear thin, translucent, revealing vertebrae beneath.

Lateral arm plates slender, widely separated; successive plates connected by soft tissue. Five to 8 arm spines near disk, smooth, thick at mid-shaft, gradually tapering toward hollow base and slender rounded tip. Spines increasing markedly in length from dorsal to ventral, 1-2 joints in length, dorsal and ventral spines compressed laterally, middle spines dorso-ventrally compressed. Two tentacle scales, thin, flat, ovoidal; scales on lateral arm plate and on ventral arm plate at right angles, incompletely covering large tentacle pore.

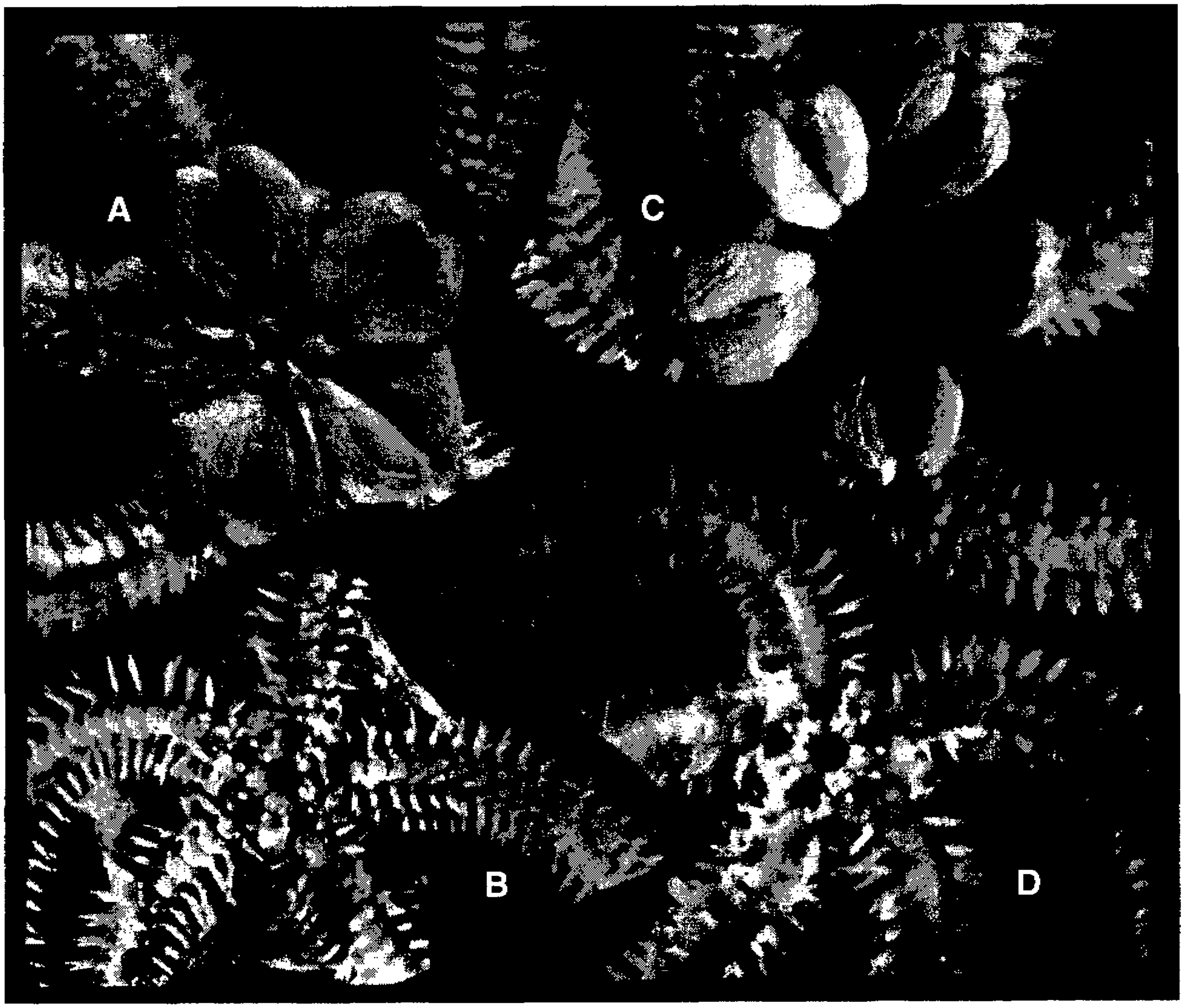

Figure 7.11. *Amphiura arcystata* H.L. Clark: A, disk, dorsal view (LACM 39-79.11; dd = 6.4 mm); B, disk, ventral view (LACM 39-100.7; dd = 10.1 mm); C, disk, dorsal view; D, disk, ventral view (LACM 39-79.11; dd = 6.4 mm). Note variability in disk scalation.

Ventral arm plates thick, opaque; first ventral arm plate in oral slit small and slender, several adjacent plates longer than wide, other proximal plates wider than long, hexagonal or octagonal, overlapping.

Color: Disk gray to violet gray or brownish, in small specimens primary plates brownish-black; radial shields brown or brownish-black with white edge or distal tip, scales surrounding radial shields tan, brown, or brownish black with white edge, ventral interradius gray, oral frame gray or tan and whitish, whitish scales border bursal slits, reddish brown stomach and gonads visible through thin body wall. Dorsal surface of arms gray, brown, or tan, with irregular bands of pale tan, cream or whitish; arm spines tan, brown, or gray, ventral surface of arms salmon colored, more cream colored distally, connective tissue on arms whitish to violet. Eggs pale pink.

Specimens in alcohol fade to pale gray, brown, and yellowish, with disk darker than arms and with dark radial shields, lateral arm plates, and arm spine bases. Densely pigmented stomach visible through naked portions of disk. Purplish muscle masses visible between joints on dorsal surface of arm.

Distribution. Mexico and Southern California to Monterey, California at 15-844 m, and in Japan at 108-848 m depths (H.L. Clark, 1911, 1915, 1940; May, 1924: Nielsen, 1932; Ziesenhenne, 1937; Hartman, 1963; A. M. Clark, 1965; Irimura, in Imaoka *et al.*, 1991).

Remarks. Juvenile and small individuals 1.5-2.5 mm dd are unlike the adults in appearance. They have prominent primary plates, the disk completely covered with thin scales, radial shields relatively larger than in mature individuals, fan-shaped dorsal arm plates, elongate ventral arm plates, modified oral papillae array, and they lack tentacle scales. H. L. Clark (1911:147) observed that small specimens have the disk almost completely scaled and the largest have scales only around the radial shields, but scale cover is not wholly related to age; "diversity in the amount of scaling on the disk and interbrachial spaces below is most remarkable, affording an unusually interesting case of resorption of calcareous matter." A.M. Clark (1965, 1970) discussed taxonomic implications of the morphological variability shown by this species.

The correct spelling of the species name is *arcystata*, although Downey's (1969) comments might be interpreted to suggest otherwise. In the original description (H. L. Clark, 1911), *acrystata* was a *lapsus* for *arcystata*, and the error was noted and corrected by the author in a later publication (H. L. Clark, 1915).

Biology. Barnard and Ziesenhenne (1961) found this species at 22% of 176 stations taken between 9-243 m depths from Pt. Conception, California to the Mexican border. They calculated a mean population density of 2.8 individuals/m^2, but densities are certainly higher at some localities where the species occurs. They found that *A. arcystata* is typically a "subdominant" in the benthic community characterized by *Amphiodia urtica*. It is a burrowing ophiuroid, and the very long arms of adult specimens suggest that the disk may be situated at least several centimeters below the surface of the sediment. I have found that the proximal tube feet are smooth and the distal tube feet are highly papillose, as is often the case in suspension feeding ophiuroids.

Amphiura diomedeae Lütken and Mortensen, 1899

Figure 7.12

Amphiura Diomedeae Lütken and Mortensen, 1899:151-152, pl. 12, figs. 1-7.

Amphiura diomedeae, H.L. Clark, 1911:10,15,17,18, 20,140-141.—1915:225.—1913:214.—1917:436-437.—Campbell, 1921b:47.—Boone, 1933:105-106, pl. 61.—Koehler, 1922:4, 158-159, pl. 67, figs. 7-10.—Fell, 1962:21.—H. L. Clark, 1939:56-57.—Hartman, 1963:86, 383, 401.

Amphiura (Section *Amphiodia*) *diomedeae*, Koehler, 1907:306.

Amphiura diomediae, A.M. Clark, 1970:39-44, 48, fig. 8n,o.

Amphiura koreae, Matsumoto, 1917:151-152, 174, 195, 198, 356 (in part ?, not *A. koreae* Duncan, 1879).—Astrahantseff and Alton, 1965:1414, 1416, 1420, 1422 (not *A. koreae* Duncan ?).

Material Examined. Oregon: Off Columbia River mouth, R/V *Commando*, 460 m (1, LACM 64-240.1). - California: Santa Maria Basin, Phase I Sta. BSS-062, 582 m (1, USNM primary voucher, [as *Amphioplus* sp. A]).—Off Santa Barbara, R/V *Velero IV* Sta. AHF 3036-55, 400 m (1, LACM 55-19.3).—Off Santa Catalina Id., *R/V Velero IV* Sta. AHF 2413-53, 375 m (11, LACM 53-112.4).—Mexico: Off Mazatlan, R/V *Albatross* Sta. 3429, 1,680 m, syntype (1, USNM 19535).—Panama: Gulf of Panama, R/V *Albatross* Sta. 3394, 935 m, syntypes (3, USNM 19533); R/V *Albatross* Sta. 3393, 1,866 m, syntypes (10, USNM 19532); off Azuero Peninsula, R/V *Albatross* Sta. 3392, 2,323 m (3, USNM 19531).—Ecuador: Off Cojimies, R/V *Albatross* Sta. 3398, 2,877 m, syntype (1, USNM 19534).—Japan: Honshu Id., off Port Arari, R/V *Albatross* Sta. 3699, 732-1,328 m (12, USNM 26630); Sagami Bay, R/V *Albatross* Sta. 5087, 1,123 m (2, USNM 26618); Suruga Gulf, R/V *Albatross* Sta. 5057, 494 m (3, USNM 27114).

Description. An amphiurid of moderate size, attaining a disk diameter of 15 mm. A specimen 7 mm disk diameter has arms over 50 mm long; one 13 mm disk diameter has arms 135 mm long.

Disk rounded, 5-lobed, indented interradially, covered with relatively few, distinct, angular, imbricating scales. Primary plates discernible; primaries and several scales between paired radial shields are largest on the disk. Radial shields prominent, 1/4 disk diameter, 2-3 times longer than wide, broadest distally, with straight, thickened distal edge, abruptly narrowing proximally; shields in contact distally or separated by single small scale, separated by wedge of scales proximally.

Jaws with sides concave and flaring, narrowing ventrally, diverging dorsally. Oral gap broad, large diastema separating proximal and distal oral papillae, broad distal end of oral slit filled by large first ventral arm plate, second oral tentacle pore conspicuous in ventral aspect. Oral papillae may vary in number and appearance among jaws of an individual. Infradental papillae flattened, often with proximal point; pairs separated, in contact, or displaced by small apical oral papilla. Buccal scales high in jaw, ranging from small, triangular to large, crescentic. Distal oral papilla spinelike, or flattened and bluntly pointed, may be single, paired, or absent on different jaws. Tentacle scale of second oral papilla adpressed, flat, operculate, set between adoral shield and first ventral arm plate. Teeth usually with constriction behind free edge.

Oral shields pentagonal to rhombic, corners rounded, with central depression. Adoral shields large, equal in length to oral shields, proximal lobes blunt, radial lobe sharply pointed. Adoral shields broadly separated by first ventral arm plate. Oral and adoral shields thin; madreporite inflated, multiperforate.

Arms gradually tapering, beginning at edge of disk; in cross section rounded above and flat below.

Proximal dorsal arm plates broadly fan-shaped; proximal end pointed, edges straight; distal end convex. Dorsal arm plates narrowly separated by lateral arm plates and wedge of connective tissue.

Lateral arm plate with prominent, thick, spine-bearing ridge. Three arm spines with thick base, gradually tapering to acute point with slight distal bend, smooth, delicate, hollow. Dorsal-most spine shortest, most slender; middle spine largest, somewhat dorso-ventrally compressed, slightly longer than the arm joint.

Ventral arm plates pentagonal, edges concave, disto-lateral corners large, lobate; broader than long on proximal joints, becoming more elongate on distal joints. Two tentacle scales rounded or bluntly pointed, covering most of tentacle pore on basal joints.

Color: As noted by H. L. Clark (1939), preserved specimens range from entirely ivory white to having grayish disks and yellowish white arms. Lütken and Mortensen (1899) described specimens in alcohol as having a bluish disk and white or pale brown arms, some with a reddish at the outer end of the radial shields.

Remarks. It is only because of the intraspecific variability of the oral formula in *A. diomedeae*, characterized by A. M. Clark (1970), that I have retained this species in the genus *Amphiura*. As shown by Hendler (1988), the homologies between the oral papillae of amphiurids suggest that distinctions between nominal *Amphiura* and *Amphioplus* species with 4 pairs of oral papillae can be baseless. Once sufficient material is available to clarify the homologies of its oral papillae, the inclusion of *A. diomedeae* in *Amphioplus* may be warranted.

H.L. Clark (1939), based on published descriptions, did not accept Matsumoto's (1917) synonymy of *Amphiura diomedeae* Lütken and Mortensen with *A. koreae* Duncan. A. M. Clark (1970) examined relevant type material, noting that most specimens of *A. koreae* (sensu Matsumoto) are referrable to *A. diomedeae* Lütken and Mortensen. In addition, she found that the holotype of *A. koreae* Duncan has oral structures unlike an *Amphiura* species.

A. M. Clark (1965, 1970) suggested that *A. diomedeae* may be synonymous with *Amphilepis diastata* Murakami and with *Amphiura caulleryi Koehler*, raising additional questions regarding its taxonomic status. Fortunately, Irimura's account (in Imaoka *et al.* 1991) of *Amphiura* (*Amphiura*) *koreae*, based on new Japanese collections, shows that additional material could be made available to evaluate the(se) species.

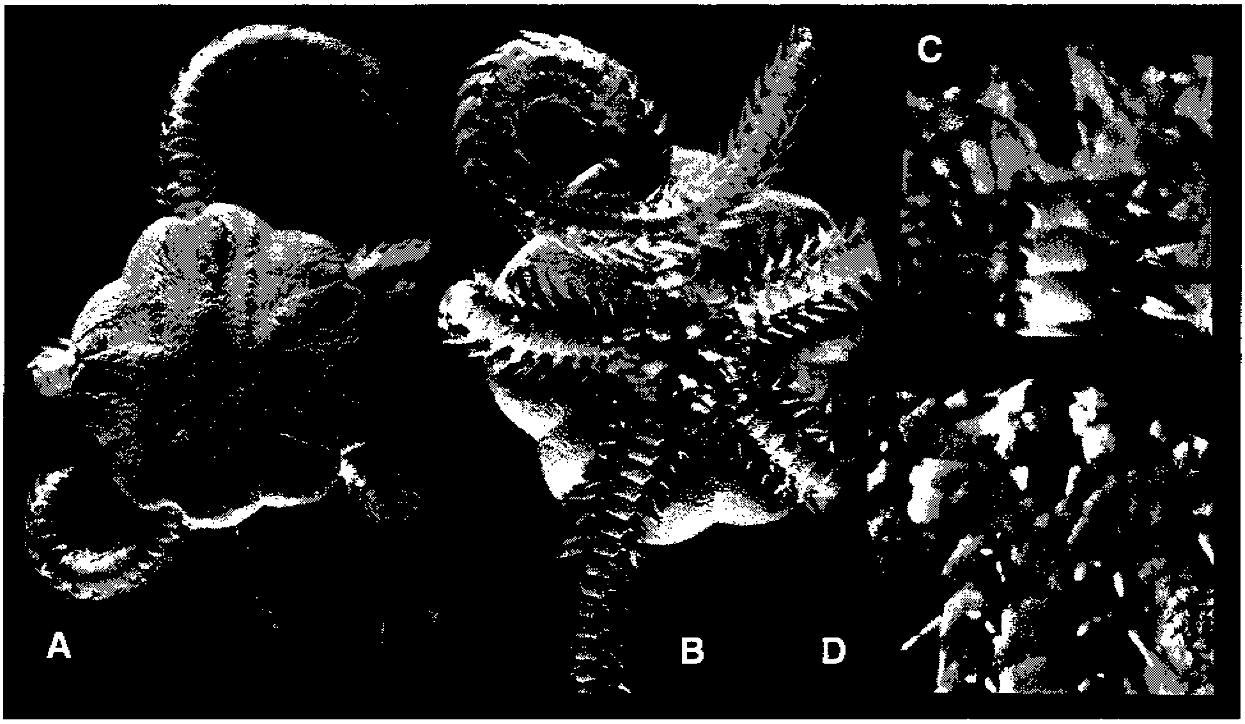

Figure 7.12. *Amphiura diomedeae* Lütken and Mortensen: A, disk, dorsal view; B, disk, ventral view; C, oral frame (USNM 19532, syntype; dd = 15.1 mm); D, oral frame (USNM 19532, syntype; dd = 11.0 mm). Note variability of *Amphioplus*-like oral papillae.

Distribution. Since its discovery, the species has been reported from off: Panama and Ecuador, 935-2,877 m (Lütken and Mortensen, 1899), Japan 71-1,369 m (H.L. Clark, 1911), California, 869-1,205 m (H.L. Clark, 1913, 1915), Tahiti, 1,325 m, Peru, 1,895 m (H.L. Clark, 1917), Philippine Islands, 368-567 m (Koehler, 1922), Costa Rica, 183 m (Boone, 1933), the Maldives, 797 m and South Arabian Coast, 1,046 m (H. L. Clark, 1939). Additional records now exist for California, Oregon, and Washington, 450-3,030 m (Hartman, 1963; Astrahantseff and Alton, 1965 [as *A. koreae*], Carey, 1990). As discussed above, some of these reports may pertain to *A. koreae* Duncan.

Biology. Summers (1993) found that *A. diomedeae* and *Amphiura carchara* H. L. Clark are the dominant ophiuroids at depths between 200 and 3,000 m off the central California continental slope. In her study area, *A. diomedeae* composed 26% of the ophiuroids sampled. Densities of individuals, when they occurred in box cores, ranged from 0.2-0.42/0.1 m^2; similar densities (as *A. koreae*) have been found off the Oregon coast (Alton, 1972).

The extensive bathymetric range of the species exposes it to a considerable range of environmental variation. Bottom temperatures recorded at collecting sites range from 1.6-20.3°C (Lütken and Mortensen, 1899; H. L. Clark, 1911, 1913, 1917).

Dougaloplus amphacanthus (McClendon, 1909)

Figures 7.13 and 7.14

Ophiocnida amphacantha McClendon, 1909:46-47, figs. 24, 25.—H.L. Clark, 1915:250.—Campbell, 1921b:48.

Amphiacantha amphacantha, Matsumoto, 1917:178.—Nielsen, 1932:296-297.—Barnard and Ziesenhenne, 1961:143.—Hartman, 1963:85, 217, 237, 285, 305, 349, 382.—Boolootian and Leighton, 1966:5, 10, fig. 15.

Dougaloplus amphacantha, A. M. Clark, 1970:33-34, 79.

Amphioplus hexacanthus H.L. Clark, 1911:10, 170.—Matsumoto, 1917:170, 172, 358.—Barnard and Ziesenhenne, 1961:135-151.—Fell, 1962: 22.—Hartman, 1963:85, 153, 217, 285.—Parker, 1964:359.—Boolootian and Leighton, 1966: 5, 10, fig. 17.—Sutton, 1976:349.

Amphilimna pentacantha H.L. Clark, 1911:10, 172-173, fig. 77a-c.—1915:259.—Campbell, 1921b:48.—May, 1924:281-282.

Amphiacantha pentacantha, Matsumoto 1917:178.

Material Examined. California: Point Reyes, R/V *Albatross* Sta. 3165, 91 m, syntypes (4, USNM 25583 [as *Amphioplus hexacanthus*]).—Monterey Bay, off Point Pinos, R/V *Albatross* Sta. 3131, 88 m, paratypes (36, USNM 27141 [*as Amphilimna pentacantha*]).—Santa Maria Basin, Phase I Sta. BSV-042, 100 m (1+, USNM primary voucher); Phase I Sta. BSR-073, 98 m (1, SBMNH secondary voucher); Phase II Sta. PJ-1, 145 m (5, CAMP voucher); Phase I Sta. BSS-064, 59 m (5, SBMNH secondary voucher [as *Amphioplus hexacanthus*]); Phase I Sta. BSR-021, 49 m (2, USNM primary voucher).—Los Angeles, off El Segundo, R/V *Velero IV* Sta. AHF 5960-58, 144 m (4, LACM 58-140.7).—Mexico: Gulf of California, off Isla las Animas, R/V *Velero IV* Sta. AHF 11837-67, 1,100-1,326 m (48, LACM 67-302.1).

Description. This moderately large amphiurid was originally described on the basis of a specimen 7.5 mm dd with arms 10 times that length. Disk soft, lobed, indented radially and/or interradially, covered with numerous small, overlapping scales bearing evenly spaced spines. Spines acute or with tip slightly expanded. Disk spines short, slender, tapered, smooth. Radial shields slender, tapering and diverging proximally, distal tips in contact.

Jaws narrow with apex jutting ventrally, oral gap teardrop-shaped. Teeth with straight, narrow tip, edge composed of imperforate stereom. Five oral papillae; infradental papillae separated, blocklike, smoothly rounded; buccal scale near ventral edge of jaw, laterally flattened, pointed; two distal papillae in contact, pointed, spinelike; oral tentacle scale rounded, flat, abutting first ventral arm plate and adoral shield. Oral shields equidimensional or longer than wide, with four lobes or ovoid with narrow distal lobe, overlapping central part of adoral shield. Madreporite more irregular in outline than oral shield, larger, thicker, with single pore. Adoral shields with small proximal lobes touching or nearly so above oral shield, adoral lobes forming acute angle between first and second ventral arm plates.

Ventral interradius with scale and spine cover similar to dorsal disk, cover reduced near oral shield. Bursal slits extending from oral shield nearly to disk edge; prominent series of overlapping scales reinforcing adradial edge of slit.

Arms long, slender, somewhat wider at midlength, narrowing proximally and distally; in cross section more rounded dorsally than ventrally, wider than high. Conspicuous band of soft tissue between arm joints.

Dorsal arm plates ovoidal, wider than long, barely in contact, lateral edges sometimes truncate; several plates near disk rounded, diamond-shaped.

Lateral arm plates narrow, with prominent spine-bearing ridge. Arm spines hollow, internal channel narrow. Up to 6 arm spines on proximal joints, upper and lowermost spines longest, pointed; middle spines with 1-2 microscopic teeth at tip; on distal joints with 3-5 spines, upper spine shortest, lowest 1-2 spines longest, second from bottom flattened with broad base, thin lateral edge microscopically roughened, 1-2 hyaline teeth at tip. In adults, upper arm spines laterally flattened, toothed arm spines dorso-ventrally flattened, ventral spine nearly round. Two (or one) tentacle scales, small, thin, leaving most of tentacle pore uncovered; scale on lateral arm plate larger.

Ventral arm plates barely in contact or slightly separated by lateral arm plates; first ventral arm plate forming knob at outer edge of oral slit; plates below disk longer than wide, distal plates nearly equilateral, octagonal to pentagonal, with rounded proximal edge, medial distal indentation.

Variation: Specimens 4 mm disk diameter or less are not truly juvenile since they have recognizable gonads, but they differ from larger individuals in having a spinelike buccal scale, distal oral papillae with rounded tips, four arm spines, numerous joints bearing only 1 tentacle scale, ventral arm plates in contact, and reduced disk spination.

Color: In alcohol disk gray; radial shields, jaws, adoral and oral shields, and lateral arm plates often with patches of yellow pigment. Arms faded reddish-pink, lateral arm plates with orange pigmentation, central portions of ventral arms plates reddish. Various authors report that preserved material is yellowish overall, or has the disk gray or greenish and the arms yellowish, or yellowish white (McClendon, 1909; May, 1924; Nielsen, 1932). Dried specimens are pale gray.

Remarks. As indicated in the synonymy above, this species was placed in *Ophiocnida* by McClendon (1909), and transferred to *Amphiacantha* by Matsumoto (1917). Nielsen (1932), proposed *A. pentacantha* (H. L. Clark) to be a junior synonym, a point that I verified by examination of H. L. Clark's type material. Since the generic name *Amphiacantha* was preoccupied, A. M. Clark (1970) provided the replacement name *Dougaloplus*, and revised the genus. She suggested that *Amphiacantha derjugini* D'yakonov is a synonym of *D. amphacanthus*, but possible differences in the arm spine shape and tentacle scale number open that conclusion to question.

I have synonymized *Amphioplus hexacanthus* with *D. amphacanthus*, based on a comparison of the syntypes of *A. hexacanthus* (Figure 7.14) with the original description and specimens recognized as *D. amphacanthus*, McClendon's original specimens of the latter presently being unavailable. I surmise that H.L. Clark would have recognized the correspondence between the two nominal species had there been dorsal disks among the 6 fragmentary specimens of *A. hexacanthus* at his disposal. My only reservation in this matter is the absence of any mention of toothed arm spines by McClendon (1909) and Nielsen (1932), a characteristic that is distinctive in this species. However, the oversight is less surprising given that H.L. Clark recognized toothed spines in *A. hexacanthus*, but ignored them in his description of *A. pentacantha*, as did May (1924); toothed spines are present in the type material of both nominal species (Hendler, prev. unpub.).

Distribution. Gulf of California (doubtful locality?), San Diego to Pt. Reyes, California, and Uraga Strait, Japan (doubtful locality, see below), at 62-1,326 m depths (McClendon, 1909; May, 1924; H. L. Clark, 1911, 1915; Nielsen, 1932; Hartman, 1963, this report). One of H. L. Clark's type lots of *A. hexacanthus* (consisting of arm fragments only, which I have not examined) reportedly originated from Uraga Strait, off Tokyo, Japan. However, the nominal species *A. hexacanthus*, has not been rediscovered from Japan (Irimura, *et al.* 1995). On that basis, I consider an amphi-Pacific distribution doubtful.

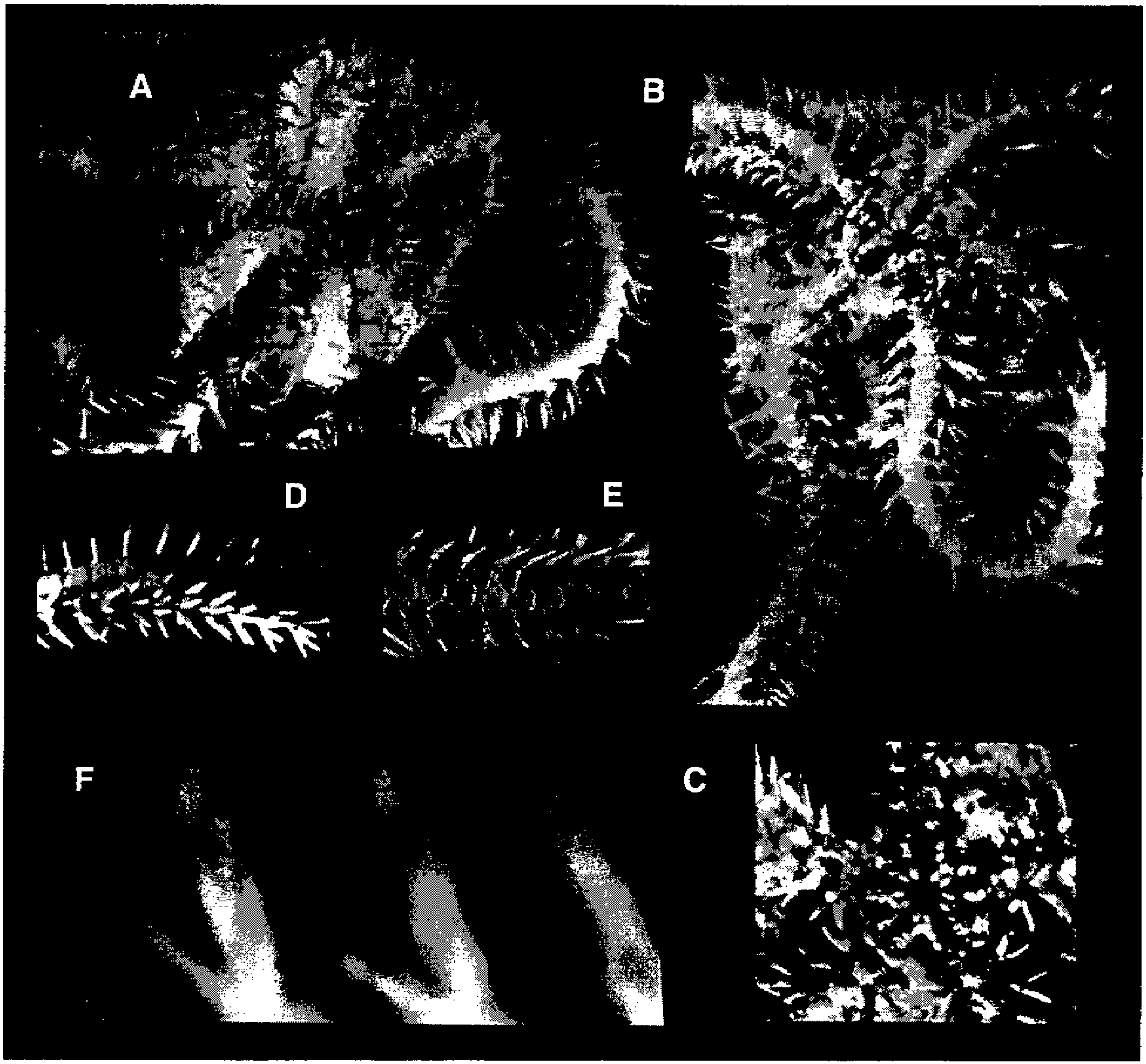

Figure 7.13. *Dougaloplus amphacanthus* (McClendon): A, disk, dorsal view; B, disk, ventral view; C, oral frame; D, arm, dorsal view; E, arm, ventral view; F, arm spines, showing glassy teeth (LACM 58-140.7; dd = 7.4 mm).

Biology. The synonymy of *Amphioplus hexacanthus* with *D. amphacanthus* has an important implication with regard to the offshore benthic ecology of Southern California. *Dougaloplus amphacanthus* would appear to be the third most abundant ophiuroid on the Southern California coastal shelf, its distribution more extensive and its population densities greater than previously recognized.

Barnard and Ziesenhenne recorded *A. hexacanthus* at 30% of 176 stations taken at 9-243 m depths from Pt. Conception, California to the Mexican border, estimating a mean population density of 13.1 individuals/m^2, with densities higher at localities where individuals are present. In the same study, *D.* (as *Amphiacantha*) *amphacanthus* was found at 15% of the stations, at lower densities than reported for *A. hexacanthus*. Presumably, the original data could be reexamined to accurately determine the distribution of *D. amphacantha*.

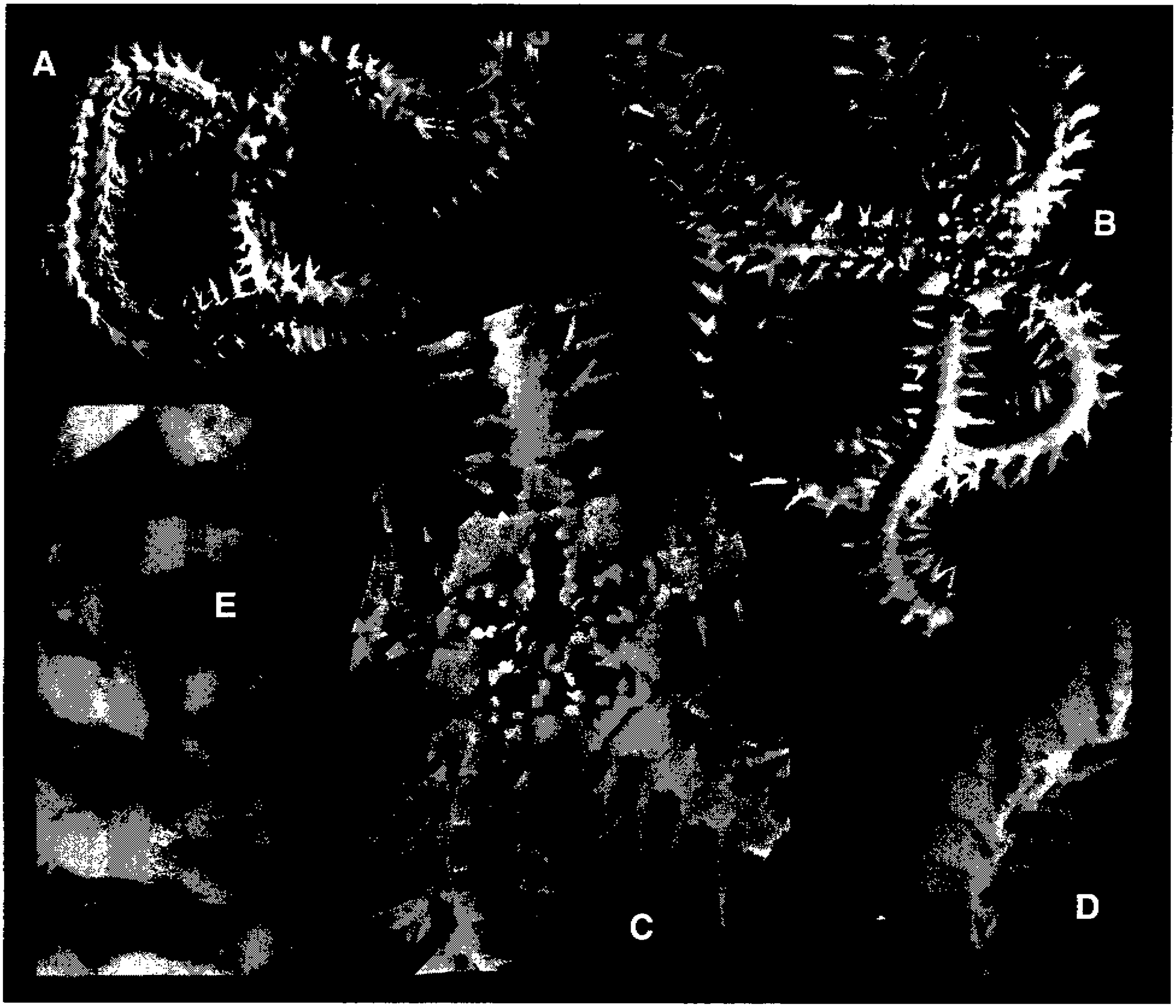

Figure 7.14. *Amphioplus hexacanthus* H. L. Clark: A, entire, dorsal view, disk missing; B, entire, ventral view; C, oral frame; D, arm, dorsal view, showing elongate, flattened, middle arm spines; E, arm spines, showing glassy teeth (USNM 25583, syntype; ofl = 2.5 mm).

Barnard and Ziesenhenne (1961) described the *Amphioplus hexacanthus* community (more correctly the *Dougaloplus amphacanthus* community) as one of three major benthic communities on the coastal shelf between Pt. Conception and Mexico, noting *Amphiodia urtica* as a community subdominant. The association was found to occur in silty-sand sediments in which silt and sand are found in nearly equal proportion, most prominently on the California shelf off San Pedro, Santa Monica, and Oceanside in 13-55 m depths, and several hundered miles to the north in deeper waters, 55-91 m, on the Monterey Bay shelf. Hartman (1955, 1966), Hartman and Barnard (1958 1960), and Jones (1969) provide additional evidence for the numerical abundance of the species.

Amphiuridae sp. juvenile

Figure 7.15

Among the many immature specimens of Amphiuridae in this collection, one was sufficiently distinctive to warrant a detailed characterization.

Material Examined. California: Western Santa Barbara Channel, Phase I Sta. BSS-087, 762 m (1, USNM primary voucher [as *Amphiodia psara*]).

Description. The specimen has a disk diameter only 3.3 mm (ofl 1.4 mm), with arms broken near the disk.

Disk rounded pentagonal, flat; cover consisting of primary plates, large interradial and marginal scales, separated by smaller, thin, overlapping scales. Radial shields half-circle shaped, twice as long as wide, in contact throughout.

Infradental papillae elongated, with distal ends pointed, diverging. Buccal scale flattened, subtriangular, situated high in jaw. Two lateral papillae, flat, free edge expanded.

Oral shields subpentagonal, about as long as wide; madreporite larger, inflated, bearing one blunt spinelet. Adoral shields nearly equal in size to oral shield, meeting broadly above oral shield; radial corner pointed, inserting between first and second ventral arm plates.

Ventral interradius scale-covered, scaling reduced in density near oral shield. Genital slit extending from oral shield to disk edge, scales bordering edges of slit.

Dorsal arm plates nearly half-circle shaped with proximo-lateral edges straight, distal edge somewhat protruding, plate about twice as wide as long; successive plates in contact.

Lateral arm plates broad, with strong, distally directed spine-bearing ridge. Three arm spines, smooth, robust, with broad base, gradually tapering, tip quite blunt; dorsal and ventral spines laterally compressed; middle spine dorso-ventrally compressed. Tentacle scales absent.

Ventral arm plates subpentagonal, as long as wide, posterolateral corners lobate, distal edge concave; successive plates narrowly separated by lateral arm plates.

Remarks. This specimen belongs to one of the amphiurid taxa with an adult oral formula consisting of 4 or more oral papillae. It does not appear to be a juvenile growth stage of a species described in the present report.

The possibility that it is an *Amphiodia* species can be ruled out. *Amphiodia* individuals of this size lack a buccal scale and show species-specific morphological features; for example juvenile *Amphiodia psara* H. L. Clark possess a long shank on the oral shield and have the arm spines laterally compressed. It is not *Amphioplus strongyloplax* or *Dougaloplus amphacantha*, both of which at a similar disk diameter have a differing and distinctive spine morphology. It does not appear to represent the Eastern Pacific *Amphioplus* species, *A. daleus* (Lyman) or *A. philohelminthius* Ziesenhenne, and does not appear to be a juvenile *Amphiura diomedeae* or a more typical *Amphiura* species. Furthermore it lacks the disk spines, granulation, oral papilla shape, and other characteristics of Eastern Pacific *Ophiocnida* and *Amphichondrius* species.

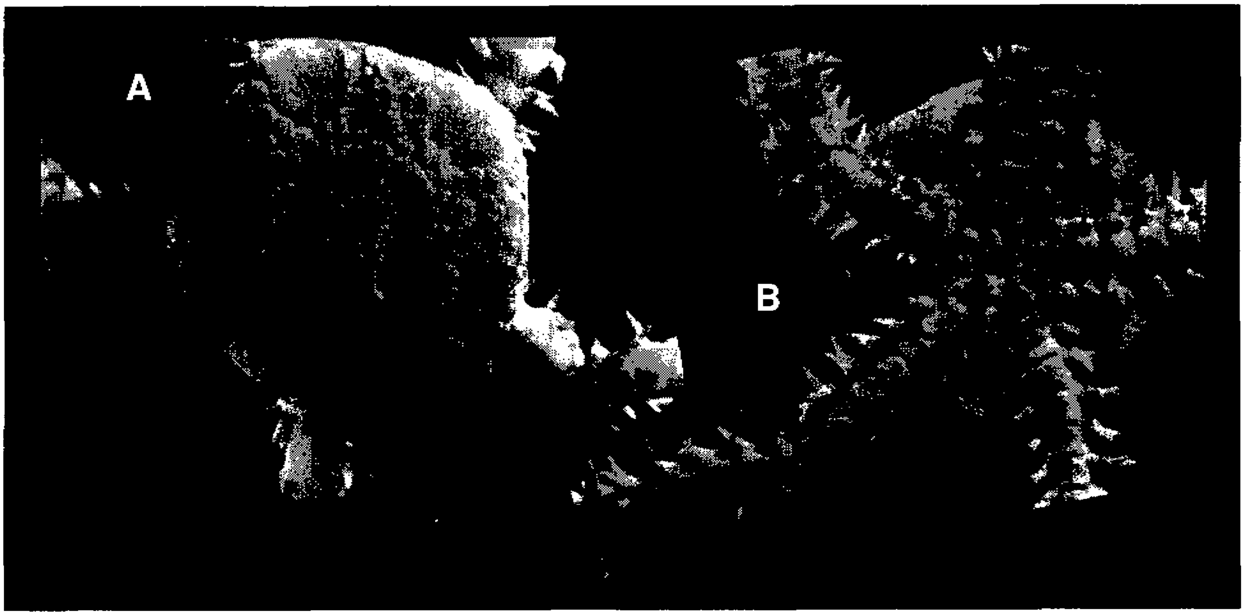

Figure 7.15. Amphiuridae sp. juvenile: A, disk, dorsal view; B, disk, ventral view (USNM, primary voucher; dd = 3.3 mm).

Family Ophiacanthidae

Ophiacantha diplasia **H. L. Clark, 1911**

Figure 7.16

Ophiacantha diplasia H. L. Clark, 1911:10, 209-211, fig. 97a-c.—1915:198.—May 1924:272-273, fig. 3a,b.—Hartman, 1963:85.—Astrahantseff and Alton, 1965:1414-1415, 1420.—Boolootian and Leighton, 1966:7, 8, fig. 30.

Ophiophthalmus diplasia, Kyte, 1982:508.

Material Examined. California: Santa Maria Basin, Phase I Sta. BRA-016, 91.5-123 m (3, SBMNH secondary voucher); Phase I Sta. BRA-027, 96-126 m (1 juvenile cf. *O. diplasia*, USNM primary voucher [as *Ophiophthalmus normani*]).—Western Santa Barbara Channel, Phase I Sta. BRA-002, 110-126 m (6, USNM primary voucher).—Monterey Bay, off Pt. Pinos, R/V *Velero III* Sta. AHF 890-38, 90-99 m (1, LACM 38-158.2).—Off Santa Barbara, R/V *Velero IV* Sta. AHF 6888-60, 113 m (6, LACM 60-276.1).—Off Santa Rosa Id., R/V *Velero III* Sta. AHF 1397-41, 132-141 m (5, LACM 41-177.2).—Off Santa Catalina Id., R/V *Velero IV* Sta. AHF 1995-50, 732 m (1, LACM 50-100.2).—Off San Clemente Id., R/V *Velero III* Sta. AHF 1023-39, 101-201 m (1, LACM 39-127.13).—Los Angeles, off Redondo Beach, Burch 40122, 90 m (3, LACM 40-341.1).

Description. An ophiacanthid species of moderate size. Largest specimens attain 25 mm dd; a specimen 23 mm dd has arms approximately 150 mm long.

Disk rounded pentagonal, flat. Densely covered with closely spaced, rough, elongate granules; granules somewhat longer and larger towards disk margin. Radial shields subtriangular, small, approximately one-tenth diameter of disk in length; broad distal edge relatively bare of granules.

Jaws broad, with apex jutting ventrally; oral gap wide, not sealed by oral papillae. Terminal oral papilla generally single, sometimes paired; 5-7 lateral oral papillae, long, spatulate, with bluntly rounded tip; proximal papillae laterally compressed, distal papillae dorso-ventrally compressed. Outer oral tentacle large, emerging at edge of oral slit, associated tentacle scale triangular, originating on first ventral arm plate. Teeth chisel-shaped, free edge unevenly rounded. Oral shields wider than long, with two large lateral lobes, narrow distal shaft; madreporite larger, more irregular in shape. Adoral shields three-lobed; proximal lobe extending above oral shield, paired shields nearly in contact.

Bursal slit widest proximally, extending from shaft of oral shield to edge of disk, adradial edge bordered by naked scales. Periphery of ventral interradius covered by V-shaped field of granules or spinelets, thin imbricating scales covering proximal region.

Arms gradually tapering, shape obscured by long arm spines; in cross section broader than tall, dorsal surface somewhat more curved than ventral surface.

First ventral arm plate U-shaped, others subpentagonal, broader than long on proximal joints, becoming equidimensional, then longer than wide and fan-shaped near arm tip; plates beneath disk depressed, those beyond disk edge with slight medial keel or thickened distal edge; successive plates barely in contact or separated by lateral arm plates.

Lateral arm plates wide, with prominent spine-bearing ridge, sharply pointed lobes intruding between dorsal and ventral arm plates; successive plates separated by narrow band of soft tissue. Maximum of 7 arm spines, decreasing in size ventrally, two uppermost spines dramatically longer, more acutely pointed than two ventral-most spines, longest spine equal in length to 4-7 arm joints. Spines erect, hollow, compressed, gradually tapered, tips truncate or bluntly rounded, lateral edges bearing microscopic echinulation. Longest spines on first two arm joints directed toward center of disk. Two tentacle scales elongate, flat; inner scale longer, narrower, more acutely pointed than outer scale.

Dorsal arm plates diamond-shaped rhombic to fan-shaped, medial portion elevated; proximal plates wider than long, in contact; distal plates longer than wide, separated by lateral arm plates.

Variations. Large specimens may have granules between or on some proximal dorsal arm plates. Specimens less than 6 mm disk diameter have all the dorsal arm plates separated. There are scattered spinelets on dorsal disk surface of individuals 1.4 - 2.4 mm dd. A juvenile specimen in this collection 1.2 mm dd has: disk covered with transparent scales bearing widely spaced irregular stumps; jaws with apical and only 3 lateral oral papillae; second oral tentacle pore opening outside the mouth angle; arm spines slender, smooth; ventral arm plates with slender waist, successive plates in contact. A juvenile *Ophiacantha normani* of similar size has: disk bearing conspicuous central primary plate and sharp spinelets; arm spines thickened at base; ventral arm plates not in contact.

Color: Living specimens with disk irregularly mottled brown and gray. Arms reddish; arm spines light brown with conspicuous white basal ligament.

In alcohol, mottled gray, white and brown; darker pigmentation retained by disk, ventral arm spines, and dorsal arm surface. Arms generally paler than disk.

Remarks. Kyte (1982) assigned this species to *Ophiophthalmus* Matsumoto, but that generic name is an invalid junior synonym (see Paterson, 1985). A new generic assignment is probably warranted for *O. diplasia* and other ophiacanthids such as *Ophiacantha* (“*Ophiophthalmus*”) *normani* Lyman, but they can be considered as *Ophiacantha* species pending a revision of the entire genus.

Distribution. Southern California to Oregon, at depths 71-1,330 m (May, 1924; H. L. Clark, 1911, 1915; Hartman and Barnard, 1958; Astrahantseff and Alton, 1965).

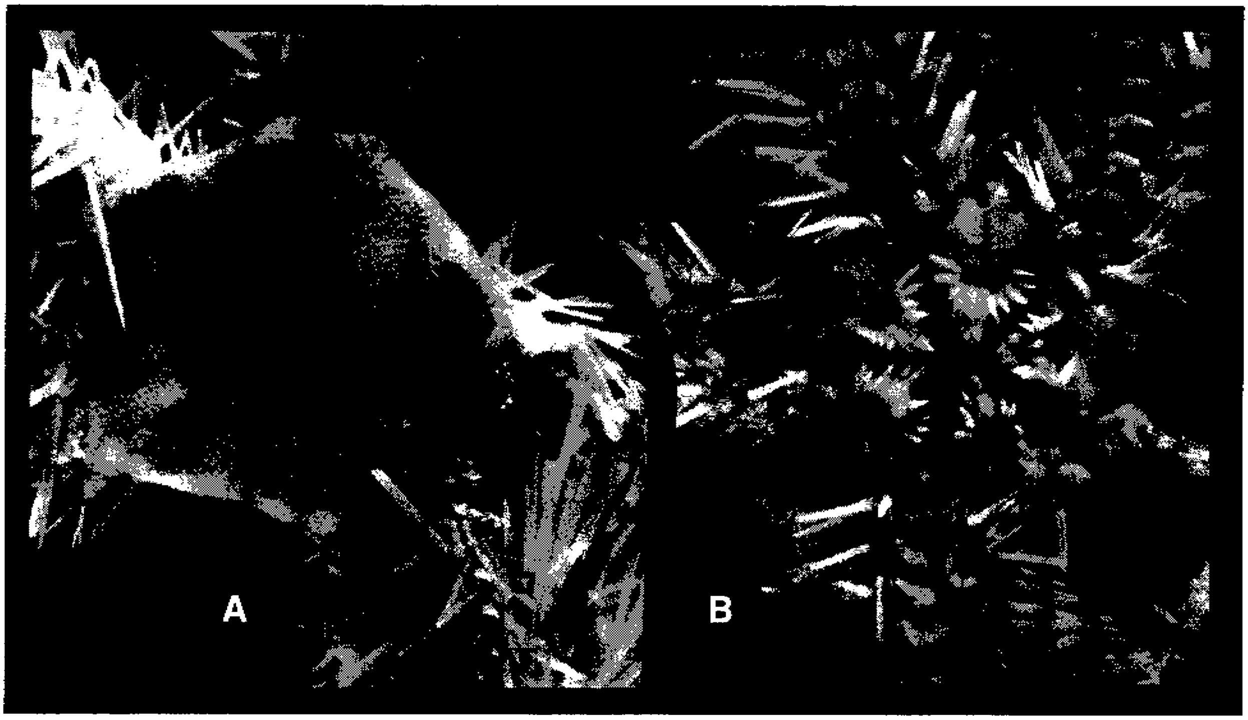

Figure 7.16. *Ophiacantha diplasia* H.L. Clark: A, disk, dorsal view; B, disk, ventral view (USNM, primary voucher; dd = 14.8 mm).

Biology. This species usually occurs on hard substrates, associated with rock structures and sessile invertebrates. Photographic records (Lissner and Benech, 1993:fig. 4.3) from off Pt. Conception, California portray it as an abundant element of a diverse hard-bottom community. Individuals take exposed or partially sheltered positions, with their arms slightly upraised. This posture is often shown by suspension feeders, and like many ophiacanthids, *O. diplasia* is probably capable of suspension feeding. Its tube feet, in alcohol preserved specimens, are large, blunt-tipped, and highly papillose. Tube foot papillae are typical, but not necessarily exclusively characteristic, of suspension feeding ophiuroids.

Family Ophiactidae

***Ophiopholis bakeri* McClendon, 1909**

Figure 7.17

Ophiopholis bakeri McClendon, 1909:41, figs. 26-27.—H.L. Clark, 1911:10, 115-116, 121-123, 128, fig. 46a-c.—1915:267.—Campbell, 1921b:48.—May, 1924:279-280, fig. 7a-c.—Berkeley, 1927:4.—Nielsen, 1932:260-262, fig. 5.—Ziesenhenne, 1937:224.—Barnard and Ziesenhenne, 1961:143.—Hartman, 1963:85, 201, 218, 366, 383, 401.—Astrahantseff and Alton, 1965:1414, 1420.—Boolootian and Leighton, 1966:7-8, fig. 28.—Kyte, 1969:1729, 1732, 1735, 1738.

Material Examined. California: Santa Maria Basin, Phase I Sta. BRA-016, 91.5-123 m (58, SBMNH secondary voucher); Phase I Sta. BRA-016, 91.5-123 m (1, juvenile *O. bakeri*? [as *Amphipholis squamata*]); Phase I Sta. BRA-025, 64.5-72 m (1 juvenile, SBMNH secondary voucher [as *Ophiothrix spiculata*]).—Western Santa Barbara Channel, Phase I Sta. BRA-002, 110-126 m (24, USNM primary voucher).—Los Angeles, off Redondo Beach, Burch Sta. 40122, 90 m (16, LACM 40-341.2).—Mexico: Pacific Coast, Baja California, off Islas San Benito, R/V *Velero III* Sta. AHF 1010-39, 130-174 m (numerous, LACM 39-114.17).

Description. An ophiactid species of moderate size. Individuals attain 10 mm dd with arms 65 mm in length. A specimen 7 mm dd has arms 32 mm long. The lateral and ventral arm plates and the major ossicles of the oral frame appear rough due to numerous microscopic bumps (EPT).

Disk round to pentagonal, interradial regions somewhat outpouched, densely covered with pointed granules and spinules borne on thin, rounded, imbricating scales and radial shields. Spinules longest, most numerous in central and lateral areas of disk, generally reduced to sharply pointed granules on radial shields. Spinules echinulate or multifid, generally with 2-5 points, up to 5 times longer than wide. Primary plates evident in small and sparsely armored specimens. Radial shields separated except distally, twice as long as wide, approximately one-fourth diameter of disk.

Jaws narrow, oral gap broad. Oral papillae 4-6 on each side of jaw, flattened to spinelike. Free edge of ventral teeth with several points or knobs, sometimes fragmented; dorsal teeth with straight tip.

Oral shields lozenge-shaped, at least twice as wide as long, lateral lobes wing shaped. Madreporite twice as large as oral shield, more rounded in outline. Adoral shields nearly equal in size to oral shield, L-shaped, distal tip touching second ventral arm plate, proximal tips extending above oral shield, in contact or nearly so.

Ventral interradial region covered with small, multifid spinules bearing 1-2 points, pointed granules near oral shield. Bursal slit narrowing distally, extending to disk margin; naked scales on edge of bursal slit.

Arms tapering. Terminal portion appearing beaded due to protruding lateral arm plates.

Dorsal arm plates inflated, rounded on proximal joints, becoming ovoidal and elongate distally, teardrop-shaped on terminal segments. Supplementary scales bordering free edges of dorsal arm plates not fully in contact, granular to slender and flat in shape, with one or two sharp points.

Lateral arm plates broad, with prominent spine-bearing ridge; successive plates separated by band of connective tissue. Up to 7 arm spines, tapering, solid, generally 2 and less than 3 arm joints in length with expanded, hoof-shaped base. Longest spines occurring dorsally, near disk, occasionally topmost spine of reduced size. Longer spines echinulate, blunt tipped; smaller ventral spines with echinulate edge and tip; lowermost spines on distal half of arm with prominent hyaline teeth, 2 teeth on terminal segments. Hooked spines arising on proximal arm segments in juvenile individuals.

Ventral arm plates octagonal, length equal to width; proximal edge convex, distal edge markedly concave. First ventral arm plate small, enclosed by adoral shields. Ventral surface of basal plates depressed, forming medial trough. Successive plates separated by connective tissue. Single tentacle scale (occasionally 2), flat, elongated, with expanded, blunt distal tip, partially covering large tentacle pore.

Variation: A 1.2 mm dd specimen of *O. bakeri* from the present survey had: central plate perforate and prominent but less than 1/3 the disk diameter, radial and central plates of almost equal size; teeth with 1 central and 2 lateral cusps; basal arm plates separated, some possessing spiny stumps; arm spines neither palmate nor webbed, short thorns on proximal arm spines, hooked arm spines with 2 hyaline teeth. It was incorrectly identified as *Ophiothrix spiculata* by survey taxonomists. Individuals of the latter species less than 2 mm dd can be distinguished as they have: disk pentagonal with interradial outpouchings, central plate covering 1/3 the disk diameter, convex, hyaline, with minute perforations restricted to edge of plate; radial plate small; dorsal arm plates lacking spiny stumps, basal plates in contact; proximal arm spines palmate,

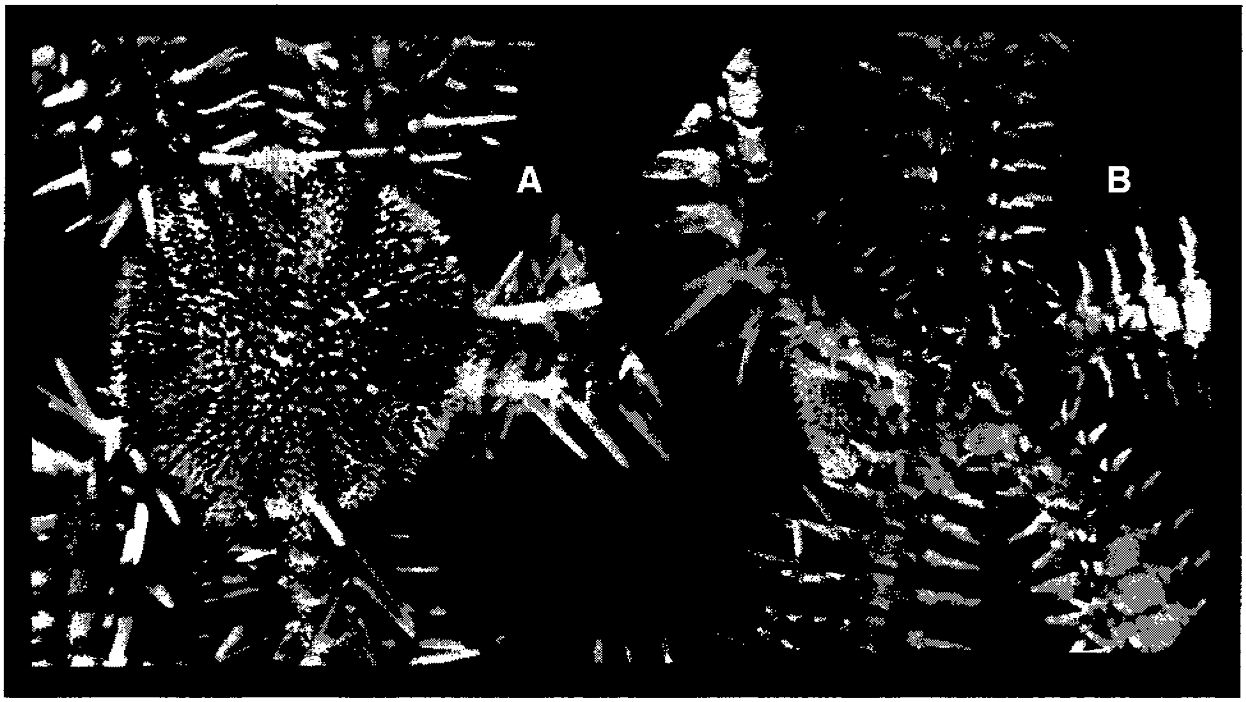

Figure 7.17. *Ophiopholis bakeri* McClendon: A, disk, dorsal view; B, disk, ventral view (LACM 40-341.2; dd = 7.9 mm).

bearing long thorns webbed with gossamer integument, other spines with small thorns; hooked arm spines with 2 hyaline teeth.

Color: In living specimen, disk reddish brown with gray central region; arms reddish brown above, yellowish-white with brown spots below, arm spines brown, tube feet yellow; conspicuous connective tissue between ventral arm plates. Ziesenhenne (1937: 224) noted that the "arms, orange in life, are pink with an occasional light band; the armspines are white or gray."

In alcohol, whitish to pink or reddish, sometimes variegated with white or brown.

Remarks. H. L. Clark (1911:116) provided a key to 5 species and 3 varieties of *Ophiopholis*: *mirabilis, brachyactis, longispina, bakeri, aculeata* (and to *aculeata* varieties *japonica, typica,* and *kennerlyi*). *Ophiopholis bakeri, longispina,* and *aculeata typica* and *kennerlyi* occur in California waters.

Full specific rank originally accorded *O. japonica* was revived by Irimura (in Imaoka *et al.*, 1990). The infraspecific status originally accorded var. *kennerlyi* by H. L. Clark (1911) has been supported by later authors (May, 1924; Nielsen, 1932).

Distribution. Baja California, Mexico, California, Oregon, Washington, British Columbia; 18-902 m (McClendon, 1909; H. L. Clark, 1911; Berkeley, 1927; Nielsen, 1932; Ziesenhenne, 1937; Hartman, 1963; Astrahantseff and Alton, 1965; Kyte, 1969).

Biology. It is likely that *O. bakeri*, like its congener *O. aculeata,* is a rheophilic suspension feeder, probably epizoic or occupying positions elevated above the sediment in hard bottom habitats (see LaBarbera, 1978, 1982). I have found it in a dead kelp holdfast recovered from Santa Monica Bay, and it likely occupies the base and holdfasts of living *Macrocystis*. It is commonly recovered from silty sand, and sand, rock and shell substrates (Kyte, 1969). Its affinity for hard substrate and rock outcroppings may account for the low numbers taken in the survey reported by Barnard and Ziesenhenne (1961).

Family Ophiodermatidae

Ophiuroconis bispinosa **Ziesenhenne, 1937**

Figure 7.18

Ophiuroconis bispinosa Ziesenhenne, 1937:228-230, fig. 2a-c.—Barnard and Ziesenhenne, 1961:143.

Material Examined. California: Santa Maria Basin, Phase II Sta. R-8, 90 m (2, CAMP voucher).—Off Santa Barbara Id., R/V *Velero III* Sta. AHF 978-39, 38-51 m (18, LACM 39-82.8).—Los Angeles, Santa Monica Bay, R/V *La Mer* Sta. C-3, 60 m (4, LACM 92-53.2).—Mexico: Islas Revillagigedo, off Isla Socorro, R/V *Velero III* Sta. AHF 924-39, 31-84 m (11, LACM 39-27.5).—Ecuador: Islas Galapagos, off Isla Española, R/V *Velero III* Sta. AHF 814-38, 37-73 m (5, LACM 38-80.9).

Description. A small, fragile species. A typical specimen is 3 mm dd with arms 17 mm long.

Disk circular to rounded pentagonal, soft, flat, loosely attached to arms. Entire disk with cover of fine, imbricating scales overlain with rounded granules, some granules at edge of disk elongate. Radial shields approximately one-fifth disk diameter, broadly in contact.

Jaws widely separated by broad oral gaps. Oral shields small, longer than wide with sharply pointed triangular proximal lobe on oral frame, round distal lobe on ventral interradius. Adorals shields narrow, curved, 4 times longer than wide, pointed proximally, in broad contact proximal to oral shield, outer end abutting first lateral arm plate. Apical and most proximal oral papilla spinelike, pointed; 3-4 distal papillae on jaw flat, rounded, largest one outermost; small papilla at corner of oral slit on first ventral arm plate.

Granules on oral frame, including few on oral shields, adoral shields, oral plate, proximal arm segments; outpouched ventral interradii with denser granule cover.

Arm long, slender, distal half tapering.

Dorsal arm plates quadrangular, widest distally, with sharp medial ridge; wider than long at base of arm, becoming much longer than wide near arm tip; successive plates overlapping except at arm tip.

Lateral arm plates broad, with sharp midlateral ridge, conspicuously etched with parallel microscopic lines. Plates broadly in contact beneath arm joint, separated above. Two arm spines at distal margin of lateral arm plate, smooth, slender, gradually tapering to rounded point; upper arm spine larger, longer than arm joint at base of arm. Accessory arm spine minute, comb-shaped, set above the larger spines (Hendler, prev. unpub.). Single tentacle scale, longer than wide, scoop-shaped, ventral surface convex; relative length increasing distally, exceeding length of arm joint near arm tip.

First ventral arm plate within oral slit small, with medial furrow; second and third ventral arm plates pentagonal; others more rectangular with curved edges, rounded corners, nearly twice as wide as long, widely separated by lateral arm plates.

Color: In living individuals, disk blotched with black-brown, brown, gray, greenish gray; jaw pale greenish brown tipped with deep brown, granules pale gray. Arms with dark and light bands of tan to pale brown, greenish, dark patches on lateral arm plates near base of spines; ventral arm plates dark, tinged with khaki; microscopic dark brown specks uniformly scattered on arm plates. Tube feet translucent, oral tentacles salmon color. Ovaries pink.

Preserved specimens retain considerable pigmentation; as described by Ziesenhenne (1937:230), "dried from alcohol...disk cream color with irregular light brown markings over the radial shields. Arms light tan with bands of brown or black, two to four segments wide (usually two), alternating with a light colored area; near disk the light bands are four segments wide, but distally they are only half as wide. Lower surface white, with some under-arm plates (usually in pairs) faintly dusky."

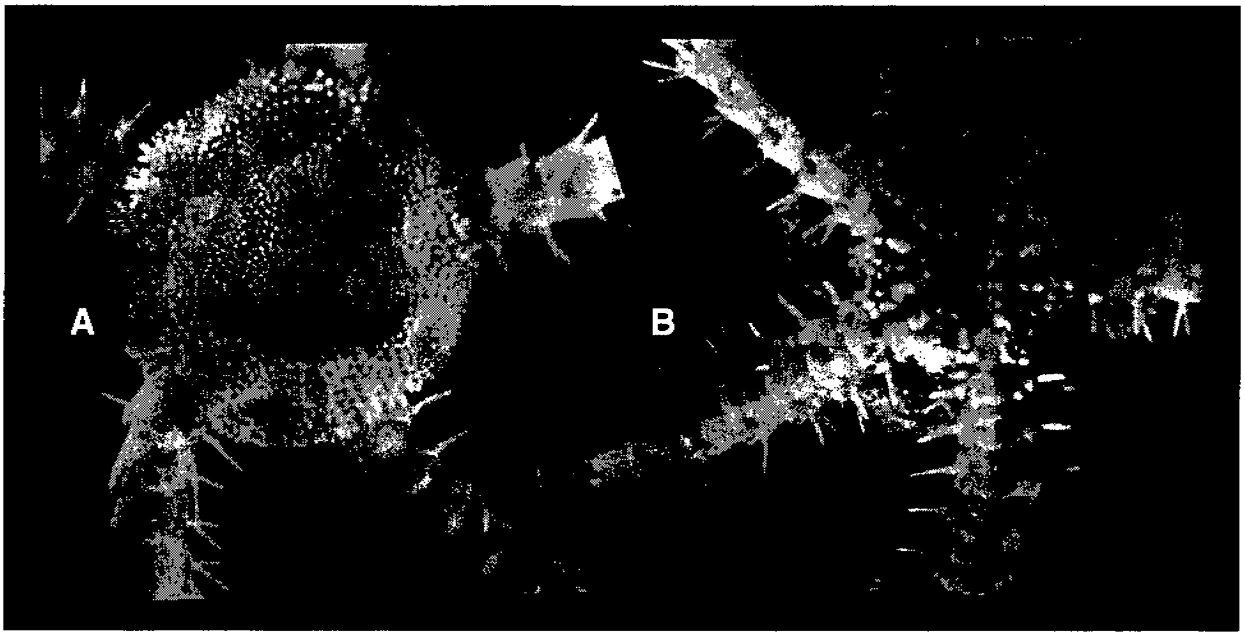

Figure 7.18. *Ophiuroconis bispinosa* Ziesenhenne: A, disk, dorsal view; B, disk, ventral view (LACM 92-53.2; dd = 2.5 mm).

Remarks. In a forthcoming publication on this species (Hendler, in prep.), its familial assignment will be revised, and the generic and specific names will be changed.

Distribution. Costa Rica, Galapagos, Mexico including Gulf of California, and southern California; 5-143 m (Ziesenhenne, 1937; this report).

Biology. Barnard and Ziesenhenne (1961) recorded *O. bispinosus* at 3% of 176 stations taken between 9-243 m depths from Pt. Conception, California to the Mexican border. Individuals from Santa Monica Bay, California, collected using a grab sampler, are capable of rapid movement, and the species appears to be epifaunal.

Family Ophiotrichidae

Ophiothrix (*Ophiothrix*) *spiculata* Le Conte, 1851

Figure 7.19

Ophiothrix spiculata Le Conte, 1851:318-319.—Lütken, 1856:22.—1859:151.—Lyman, 1865:167.—1882: 214, 216, 226, 312, 325.—Ljungman, 1867:331.—Verrill, 1867: 320, 332-333, 342.—Lyman, 1865: 13, 153, 167-169.—1875:5.—1880:35.—1882:226.—Ives, 1889:178.—Lütken and Mortensen, 1899:181.—H.L. Clark, 1902:525-526.—1910:342.—1911:10, 262-263, fig. 129a-c.—1913: 218.—1915:278-279.—1917: 439.—1923:157.—1940:340.—Koehler, 1907:338.—McClendon, 1909:50-51, figs. 38, 39.—Campbell, 1921a:3, fig.7.—1921b:48.—1922:38-39, pl. 1, figs. a-i.—May, 1924:274-276, fig. 5a-c.—Ziesenhenne, 1937:225.—Caso, 1961:201-204, fig. 85.—Barnard and Ziesenhenne, 1961:133, 143.—Hartman, 1963: 85, 154, 305.—Boolootian and Leighton, 1966:6, 8, fig. 26.—Austin and Hadfield, 1980:151, pl. 49, fig. 10.6.

Ophiothrix (*Ophiothrix*) *spiculata*, A.M. Clark, 1966:647.

Ophiothrix dumosa Lyman, 1860:252-254.—1865:13, 153, 169-171.—Lyman, 1880:35.—Ljungman, 1867:331.—Verrill, 1867:270, 326, 329.—Lyman, 1882:226.—Ives, 1889:178.—H.L. Clark, 1915:270, pl. 12, fig. 6.—May, 1924:274-276, fig.5a-c.

? Young ophiurid Nielsen, 1932:342-3, figs. 41-42.

Material Examined. California: Santa Maria Basin, Phase I Sta. BRA-025, 64.5-72 m (2 juvenile, SBMNH secondary voucher).—Western Santa Barbara Channel, Phase I Sta. BRC-001, 73.5-78 m (2 juvenile, USNM primary voucher).—Off Santa Barbara Id., R/V *Velero III* Sta. AHF 975-39, 46-49 m (20, LACM 39-79.10).—Mexico: Gulf of California, off Bahia Concepcion, R/V *Velero III* Sta. AHF 683-37, 22 m (16, LACM 37-85.1).

Description. An ophiotrichid of moderate size, growing to 18 mm dd with arms 5-8 times as long. A 14 mm dd specimen has 62 mm arms, and one 7 mm dd has 53 mm arms.

Disk pentagonal with interradial outpouchings. Disk fully covered, radial shields sparsely covered with rough spinelets and multifid spinules. Radial shields tapering proximally to a point, distally to a short straight edge, separated by series of narrow scales, length approximately one-fourth to one-fifth disk diameter.

Jaws with conspicuous central cavity proximal to oral shield. Oral gap quite broad. Oral papillae absent. Dental papilla cluster at ventral apex of jaw, with central papillae shortest; chisel-shaped teeth high in oral cavity. Oral shields wider than long, with medial points on proximal edge, lateral sides lobate; madreporite larger, more irregular in outline. Adoral shields small, subtriangular, in contact, confined to inner side of oral shield. Ventral interradius covered with spines and minute scales. Large genital scale evident at distal end of bursal slit.

Arms tapering to filiform tip; arm joints with narrow waist due to proximally constricted lateral arm plates.

Dorsal arm plates saddle-shaped, raised medially, proximo-lateral edges concave, narrow proximal end depressed, disto-lateral edges convex, broad distal end upraised.

Lateral arm plates in contact, with very prominent, flaring spine-bearing ridge. Up to 8 thorny arm spines with thickened, round base, sides of shaft compressed; topmost spine often short, second or third the longest, 4.5 times length of joint, spines decreasing in length ventrally. Beyond base of arm, most evidently near tip, ventral-most spine with 3 hyaline teeth; terminal tooth largest, curved. Tentacle scale single, small, edge bearing sharp tooth.

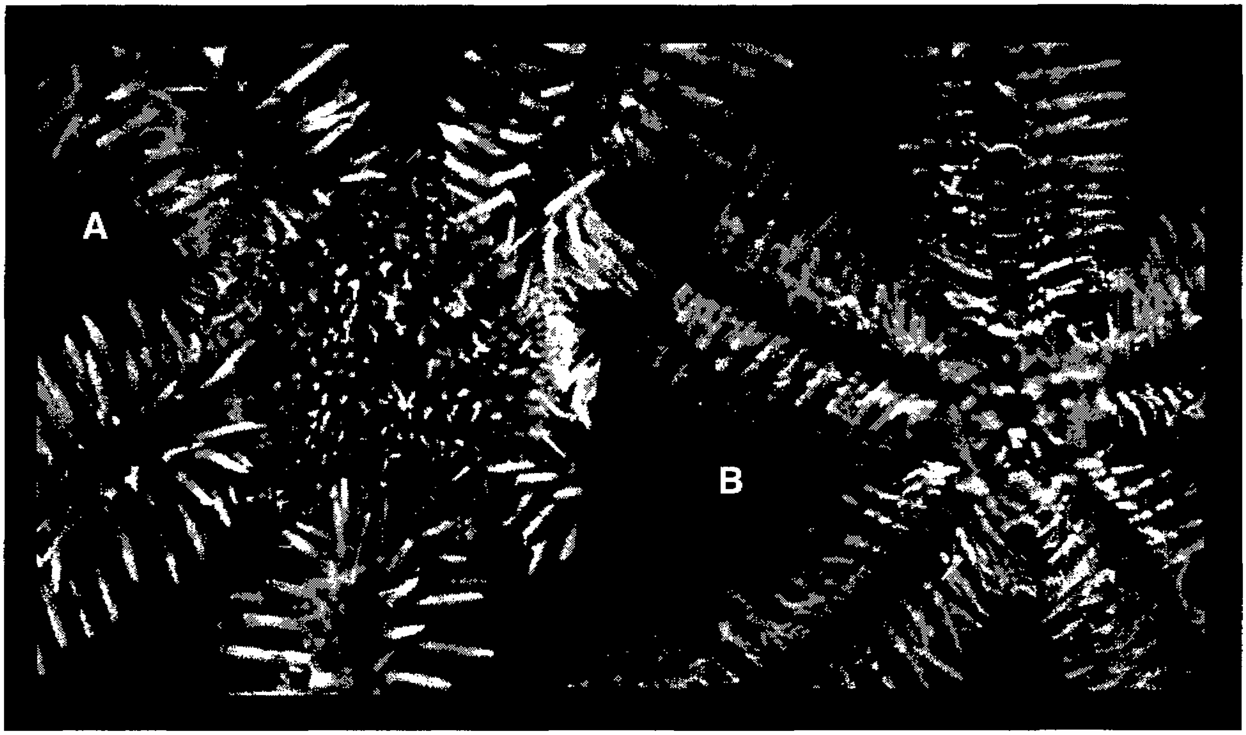

Figure 7.19. *Ophiothrix* (*Ophiothrix*) *spiculata* Le Conte: A, disk, dorsal view; B, disk, ventral view (LACM 37-85.1; dd = 6.6 mm).

Basal ventral arm plates longer than wide, depression at center creating medial ventral arm furrow; proximal plates wider than long, broadest near distal edge, with thickened distal and proximal edges; distal plates longer than wide. Connective tissue filling gaps between successive plates.

Variation: See *Ophiopholis bakeri* above, for description of juvenile.

Color: Living individuals with variable color patterns. Generally greenish brown or brown to greenish yellow above, sometimes with patches or spots of white, gray, orange, or garnet on the disk; the the arms spotted, blotched or regularly banded with red, orange, pink, brown, maroon, or gray. Ventral surface with whitish oral region, otherwise disk and arms pigmented as dorsally, the arms often banded (see McClendon, 1909; May, 1924; Ziesenhenne, 1937, for extensive color notes). Tube feet grayish with microscopic brown specks. Ovaries and eggs orange-salmon or orange-peach colored.

Preserved specimens fade and change color. The "characteristic blue...coloring of the species" noted by H. L. Clark results from the degradation of green pigments, a phenomenon seen in other alcohol preserved ophiotrichids (Hendler *et al.*, 1995).

Distribution. Northern Chile and Galapagos Islands to Moss Beach, California; intertidal to 211 m (Lütken and Mortensen, 1899; McClendon, 1909; May, 1924; H. L. Clark, 1911, 1913, 1915, 1917, 1923, 1940; Nielsen, 1932; Caso, 1961; Hartman, 1963; Castillo Alarcón, 1968; Austin and Hadfield, 1980).

Remarks. The synonymy of *Ophiothrix dumosa* with *O. spiculata* has withstood repeated examinations (Ives, 1899; May, 1924; Neilsen, 1932). H.L. Clark (1902, 1915, 1917) eventually retracted his proposal that specimens of *Ophiothrix galapagensis* Lütken and Mortensen are the young of *O. spiculata*.

The only sympatric congener of *O. spiculata* in California waters is *Ophiothrix rudis* Lyman, and Nielsen (1932) provides a detailed discussion of distinctions between the species.

Some features of juvenile *Ophiothrix spiculata* are evident in Nielsen's illustration of a "Young ophiurid from the Gulf of Panama" (Nielsen, 1932: figs. 41, 42), especially the large, smooth central plate and palmate basal arm spines. However, the differences from *O. spiculata* in the shape of major plates suggest that other features are inaccurately rendered, or another species of *Ophiothrix* is depicted.

Biology. Austin and Hadfield (1980) summarized the natural history of *O. spiculata.* The species occurs in shallow water under rocks, in rock crevices, in algae and algal holdfasts and subtidally on hard bottom such as shaley pebbles (Barnard and Ziesenhenne, 1961). Individuals use the hooked arm spines to secure themselves to the substrate and probably to each other. Small *O. spiculata* are often seen in shallow-water tide pools. They are found amongst algae, clinging to sponges, in mussel beds, and within interstices of *Macrocystis* kelp holdfasts. Scuba divers at the Channel Islands and other islands off Southern California and Mexico report great numbers of this species, sometimes 80 individuals/0.1 m^2, carpeting the substrate in areas of strong currents. These aggregations exhibit the "gregariousness" behaviors reported for *Ophiothrix fragilis* in European waters (Hendler, 1991).

Individuals suspension feed using the mucus coated arm spines and tube feet to strain plankters and particulate material from the water. They are also capable of gleaning food from the intertidal surface film and capturing macroscopic items. *O. spiculata* lacks the ciliary tracts postulated by MacGinitie (1949). The species falls prey to fish including rock wrasse, pile perch, and sand bass, as well as the sea star *Astrometis sertulifera* (Xantus). I have found the egg diameter to be 0.11 mm, consistent with the production of an ophiopluteus larval form.

Family Ophiuridae

Ophiosphalma jolliense (McClendon, 1909) new combination

Figure 7.20

Ophiomusium jolliensis McClendon, 1909:36, figs. 2, 3.—H. L. Clark, 1911:9, 20, 111-113, fig. 41a-c.—Campbell, 1921b:46.—Astrahantseff and Alton, 1965:1414, 1421.—Thompson *et al.*, 1993:30, 38.

Ophiomusium jolliense, H.L. Clark, 1915:330.—1917:450.—1923:154.—Matsumoto, 1917:285, 291, 359.—Hartman, 1963: 85, 170, 185, 261, 305, 320, 383, 401.—Boolootian and Leighton, 1966:6, 10, fig. 21.

Ophiomuseum jolliensis, Thompson and Jones, 1987:5.

Material Examined. California: Santa Maria Basin, Phase I Sta. BSS-062, 582 m (3, USNM primary voucher; 1 LACM 83-232.1 [as *Ophiomusium jolliensis*]).—Western Santa Barbara Channel, Phase I Sta. BSS-078, 762 m (1, LACM 83-230.1 [as *Ophiomastus* sp. A]).—Off Santa Catalina Id., R/V *Velero III* Sta. AHF 1425-41, 512 m (8, LACM 41-205.2).—Off Redondo Beach, R/V *Velero IV* Sta. AHF 2788-54, 17 m (1, LACM 54-104.2).—Off Newport Beach, R/V *Velero IV* Sta. AHF 7352-61, 420-521 m (3, LACM 61-168.1).

Description. An *Ophiomusium* species of moderate size. The largest specimens have disk diameters of 20, exceptionally 30 mm. An individual 15 mm dd has arms over 62 mm long, though relatively shorter arms have frequently been reported. Large ossicles appear rough due to numerous microscopic bumps (EPT).

Disk rounded pentagonal, central region depressed, margins somewhat raised. Central half of disk covered by thickened, rounded and angular tesselate scales. Primary plates present, slightly larger than other scales. Largest scale, about half size of radial shield, at disk edge midway between arms. Radial shields narrowing proximally to acute point, with broad, rounded lobe near arm base; shields approximately twice as long as wide, length one-fourth diameter of disk. Series of narrow, angular scales between paired radial shields continuing onto base of arm, overlapping first dorsal arm plate.

Jaws broad. Oral slits narrow, nearly sealed by oral papillae. Oral papillae 6-7 on a side, in continuous series; lateral papillae subquadrilateral, flattened; apical papilla pointed. Teeth spinelike, sharply pointed, dorso-ventrally flattened. Oral shields small, nearly twice as long as wide, spearhead-shaped with sharp proximal point, prominent shaftlike distal extension fused to interradius. Adoral shields as large or larger than oral shield, broad distal edge abutting first ventral arm plate; paired shields with acutely pointed tips meeting proximal to oral shield. Ventral interradii with scales similar to dorsal disk surface. Bursal slit prominent, spanning oral shield nearly to edge of disk; proximal end bifurcate, short branches diverging at postero-lateral edge of oral shield; slit fringed with continuous series of minute, flat, quadrilateral scales on radial edge and on outer adradial edge.

Arms gradually tapering, distal portion filiform; in cross section dorsal surface with shallow medial ridge, ventral surface flattened, with medial indentation; sharp notched indentations between arm joints. Base of arm with small, lateral fields of microscopic, angular granules between distal edges of radial shield and bursal slit. First three joints beneath disk broad, bearing large tentacle pores; distal arm joints lacking apparent pores.

Dorsal arm plates except first diamond-shaped, slightly longer than wide; first several plates touching or nearly in contact, remainder considerably smaller, widely separated by lateral arm plates.

Lateral arm plates large, broad, flat, lacking prominent spine-bearing ridge, covering most of dorsal and ventral surface of arm, meeting below and above except on first few joints.

Ventral arm plate at edge of oral slit minute, situated between distal-most oral papillae, adoral shields, and first lateral arm plates. Remaining ventral arm plates with inner edges joining at sharp proximal point, lateral edges narrowing beside tentacle pore, distal edges lobate. Lobes prominent on first three joints, thereafter decreasing in size, plates becoming diamond-shaped, wider than long. Ventral arm plates absent near arm tip. Single tentacle scale on first three joints, hinged to lateral arm plate, flat, rounded, operculate, sealing tentacle pore; sometimes additional minute scale present on ventral arm plate. Arm spines small, approximately one-fifth length of arm joint, affixed to distal edge of lateral arm plate near ventral arm surface; 1 spine on fourth joint, 2 on next several joints, 3 spines by tenth joint. Ventral-most spine tapering, pointed; dorsal spines hook-shaped with proximally directed, hyaline, terminal teeth.

Variation: The juvenile specimens (1.6-4.3 mm dd) are quite unlike the adults in appearance: dorsal surface of disk covered by thickened primary plates, radial shields, and one or two marginal scales; ventral surface covered by the oral shield and several interradial scales; genital slit papillae absent in specimens less than 2.8 mm dd. Oral papillae in smallest specimens consist of: apical papilla, 2 small proximal papillae, elongate distal papilla; number of papillae increasing during ontogeny. Successive dorsal and ventral arm plates widely separated by lateral arm plates. Tentacle scales flattened.

Color: The description in Boolootian and Leighton (1966:10) as "dark brown aborally, tan or yellow orally," may have been based on living material. Preserved specimens pale brown, yellowish, to cream or gray; juvenile specimens translucent white.

Remarks. H.L. Clark (1941) proposed the new genus name *Ophiosphalma* for species with 3 pairs of proximal tentacle pores, restricting the genus *Ophiomusium* to species with only 2 basal tentacle pores. It is on that basis alone that this species is referred to *Ophiosphalma*. The correct nominative singular ending for the specific epithet is the neuter form "*jolliense.*"

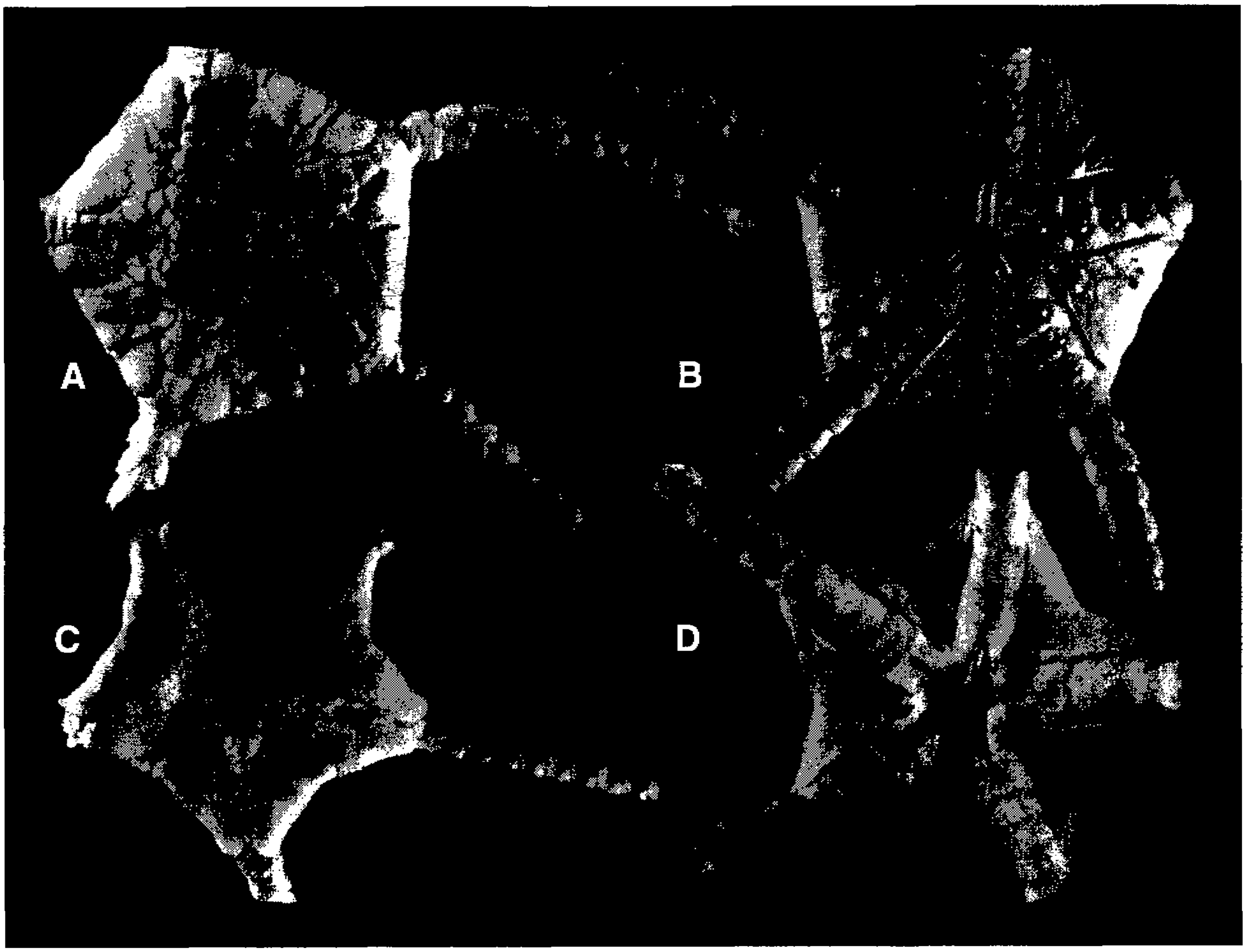

Figure 7.20. *Ophiosphalma jolliense* (McClendon): A, disk, dorsal view; B, disk, ventral view (LACM 41-205.2; dd = 12.0 mm). *Ophiosphalma variabile* (Lütken and Mortensen): C, disk, dorsal view; D, disk, ventral view (USNM 19502, syntype, *Ophiomusium variabile*; dd = 13.9 mm).

Ophiomusium (= *Ophiosphalma*) *variabile* Lütken and Mortensen (1899) is similar to *O. jolliense* in overall appearance and details such as the distinctive shape of the oral shield (Figure 7.20). Examination of type specimens of *O. variabile* (USNM 19502) revealed that it differs in having: marked interradial indentation of the disk; large radial shields greater than twice as long as broad, widest at mid-length, in contact distally; edges of lateral arm plates straight or concave in dorsal view; conspicuous gap between distal-most oral papillae. H. L. Clark (1911) delineated the similarities and diagnostic differences of *O. jolliense* and its congeners *O. cancellatum* Lyman, *O. armigerum* Lyman, and *O. eburneum* Lyman.

Juvenile *O. jolliense* and the juveniles of an undetermined Ophiurine species both, were mistakenly identified by survey taxonomists as an *Ophiomastus* species. The identity of the juvenile *Ophiosphalma* was confirmed by comparison with a growth series of *O. jolliense*. Individuals of the juvenile Ophiurinae species, 1.5 mm dd or smaller, were found at only one locality, Phase I Sta. BSS-069, 927 m (specimens: 1, USNM primary voucher; 1, SBMNH secondary voucher, 1 LACM 83-231.1). Unlike the juvenile *O. jolliense* they have four, rather than three evident tentacle pores, and a rudimentary arm comb.

Distribution. Cabo San Lucas, Mexico to Oregon, and Japan, generally from 155-1,463 m (McClendon, 1909; H. L. Clark, 1911; Hartman, 1963; Astrahantseff and Alton, 1965; Irimura *et al.*, 1995). The LACM specimen from 17m reported herein is a juvenile. Records for occurrences off the Galapagos (H. L. Clark, 1917) and at depths to 4,300 m (Carey, 1990) require confirmation.

Biology. Thompson and Jones (1987) provide underwater photographs of large numbers of ophiuroids, identified as *O. jolliense*, inhabiting soft bottom at 698 m, on the lower slope of the San Pedro Basin off Southern California. Individuals have the distal part of arms upraised and sinuously bent; some occur in the open, others in depressions, or perched on small, hard structures.

Thompson *et al.* (1993) determined that this species is among the most abundant megabenthic invertebrates trawled at the mid and lower slope depths (300-780 m) of San Pedro and Santa Monica Basins. They suggested its population density may have increased by an order of magnitude following an El Niño event.

Ophiura leptoctenia H. L. Clark, 1911

Figure 7.21

Ophiura leptoctenia H.L. Clark, 1911:4, 9, 15, 18-19, 51-55, 58-59, 60, fig. 12a-c.—1913:208-209.—1915:321.—1923:153.—Matsumoto, 1917:268, 270, 277, 354.—Campbell, 1921b:47.—May, 1924:291, fig. 13a-c.—Nielsen, 1932:315, 317-321, figs. 27b, 29a,b, 30a-c.—D'yakonov, 1954:105-106.—Hartman, 1963: 86, 350, 383, 391, 401.—Astrahantseff and Alton, 1965: 1414, 1422.—Kyte, 1969:1729, 1731, 1735, 1739.—A. M. Clark, 1965:68.

Material Examined. Oregon: Off Columbia River mouth, R/V *Commando*, 460 m (3, LACM 64-240.2).—California: Santa Maria Basin, Phase I Sta. BSS-063, 930 m (1, SBMNH secondary voucher).—Off Santa Catalina Id., R/V *Velero IV* Sta. AHF 9168-63, 1,262-1,298 m (13, LACM 63-203.1).

Description. A small ophiurid, most individuals 8 mm disk diameter or smaller, although H. L. Clark (1911) reports a specimen 11 mm dd with arms 30 mm long.

Disk round, flat, covered with thin, irregularly shaped, imbricating scales; primary plates larger than all other scales. Radial shields large, longer than wide, length approximately one-fourth dd, separated or in contact distally. The disk sometimes bearing scattered small, slender spinelets, numbering up to 25 according to Nielsen (1932).

Oral shields longer than wide with pointed proximal edge and broad semicircular distal edge. Adoral shields small, narrowed proximally to oral shield, with long radial extension joining first lateral arm plate. Oral papillae 5 or more, narrow, sharp, spinelike near apex of jaw, broader at jaw base, sometimes with serrate free edge. Teeth narrow, pointed. Ventral interradial area covered with fine scales. Bursal slit extending from oral shield to dorsal side of disk; genital scales large; series of minute spines along each scale continuing dorsally, increasing in size, forming arm comb. Arm comb of approximately 12 slender spines, middle ones longest; opposed by smaller V-shaped secondary comb at base of arm.

Proximal dorsal arm plates fan-shaped with proximal edge concave, distal edge convex; some basal plates wider than long, others longer than wide, becoming triangular toward tip of arm; successive plates in contact, except near arm tip.

Lateral arm plates wide, broadening ventrally, meeting below arm. Three slender, sharp arm spines; uppermost longest, length equaling or exceeding joint on first several joints. Tentacle pores large; 9 scales surrounding oral pore, 5 on jaw, 4 arising from first ventral arm plate; on first arm joint 1-2 scales on lateral arm plate, 2-3 on ventral arm plate, within several joints tentacle scales reduced to only 1 on lateral arm plates.

First ventral arm plate within jaw, bilobed, with medial furrow. Second ventral arm plate triangular, remainder wider than long, with sharp projection from proximal edge; successive plates separated a distance exceeding their length by lateral arm plates. In large specimens, ventral surface of basal arm segments depressed, forming a medial furrow.

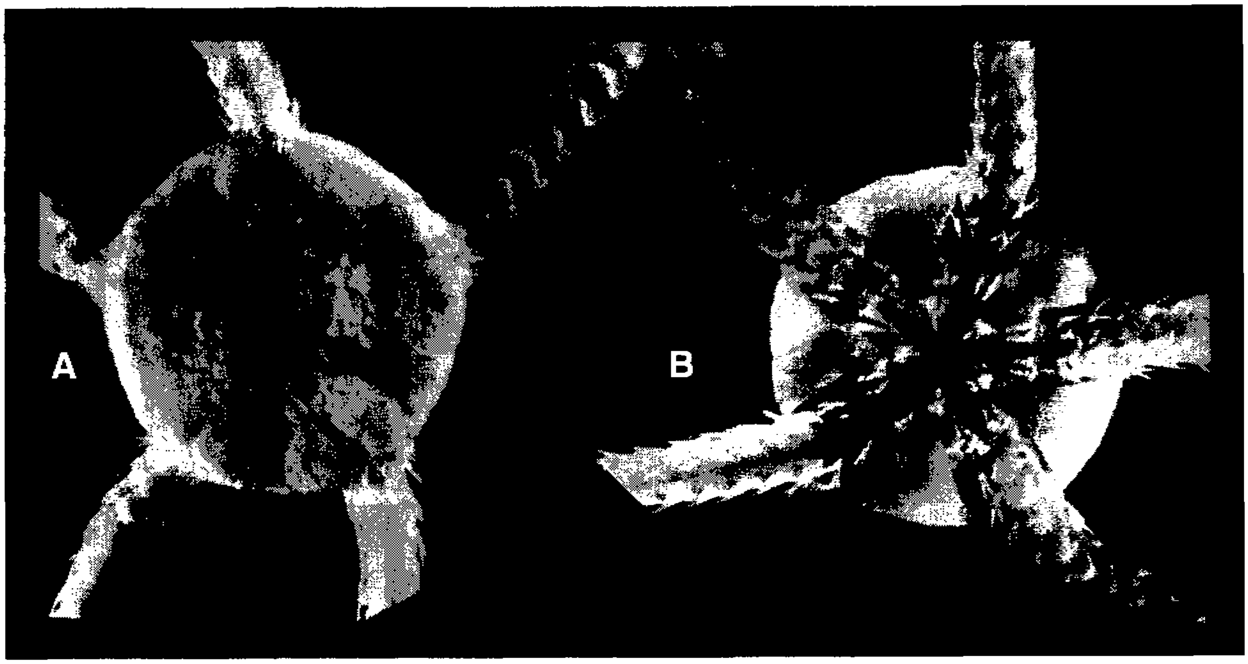

Figure 7.21. *Ophiura leptoctenia* H. L. Clark: A, disk, dorsal view; B, disk, ventral view (LACM 64-240.2; dd = 6.1 mm).

Variation: Juveniles have: disk covered by primary plates, radial shields, and few additional scales; fewer oral papillae than adults; pear-shaped oral shield with narrow triangular lobe merging with oral frame, rounded distal lobe occupying most of ventral interradius; dorsal arm plates fan-shaped, separated. An arm comb first appears in individuals 1-2 mm dd, the inner comb arises later in ontogenesis. On one jaw of one specimen from the present survey the adoral shield bears a spine, but this condition may be aberrant.

Color: Living individuals reddish brown or gray and khaki above, pale gray below. Eggs orange-salmon and pink. Preserved specimens fade to white, yellowish, or gray.

Remarks. Nielsen (1932) specified features that may differ between typical individuals and those from British Columbia. H. L. Clark (1911) compared and contrasted *O. leptoctenia* with congeners from northern waters, including *O. quadrispina* H.L. Clark, *O. ljungmani* (Lyman), *O. kinbergi* Ljungman, *O. sarsii* Lütken, and *O. luetkenii* (Lyman).

Distribution. Channel Islands to northern California, Oregon, British Columbia to western Aleutian Islands and Bering Sea (to 55° 35'N); also, Sea of Japan to Sakhalin Island. H. L. Clark (1911) noted the peculiar gap between Sakhalin and the Aleutians, depite the *Albatross* sampling stations in intervening waters. Bathymetric range 122-3,239, with poorly documented reports for 9-16 m (H. L. Clark, 1911, 1913, 1915; May, 1924; Nielsen, 1932; D'yakonov, 1954; Hartman, 1963; A. M. Clark, 1965; Astrahantseff and Alton, 1965; Kyte, 1969).

Biology. H. L. Clark characterized *O. leptoctenia* as one of the most common of the North Pacific ophiuroid species, with over 2,000 specimens in the collection he examined. *Ophiura luetkenii* was a close runner-up with 658 specimens. On the offshore basin slopes of Southern California, densities of *O. leptoctenia* reach 44 individuals/m^2 (Thompson and Jones 1987). On the Central California continental slope, this species and *Ophiacantha normani* Lyman are the dominant ophiuroid species. At 1000-2000 m depths, *O. leptoctenia* comprises 50% of the ophiuroids sampled. Its density peaks near 1,500 m where there are in excess of 30 individuals/0.1 m^2 (Summers, 1993).

The upper bathymetric limit of the species may coincide with the lower edge of the oxygen minimum zone off Central California (Summers, 1993). H. L. Clark pointed out the remarkably wide bathymetric range of *O. leptoctenia*, and provided information on bottom temperature at sampling localities. However, he failed to note that their depth of occurrence may be related to temperature, with populations tracking cold water masses and ranging from shallow depths in norther localities to deeper water in southern localities.

Sokolova (1959) characterized the species as omnivorous and carnivorous, but gut contents of specimens from 2,900-3,140 m consisted primarily of flocculent detritus, radiolarian and diatom remains, and Cumacea; of the latter there was generally only one per ophiuroid, some remaining in good condition.

The eggs of this species are approximately 0.2 mm diameter, a size consistent with an abbreviated mode of development or an ophiopluteus larval form.

Ophiura luetkenii (Lyman, 1860)

Figure 7.22

Ophioglypha Lütkenii Lyman, 1860:197-198.—1865:10, 40, 47-48.

Ophioglypha Lütkeni, Lyman, 1875:4.—1880:7.—Koehler, 1907:294, pl. 10, figs. 9-10.

Ophioglypha lütkeni, Lyman, 1882:35, 76, 310, 313.—Ives, 1889:176.—H.L. Clark, 1901:330.

Ophiura Lütkenii, Verrill, 1867:325.

Ophiura lütkeni, McClendon, 1909:37-38, figs. 32, 33.—H.L. Clark, 1911:5, 11, 19, 44-47, 55.—1915, 322.—Ziesenhenne, 1937:210, 230.—D'yakonov, 1954:102, fig. 38.—Matsumoto, 1917: 267.—Hartman, 1963: 85, 218, 305, 335, 350, 365, 382.—Kyte, 1969:1729, 1731, 1735, 1739.

Ophiura lütkini, Campbell, 1921b:47.

Ophiura lütkenii, May, 1924:291-294, fig. 1a-b.—Berkeley, 1927:5.—H.L. Clark, 1940:331, 343-344.

Ophiura Lütkeni, Nielsen, 1932:315, 316-18, figs. 27a, 28a,b.

Ophiura lutkeni, Barnard and Ziesenhenne, 1961:143.—Boolootian and Leighton, 1966:6, 9, fig. 20.—Alton, 1972:506-507.—Scanland, 1995:107.

Material Examined. California: Off Farallon Id., R/V *Velero III* Sta. AHF 887-38, 68 m (23, LACM 38-155.5). - Santa Maria Basin: Phase I Sta. BRC-013, 88.5-100.5 m (1, USNM primary voucher [as *Ophiura lutkeni*]); Phase I Sta. BSS-042, 100 m (1, SBMNH secondary voucher [as *Ophiura lutkeni*]); Phase I Sta. BSV-042, 100 m (1, USNM primary voucher [as *Ophiura leptoctenia*]); Phase II Sta. R-4, 92 m (1, CAMP voucher [as *Ophiura luetkeni*]). - Off San Clemente Id., R/V *Velero III* Sta. AHF 1012-39, 101-126 m (numerous, LACM 39-116.20).

Description. This is an ophiurid of moderate size; specimens as large as 27 mm dd have been reported. An individual 18 mm dd has arms 90 mm long; one 13 mm dd has 85 mm arms.

Disk pentagonal, flattened, covered by flat, imbricating scales; primary plates prominent; large radial, interradial, and mid-marginal scales surrounded by small, rounded scales. Radial shields subpentagonal, somewhat longer than wide, length approximately one-fifth diameter of disk. Paired radial shields separated proximally by wedge of scales, distally by series of scales aligned with dorsal arm plates. Arm combs of flat, nearly square scales in tight contact; up to 10 scales in the comb aligned with series of smaller scales fringing the radial shield and adradial edge of bursal slit.

Jaws narrowing ventrally, expanding to form a shelf within the oral gap. Apical oral papillae spinelike, arranged in cluster resembling dental papillae in large individuals; 5 flattened outer oral papillae on jaw opposed by 3 pointed papillae on first ventral arm plate. Teeth slender, with bluntly pointed tip. Oral shield large, partially covering ventral interradius, about as wide as long, rounded pentagonal with deeply notched lateral edges. Adoral shields narrow, approximately 1/2 size of oral shield, with proximal edges broadly in contact. Ventral interradii covered with thin, imbricating scales. Bursal slit spanning middle of oral shield to edge of disk, extending above arm base.

Arms tapering markedly toward tip; rounded triangular in cross section.

Dorsal arm plates overlapping, fan-shaped to subquadrate in dorsal view, with medial keel.

Lateral arm plates large, covering much of lower arm surface, somewhat figure-8 shaped in lateral aspect with dorsal lobe bearing spines on the distal edge, ventral lobe intruding between ventral arm plates. Three arm spines, tapering abruptly to sharp tip, laterally compressed; upper spine distinctly largest and longest at base of arm, length equaling 1.5 joints, relative size decreases distally; distal spines of equal size.

First ventral arm plate subtriangular with medial furrow; remaining ventral arm plates beneath disk more than twice as wide as long, proximal edge with protruding medial point, lateral edges narrow, rounded; plates beyond disk edge smaller, thinner; basal plates inflated in large individuals. Tentacle scale on lateral arm plate single, small, bluntly pointed; opposing scale on ventral arm plate present in large individuals.

Variation: Nielsen (1932) discussed the ontogenesis of the oral papillae and arm comb in this species. The arm comb is absent in individuals less than 2.5 mm dd, making it difficult to distinguish juveniles of this species from congeners such as *Ophiura sarsii*. Specimens of this size and smaller also differ from adults in having: reduced number of dorsal disk scales, arm spines, and tentacle scales; comb scales with free end pointed, dorsal arm plates overlapping only at base of arm.

Color: Living individuals were described as "salmon red with cinnamon" (May, 1924). Individuals from Santa Monica Bay, California are greenish-brown and reddish, mottled with black, pink, and white, the darker pigments sometimes forming a medial stripe on the arm; the lower surface is pale gray or whitish; the ovaries are salmon colored. The pigmentation pattern varies considerably from one individual to another. Color is retained for a time in preserved specimens, which have an intense gray dorsal surface, with black and white markings, and the ventral surface grayish white. Alcohol preserved material can fade to white.

Distribution. Cedros Island, Mexico, California, Oregon, Washington, British Columbia and Alaska to Bering Sea, at 9-1,265 m (Lyman, 1882; McClendon, 1909; H. L. Clark, 1911, 1940; May, 1924; Berkeley, 1927; Nielsen, 1932; Hartman, 1963; Kyte, 1969).

Remarks. H. L. Clark (1911) provides a key distinguishing *O. luetkenii* from the congeners, *O. sarsii* and *O. kinbergi*, with which it might be confused.

The epithet "*luetkenii*" is adopted because the specific name, originally published with a diacritic mark, is regarded as an incorrect original spelling to be corrected. In such a case, the ICZN indicates "...when in a name published before 1985 and based upon a German word, the umlaut sign is deleted from a vowel, the letter 'e' is to be inserted after that vowel (if there is any doubt that the name is based upon a German word, it is to be so treated)" (ICZN 32di[2]). Furthermore, the *-ii* genitive ending of the original name is retained as required (ICZN 33d).

Biology. This species occurs in great abundance in suitable habitats. For the southern end of its range in the Gulf of California and adjacent waters, Ziesenhenne (1937: 230) reported "bushelsful" of *O. luetkenii* taken in a single trawl haul. It has been characterized as "the most abundant deep-sea species in Monterey Bay" (May, 1924:294). However, its distribution may be patchy; Barnard and Ziesenhenne (1961) report it at 15% of 176 stations sampled between Pt. Conception, California and the Mexican border. It inhabits sand habitats with varying amounts of silt or mud, but also is found on shell or gravel bottoms (Kyte, 1969).

O. luetkenii is epifaunal, as are most of its congeners. A bottom photograph from off Pt. Conception (Lissner and Benech, 1993:fig. 4.7), shows a number of grayish-colored individuals resting on the surface of the sediment, with the ends of their arms upraised. MacGinitie (1949) characterized the species as a detritus feeder, but it is unlikley to use cilary tracts to transport food in the manner he suggested. According

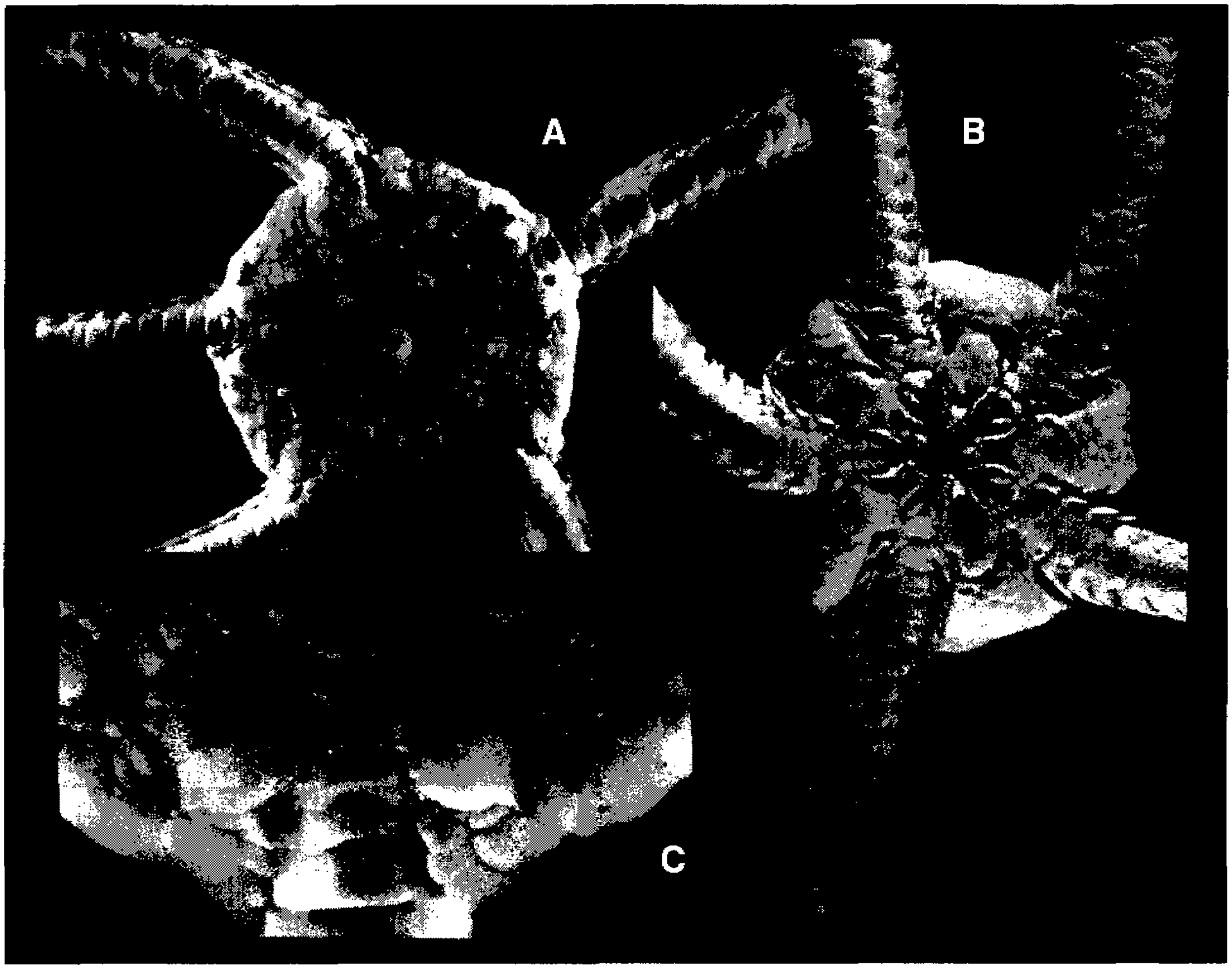

Figure 7.22. *Ophiura luetkenii* (Lyman): A, disk, dorsal view; B, disk, ventral view; C, disk edge, showing blunt, close-set scales of the arm comb (LACM 38-155.5; dd = 13.9 mm).

to Kyte (1969) it feeds on material from the surface of the sediment including protozoans, small animals, and detritus. Scanland (1995) reported a barred sand bass that gorged on *O. luetkenii* off the Orange County California ocean outfall, and Dover sole off Oregon, as well as copper rockfish off British Columbia (Murie, 1995) also prey on the species.

Acknowledgements

This study was funded by the Pacific Outer Continental Shelf Region of the Minerals Management Service, U. S. Department of the Interior, Washington, D. C. J. Blake and A. Lissner offered the MMS collection for study and arranged for its deposition at LACMNH.

D. Pawson and C. Ahearn (NMNH), R. Woolacott (MCZ), M. Jensen (Zoological Museum, Copenhagen), and F.A. Solis-Marin (UNAM, Mexico City) made available specimens in their care. Danish and German translation was provided by K. Friedmann, Russian by T. Ross, and Japanese by K. White. J. Dearborn and D. Pawson reviewed a draft of the manuscript.

Opportunities to collect and study living ophiuroids were provided by personnel of Hyperion Water Treatment Plant (Department of Sanitation, City of Los Angeles) and Southern California Control Water Research Project (SCCWRP). SCCWRP also provided partial support for taxomomic study of *Amphiodia* species. J. Watanabe (Hopkins Marine Station) furnished living material from Monterey Bay. I am grateful to all those acknowledged, for their assistance with this chapter.

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8. CLASS ECHINOIDEA

by

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Introduction

Echinoids, commonly known as sea urchins, heart urchins, and sand dollars, are a class of spherical or flattened echinoderms containing approximately 900 living species (Figures 8.1 and 8.2). General references utilized for this section are Hyman (1955), Barnes (1980), and Durham *et al.* (1980). Echinoids occur in all oceans and can tolerate salinities ranging from 57 percent to 110 percent seawater. Echinoids may be herbivorous or omnivorous. Most regular urchins feed on macroalgae. Irregular echinoids such as heart urchins ingest sediment, digesting the organic material, while sand dollars typically gather particulates from the substrate or water column, moving food items to the mouth via tube feet.

The name Echinoidea, meaning "like a hedgehog," describes the many spines arranged around the animal's test (Figure 8.1). Spines may be few in number and elongate, to numerous and short, and function in defense, burrowing, and locomotion. The longer spines are called primaries and the smaller spines are secondaries or miliaries (Figure 8.1).

Stalked pedicellaria are typical of all echinoids, generally consisting of three articulating jaws. They can occur over the general body surface (Figure 8.3) and are used for defense, prey capture, and cleaning.

Echinoids are dioecious, although some examples of hermaphroditism are known (Boolootian and Moore, 1956; personal observation). Fertilization and larval development are primarily external; however, brooding is utilized by some cold-water sea urchins and heart urchins, and is present in at least one species of sand dollar.

Regular Urchins

In the regular or radial urchins, each test plate has only one primary spine (Figure 8.1). The oral surface is located on the flattened, ventral side, while the aboral surface is moderately to highly arched. Spines on the oral and aboral surfaces typically are shorter than those on the sides. The oral surface has five ambulacral areas containing five double rows of podia that extend in a pentaradiate pattern from the oral to the apical region (Figure 8.1). Podia usually are equipped with terminal disks and are extendable beyond the spines. Sea urchins use both spines and podia for locomotion.

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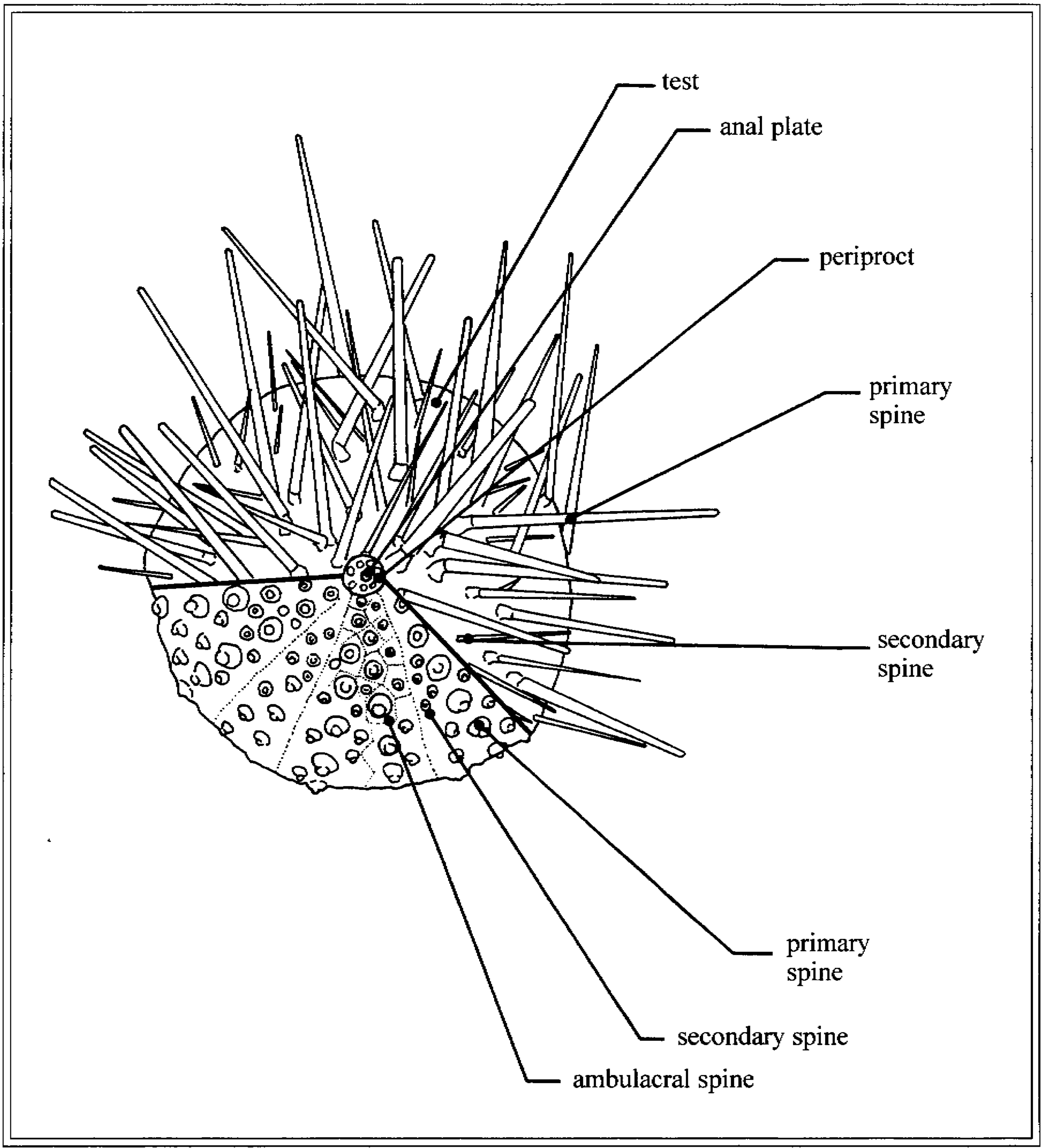

Figure 8.1. Typical aboral morphology of regular echinoid (after Word and Charwat, 1975).

The mouth is located in the center of the oral surface. The urchin's chewing apparatus, termed Aristotle's lantern, is composed of an elaborate system of muscles surrounding 40 calcified ossicles. Five of these ossicles form hard teeth used to graze food. A membranous area, the peristome, encircles the mouth forming a thickened rim (Figure 8.3). At the edge of the peristome are five pairs of bushy gills. The aboral surface also has a membranous central area, the periproct. The periproct may have one to many embedded endoskeletal plates and also contains the anus. The axis of symmetry extends from the center of the periproct to the mouth, and body parts are arranged pentamerously around the axis.

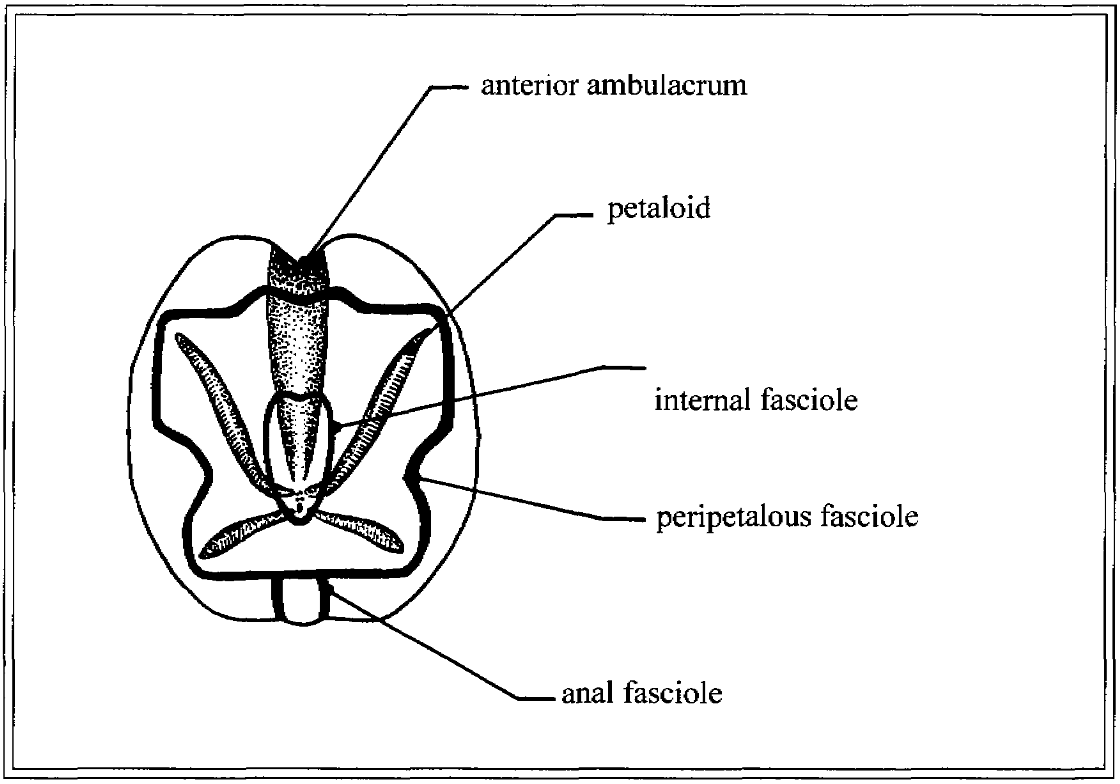

Figure 8.2. Typical aboral morphology of irregular echinoid (after Word and Charwat, 1975).

The endoskeletal test typically is formed of tightly fitted, rigid calcareous plates. However, some diademids and echinothuriids may have overlapping plates which give their tests a more flexible or leathery appearance.

Irregular Echinoids

In the irregular echinoids such as heart urchins and sand dollars, the periproct and anus are shifted from the center of the aboral surface to a posterior area between ambulacra, the posterior interambulacrum (Figure 8.2). This migration establishes an axis of bilateral symmetry that is more effective for burrowing by these species.

Heart urchins have a more or less ovoid shape with flattened oral and convex aboral surfaces. The peristome and mouth have migrated anteriorly, and the periproct and anus posteriorly, while the center of the aboral surface remains at the center of the dorsal surface. Some heart urchins have spines grouped in narrow bands (fascioles) on the upper body surface. These smaller spines are associated with numerous cilia that, when beating in unison, create currents that assist in feeding, respiration, and cleaning of the surface. Podia are degenerate in these species except for areas around the oral and aboral surfaces.

Sand dollars have flattened bodies with circular circumferences. In these species, the oral and aboral surfaces are centrally located, with the periproct ventral and situated in the posterior interambulacrum.

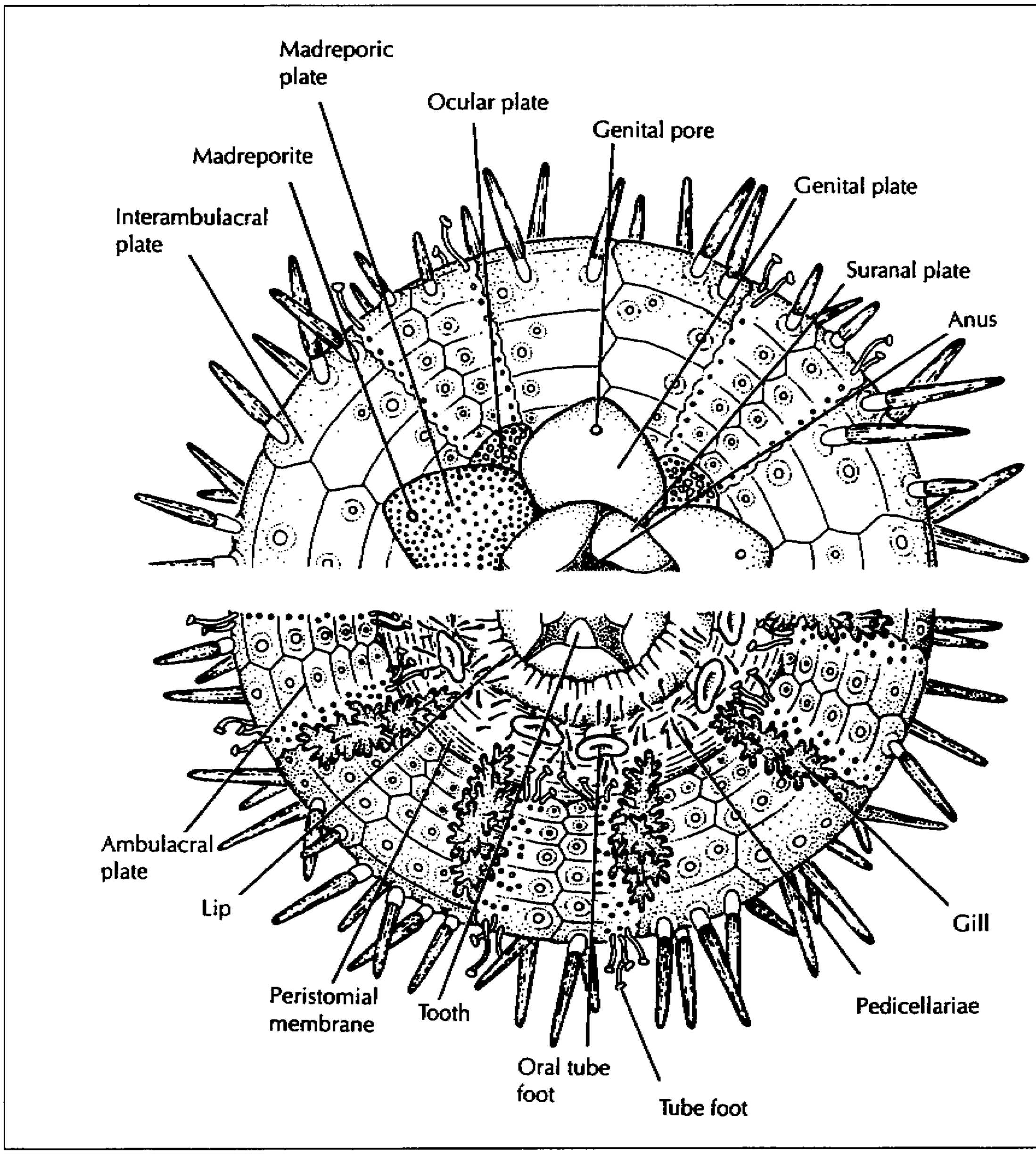

Figure 8.3. Oral (upper) and aboral (lower) views of regular echinoid (after Pierce and Maugel, 1987).

Taxonomic History

The distinctive morphology, color, and relatively large size of most California echinoids have made them the subject of numerous scholarly and popular presentations on their taxonomy and distinguishing characteristics. Important taxonomic monographs for echinoids worldwide include Mortensen (1928-1951), Durham and Melville (1957), and Durham *et al.* (1966), with Pacific Coast taxa addressed more specifically by Grant and Hertlein (1938), Clark (1948), Swan (1952), Jensen (1974), and Durham *et al.* (1980). Another classic reference that summarizes key distinctions among Orders and Families of echinoids, as well as considerable species-specific information on West Coast taxa is Hyman (1955). A very useful, popular reference, including color plates of shallow subtidal species, is Gotshall and Laurent (1979). Other relevant summaries of species distributions and their natural history are presented in Ziesenhenne (1941), Hartman (1955), and Hartman and Barnard (1958), Pequegnat (1964), Turner *et al.* (1968), and Lissner and Dorsey (1986). Important synopses of taxonomic collections of echinoids and distributions, including those from southern California, are provided in Muscat (1980), Luke (1982), and Maluf (1988).

Morphology

Key features that are useful in identifying echinoids include the body shape, size and type of primary spines, location and shape of petaloids for heart urchins, and, in most fresh and preserved specimens, body and spine color. Important characters that must be recognizable to use the taxonomic key in this chapter include anterior ambulacrum, petaloids, fasciole, and ambitus (Figures 8.1 and 8.2).

The taxonomic key for the echinoids was developed in part with, and the identifications were made with the aid of, the monographs of Mortensen (1928-1951). Many specimens also were compared with the echinoid collection of the Allan Hancock Foundation, University of Southern California.

Glossary

Anterior ambulacrum. Antero-dorsal furrow, prominent in most irregular echinoids, containing tube feet and produced by a depression in the skeletal plates.

Fasciole. Clusters of spines, usually on the aboral surface, that often are darker colored (e.g., brown or black) in several heart urchin species and which are arranged in characteristic patterns such as ovals, kidney bean-shaped (reniform), or margin contours.

Petaloids. Petal-like, ambulacral furrows, usually four in number, located on the dorsal surface of most irregular echinoids, posterior to the anterior ambulacrum.

Methods of Laboratory Examination

Identification of echinoids was accomplished using the unaided eye to distinguish gross morphological features such as color and general shape, and a stereomicroscope to verify spine or anterior ambulacrum/ petaloid type and location in small individuals (less than approximately 10 mm). Microscopic spicules, which can be examined under a compound microscope by dissolving a piece of tube foot in sodium hypochlorite (bleach), are sometimes used as taxonomic features; however, this was not necessary to identify the present species. The first distinction was based on whether the test was circular or ovoid (irregular) in outline, thereby separating the regular urchins from the heart urchins, respectively. The regular urchins then could be distinguished based on color, which is conservative in preserved specimens and unique (pink or whiteish) for the species in the study area. For the heart urchins, the light green to brown color (also conservative in preservation) indicated that the specimens belonged to either *Brisaster* or *Brissopsis* in the study area; other genera are either whitish or purple. The arrangement and shape of the anterior ambulacrum and petaloids then distinguished the species.

List of Species

Class Echinoidea
    Order Temnopleuroida
        Family Toxopneustidae
            Lytechinus pictus (Verrill, 1867)

    Order Echinoida
        Family Strongylocentrotidae
            Allocentrotus fragilis (Jackson, 1912)

    Order Spatangoida
        Family Schizasteridae
            Brisaster latifrons (A. Agassiz, 1898)
        Family Brissidae
            Brissopsis pacifica (A. Agassiz, 1898)

Key to the Species of Echinoidea Collected from the Santa Maria Basin and Western Santa Barbara Channel

(Note: other species may occur in the region but were not collected in the present study)

1A. Test oval to heart-shaped (irregular urchins) 3
1B. Test globose, circular in outline (regular urchins) 2

2A. Color of test and spines pink; spines distributed evenly over surface of test; spines thin and delicate; (note: spine color visible in juveniles greater than 2-3 diameter) .... *Allocentrotus fragilis*
2B. Color of test and spines on aboral surface dirty white to dark "blotched" and white to tan on oral surface; "skirt" of primary spines around circumference of test; primary spines robust .... *Lytechinus pictus*

3A. Anterior ambulacrum deeply notched; subanal fasciole not evident; posterior petaloids typically less than half the length of anterior petaloids; color of test and spines light brown to brownish-green in fresh specimens .... *Brisaster latifrons*
3B. Anterior ambulacrum only slightly notched; prominent, brown to black, reniform subanal fasciole; posterior and anterior petaloids almost equal in length; color of test and spines light green to brown in fresh specimens .... *Brissopsis pacifica*

Descriptions of Species

Order Temnopleuridae

Family Toxopneustidae

Lytechinus pictus (Verrill, 1867)

Figure 8.4

Psammechinus pictus Verrill, 1867.
Lytechinus pictus: Clark, 1912.

Material Examined. California: Santa Maria Basin, Sta. BRA-001 (USNM), approximately 70 m (one specimen, 23 mm test diameter); Sta. 002 (SBMNH), 200 m (one specimen, 12 mm test diameter); Sta. PJ-1 Rep. 1 (note: secondary label in specimen jar lists station as RI-1, presumably in error since it does not match a known station code), 145 m (one specimen, 23 mm test diameter).

Description. Test domed aborally and flattened orally, with diameter to approximately 40 mm; primary spines to 25 mm in length (Tyler, 1944; Durham *et al.*, 1980), commonly observed as a "skirt" of spines around ambitus (Lissner, 1980). Primary tubercles of interambulacra small and imperforate (Figure 8.4); pore pairs of ambulacra in 3oblique rows. Test color ranges from off-white to yellowish, particularly on oral surface and sides of test, but including grayish to purple "blotches" on aboral surface, extending to irregular banding on some spines (Durham *et al.*, 1980; Lissner, 1980).

Biology. *Lytechinus pictus* is one of the most common megabenthic invertebrates collected on the California shelf (Thompson *et al.*, 1987a), occurring in densities up to 20 individuals m^2, but noted up to 192 individuals m^2. Populations may appear in vast "herds", usually on sandy bottoms (Dean *et al.*, 1984) or in eelgrass beds (e.g., in bays off Baja California). The range of substrate types includes rocks, shells, sand, and mud (Maluf, 1988). Their diet appears to be omnivorous (Thompson *et al.*, 1987a), but they are best known from field studies (e.g., Dean *et al.*, 1984) that documented extensive grazing effects on juvenile kelp, the extent of which appears to be mediated by predation from the seastar *Patiria miniata* (Schroeter *et al.*, 1983).

Remarks. Maluf (1988: page 144) notes that *Lytechinus anamesus* is considered to be a synonym of *L. pictus*. Unpublished comparisons (Lissner, pers. obs.) of spicules in tube feet also could not distinguish any differences between these two morphological types, and similarly treat them as synonomous in this chapter. These conclusions are supported further by laboratory results which indicated the two "sympatric" species are completely cross-fertile (Cameron, 1984).

Distribution. The species occurs from Monterey, California to La Plata Island, Baja California, ranging in depth from the intertidal to 300 m. This is a much broader depth range than noted in earlier references (e.g., Gotshall and Laurent, 1979), and likely reflects the distributions of both *L. pictus* and *L. anamesus*, as combined by the synonomization of these species (noted in Maluf, 1988; see remarks).

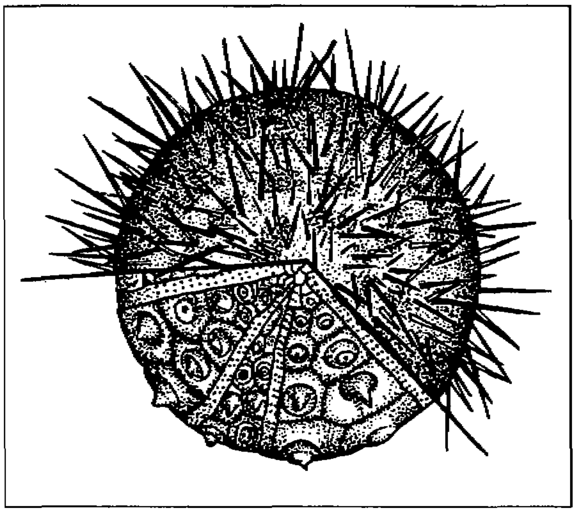

Figure 8.4. Aboral view of undisturbed test and spines of *Lytechinus pictus* (upper) and cleaned test (lower) (after Word and Charwat, 1975).

Order Echinoida

Family Strongylocentrotidae

Allocentrotus fragilis **Jackson, 1912**

Figure 8.5

Allocentrotus fragilis Jackson, 1912.—Mortensen, 1942, 1943.
Strongylocentrotus fragilis: Clark 1912.

Material Examined. California: Santa Maria Basin, Sta. 095 (USNM), 198 m (one specimen, 80 mm test diameter, labelled/spelled incorrectly as *A. fragile*); Sta. R-6, Rep. 1, 410 m (one fragmented specimen, oral half only, approximately 50 mm test diameter).

Description. Color of test and spines pink, although irregular dark and white spine-banding also evident, particularly on primary spines; spines thin and delicate (Figure 8.5); test somewhat flattened dorsoventrally. No genital papillae in males or females (Lawrence, 1987). Color retained quite well in dried and preserved specimens, and evident in juveniles of at least 2-3 mm test diameter. *Allocentrotus fragilis* is the only pink sea urchin collected on the shelf and slope of the Pacific Coast.

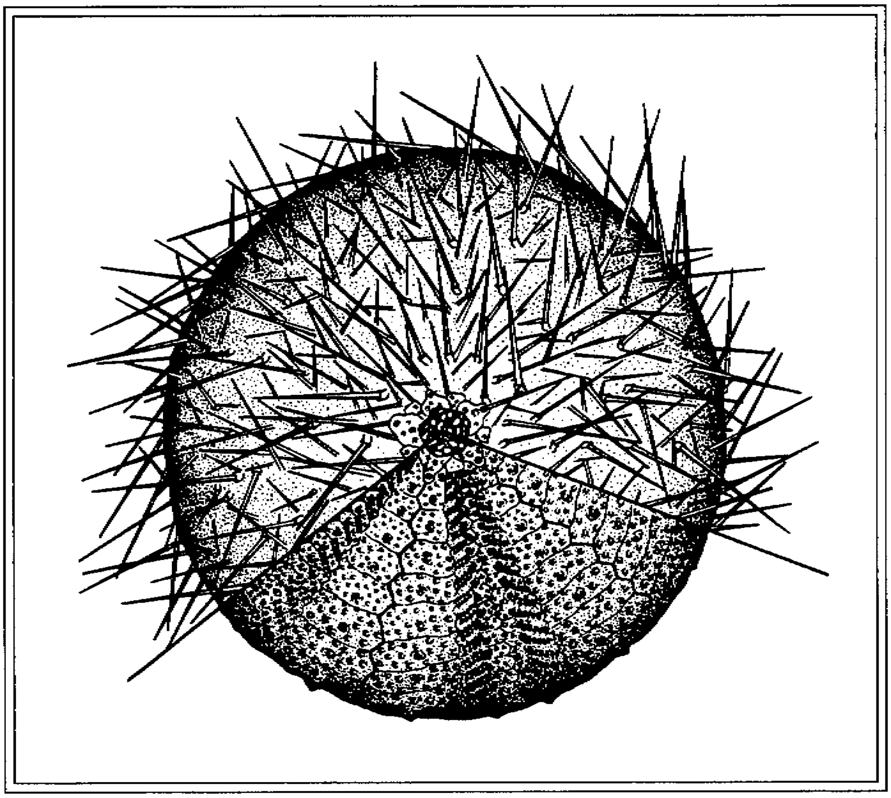

Figure 8.5. Aboral view of undisturbed test and spines (upper) and cleaned test (lower) of *Allocentrotus fragilis* (after Word and Charwat, 1975).

Biology. *Allocentrotus fragilis* often occurs in large aggregations at depths ranging from 50-1200 m, and has been characterized as the most abundant sea urchin off the California coast (Pearse, 1975), although Thompson *et al.* (1987) reported that the predominate depth range within the southern California borderland is from 150-480 m. The species often dominates (abundance and/or biomass) trawl catches at upper slope sites; densities have been recorded up to 6.2 individuals/m^2(Thompson *et al.*, 1987). No correlation of distribution and abundance with grain size is evident, with populations ranging primarily from fine sand to very fine, silty-clay habitat, but also occurring on hard substrate (Maluf, 1988), particularly in ecotone regions (Lissner, pers. obs.). Their feeding type is characterized as predator-scavenger, consistent with the overlap of their highest abundances with areas of highest infaunal diversity. *Allocentrotus fragilis* also are common scavengers on food falls (e.g., fish and algae) observed within their depth range (Lissner, pers. obs.).

Distribution. The species is reported from Vancouver, Canada, to Isla Carmen, Baja California, ranging in depth from 50-1,200 m (Maluf, 1988).

Order Spatangoida

Family Schizasteridae

***Brisaster latifrons* (A. Agassiz, 1898)**

Figures 8.6 and 8.7

Schizaster latifrons A. Agassiz, 1898.

Schizaster townsendi A. Agassiz, 1898.

Schizaster (*Brisaster*) *townsendi:* Mortensen, 1907.

Brisaster latifrons: Clark, 1913, 1917, 1937.—Koehler, 1924.—Grant and Hertlein, 1938.—McCauley, 1967.

Brisaster townsendi: Clark, 1917 (according to McCauley, 1967).

Oppissaster latifrons: Lambert and Thiery, 1924.

Material Examined. California: Santa Maria Basin, Sta. 097 (USNM), 393 m (one specimen, 49 mm length, ratio of anterior/posterior petaloids is 26 mm/19 mm); Sta. 088 (SBMNH), 393 m (one specimen, 40 mm length, ratio of anterior/posterior petaloids is 25 mm/15 mm); Sta. R3 Rep. 3, 409 m (two specimens, 40 and 47 mm lengths, ratios of anterior/posterior petaloids are 27 mm/15mm and 27 mm/17 mm, respectively).

Description. Petaloids deeply sunken; anterior petaloids long, reaching almost to margins of test; posterior petaloids shorter, approximately one-half length of anterior ones (1.0:0.5) (Word and Charwat, 1975; Figures 8.6 and 8.7); however, ratios measured in material examined approximately 1.0:0.6. Anterior ambulacram deeply notched. Peripetalous fasciole present (Figure 8.7), ranging even in preserved specimens from dark brown (thereby contrasting sharply with the lighter brown test) to light brown (blending with the test color).

Biology. *Brisaster latifrons* is a very common heart urchin of the California continental shelf and slope, occurring in "kilometer-scale herds" on the slope (Thompson, 1993), and sometimes representing the dominant (abundance and/or biomass) megabenthic invertebrate in these communities (Thompson *et al.*, 1987). Densities on the upper slope can range up to 30 individuals/m^2. Maximum lengths from Thompson *et al.* were 73 mm. Individuals burrow up to 15 cm below fine-grained sand or muddy substrates, feeding on organic material in the sediments (Nichols *et al.*, 1989).

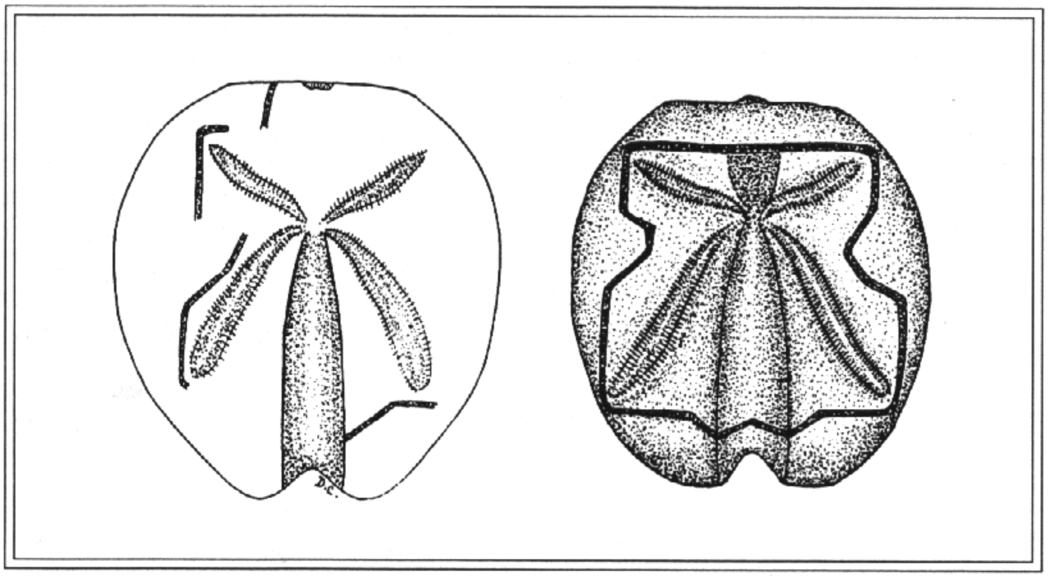

Figure 8.6. Aboral view of cleaned test of *Brisaster latifrons* (after Word and Charwat, 1975).

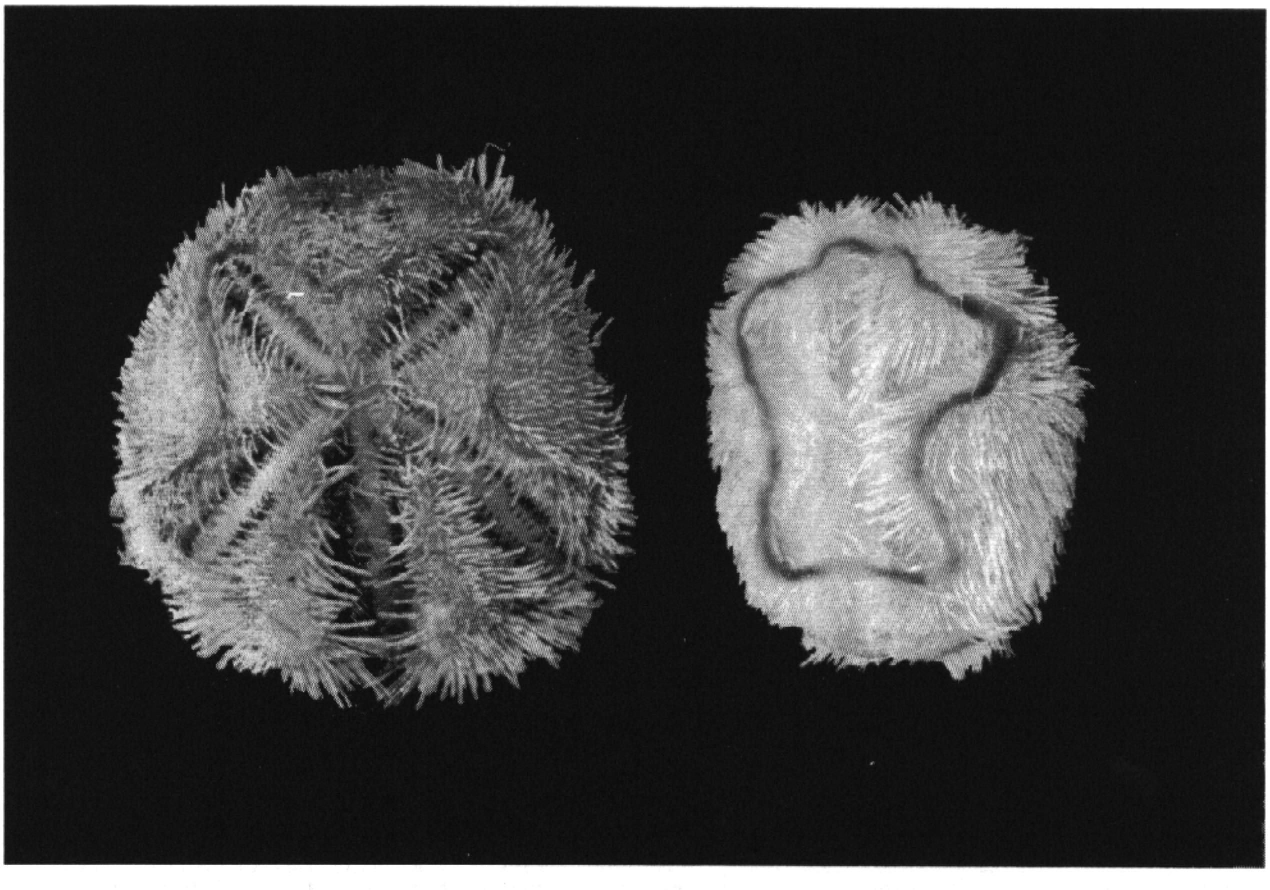

Figure 8.7. Aboral views of *Brisaster latifrons* (left) showing sunken petaloids, notched anterior ambulacrum, and faint peripetalous fasciole; and *Brissopsis pacifica* (right) indicating "shallow" petaloids and prominent peripetalous fasciole. Specimens are from Stations 088 and 025, respectively.

Distribution. This species is panamic, extending along the entire Pacific coast of North America (Clark, 1914), with an overall range from the Bering Sea to the Galapagos Islands (Maluf, 1988). The reported depth range is from 9-2,817 m.

Family Brissidae

Brissopsis pacifica A. Aggasiz, 1898

Figures 8.8 and 8.9

Brissopsis pacifica A. Aggasiz, 1898.

Toxobrissus pacificus: A. Agassiz, 1904.

Brissopsis pacifica: Mortensen, 1907.—Clark, 1917, 1923, 1948.—Grant and Hertlein, 1938.— Zeisenhenne, 1937.

Kleinia pacifica: Lambert and Thiery, 1925.

Material Examined. California: Santa Maria Basin, Sta. 066 (USNM), 201 m (two specimens, 29 and 49 mm lengths, ratios of anterior/posterior petaloids 10 mm/10 mm and 13mm/13 mm, respectively, and one broken specimen, approximately 32 mm length, no ratio determination possible); Sta. 025 (SBMNH), 390 m (one specimen, 38 mm length, ratio of anterior/posterior petaloids 13 mm/10 mm); Sta. PJ-1 Rep. 1, 145 m (one specimen, 47 mm length, ratio of anterior/posterior petaloids 17 mm/17 mm).

Description. Body and spines light green to brownish in fresh specimens, fading to light green to light tan in preserved material (Durham *et al.*, 1980; Lissner, pers. obs.); prominent brown to black peripetalous fasciole (Word and Charwat, 1975) and reniform subanal fasciole are present (Figure 8.7 and 8.9); petaloids not deeply sunken, anterior and posterior petaloids approximately same length (see material examined ratios); anterior ambulacram relatively flush with test edge.

Biology. *Brissopsis pacifica* is one of three echinoids (along with *Allocentrotus fragilis* and *Brisaster latifrons)* that dominate (abundance and/or biomass) their respective communities on the California continental slope (Thompson *et al.*, 1987), sometimes occurring in "kilometer-scale herds" (Thompson, 1993). Highest abundances (e.g., approximately 20 individuals/m^2, but ranging up to 42 individuals/m^2) occur at mid-slope depths from 300-600 m. Maximum test lengths from Thompson *et al.* were almost 60 mm. The species is characteristic of fine-grained substrates, ingesting organic material from the sediments.

Distribution. This species ranges from the Channel Islands and coast of southern California to Panama and the Galapagos Islands (Feder, 1980), and the western Indo-Pacific (Maluf 1988), at depths from 9-3,279 m.

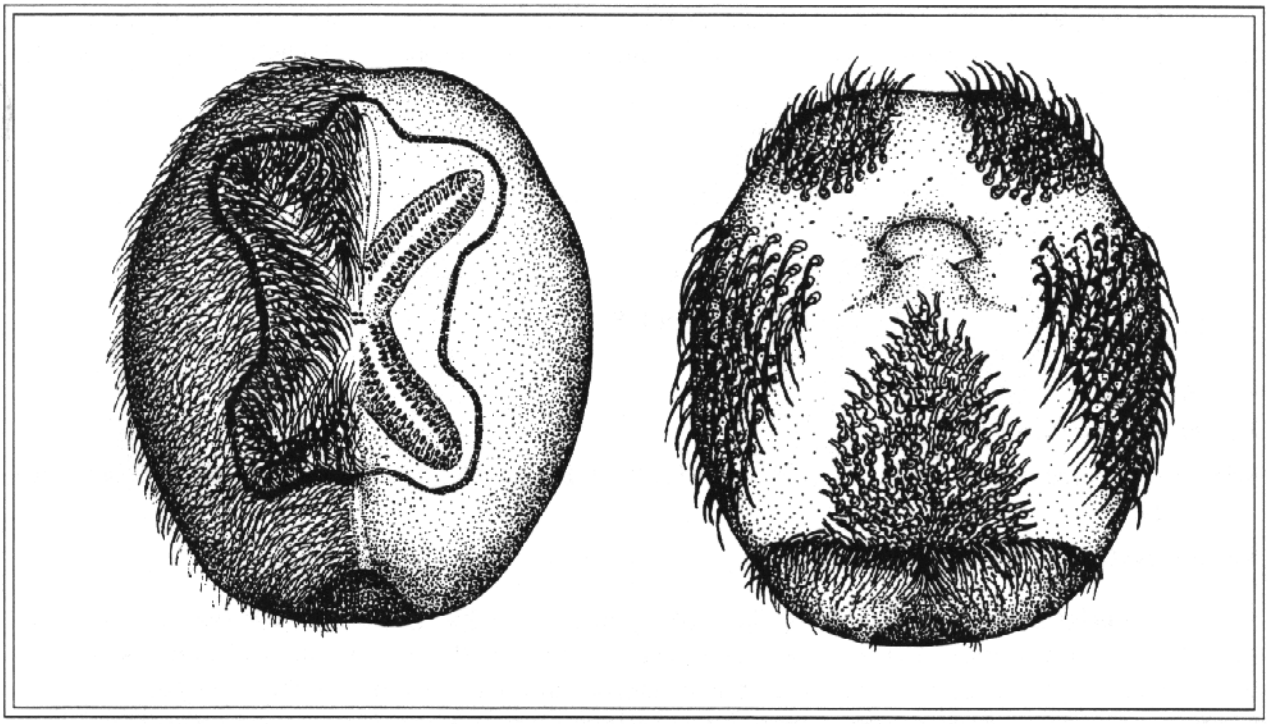

Figure 8.8. Aboral view (left) of undisturbed test and spines (left-side) and cleaned test (right-side), and oral view (right) of undisturbed test and spines of *Brissopsis pacifica*. Source: Word and Charwat, 1975.

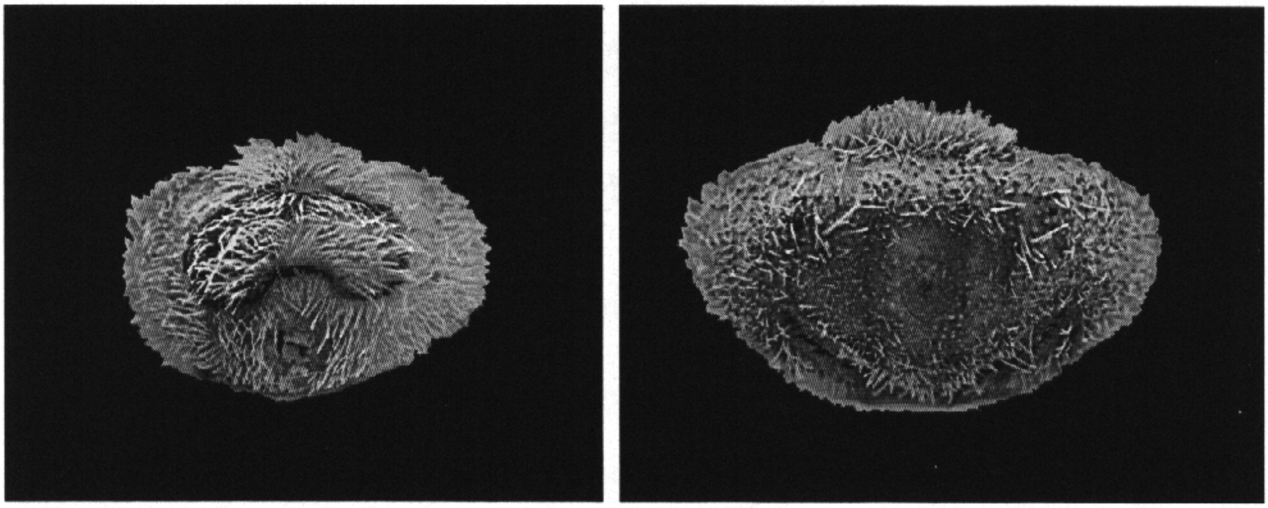

Figure 8.9. Posterior views of *Brissopsis pacifica* (right) showing prominent subanal fasciole, contrasted with *Brisaster latifrons* (left). Specimens are from Stations 025 and 088, respectively.

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9. CLASS HOLOTHUROIDEA DE BLAINVILLE, 1834

Including Keys and Descriptions to all Continental Shelf Species from California

by

Mary Bergen[1]

Introduction

Holothuroids are common members of benthic communities in California. They are found in both hard- and soft-bottom habitats, from the intertidal zone to abyssal depths.

Holothuroids are most often soft-bodied and cylindrical, with tentacles at one end. Their kinship with the echinoids and asteroids is not immediately apparent because bilateral symmetry has been superimposed over pentamerous symmetry and the plates of the exoskeleton have been reduced to microscopic particles in the body wall. One external clue, however, that a worm-like creature is a holothuroid is that the number of tentacles is a multiple of five. On dissection, the presence of the water vascular system and muscle bands in multiples of five clearly show that holothuroids are, indeed, echinoderms.

Morphology

Most holothuroids have cylindrical bodies, with the tentacles and mouth at one end and the anus at the other. Some holothuroids are somewhat U-shaped; in extreme cases, the body wall becomes foreshortened so that the mouth and anus are adjacent. Some holothuroids are flattened dorsoventrally, with a distinct soft sole sometimes developed.

The number and shape of the tentacles is an important taxonomic character. Most California holothuroids have 10 or 15 tentacles; however, the apodous holothurians have 12 tentacles. Tentacles may be a simple digitate, pinnate, shaped like a shield or profusely branched (Figure 9.1). In dendrochirote holothurians, the tentacles can be retracted into the body; the area between the tentacles and the body is called the introvert.

The body wall is divided by five radii that extend from the mouth to the anus. In each radius there is a longitudinal muscle, a nerve strand and a water-vascular canal. The water-vascular canal is a vessel which carries fluid to the tube feet (= podia). In the apodous holothurians both tube feet and water-vascular canals are absent. In most cases, there are three ventral radii that contact the substrate and two dorsal radii.

The portion of the body wall with the longitudinal muscle and tube feet is called the ambulacrum or radius. The spaces between ambulacra are called the interambulacra or interradii.

Tube feet may be restricted to the ambulacra or scattered over the entire body wall. In most cases, interambulacral feet are not present in small holothuroids; rather, they first appear when the animal is about one centimeter long. The podia are modified into papillae in some aspidochirote holothurians.

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[1] Southern California Coastal Water Research Project, 7171 Fenwick Lane, Westminster, CA 92683.

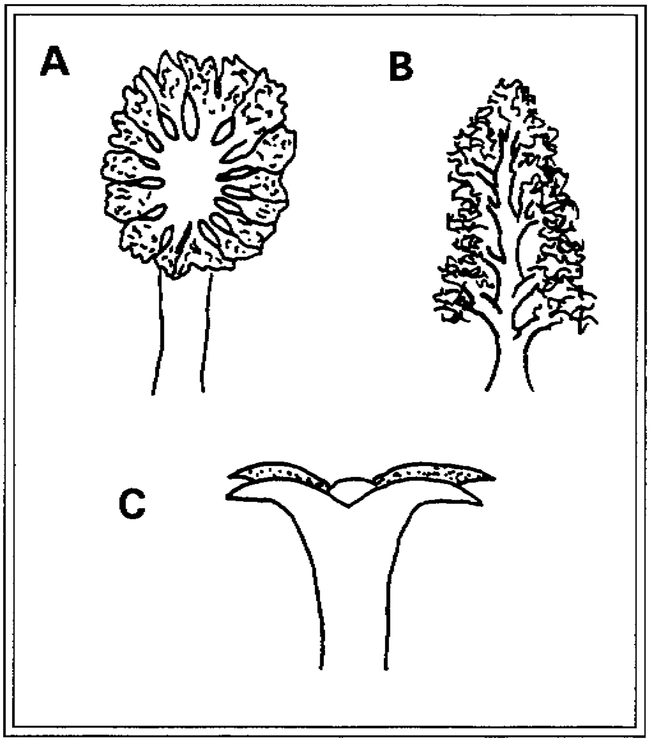

Figure 9.1. Types of tentacles: A, peltate; B, digitate; C, tentacle with 2 pairs of digits and no terminal digit.

Internally, the gut is divided into an esophagus, intestine and, sometimes, a cloaca (Figure 9.2). The esophagus is surrounded by a calcareous ring that provides support and is a point of attachment for the radial muscles. In dendrochirote holothurians, retractor muscles, which pull the tentacles into the body, also attach to the calcareous ring.

Immediately posterior to the calcareous ring is the water-vascular ring. Connecting to the water-vascular ring is one or more polian vesicles which act as reservoirs. In some groups, e.g., the Molpadiidae and the Stichopodidae, reservoirs for the tentacles, called tentacle ampullae, are also present. There is also one or more stone canals terminating in a madreporite which allow exchange of fluid between the water-vascular system and the coelom.

The gonad is a tuft of tubules which, when ripe, can occupy much of the coelom. The gonoduct runs anteriorly along the middorsal interradius to an external opening near the ring of tentacles. Except in elasipods and apodous holothurians, the coelom also contains respiratory trees which arise from the cloaca. The respiratory trees assist in gaseous exchange.

Some holothuroids, such as the Psolidae, have a test of large overlapping plates. In others, the plates are small, but so closely packed as to form a hard surface. In most cases, with the exception of the Psolidae, the plates are embedded in the body wall, and are microscopic in size. These microscopic ossicles (sometimes also called spicules or calcareous deposits) are a primary character used in identification.

The ossicles assume a wide variety of shapes, including anchors, tables and plates (Figure 9.3). Plates are more or less flat while tables have a spire attached to a flat disk. The key to species has illustrations of the different ossicle types. The ossicles in the body wall, tube feet and the tentacles are generally different. The tube feet have supporting tables and, in some cases, an end plate. The disk of the supporting table is curved. The end plate is a sieve-like plate found in the end of the tube foot. The ossicles in the tentacles are usually rods. They are so variable in size and shape that they are rarely used in identification.

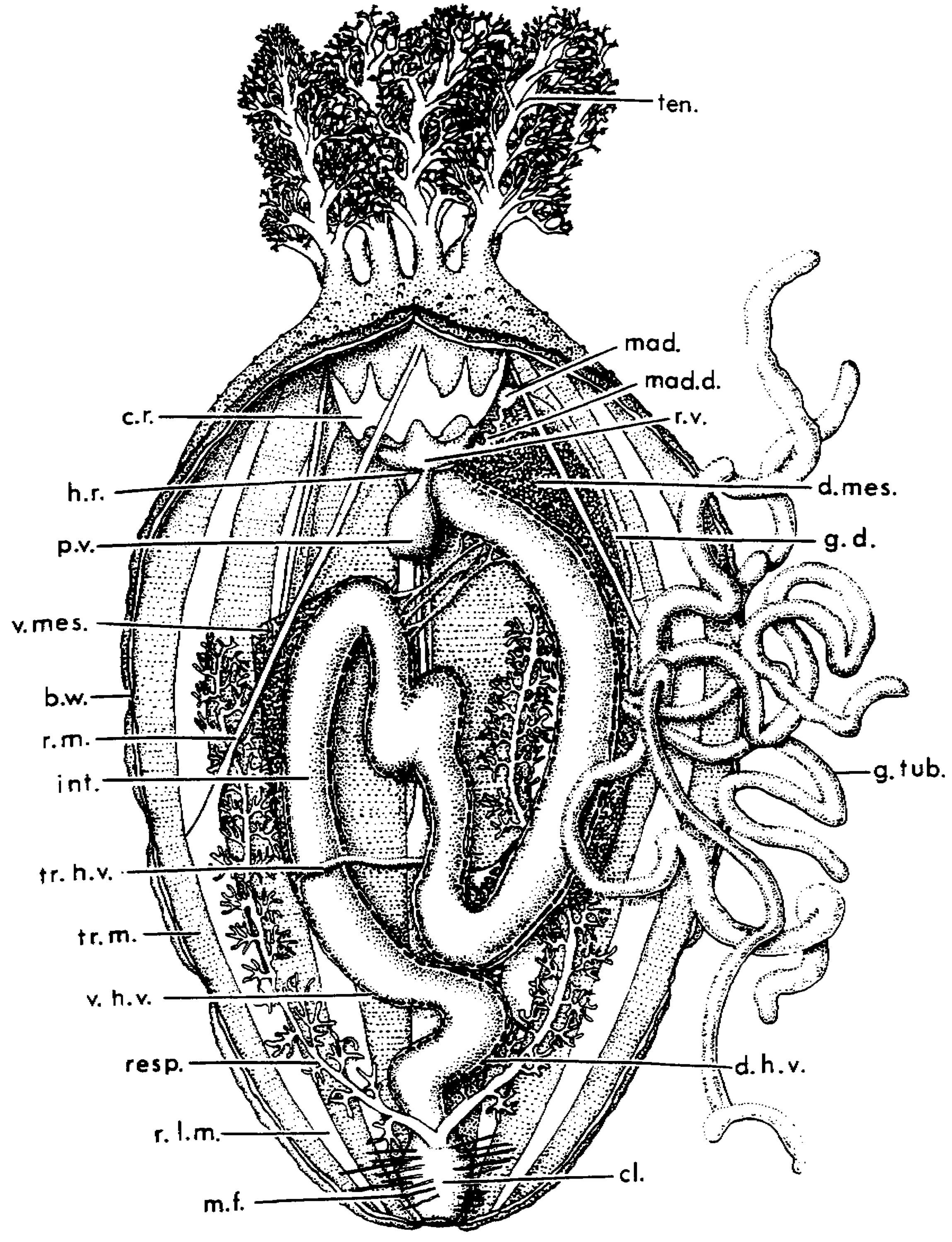

Figure 9.2. Whole animal, dissected to show internal morphology (from Pawson, 1970).

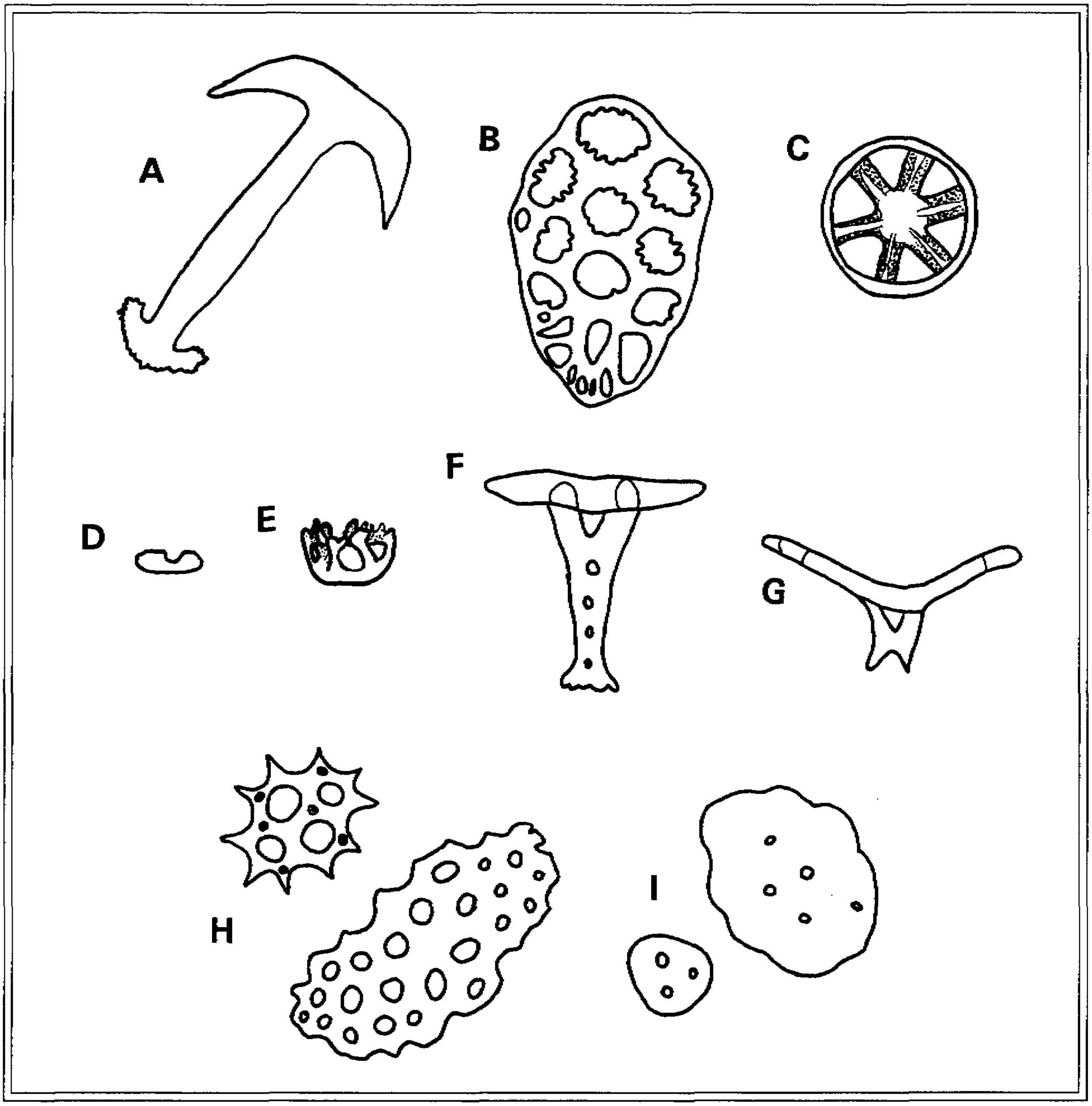

Figure 9.3. Types of ossicles: A, anchor; B, anchor plate; C, wheel; D, miliary body or granule; E, cup; F, table; G, supporting table; H, plates; I, buttons.

Glossary

Ambulacrum (Plural: Ambulacra). The radius. The portion of the body wall that includes the longitudinal muscle and tube feet.

Anchor. An ossicle shaped like an anchor.

Apodous. Lacking tube feet.

Button. A round thick ossicle.

Calcareous ring. A ring of calcareous plates surrounding the pharynx; the ring supports the water vascular ring, and provides attachment for the longitudinal muscles.

Caudal appendage. A tail-like extension of the posterior body wall found in molpadiid holothurians.

Ciliated funnels. Small funnel-shaped structures attached to the mesenteries and/or the body wall in apodous holothurians.

Cup. An ossicle with raised sides shaped like a cup.

Cuvierian organs. Sticky tubules that can be ejected from the anus as a defense against predators.

Digitate. Shaped like a finger.

End plate. A sieve-like plate found at the end of a tube foot.

Interambulacrum. Interradius. The portion of the body wall between the ambulacra.

Introvert. In dendrochirote holothurians, the part of the body wall between the tentacles and main body which allows inversion of the tentacles.

Madreporite. A calcareous structure at the terminus of the stone canal which allows for passage of fluid between the water vascular system and the coelom.

Miliary granules. Small, compact ossicles found in the longitudinal muscles of apodous holothuroids.

Ossicles. Microscopic calcareous particles, also known as spicules, embedded in the body wall which act as a skeletal structure.

Phosphatic body. Round to oval granules of iron phosphate formed from ossicles in Molpadiida.

Pinnate. Shaped like a feather.

Papillae. Tube feet lacking a suction cup at the end.

Peltate. Shaped like a shield.

Plate. A flat ossicle usually with perforations.

Podia. See **Tube feet.**

Polian vesicle. A sac-like protrusion from the water vascular ring that acts as a reservoir for the water vascular system.

Radius (plural: radii). Ambulacrum. A longitudinal division of the body wall having a muscle, a nerve strand and, except in apodous holothurians, a water-vascular canal.

Respiratory trees. Branching tubules arising from the cloaca that assist gaseous exchange.

Rod. A cylindrical ossicle.

Rosette. A small ossicle with short rounded lateral branches.

Sigmoid body. An ossicle in the form of curved rod with both ends recurved. Found in some apodous holothurians.

Spicules. See ossicles.

Stone canal. A tube arising from the dorsal side of the water vascular ring which terminates in madreporite.

Supporting table. A table found in the tube feet; supporting tables usually have a curved disk.

Table. An ossicle having a spire attached to a disk.

Tentacles. Feeding structures, variously shaped, surrounding the mouth.

Tentacle ampullae. Sac-like protrusions from the water vascular system that act as reservoirs for fluid supporting the tentacles.

Test. A framework of overlapping plates forming an exterior skeleton.

Tower. A hollow cylindrical ossicle with straight sides.

Tube feet. Cylindrical projections from the body wall with suction cups at the end, which aid in locomotion. Also known as **podia**.

Water vascular ring. A part of the water vascular system that encircles the esophagus.

Water vascular system. A system of vessels filled with fluid that acts as a hydrolic system, providing skeletal support and the means to move the tentacles and tube feet.

Wheel. A circular ossicle with spokes.

Taxonomic History

The California holothuroids have a long taxonomic history. The literature is scattered, and to date there has been no comprehensive study of temperate eastern Pacific holothurians. Between 1829 and 1886, Eschscholtz (1829), Brandt (1835), Ludwig (1881) and Stimpson (1857, 1864) described some 16 species from the Pacific coast, mostly from Alaska and Puget Sound. Between 1900 and 1925, Hubert Lyman Clark described approximately seven species from California. Between 1935 and 1965, Elizabeth Deichmann worked extensively on eastern Pacific holothurians, publishing descriptions of numerous species, including six species from California. Several authors, including Cowles (1907), Pawson (1967), and Yingst (1972) have described additional species.

The taxonomic classification used herein is that proposed by Pawson and Fell (1965). This classification is based on the shape of the tentacles, the form of the ossicles, and the shape of the calcareous ring. In earlier classifications for dendrochirote holothurians, the number of tentacles was given taxonomic precedence over the shape of the calcareous ring. Based on examination of recent and fossil species, Pawson and Fell concluded that the shape of the calcareous ring was more important than the number of tentacles.

In Pawson and Fell's classification, the dendrochirote holothurians that do not have a test are divided into three families: (1) the Cucumariidae, which have a simple calcareous ring, (2) the Phyllophoridae, which have a ring with long projections divided into many small pieces, and (3) the Sclerodactylidae, which have undivided processes (Figure 9.4). Unfortunately, California species do not exactly fit into this scheme because in species with a calcareous ring with long projections, the projections are divided into two or three big pieces. In this chapter, I have changed the keys and descriptions to reflect this difference, assuming that the California species belong in the Phyllophoridae. Further study is needed to determine if the California species should be put into a different family.

The generic classification used for dendrochirote holothurians in this chapter is that proposed by Panning (1949) as modified in Panning (1964, 1966, 1971). In a postscript to his 1949 paper, Panning noted that *Havelockia* has processes divided into several large pieces, and moved this genus into the Sclerodactylidae. Given that all the California species in this group, not just *Havelockia*, have this characteristic and that the species clearly do not belong in this family, this change in the classification has not been followed.

In his papers, Panning assigns California species to genera. However, because he based his assignments on published papers, some species were misplaced. In this paper, I have reassigned the species as best I can. However, the relationship of California species to the generic classification and the generic classification itself are in need of additional study.

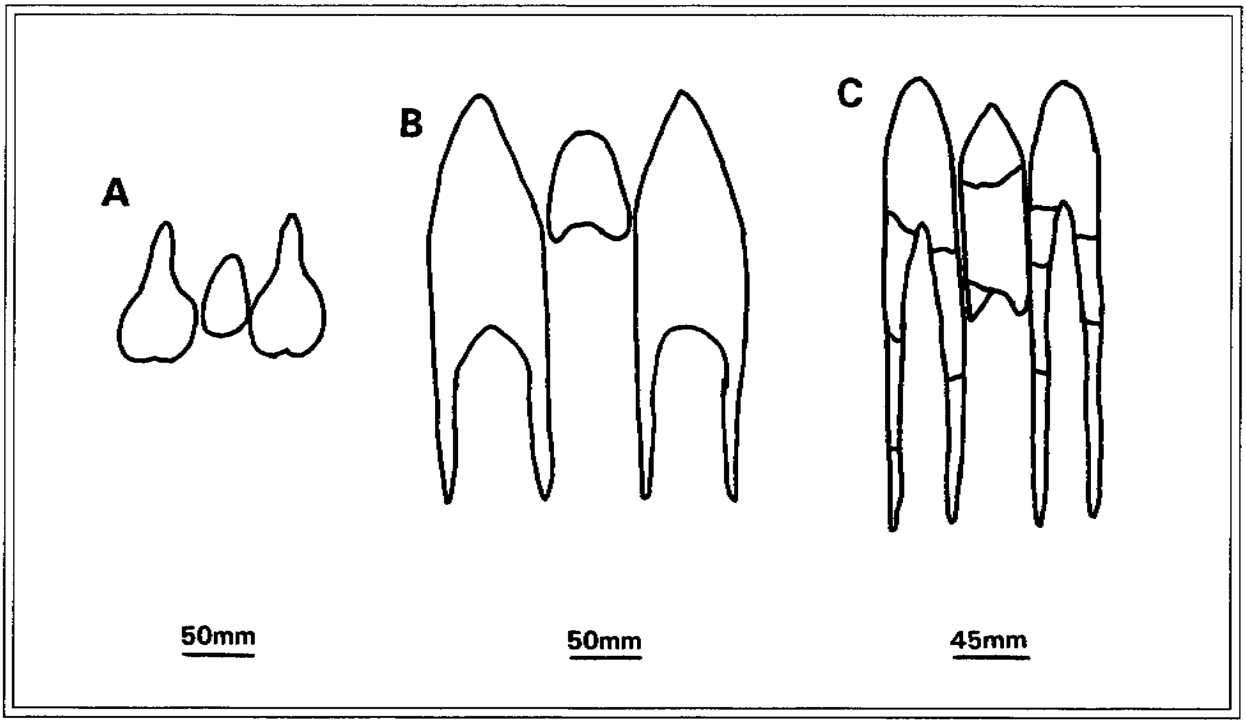

Figure 9.4. Types of calcareous rings: A, simple ring; B, ring with short processes; C, ring with long processes.

The classification of apodous holothurians used herein is that proposed by H.L. Clark (1907). In addition, the genus *Rynkatorpa*, proposed by Rowe and Pawson (1967) is included.

Heding (1928) published a paper on the Synaptidae (apodous holothurians with ossicles as anchors or wheels) including descriptions of several new species from California. He modified the classification of the Synaptidae by elevating the importance of two characters: (1) the number and structure of ciliated funnels attached to the inside of the body wall or the mesenteries and (2) the shape of the miliary granules, small ossicles found in the body wall and longitudinal muscles. He also differed with H.L. Clark (1907) on synonyms for several species. Since it has not been possible to sufficiently study Heding's characters and the identity of the species is unclear, I have not identified the Synaptidae in this chapter to species. More information about nominal species and their descriptions is given in the generic description.

Dissection and Slide Preparation

The calcareous ring and other internal organs can be exposed by cutting along the lateral body wall from the tentacles to the posterior end. By making the cut along the side of the specimen, dorsal mesenteries and other important organs are left intact.

In dendrochirotids when the tentacles are not retracted, it may be necessary to cut open the introvert to expose the calcareous ring. When the tentacles are retracted, the introvert forms a tube between the top of the body wall and the calcareous ring. The tentacles are inside the calcareous ring. To see the tentacles, the ring must be cut and laid open.

To make a temporary slide of the ossicles in the body wall, introvert or tube feet, dissolve a piece of the tissue in household bleach. For specimens with thin tissue and relatively few ossicles, a small piece of tissue can be put directly on the slide and a drop or two of bleach added. When the tissue is dissolved, and no more bubbles are being formed, a cover slip can be added and the slide examined on the microscope. For specimens with thick tissue or abundant ossicles, it is easier to dissolve the tissue in a spot plate or watch glass. Then a sample of the ossicles can be transferred to a slide with a pipette.

To make a permanent slide, the bleach must be washed from the ossicles. When there are relatively few ossicles, it is best to allow a drop of bleach with ossicles to dry in the center of the slide. Then a drop of distilled water is added to each side of the drop of bleach so that the distilled water barely merges with the bleach. This procedure dilutes the bleach without removing the ossicles from the center of the slide. The slide is allowed to dry, preferably on a drying plate. A squirt bottle with distilled water is then used to wash the edges of the slide, removing bleach but not the ossicles. This procedure is repeated until the bleach is sufficiently diluted that mounting medium and a cover slip can be added.

When there are sufficient ossicles, it is easier to wash them in a small vial. Distilled water is added and then decanted with a pipette, with care being taken to keep the ossicles at the bottom of the vial. When sufficiently clean, the ossicles are transferred to a slide in a drop of water. When the slide is dry, mounting medium and a cover slip added.

Ossicles in some species degenerate as the animal grows. Adults of some species, such as *Caudina arenicola*, have no ossicles at all. In molpadids, the ossicles become converted into phosphatic bodies, round to oval granules of iron phosphate that are red in color. However, ossicles can usually be found in the tip of the tail. In chiridotids, ossicles are often scattered in bundles on the surface of the body wall; the bundles, if present, may be found by scanning the body wall with a dissecting microscope.

Biology

Holothurians are largely benthic, although some deep-sea species are known to make swimming excursions. They occur in both hard- and soft-bottom habitats. Some are members of the epifauna, others nestle in cracks or under rocks and others burrow or form tubes in soft substrates.

Many species of holothurians are filter feeders. These species extend tentacles covered with mucus into the water. Then, from time to time, they insert a tentacle into the esophagus, removing the mucus with its meal of planktonic organisms and detritus. Other species, such as *Parastichopus*, sweep the tentacles across the substrate, picking up detritus. These species also use the esophagus to remove food from the tentacles. Some species, such as *Leptosynapta*, burrow through mud and sand, engulfing the substrate whole. Other species, such as *Molpadia*, feed head down in a burrow. These feed on mud at the bottom of the burrow, passing the mud through the intenstine to be deposited in a mound on the surface.

Most holothurians are dioecious broadcast spawners. Many of these species raise the anterior portion of the body away from the substrate while spawning; spawning may be accompanied by swaying or tentacle waving (McEuen, 1988). Some species, such as *Pseudocnus lubricus* and *Cucumaria pseudocurata*, brood eggs under the ventral surface of the body. Other species such as *Pachythyone* retain the eggs, giving birth to the young through special pores or by rupture of the body wall.

As a defense against predators, some species of aspidochirotid holothurians have sticky tubules, the Cuvierian organs, that are ejected through the anus when the animal is disturbed. Other species of holothurians will eject the whole viscera through the mouth or anus when disturbed. A new viscera is regenerated in a few weeks.

Key to Families, Genera and Species from Shallow Water and Continental Shelf Depths of California

1A. Tube feet and papillae absent 2

1B. Tube feet and/or papillae present 8

2A. Body cylindrical; ossicles as anchors and plates or wheels or sigmoid bodies, but not as tables or phosphatic bodies .... Order Apodida 3

2B. Body more or less tapering posteriorly to a caudal appendage; ossicles as tables, fusiform rods or perforated plates, anchors sometimes present, wheels and sigmoid bodies absent, phosphatic bodies often present .... Order Molpadiida 6

3A. Ossicles as anchors and anchor plates .... Family Synaptidae 4

3B. Ossicles as wheels 5

4A. Anchor plates elongate, irregular in outline .... Genus *Rynkatorpa*

4B. Anchor plates oval, regular in outline .... Genus *Leptosynapta*

5A. Wheels with 8 or more spokes .... Family Myriotrochidae: Genus *Myriotrochus*

5B. Wheels with 6 spokes .... Family Chiridotidae: Genus *Chiridota*

6A. Tentacles claw-shaped; phosphatic bodies present; ossicles in caudal appendage as tables with round to fusiform disk or as anchors and racquet-shaped plates .... Family Molpadiidae: Genus *Molpadia*: *M. intermedia*

6B. Tentacles with 2 pairs of digits and no terminal digit; phosphatic bodies absent .... Family Caudinidae 7

7A. Pseudomesenteries absent; ossicles as large spiny plates with large perforations .... Genus *Hedingia*: *H. californica*

7B. Pseudomesenteries present; ossicles as perforated plates or rods or, in juveniles, small tables; ossicles often reduced or entirely lacking .... Genus *Caudina*: *C. arenicola*

8A. Tentacles peltate, ventrally placed; retractor muscles absent; tube feet restricted to ventral surface; dorsal surface with papillae .... Order Aspidochirotida: Family Stichopodidae: Genus *Parastichopus* 9

8B. Tentacles digitate; retractors present .... Order Dendrochirotida 11

9A. Dorsal papillae mostly large and conical; mean number of spines on spire of tables from dorsal body wall greater than 12 10

9B. Dorsal papillae mostly small, black tipped in live specimens; mean number of spines on spires of tables less than 12; diameter of table disks less than 75 µm .... *Parastichopus parvimensis*

10A. Mean diameter of table disks greater than 100 µm; yellowish white when alive .... *Parastichopus johnsoni*

10B. Mean diameter of table disks less than 100 µm; mottled brown to reddish brown when alive .... *Parastichopus californicus*

11A. Body flattened, bilaterally symmetrical; distinct sole present .... Family Psolidae 12

11B. Body cylindrical; distinct sole absent 15

12A. Dorsal scales present, but covered by a layer of deposits including hour-glass shaped ossicles; tube feet present on the dorsal surface .... Genus *Lissothuria* 13

12B. Dorsal scales naked; tube feet absent from the dorsal surface .... Genus *Psolus* 14

13A. Dorsal scale covering incomplete; dorsal scales overlain with towers, and hourglass-shaped ossicles; ossicles of sole perforated plates with raised marginal projections and cups ... *Lissothuria nutriens*

13B. Dorsal scale covering complete; dorsal scales overlain with hourglass-shaped ossicles; towers absent; ossicles of sole large heavily knobbed plates, which tend to become 2-layered, smaller plates with knobbed margin and hourglass-shaped ossicles .... *Lissothuria deichmannae*

14A. Approximately 12 scales between oral and anal scales; scales granulated; ossicles in sole plates with 2-4 holes and marginal projections, often reduced with age .... *Psolus squamatus*

14B. Approximately 4 scales between oral and anal scales; scales smooth; ossicles in sole oval buttons with multiple perforations, often forming a reticulated mass .... *Psolus chitinoides*

15A. Calcareous ring simple, lacking posterior processes .... Family Cucumariidae 16

15B. Calcareous ring complex, with paired or unpaired posterior processes 21

16A. Ossicles thin, flat, sometimes with spines .... Genus *Cucumaria* 17

16B. Ossicles three-dimensional, knobbed, sometimes with a dentate handle .. *Pseudocnus*: *P. lubricus*

17A. Ossicles with spines 18

17B. Ossicles without spines 19

18A. Ossicles mostly rounded, with large holes and spiny margins; single stone canal .... *Cucumaria piperata*

18B. Ossicles mostly oblong; perforations small, margin of ossicle smooth; multiple stone canals .... *Cucumaria miniata*

19A. Tube feet not restricted to the ambulacra; maximum length 2.5 cm; dorsal side black, ventral side yellowish; ossicles mostly small rounded buttons with 4-8 holes .... *Cucumaria curata*

19B. Tube feet restricted to the ambulacra 20

20A. Ossicles mostly small buttons with 4-8 holes; maximum size 10-15 cm .... *Cucumaria salma*

20B. Ossicles mostly round plates with 15 or more perforations; maximum size 2-3 cm .... *Cucumaria pseudocurata*

21A. Processes short, entire .... Family Sclerodactylidae 22

21B. Processes long, in pieces .... Family Phyllophoridae 23

22A. Tube feet restricted to ambulacra; ossicles knobbed plates and baskets or cups .... Genus *Eupentacta*: *E. quinquesemita*

22B. Tube feet not restricted to the ambulacra; ossicles reticulated plates and regularly-knobbed 4-holed buttons; no baskets or cups present .... Genus *Pachythone*: *P. rubra*

23A. Ossicles in body wall predominantly plates 24

23B. Ossicles in body wall mostly tables or a mixture of tables and plates 28

24A. Lozenge-shaped plates, 0.05-0.15 mm long, common; supporting tables in tube feet with well-developed spire .... *Pentamera lissoplaca*

24B. Lozenge-shaped plates rare or absent 25

25A. Spire on supporting tables in tube feet well developed 26

25B. Spire on supporting tables in tube feet reduced or lacking 27

26A. Spire on supporting tables with 4 pillars ending in a spiny mass; body wall ossicles plates, usually oblong, often covered with spines and knobs .... *Stolus trachyplaca*

26B. Spire on supporting tables with 2 pillars, sometimes elongate and flattened; body wall ossicles large, irregularly-shaped plates, 0.2-0.4 mm in diameter; star-shaped tables occasionally present. .... *Pentamera pseudocalcigera*

27A. Body wall ossicles oval buttons with 2 central and up to 8 marginal knobs .... *Thyone montereyensis*

27B. Body wall ossicles flat, irregularly shaped plates and smaller, more delicate rectangular plates, often with two enlarged central holes; buttons sometimes present .... *Havelockia benti*

28A. Lozenge-shaped plates common .... *Pentamera lissoplaca*
28B. Lozenge-shaped plates absent 29

29A. Discs on tables oblong, regular in outline; spire long with 3-6 crossbars ..... *Havelockia charlottae*
29B. Discs irregular in outline; spire short with 1-2 crossbars 30

30A. Teeth on spire of supporting tables bifurcate .... *Pentamera pseudopopulifera*
30B. Teeth on spire of supporting tables not bifurcate 31

31A. Four-holed tables common; star-shaped tables absent .... *Havelockia benti*
31B. Four-holed tables not common; star-shaped tables present .... *Pentamera populifera*

Descriptions of Species

As noted earlier, there has been no comprehensive review of the systematics of northeastern Pacific holothurians. Information about holothuroids is scattered in a variety of publications, many of which are difficult to obtain. For this reason, I decided to expand the scope of this chapter to include all species in California, either reported in the literature or personally identified, that are found from the intertidal zone to a depth of 200 meters. In addition, some species not reported from this area are included. I have not included groups such as the Elasipodida or the Synallactidae that are found only in deep-water habitats.

The following descriptions are based on an extensive review of the literature, including a manuscript on the eastern Pacific holothurians that was being written by Elizabeth Deichmann at the time of her death. This manuscript was kindly given to me by the American Museum of Natural History.

The descriptions are also based on examination of the large collections of specimens in the U.S. National Museum of Natural History (USNM) and the Allan Hancock Foundation (AHF) collection which is now housed in the Natural History Museum of Los Angeles County. I also examined material from the American Museum of Natural History(AMNH), Museum of Comparitive Zoology, Havard (MCZ), the Santa Barbara Museum of Natural History (SBNMH), the British Columbia Provincial Museum (BCPM) and Scripps Institute of Oceanography (SIO). In addition to the material collected in Bureau of Land Management (BLM) and Minerals Management Service (MMS) surveys, I have included material collected by individuals and groups, including Marine Ecological Consultants (MEC), the Southern California Coastal Water Research Project (SCCWRP), Pacific Biomarine (PBM), and myself (MB).

Order Apodida Brandt, 1835

Diagnosis. Body cylindrical, worm-like. Body wall smooth, rough or with warty surface. Tube feet absent. Anal papillae, tentacle ampullae, and respiratory trees absent. Tentacles 10-25, pinnate or digitate in form. Ossicles include wheels and anchors, may be reduced with age.

Remarks. Two families of Apodida, the Synaptidae and Chiridotidae, are common in shallow water soft-bottom habitats in California. I have included a third family, the Myriotrochidae, in the key. This group primarily occurs in deep water; however, occasional specimens are taken in shallower water.

Family Synaptidae Burmeister, 1837

Diagnosis. Tentacles cylindrical or terete, not widened distally, either pinnate or digitate in form. Ossicles as anchors and anchor plates.

Remarks. Only one genus (*Leptosynapta*) of Synaptidae is known to occur in California. However, I have included the genus *Rynkatorpa* Rowe and Pawson, 1967 in the key because there is a possibility that *Rynkatorpa duodactyla* (H.L. Clark, 1907) may occur in California. This species is distinguished by the irregular shape of the anchor plates and the presence of two digits on the tentacles. It is known to occur from the Aleutian Islands to Grays Harbor, Washington.

Genus *Leptosynapta* Verrill, 1867

Type Species. *Holothuria inhaerens* O.F. Müller, 1776, designated by Verrill (1867).

***Leptosynapta* spp.**

Figure 9.5

Material Examined. California: Mugu Lagoon, intertidal (1), (BLM sandy beach, Winter 1977, Sta 4A); Corona del Mar, intertidal (1), (BLM sandy beach, Winter 1977, Sta 13c); Pt Dume, 60 m, (3), (SCCWRP R15-60); Pt Arguello, (1: 0.3 cm) (MMS CAMP 1-1, PJ7); Pt Arguello, (1: 0.5 cm), (MMS CAMP 1-2, R-1); Pt Arguello, (13), (MMS CAMP 1-2, R-8); Pt Arguello, (2), (MMS CAMP 2-3, R-8); BLM 23201; BLM 23206; BLM 23149; USNM BSS-63; SBMNH BSR-79; (MMS Camp 3-4, R1); (MMS CAMP 3-1, R-8).

Diagnosis. Tentacles pinnate, 10-13 in number. Sense organs on tentacles as small cups, pigment spots absent. Stocks of anchors with fine teeth, not branched. Anchor arms usually with small teeth, vertex of anchor smooth. Anchor plates oval or somewhat elongated, usually with 6-7 large dentate holes; several smaller smooth holes present at narrow end of plate.

Biology. Species of *Leptosynapta* live in sandy or muddy habitats. They are thought to burrow beneath the surface, engulfing sediment as they move. However, during the spawning season in Puget Sound (November-December), McEuen (1988) found *Leptosynapta* in vertical burrows in aggregations of 2 to 4 individuals. Fertilization and early development occurs within the ovary in *Leptosynapta*.

Remarks. As noted in the Introduction, the identity of species in this genus is uncertain at present. H.L. Clark (1907) recognized only one species from the west coast of North America: *Leptosynapta inhaerens*. He considered *Synapta albicans* Selenka, 1867, a synonym of *inhaerens*, a circumpolar species occurring in Europe, the western Atlantic and eastern Pacific.

Heding (1928) considered the European, western Atlantic and Pacific forms of *inhaerens* to be distinct species. However, he did not believe that the Pacific forms could be referred to *albicans*; rather he described them as a new species: *L. clarki*.

Heding recognized five species of *Leptosynapta* from the eastern Pacific: *albicans*, *clarki*, *lens*, *roxtona*, and *transgressor*. He considered *lens* and *albicans* to be closely related, possibly the same species, being differentiated primarily by the presence (*albicans*) or absence (*lens*) of rods in the tentacles.

The two provisional species designations (Sp. A and Sp. B) given for specimens of *Leptosynapta* are based on the size of the anchors: Species A has relatively large anchors compared to Species B. However, anchor size can be quite variable; sometimes the anchors in the anterior and posterior portions of the body are distinctly different. A thorough study of many specimens from a variety of locations is needed to establish the range of variability in species characteristics and determine the identity of the species of *Leptosynapta* occurring in California.

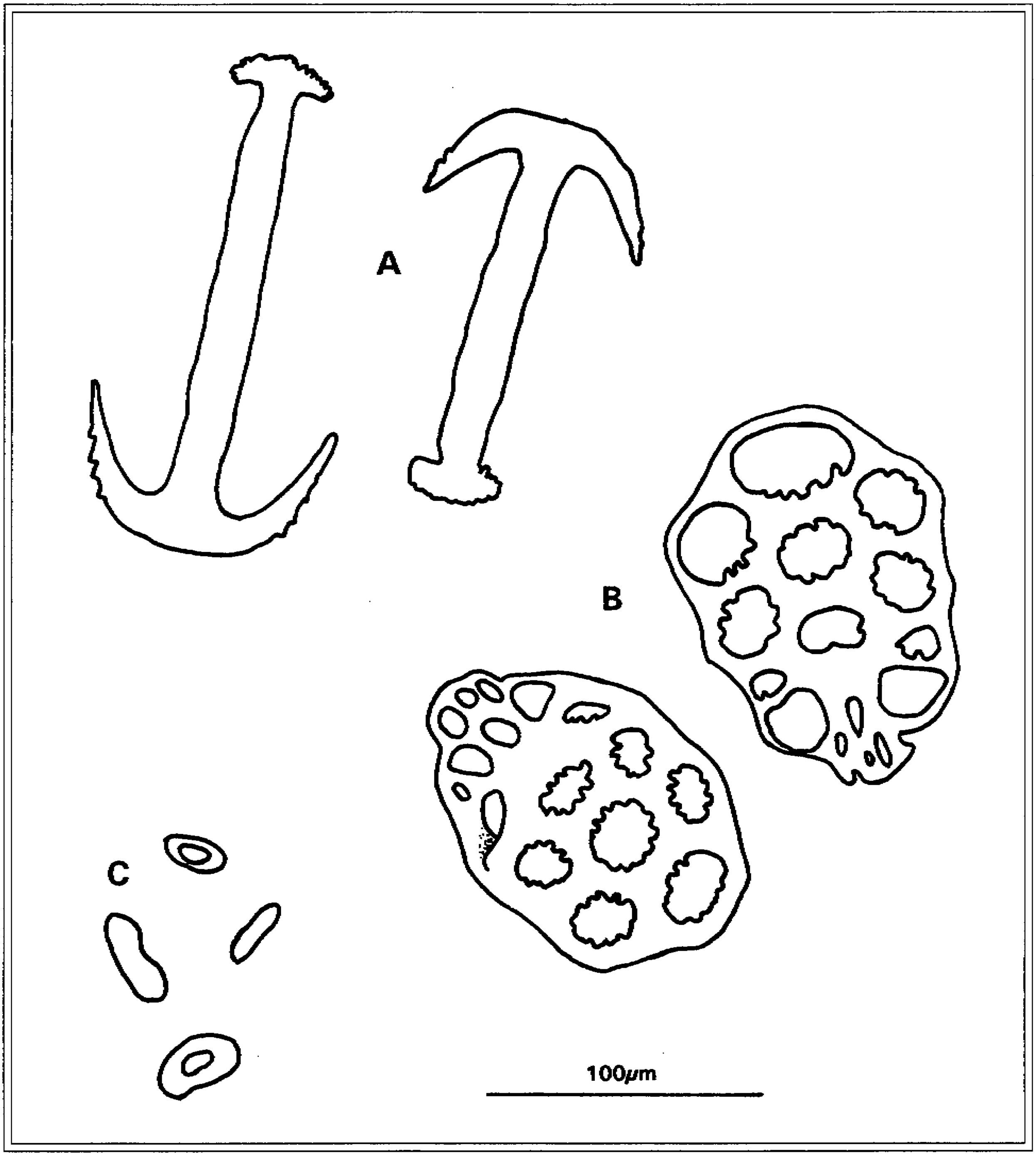

Figure 9.5. *Leptosynapta* spp.: A, anchors; B, anchor plates; C, miliary granules.

Family Chiridotidae Ostergren, 1898

Diagnosis. Tentacle stalks short, widened distally, with 3-10 digits on each side of the distal end. Ossicles as 6-spoked wheels; sigmoid or C-shaped rods may or may not be present; ossicles sometimes lacking.

Genus *Chiridota* Eschscholtz, 1829

Type Species. *Chiridota discolor* Eschscholtz, 1829, by original designation.

Chiridota spp.

Figure 9.6

Material Examined. California: BLM 24242; Santa Catalina Basin, 1300 m (NOFAC Sta. 1).

Diagnosis. Twelve tentacles present, rarely 13-14. Polian vesicles numerous. Ossicles as 6-spoked wheels collected into papillae; sigmoid ossicles absent; small curved rods with enlarged ends may be present; tiny oval particles may be present in the longitudinal muscles.

Remarks. As noted in the Introduction, the identity of species in this genus is uncertain at present. In his discussion of the genus *Chiridota,* Clark (1907) notes that the characteristics used to differentiate the species (the number and arrangement of wheel papillae, the number and length of digits on the tentacles, the presence or absence of miliary granules) are highly variable. He provisionally identified two species as ranging from Alaska to Baja California: *C. discolor* Eschscholtz, 1829 and *C. laevis* (Fabricius, 1780). However, he noted that the identifications were tentative and that additional species may be present.

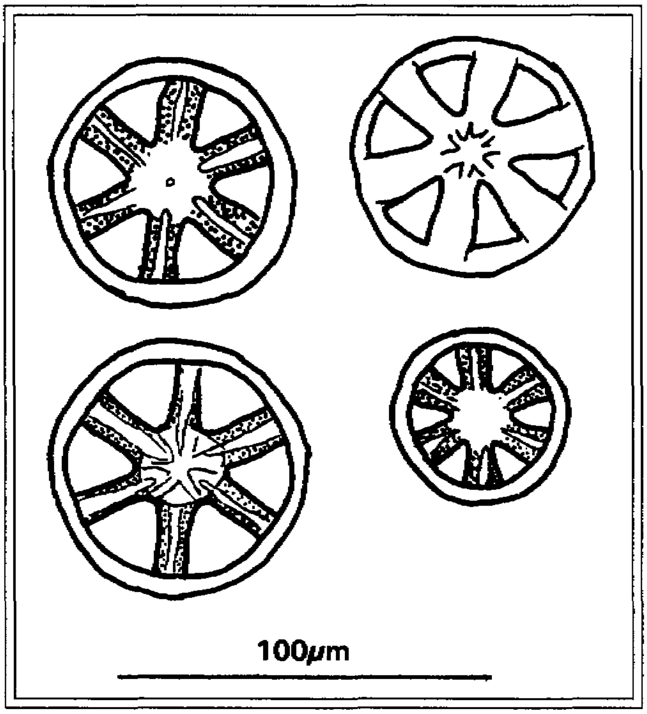

Figure 9.6. *Chiridota* spp.: Wheels from body wall.

Heding (1928) also recognized the variability of many characteristics used to identify species in the genus *Chiridota*. However, he believed that the size, arrangement and shape of the ciliated funnels, the shape and arrangement of miliary granules in the body wall and the shape of the calcareous ring could be used to differentiate species.

Heding (1928) described two new species from the north eastern Pacific: *C. pacifica*, from La Jolla, California, and *C. nanaimoensis*, from Nanoose Bay, British Columbia. He notes that *C. pacifica* is closely related to *C. albatrossi* Edwards, 1907 and *C. laevis*, both of which occur in the northern Pacific. He indicates that the specimens identified by Clark (1907) represent three species: *C. albatrossi, C. pacifica*, and *C. laevis*. Since there is no discussion of *C. discolor*, the status of this species is unclear.

Heding (1928) differentiates *C. pacifica* from *C. albatrossi* and *C. laevis* by the shape and size of the ciliated funnels, the shape of the madreporite, and the presence or absence of rods in the anterior portion of the body wall. A study to determine the range of variability in these characters is needed in order to determine the status of these species.

Order Molpadida Haeckel, 1896

Diagnosis. Body stout, tapering to a more or less distinct tail. Fifteen tentacles present. Respiratory trees and tentacle ampullae present. Ossicles may include tables, anchors, fusiform rods, or perforated plates. Red phosphatic ossicles often present.

Family Molpadiidae Müller, 1850

Diagnosis. Tentacles claw-shaped or with lateral digits. Tentacle ampullae long. Ossicles in tail tables or fusiform rods. Phosphatic bodies often present.

Genus *Molpadia* Risso, 1826

Type Species. *Molpadia musculus* Risso, 1826, by original designation.

Diagnosis. Tentacles with 1, sometimes 2, pairs of digits and a terminal digit. Ossicles as tables, plates or fusiform rods. In young individuals, racquet-shaped plates and anchors sometimes present. Phosphatic bodies usually present.

***Molpadia intermedia* (Ludwig, 1894)**

Figure 9.7

Trochostoma intermedium Ludwig, 1894:161, pl. 16, figs. 7-21.

Molpadia intermedia H.L. Clark, 1907:33, pl. 12, figs. 5-15.—Heding, 1931:279.—Deichmann, 1937:174.

Material Examined. West coast tropical America: (syntype, USNM 18202).—Califonia: *USNM Albatross* 2937, 33°04'30"N, 117°42'00"W, 464 fms, mud (1:6.5 cm); USNM*Albatross* 4475, 9.7 mi S15°W Pt. Piños lighthouse, 58-142 fms, mud (3:7.3-7.8 cm); USNM *Albatross* 4509, 8.6 mi S13°W Pt. Piños lighthouse, 152-286 fms, mud (1:10 cm); MEC, Pt. Arguello (1); MBC, N side of Coronado Canyon (1); MBC, off Pt. Loma, 187 m (1:3.5 cm); Chambers, Pt. Arguello (1); SCCWRP, Pt. Dume (1); CAMP 1, R-

1 (2:0.5, 2 cm); PJ-1 (1: 0.5 cm); CAMP 1-2, R-1 (1: 2 cm); R-4 (1); R-8; CAMP 1-3, R-5 (1); CAMP 2-3, R-1 (2); R-9 (1); CAMP 2-4, R-2 (1: 5.5 cm); R-1 (1: 2.4 cm); R-5 (1: 1.8 cm); CAMP 2-5, R-1; R-8 (1); CAMP 3-1, R-1 (1); CAMP 3-4, R-1 (2); USNM BSS-058; SBNMH BSS-102.

Description. Body stout, globose, tapering to distinct caudal tail, brown in smaller specimens, mottled magenta in larger specimens. Tentacles with unpaired terminal digit. In small individuals ossicles in body wall tables and racquet-shaped plates and anchors, sometimes as rosettes. With age, ossicles in body wall converted to phosphatic bodies. Ossicles in caudal appendage tables with round to fusiform disk.

Biology. *Molpadia intermedia* is one of the most common holothurians in muddy bottoms in California from 60 to at least 900 m. The species lives head-down, engulfing mud at the bottom of the burrow. The mud is passed through the gut and deposited in a mound on the surface of the substrate. In Puget Sound, *M. intermedia* spawns during the winter (McEuen, 1988). To spawn, the adults emerge from the substrate, raising the anterior end of the body 4-8 cm above the substrate. Eggs are expelled into the water in one short burst.

Type Locality and Type Specimens. West coast of tropical America, syntype (USNM 18202).

Distribution. From Alaska to South America, 60-900 m.

Family Caudinidae Heding, 1931

Diagnosis. Tentacles with 1-2 digits, no terminal digit. Skin may show coloration, but does not contain phosphatic bodies. Ossicles tables, plates, small crossed cups or irregularly-shaped bodies.

Genus *Caudina* Stimpson, 1853

Type Species. *Caudina arenata* Gould designated by Stimpson (1853).

Diagnosis. Body stout, tapering toward the posterior end. Fifteen tentacles with 2 pairs of digits, no terminal digit. Pseudomesenteries present. Ossicles as tables, or plates; ossicles sometimes lacking. Phosphatic bodies absent.

***Caudina arenicola* (Stimpson, 1857)**

Liosoma arenicola Stimpson, 1857:525.

Trochostoma arenicola Theél, 1886.

Molpadia arenicola H.L. Clark, 1907:33, 171, pl. 7, figs. 1-2.—Ricketts and Calvin, 1968:292, fig. 219.

Caudina arenicola Deichmann, 1938:112, text-fig.

Material Examined. Off Pt. Loma, California, 195 ft, (1) (City of San Diego, Sta. B-3).

Description. Large form, with stout body tapering slightly in posterior end. Skin smooth, slippery, with yellowish-brown mottling. Ossicles in posterior end small perforated plates, with 2-4 holes, and branched rods. Ossicles in juveniles small tables. Ossicles reduced with age, often absent.

Remarks. Because of its shape and color, this species is commonly known as the "sweet potato". Surprisingly, very little is known about its distribution or habits.

Type Locality and Type Specimens. San Pedro, California, types missing.

Distribution. In sandy areas from San Pedro south to northern Baja California.

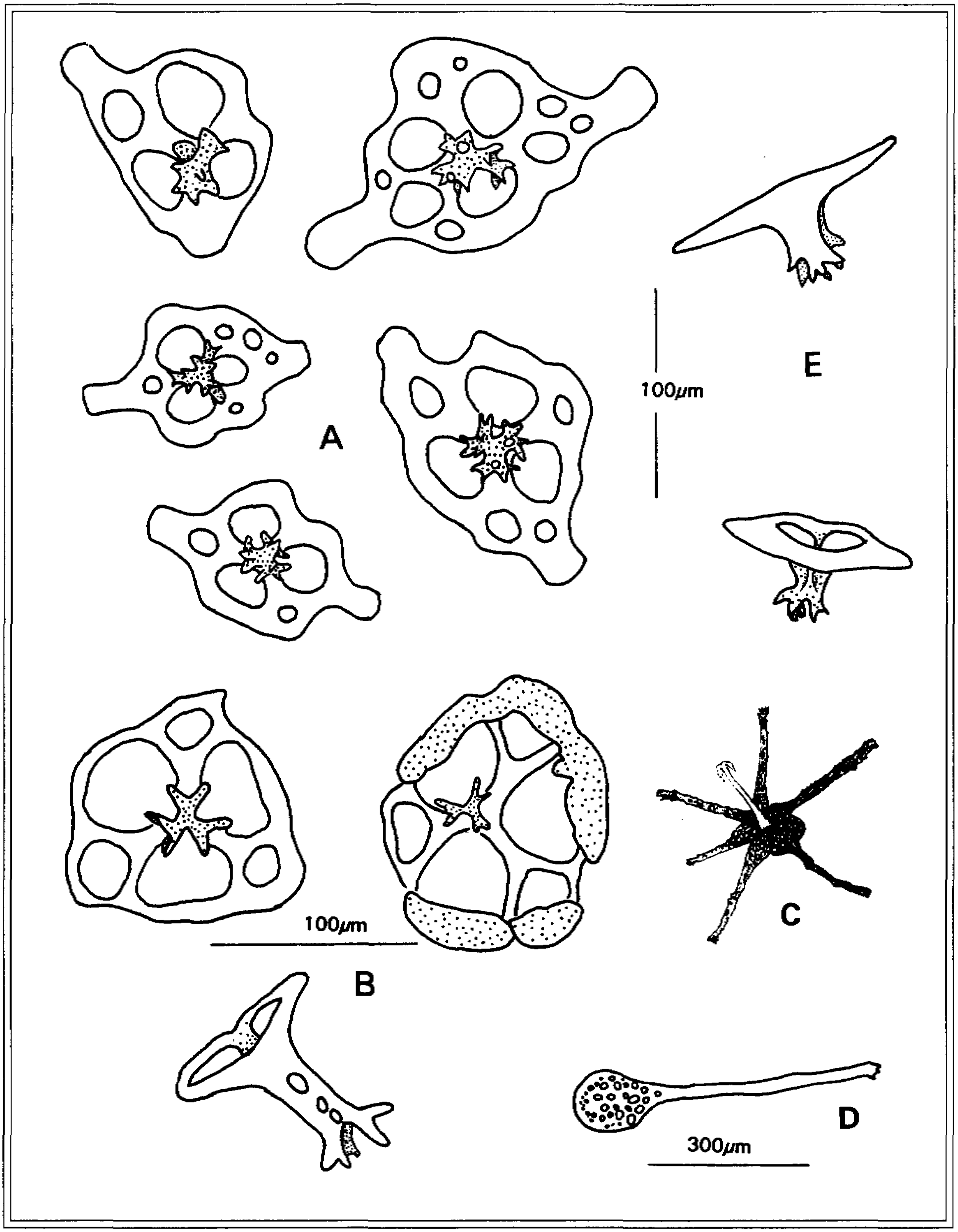

Figure 9.7. *Molpadia intermedia*: A, tables from caudal appendage; B, tables from body wall of small individual, table at right forming phosphatic bodies; C, rosette of raquet-shaped plates with anchor (not to scale, copied from H.L. Clark, 1907); D. racquet-shaped plate.

Genus *Hedingia* Deichmann, 1938

Type Species. *Trochostoma albicans* Théel, 1886, designated by Deichmann (1938b).

Diagnosis. Fifteen tentacles, with 2 pairs of digits, without terminal digit. Pseudomesenteries absent. Ossicles huge tables or plates with large perforations and smooth or spinous surface.

Hedingia californica (Ludwig, 1894)

Figure 9.8

Caudina californica Ludwig, 1894.—H.L. Clark, 1907:37; 1935:279.
Hedingia californica Deichmann, 1938b:112.

Material Examined. Gulf of California, syntype (USNM 18164).

Diagnosis. Ossicles large spiny plates with many perforations; spines sometimes mounded.

Remarks. Very little is known about this species. It was described from deep water in the Gulf of California. Clark (1907) ascribes two other specimens to this species: one from 85 m off Baja California and the other from "Southern California probably". Deichmann (1938) considers all members of the genus *Hedingia* to be deep-water forms. It may be that the shallow-water specimens identified by Clark (1907) were young *Caudina arenicola*.

Type Locality and Type Specimens. Gulf of California, syntype, *Albatross* Station 3434 (USNM 18164)

Distribution. Uncertain, see Remarks.

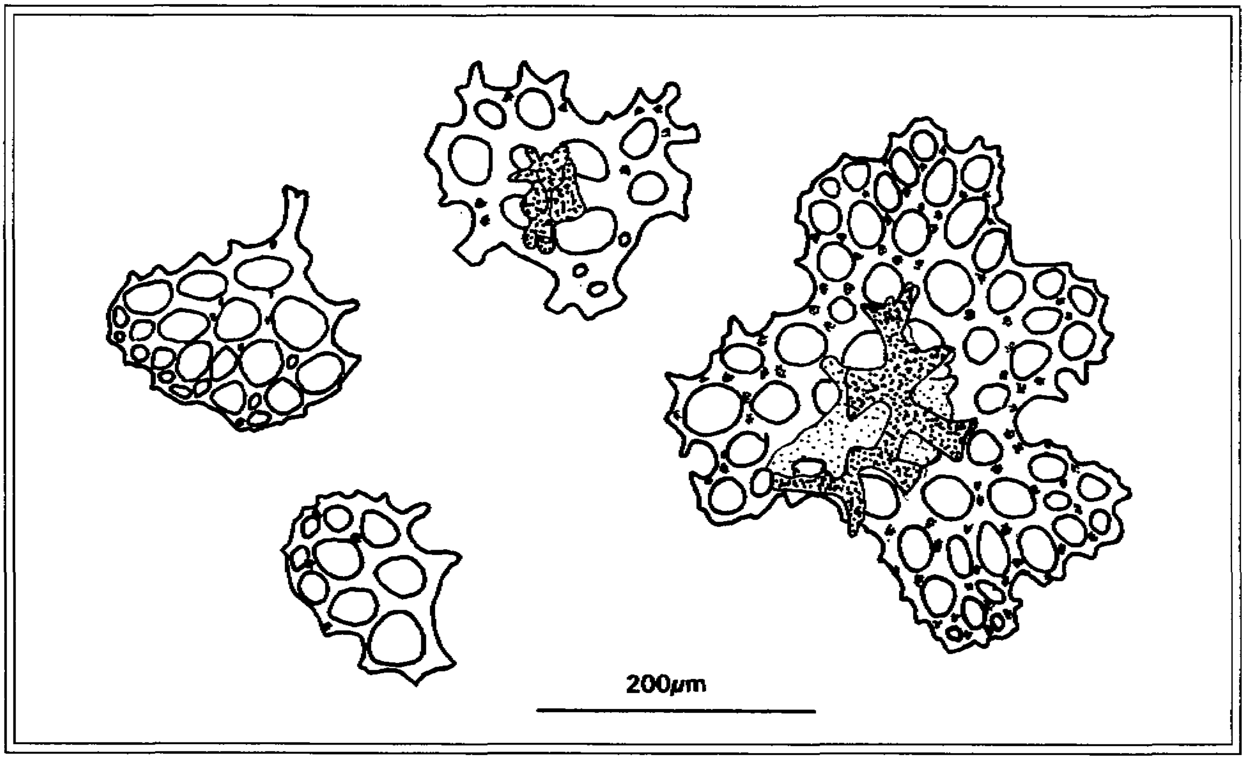

Figure 9.8. *Hedingia californica*: ossicles from caudal appendage of syntype.

Order Aspidochirotida Grube, 1840

Diagnosis. Tentacles peltate, 15 to 30 in number. Respiratory trees present. Mesentery of posterior loop of intestine attached to right ventral interradius. Gonad in 1 or 2 tufts. Ossicles usually include tables.

Family Stichopodidae Haeckel, 1896

Diagnosis. Tentacle ampullae present. Gonads in 2 tufts, one on either side of dorsal mesentery. Dorsal side of body usually with papillae or warts. Ossicles as tables and sometimes C-shaped rods and buttons.

Genus *Parastichopus* H.L. Clark, 1922

Type Species. *Stichopus tremulus* Gunnerus, 1770, designated by Deichmann (1937).

Diagnosis. Body cylindrical, mouth ventrally placed, anus terminal. Dorsal side with large conical papillae and smaller feet; ventral side with cylindrical tube feet more or less arranged in bands. Ossicles tables and buttons with several holes along sides, no terminal hole.

Remarks. This genus was proposed but not described by Clark (1922). Deichmann (1937) defined the genus.

***Parastichopus californicus* (Stimpson, 1857)**

Holothuria californicus Stimpson, 1857:524.

Stichopus californicus H.L. Clark, 1901b:164, 1922:70, pl. 1, figs. 8-12.

Stichopus fuscus Theél, 1886:5.

Parastichopus californicus Deichmann, 1937:163.—Lambert, 1986:2267, fig. 3B.

Material Examined. Califonia: USNM *Albatross* 4534, 4 mi S80°E Pt. Piños Lighthouse, 76-86 fms, hard grey sand (1:15 cm); USNM *Albatross* 2906, 34°23'30"N, 129°19'30", 96 fms (1:13 cm); USNM 2964, 34°22'45", 119°40'00"W, 21.5 fms, sand, stones (1); Bodega Bay, intertidal (2:11.6, 16.4 cm) (AHF 295.36); USNM BRC-001; SBMNH BRA-1.

Description. Body cylindrical, with numerous large dorsal papillae. In life, mottled brown to reddish brown, rarely white; papillae flesh colored. Ossicles tables, 0.06-0.12 mm in diameter, and oblong plates, 0.13-0.24 mm long.

Biology. *Parastichopus californicus* is a common member of the epifauna in both hard- and soft-bottom habitats. It feeds by sweeping its tentacles across the substrate, picking up surface detritus. In Puget Sound, *P. californicus* spawns in the spring (McEuen, 1988). Oogenesis in this species has been described by Smiley (1988).

Type Locality and Type Specimens. California, Tomales Bay, types lost.

Distribution. Alaska to Cedros Island, Baja California, intertidal to 216 m.

Parastichopus johnsoni (Theél, 1886)

Figure 9.9

Stichopus johnsoni Theél, 1886:4.—H.L. Clark, 1922:69, pl. 1, figs. 15,16.
Parastichopus johnsoni Lambert, 1986:2271.

Material Examined. California: 30 mi S of Santa Barbara, 22 fms (1) (holotype, MCZ 767); USNM BRA-17.

Description. Body cylindrical, form and color uncertain, possibly yellowish in life. Ossicles tables 0.10-0.17 mm in diameter, oblong plates, 0.14-0.22 mm long.

Remarks. Deichmann (1937) considered *Parastichopus johnsoni* to be an immature form of *P. californicus*. However, after measuring the ossicles in a number of specimens, Lambert (1986) determined that tables in *P. johnsoni* were significantly larger than the tables in *P. californicus*. He considered these two species to be distinct.

Type Locality and Type Specimens. California, 30 mi S of Santa Barbara, holotype (MCZ 767).

Distribution. California, Point Conception south to Baja California, 40-140 m.

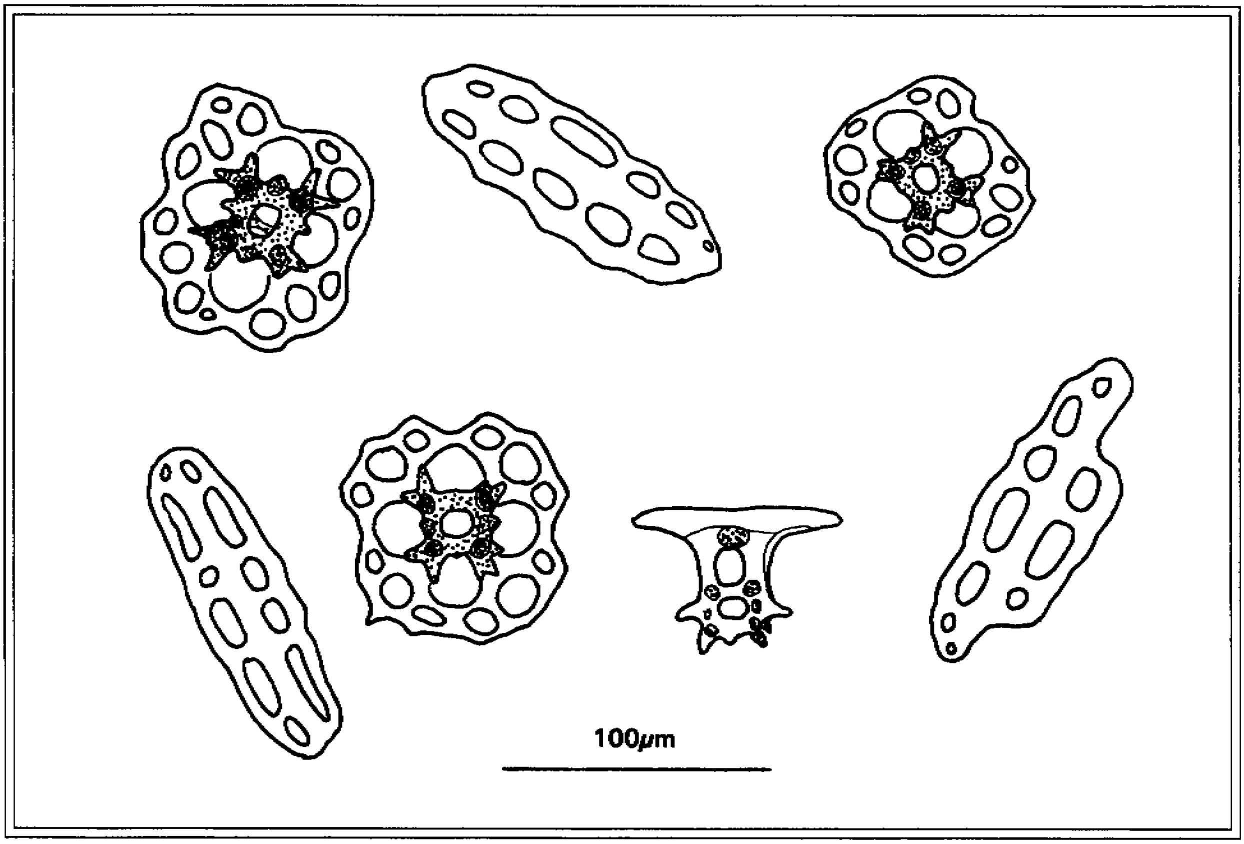

Figure 9.9. *Parastichopus johnsoni*: ossicles from the body wall of the holotype.

Parastichopus parvimensis (H.L. Clark, 1913)

Stichopus parvimensis H.L. Clark, 1913:234, 1922:70, pl 1, fig. 13-14.

Parastichopus parvimensis Deichmann, 1937:163.—Lambert, 1986:2267, fig. 3C.

Material Examined. California: Fourth of July Cove, Catalina I, 1-2 fms (1:11 cm) (AHF 339.29); Santa Monica Bay, 60 m (1) (SCCWRP SMB 6.4 No. 1).—Mexico: Cedros I, Baja California (holotype, USNM Acc. No. 55337).

Description. Body cylindrical with numerous small dorsal papillae and 3-6 large papillae. In life, body light brown, small papillae with black tips. Ossicles tables, 0.04-0.06 mm in diameter, and oblong plates, 0.07-0.14 mm long.

Biology. The habits and habitat of *Parastichopus parvimensis* and *P. californicus* are similar; however, *P. parvimensis* has a more southerly distribution.

Type Locality and Type Specimens. Mexico, Baja California, Cedros I, 1 m, holotype (USNM Acc. No. 55337).

Distribution. Central California to Baja California, intertidal to 64 m.

Order Dendrochirotida (Grube, 1840)

(Restricted Pawson and Fell, 1965)

Diagnosis. Tentacles highly branched, 10-30 in number. Calcareous ring simple or complex; retractor muscles present.

Family Psolidae Perrier, 1902

Diagnosis. Dorsal body wall more or less completely covered by scales. Ventral body wall flat, not covered by scales, functioning as a "sole". Mouth and anus dorsal, usually protected by valves.

Genus *Psolus* Oken, 1815

Type Species. *Holothuria phantapus* Strussenfeldt, 1765, designated by Oken (1815).

Diagnosis. Body oval with distinct sole, with marginal tube feet; tube feet sometimes present in the midventral ambulacrum. Dorsal side covered with scales; oral and anal apertures with or without operculum of triangular scales. Dorsal side without appendages except for anal papillae and, in some cases, a few tube feet on introvert. Ten tentacles present. Ossicles in sole plates or buttons, smooth or knobbed; ossicles sometimes develop reticulations or may be reduced with age.

Psolus chitinoides H.L. Clark, 1901

Figure 9.10

Psolus chitinoides H.L. Clark, 1901a:335, pl. 3, figs. 4-5, pl. 4, figs. 6-10; 1924:57.

Material Examined. Washington: 74 m, rocky (1:4.9 cm) (USNM E1992).—California: Pt Arguello, 1 (Nekton).

Description. Medium-sized form, up to 7.0 centimeters long. Oral and anal opening surrounded by triangular plates. Dorsal plates smooth, without granulations. Approximately 4 rows of plates between oral and anal scales. Ossicles in sole knobbed buttons, approximately oval in shape, with many knobs and perforations; reticulated mass often present.

Biology. *Psolus chitinoides* is found on top of rocks and in cobble fields. They are generally sessile, but may move at times. In Puget Sound, *P. chitinoides* spawns in March and May (McEuen, 1988; McEuen and Chia, 1991). The females extrude ropes of brick red eggs, which float to the surface. After 10 to 15 minutes, the gelatinous material binding the eggs dissolves, releasing the eggs.

Type Locality and Type Specimens. Type locality unknown, holotype (MCZ 309)

Distribution. British Columbia to Pt Arguello, California; intertidal to at least 74 m, rocky habitats.

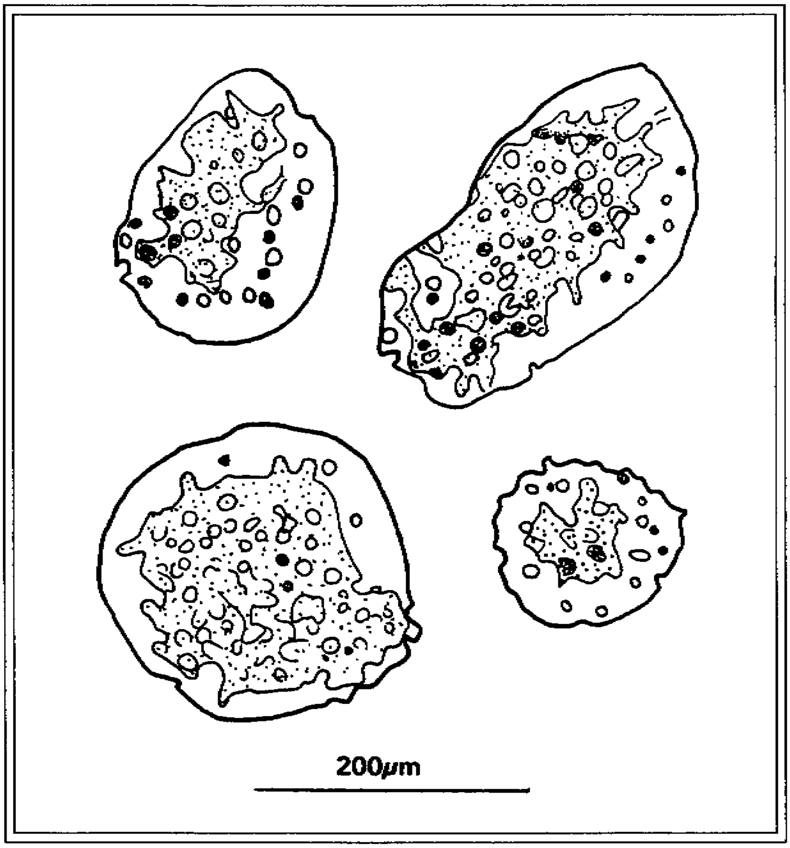

Figure 9.10. *Psolus chitinoides:* buttons from sole.

Psolus squamatus (Koren, 1844)

Figure 9.11

Cuvieria squamata Koren, 1844:211, pl. 2-3.

Psolus squamatus H.L. Clark, 1901b:165, 1901c: 491.—Mitsukuri, 1912:225, pl. 7, figs. 61-62, text-fig. 42.—Oshima, 1915:280.

Psolus squamatus var. *segregatus* Perrier, 1905:59.—Ekman, 1925:136, fig. 33.—Deichmann, 1941:147, pl. 30, fig. 7.

Psolus pauper Ludwig, 1894:139.

Material Examined. Califonia: Gull Islet, S coast of Santa Cruz I, 97-281 fms, sand, rock, pebbles (3:6.1-7.6 cm) (USNM *Albatross* 4430); 7.6 mi S of East Pt, San Nicolas I, 216-339 fms, sand, pebbles, rock (1:9.2 cm) (USNM *Albatross* 4423); 6.9 mi N8°E SW rock, Santa Barbara I, 238-310 fms, mud, sand, rock (2:6.0-6.8 cm) (USNM *Albatross* 4418); off southern California, 33°49'45"N, 119°24'30"W, 603 fms, green mud (1) (USNM *Albatross* 2980); 276 fms (1: 5.3 cm) (USNM E2000); northern California, 239 fms (2: 3.6, 4.6 cm) (USNM E2001); USNM BRA-02; SBNMH BRA-04.

Description. Large form, up to 13 cm long. Oral and anal opening surrounded by triangular scales. Dorsal scales granulated; approximately 12 scales between oral and anal plates. Ossicles of sole plates with 2-4 holes and marginal projections; ossicles often reduced with age.

Type Locality and Type Specimens. Patagonia, types missing.

Distribution. Southern Bering Sea to Cape Horn; in northern hemisphere, 194 to 1206 m.

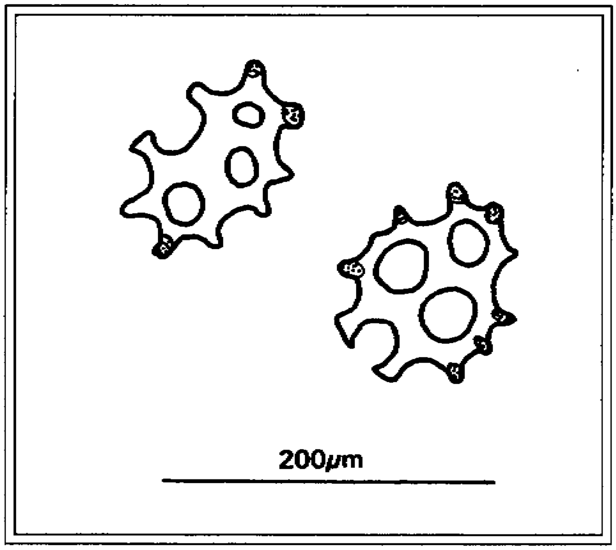

Figure 9.11. *Psolus squamatus:* plates from sole.

Genus *Lissothuria* Verrill, 1867

Type Species. *Lissothuria ornata* Verrill, 1867, by original designation.

Diagnosis. Small to medium-sized form with distinct sole. Dorsal scales present, covered by a layer of ossicles, including hour-glass shaped bodies or towers or both. Ossicles in sole as knobbed or smooth plates; cups sometimes present.

Lissothuria nutriens (H.L. Clark, 1901)

Figure 9.12

Thyonespolus nutriens H.L. Clark, 1901a:169, 1901b:491.—Deichmann, 1930:193, 1937:174, 1941:138, pl. 26, figs. 1-5.

Psolidium nutriens Ludwig, 1904:689.

Lissothuria nutriens Pawson, 1967:6.

Material Examined. California: Talcott Shoals, Santa Rosa I (2) (MB); SE of Carrington Pt, Santa Rosa I (1) (MB); E of pier, Johnson's Lee, Santa Rosa I (1: 1.2 cm) (MB); Pacific Grove (1: 1.8 cm) (USNM 22458).

Description. Small, up to 2 cm long. Dorsal scale covering incomplete, with scales absent from dorsal midline. Dorsal ossicles towers and hourglass-shaped deposits; cups absent. Ossicles in sole perforated plates with raised marginal projections and cups. Ossicles in tentacles perforated plates or buttons and rods; rosettes lacking.

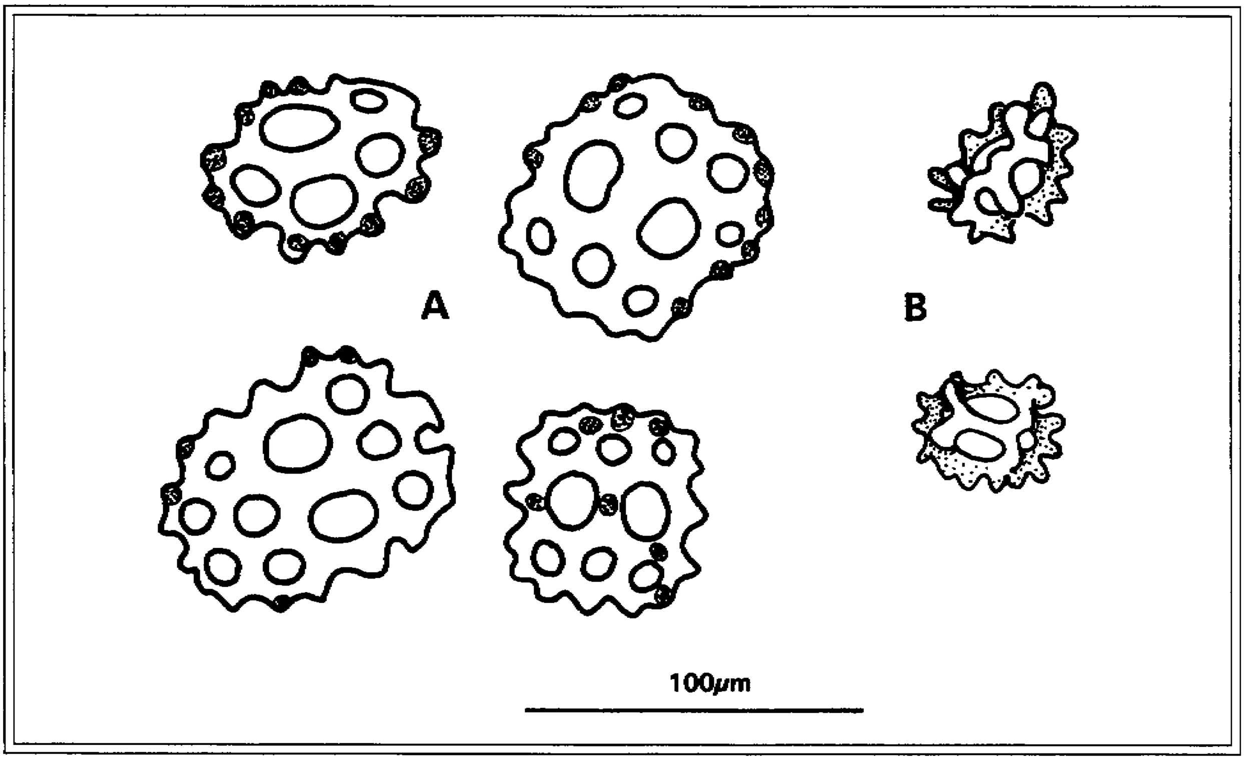

Figure 9.12. *Lissothuria nutriens*: ossicles from sole, A, plates; B, cups.

Biology. *Lissothuria nutriens* is red in life with a pinkish sole. The female produces a small number of large eggs that are brooded in pits on the dorsal surface. When ready to leave the mother, the young have ten tentacles and six tube feet. By the time the animal has grown to 2 mm in length, the sole is fully developed.

Type Locality and Type Specimens. California, Monterey Bay, Pacific Grove, intertidal (MCZ 244).

Distribution. In rocky habitats, Monterey Bay south to Catalina Island, intertidal to 20 m.

Lissothuria deichmannae Pawson, 1967

Lissothuria deichmannae Pawson, 1967:14, fig. 5.

Description. Dorsal scale covering complete. Dorsal ossicles hourglass-shaped deposits and flat plates; towers absent. Ossicles in sole large plates with conspicuous knobs which become multilayered with growth. Small hourglass-shaped plates also present.

Remarks. Pawson (1967) described *Lissothuria deichmannae* from one specimen collected in the intertidal zone on Santa Cruz Island. It is distinguished from *L. nutriens* by the large plates in the sole that tend to become multilayered. At present, little is known about its distribution or habits.

Type Locality and Type Specimens. California, southwest shore of Smugglers Cove, Santa Cruz Island, intertidal, holotype (AHF 325.1).

Distribution. At present known only from the type locality.

Family Cucumariidae Ludwig, 1894
emend. Pawson and Fell, 1965

Diagnosis. Body wall not enclosed by test of imbricating plates. Calcareous ring simple, lacking posterior prolongations.

Subfamily Cucumariinae Panning, 1949

Diagnosis. Ten tentacles. Ossicles in body wall as knobbed or smooth plates; no cups or plates with spires.

Remarks. In Panning's (1949) classification, the genera of Cucumariinae are differentiated by the form of the plates in the body wall. Accordingly, species in the genus *Cucumaria* have thin, spiny plates. Species in *Pseudocnus* have thick knobby plates. These plates are either round or are oblong with a tendency to develop a dentate handle. I have attempted to allocate California species to the appropriate genus; however, in some cases, the allocation is uncertain. In particular, *C. piperata* is problematic. While most ossicles in this species are flat and spiny, some are knobby with a dentate handle.

Genus *Cucumaria* Blainville, 1834
emend. Panning, 1949

Type Species. *Holothuria frondosa* (Gunner, 1767) designated by Panning (1949).

Diagnosis. Ossicles thin plates, smooth or with spines.

Cucumaria curata Cowles, 1907

Figure 9.13

Cucumaria curata Cowles, 1907:2.—Panning, 1949:416.—Rutherford, 1977: 165, figs. 3-5.—Lambert, 1984:437, fig. 1.

Material Examined. California: Carmel Bay, intertidal (1: 2.4 cm) (AHF Acc. 1234); San Clemente, intertidal (multiple) (BLM 2A28376).

Description. Small form, up to 2.5 cm long. Ten tentacles, approximately equal in size. Dorsal body wall and tentacles purplish brown to black, with tube feet scattered in interambulacra. Ventral body wall yellowish. Single stone canal. Ossicles of the body wall as small buttons with 4-6 holes and larger plates with 20 or more holes.

Remarks. Rutherford (1977) considered *Cucumaria pseudocurata* to be a synonym of *C. curata*. However, Lambert (1985) concluded that both *C. curata* and *C. pseudocurata* were valid species. He believed that *C. curata* was very limited in distribution, only occurring at Pacific Grove in Monterey Bay. He, therefore, believed that Rutherford had only collected and studied *C. pseudocurata*.

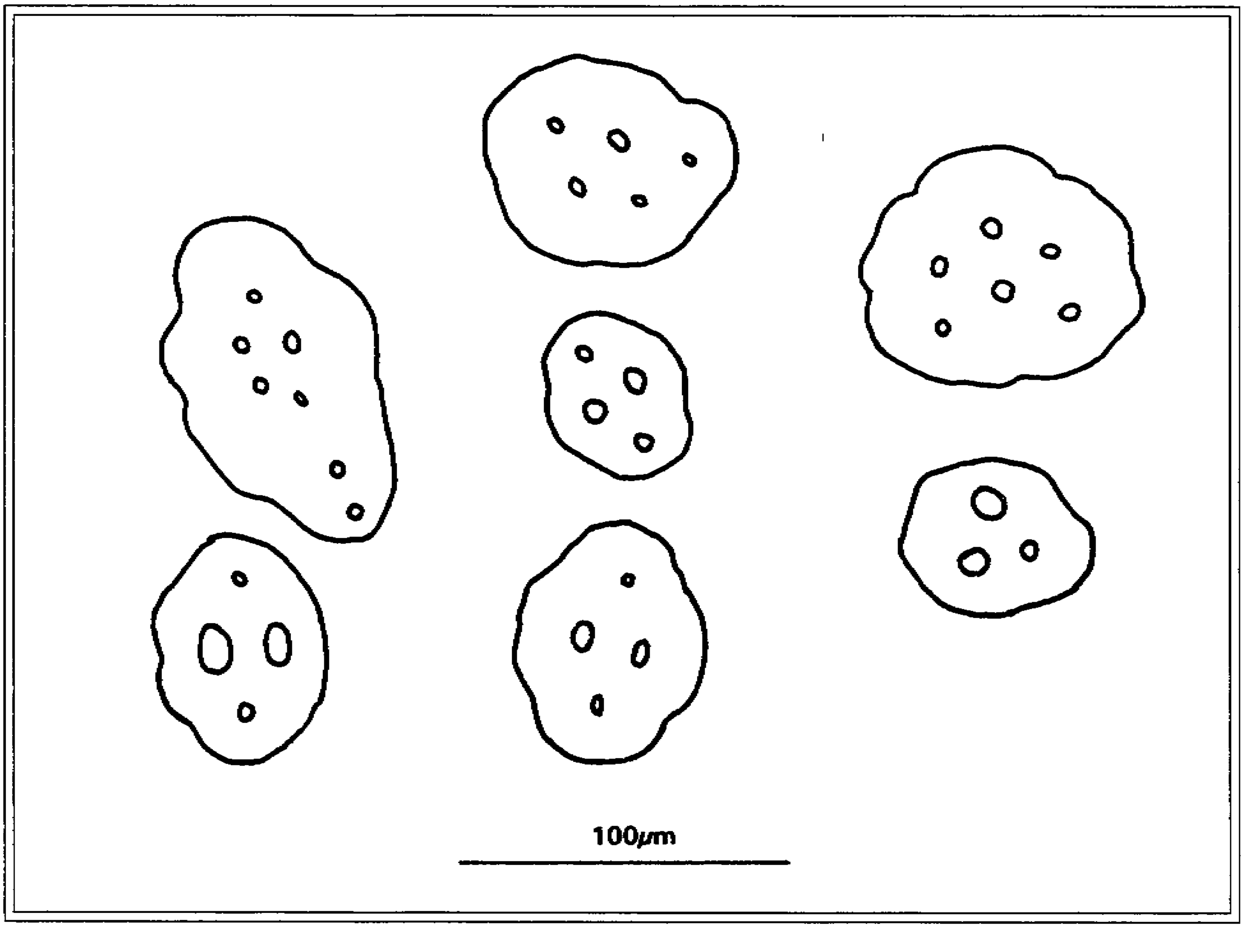

Figure 9.13. *Cucumaria curata*: ossicles from body wall.

The specimens listed under Material examined above agree well with Cowles' and Lambert's description of *C. curata*. Since they seem distinctly different, I have herein treated *C. curata* and *C. pseudocurata* as separate species. Additional studies are needed to determine the status of these two species.

Cowles named this species "*curata*" for its habit of brooding its eggs under the ventral surface of the body wall.

Type Locality and Type Specimens. Cypress Point, Monterey Bay, intertidal, types missing.

Distribution. Uncertain, presumably near Pacific Grove, Monterey Bay, intertidal in rocky habitats (see Remarks).

Cucumaria miniata (Brandt, 1835)

Figure 9.14

Cladodactyla (Polyclados) miniata Brandt, 1835:44.

Cucumaria miniata Selenka, 1867:350.—H.L. Clark, 1924, p. 56.—Edwards, 1910:604, pl. 19, figs. 17-21.

Cucumaria albida Selenka, 1867:350, pl. 20, fig. 109.

Cucumaria japonica Lampert, 1885:143.—H.L. Clark, 1902:562-564.—Edwards, 1907:61-62.

Material Examined. California: Midway between Twin and Platts Harbor, Santa Cruz I, 10-50 ft., rock (1: 7.3 cm); Santa Barbara I, 321 fms (1: 3.9 cm) (*Velero* 1856-49); off UCSB marine lab, Santa Barbara, 30 ft (1: 5 cm) (SBNMH 49001); 1.5 mi E of Cardwell Pt, San Miguel I, 20-21 fms (3:4.0-10.0 cm) (*Velero* 1415-41); Anacapa Passage, 33°59'00"N, 119°32'08"W, 15-50 fms (2: 7.4, 11.1 cm) (*Velero* 1190-40); 1 mi S of East Pt, Santa Rosa I, 15-16 fms (2: 7.0, 9.4 cm) (*Velero* 1284-41b); 5 mi 152° from San Pedro breakwater, 18-19 fms (1) (*Velero* 1232-41b); S side of North jetty, Bodega Bay, intertidal (8:1.0-9.0 cm) (AHF 342.15); 1.5 mi E of Cardwell Pt, San Miguel I, 20-21 fms (3: 7.4-12.0 cm) (*Velero* 1415-41); E of pier, Johnson's Lee, Santa Rosa I, (1:6.7 cm) (MB); Campbell Cove, Bodega Harbor, (2:7.3, 8.8 cm) (AHF 342.6); Cambria, San Luis Obispo Co, (1:2.3 cm) (*Velero* 1581-47); North jetty, Bodega Bay, intertidal (4:6.9-11 cm) (AHF 342.1); Point Arena, Mendocino Co (1) (*Velero* E.B. 41-49); 1.5 mi East of Cardwell Pt, San Miguel I, 20-21 fms (2:3.4, 8.5 cm) (*Velero* 1415-41).—Mexico: 5.5 mi S of San Benito I, 66-81 fms (1: 1.9 cm) (AHF 403.9).—Oregon: North Bay, Cape Arago State Park, intertidal (1:12.5 cm) (*Velero* 1489-42).

Description. Large form, up to 20 cm long. Body cylindrical, with 10 equal tentacles. Color in life red, brownish in preserved specimens. Tube feet restricted to ambulacra. Twenty or more stone canals present. Ossicles in body wall small oblong plates, with 3-7 holes and spines scattered on the surface. Plates often narrowed at one end.

Biology. *Cucumaria miniata* is found under rocks and in crevices in hard-bottom habitats. In Puget Sound, it spawns in spring (McEuen, 1988).

Remarks. This species is differentiated by it large size, red color, lack of interambulacral feet, multiple stone canals and small flat spiny ossicles.

Type Locality and Type Specimens. Sitka, Alaska, types missing.

Distribution. Alaska south to San Benito Island, Baja California, intertidal to 35 m, rocky habitats.

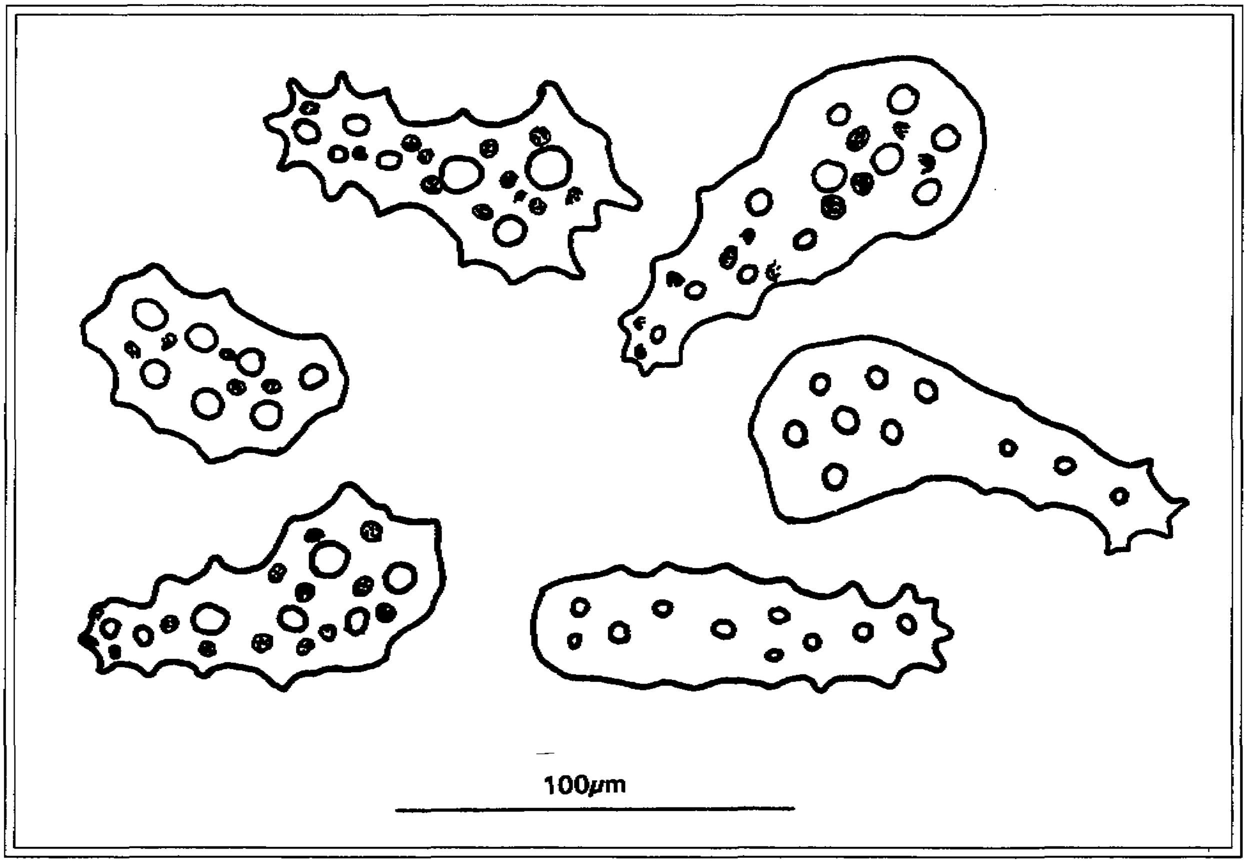

Figure 9.14. *Cucumaria miniata*: ossicles from body wall.

Cucumaria piperata (Stimpson, 1864)

Figure 9.15

Pentacta piperata Stimpson, 1864:161.—H.L. Clark, 1901b:171.

Cucumaria piperata H.L. Clark, 1924:56.—Deichmann, 1937:169.—Panning, 1962:77, fig. 20.-Lambert, 1990:913, fig. 1,4.

Cucumaria fisheri Wells, 1924:114, text-fig. 1, pl. 3, fig. 1-2.

Material Examined. Washington.—Friday Harbor, Puget Sound, (1) (USNM Acc. 102730).—California: 18.5 mi S of San Nicolas I, 57 fms (1:4.3 cm) (AHF 403.13); 1 mi N of west end of Anacapa I, 45-46 fms (3:0.9-1.7 cm) (AHF 403.15); 4.25 mi NE of Sandy Pt, Santa Rosa I, 35-36 fms (1:3.2 cm) (AHF 403.12); 4 mi SE of east end of Santa Catalina I, 104-135 fms (2:3.6, 4.6 cm) (AHF 403.16); 0.5 mi S of west end of Anacapa I, 25-26 fms (4:0.8-1.5) (AHF 403.7); 0.35 mi SW of Ship Rock, Santa Catalina I, 34-43 fms (1:1.8 cm) (AHF 515.1); off Del Monte, Monterey Bay, 5 fms (2:1.5, 2.3 cm) (USNM Acc. 152709); 3.25 mi NE of San Pedro Pt, Santa Cruz I, 46-47 fms (1:1.7 cm) (*Velero* 1418-41); 10.75 W of Pt Dume, 47-48 fm (1:3.6 cm) (*Velero* 1276-41a); 1.5 mi NW of Cavern Pt, Santa Cruz I, 54-56 fms (1:2.5 cm) (*Velero* 1300-41b); E of pier, Johnson's Lee, Santa Rosa I, (1:2.4 cm) (MB); SE of Carrington Pt, Santa Rosa I, (2:2.8, 4.4 cm) (MB); East Pt, Santa Rosa I, (1:2.0 cm) (MB); Tajiguas, Santa Barbara Co, 20 ft (3) (SBMNH 49004m); W of Dutch Harbor, San Nicolas I, 8-9 fms (1:1.7 cm) (*Velero* 1204-40); Pt Dume, 150 m (1:1.8

cm) (SCCWRP R15-150).—Mexico: Ranger Bank, off Cedros I, Baja California, 81-83 fms (4:0.5-1.5 cm) (AHF 403.2); 5 mi S of San Benito I, Baja California, 87-95 fms (50:1.5-4.7 cm) (*Velero* 1119-40); off San Benito I, Baja California, 92-95 fms (5s: 0.9-7.1 cm) (*Velero* 1010-39); 5.5 mi S of San Benito I, Mexico, 66-81 fms (1:2.3 cm) (AHF 403.9);

Description. Medium-sized form, up to 7 cm long. Body cylindrical with 10 equal tentacles. Color in life yellowish with brown spots; tentacles brown. Tube feet restricted to ambulacra. Single stone canal. Ossicles round to oblong plates with a spiny margin and spiny or slightly knobbed surface. Some plates with dentate handle.

Biology. *Cucumaria piperata* is found in both hard- and soft-bottom habitats, sometimes in great numbers. McEuen (1988) reports seeing *C. piperata* in "vast beds on soft bottoms" in Puget Sound. On Santa Rosa Island *C. piperata* was found clinging to coralline algae in a mixed aggregation with *Pseudocnus lubricus* and *Pachythone rubra* (M. Bergen, unpublished).

Remarks. Lambert (1990) synonymized *Cucumaria fisheri fisheri* Wells, 1924 with *Cucumaria piperata*. A discussion of the status of *Cucumaria fisheri astigmata* Wells, 1924 is included under the remarks for *Pseudocnus lubricus*.

Type Locality and Type Specimens. *Cucumaria piperata*: Washington, Puget Sound, type missing; *C. fisheri fisheri*: California, Monterey Bay, 24 m, holotype (USNM E1198).

Distribution. Washington, Puget Sound south to San Benito Island, Baja California, 6-250 m.

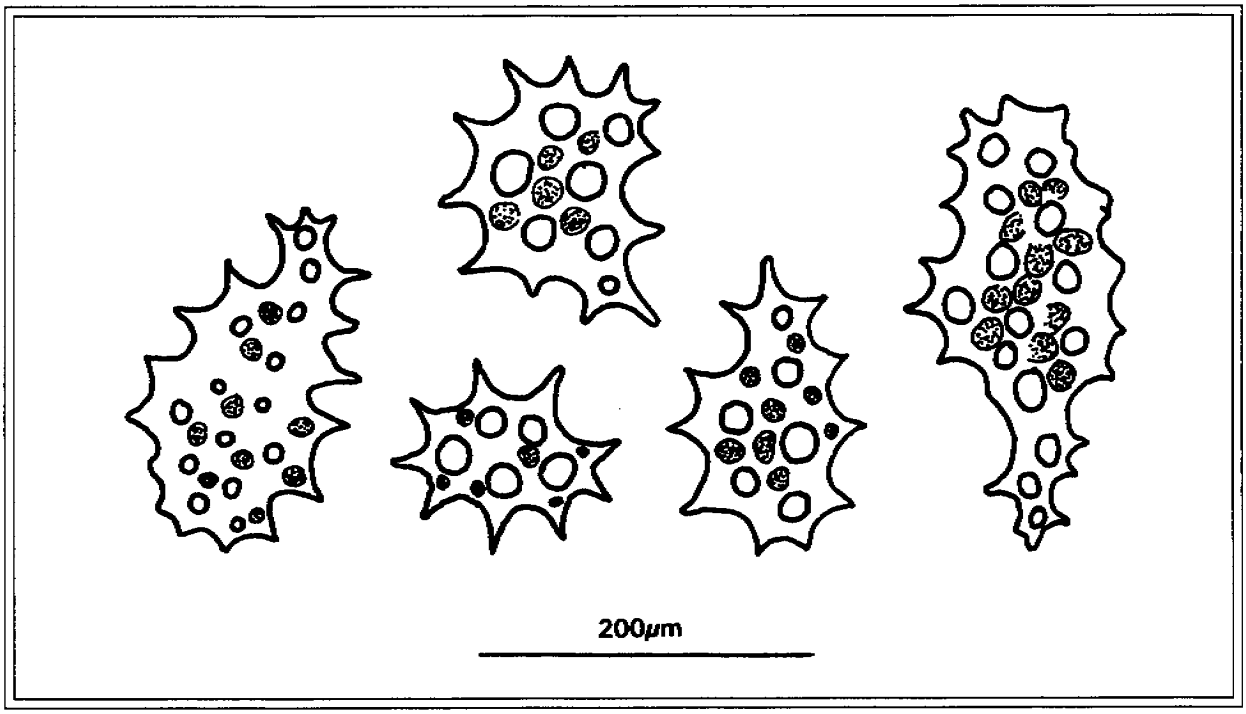

Figure 9.15. *Cucumaria piperata*: ossicles from body wall.

Cucumaria pseudocurata Deichmann, 1938

Figure 9.16

Cucumaria pseudocurata Deichmann, 1938:104, fig. 1.—Rutherford, 1977: 165, figs. 3-5.—Lambert, 1985: 437, fig. 2.

Cucumaria curata: Smith, 1962:233-246. *Not* Cowles, 1907.

Material Examined. California: San Mateo, (1) (cotype, MCZ 356). *Velero* EB23, Zone 3, Mendocino Co, Cormorant Cove, intertidal; *Velero* M1-48, Dillon Beach, intertidal. Oregon: *Velero* 1492-42, Cape Arago State Park, intertidal (multiple); Agate Beach, intertidal (multiple); Agate Beach, under Yaquina Head Light, intertidal (21:0.7-1.8 cm) (*Velero* 1477-42).

Description. Small form, 2-3 cm long. Ten tentacles, approximately equal in size. Dorsal body wall purplish brown to black; ventral body wall yellowish. Tube feet restricted to ambulacra. Ossicles in body wall oblong to round plates, often with 20 or more holes, and rods.

Biology. *Cucumaria pseudocurata* is found in dense aggregations in the lower intertidal zone in rocky intertidal habitats. Spawning occurs in December and January (McEuen, 1988; Rutherford, 1973; Smith, 1962). When spawning, the females deposit the eggs under the ventral surface of the body wall, where they are brooded. After about a month the eggs hatch and the young move away from the female.

Remarks. According to Lambert (1985), the small black holothuroid commonly found in rocky intertidal areas in northern California is *C. pseudocurata*; *C. curata* is restricted to a small area near Pacific Grove, Monterey Bay (See Remarks under *C. curata*). Lambert (1985) also suggests that *C. pseudocurata* and *C. vegae* Theél, 1886, a species described from the Aleutian Islands, may be synonyms.

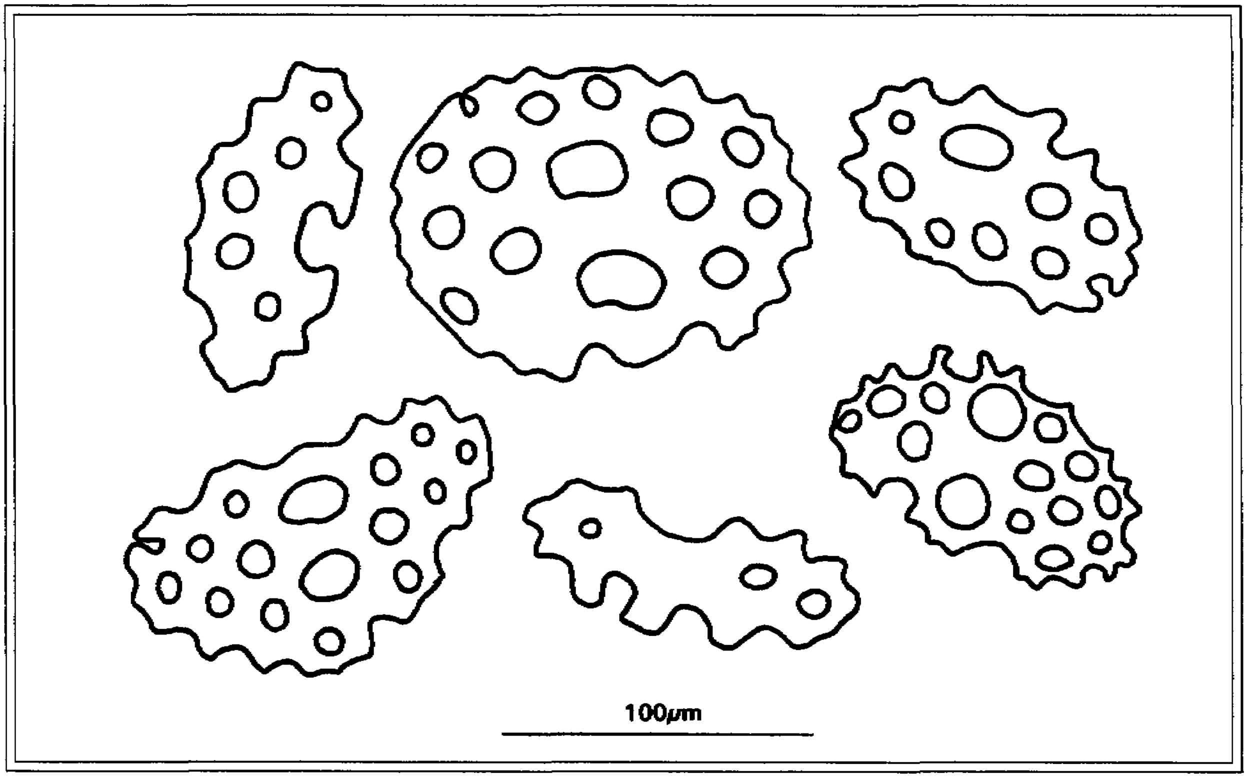

Figure 9.16. *Cucumaria pseudocurata*: ossicles from body wall.

Type Locality and Type Specimen. Southern California, San Mateo, cotype (MCZ 2356). (Note: The type locality for this species is uncertain as San Mateo is in northern, not southern California).

Distribution. Queen Charlotte Islands, British Columbia south to Monterey Bay, California, intertidal, rocky habitats.

Cucumaria salma Yingst, 1972

Figure 9.17

Cucumaria salma Yingst, 1972:142, figs. 1-3.

Material Examined. California: 1 mi S of East Pt, Santa Rosa I, 15 fms, loose rock, sand (1:4.5 cm) (*Velero* 1284-41); San Miguel Passage, 37-39 fms, shale, gray sand (1:0.9 cm) (*Velero* 990-39); 0.5 mi E San Pedro Pt, Santa Cruz I, 26-40 fms, rock (1:1.9 cm) (*Velero* 1297-41); 1 mi N of San Pedro Pt, Santa Cruz I, sand, broken shell (1:1.5 cm) (*Velero* 1298-41); off Anacapa I, 2-20 ft (1:2.5 cm) (SBMNH 49049m); Becher's Bay, Santa Rosa I, (1:2.2 cm) (AHF Hubbs 47-86a); 0.5 mi N of Platt Pt, Santa Cruz I, 36-47 (2:0.9, 1.1 cm) (*Velero* 1303-41a); 0.5 mi N of Platt Pt, Santa Rosa I, 36-47 fms (3:0.5-1.1 cm) (*Velero* 1303-41b); Smugglers Cove, Santa Cruz I, 40 ft (1:4.1 cm) (SBMNH 49010); 5 mi 152° from San Pedro breakwater, 18-19 fms (6:2.5-5.0 cm) (*Velero* 1232-41a); Becher's Bay, Santa Rosa I, 13-16 fms (8) (*Velero* 1004-39b); 4.25 mi NE of Sandy Pt, Santa Rosa I, 46-47 fms (1:1.5 cm) (*Velero* 1417-41b); E of pier, Johnson's Lee, Santa Rosa I (1:3.9 cm) (MB); off Pt La Jolla, 55 m (1:6.1 cm) (Scripps E2659); N face of Bird Rock, Catalina I, 40 ft (1) (holotype, AHF 61).

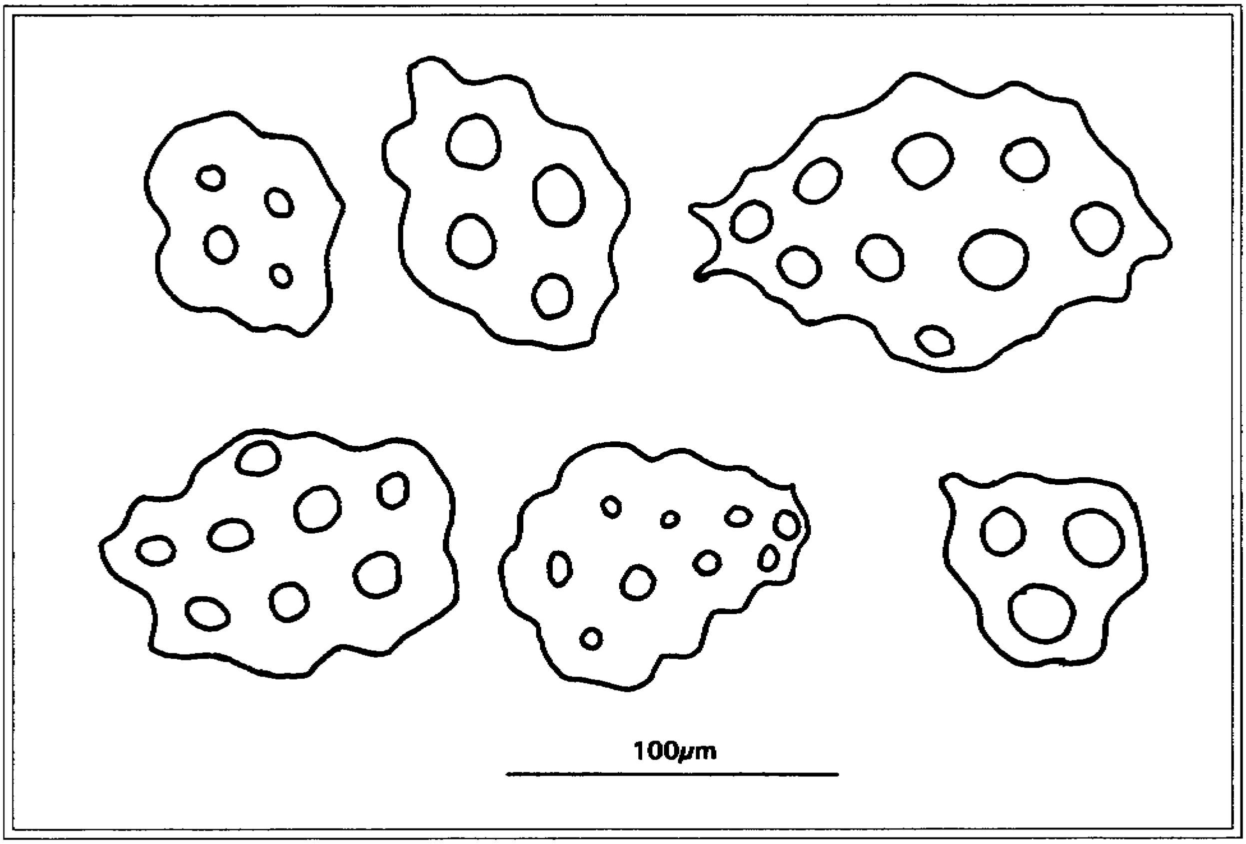

Figure 9.17. *Cucumaria salma*: ossicles from body wall.

Description. Medium-sized, up to 10 cm long. Body cylindrical with 10 equal tentacles. Color in life salmon; anterior end black; tentacles and buccal membrane black mottled with white. Tube feet restricted to ambulacra. Three to 4 stone canals present. Ossicles in body wall smooth plates with undulating margin and 2-20 or more perforations.

Remarks. *Cucumaria salma* lives in crevices in rock reefs. Black dendrochirote tentacles protruding from a rock wall are often the only evidence that this species is present. The ossicles of *C. salma* and *Cucumaria crax* Deichmann, 1941, a species described from Baja California, are similar. It is possible that further study will show these two species to be synonyms.

Type Locality and Type Specimens. California, Catalina I, Bird Rock, 13 m (holotype and paratypes, AHF 61).

Distribution. California, Santa Rosa Island south to Point Loma, San Diego County.

Genus *Pseudocnus* Panning, 1949

Type Species. *Cucumaria dubiosa* Semper, 1868, designated by Panning (1949).

Diagnosis. Ossicles in body wall thick, knobby, either round or oval with one end tending to form a dentate handle.

Pseudocnus lubricus (H.L. Clark, 1901)

Figure 9.18

Cucumaria lubrica H.L. Clark, 1901a:334, 1924:55.

Cucumaria fisheri astigmata Wells, 1924:114, text-fig. 1, pl. 3, fig. 1-2.

Pseudocnus astigmatus Lambert, 1990:913, fig. 2,3.

Material Examined. Califonia: Paradise Cove, (1) (USNM Acc. No. 261891); 3.5 mi S of Fraser Pt, Santa Cruz I, 25-28 fms, sand, broken shell (1:0.8 cm) (*Velero* 1287-41); 0.5 mi S of Gull I, Catalina I, 34-41 fms, sand, shell (7) (*Velero* 1294-41); 2.6 mi E of East Point, Santa Rosa I, 47-49 fms, green mud (2:0.9, 1.7 cm) (*Velero* 1289-41); 3 mi NW Anacapa I light, 47 fms, gray, green sand (multiple) (*Velero* 1267-41a); W of Dutch Harbor, San Nicolas I, 8 fms, rocky (7:1.4-2.4 cm) (*Velero* 1204-40); S. side of Santa Cruz I, 38 fms (12:1.2 - 3.7 cm) (*Velero* 1191-40); off Del Monte, Monterey Bay, 5 fms (10:0.4-3.5 cm) (USNM Acc. 152709); Monterey Bay, 16 fms (2:1.2, 2.3 cm) (USNM Acc. 152709); Chinese Harbor, Santa Cruz I, 25 ft (1:2.0 cm) (SBMNH 49001m); Becher's Bay, Santa Rosa I, 13-16 fms (17) (*Velero* 1004-39a); 2.5 mi E of South Pt, Santa Rosa I, 17-18 fms (11) (*Velero* 1282-41b); 2.25 mi E of South Pt, Santa Rosa I, 23-28 fms (7:0.8-2.5 cm) (*Velero* 1283-41b); Monterey Bay, 8 fms (2:0.9, 2.1 cm) (*Velero* 1456-42); San Luis Obispo Bay, (1:1.8 cm) (*Velero* 885-38a); S of San Miguel I, 5-15 fms (2:0.9, 1.9 cm) (*Velero* 894-38); 1 mi S of East Pt, Santa Rosa I, 15-16 fms (3:0.8-2.3 cm) (*Velero* 1284-41b); 9.5 mi NW of buoy, Cortez Bank, 50 fms (*Velero* 1342-41); Nifty Rock, San Miguel I, (1:2.2 cm) (MB); SE of Carrington Pt, Santa Rosa I, (7:0.8-2.2 cm) (MB); East Pt, Santa Rosa I, (12:0.5-1.5 cm) (MB); E of pier, Johnson's Lee, Santa Rosa I, Ca (6:1.0-3.8 cm) (MB); W of pier, Johnson's Lee, Santa Rosa I, (1:2.3 cm) (MB); 4 mi S of Gaviota, (1:2.0 cm) (SBMNH 48998); Pelican Cove, Santa Cruz I, 20-60 ft (2) (SBNMH); reef midway between Twin and Platts Harbors, Santa Cruz I, 10-50 ft (1) (SBNMH 48845m); Tajiguas, Santa Barbara Co, 20 ft (3) (SBNMH 48849); Chinese Harbor, Santa Cruz I, (1) (SBNMH 49004m); Hope Ranch, Santa Barbara Co, (1) (SBNMH 49000); 1 mi N of W end of Anacapa I, 46 fms (10:0.7-1.6 cm) (*Velero* 1419-41); 4.25 mi N of Sandy Pt, Santa Rosa I, 35 fms (2:1.2, 1.7 cm) (*Velero* 1417-41); 2 mi W of Cardwell Pt, San Miguel I, 35 fms (1:3.1 cm) (*Velero* 1413-41); 3.6 mi off S coast, near E end, Santa Rosa I, (2:0.5, 0.9 cm) (Hubbs 47-85); 1 mi NW of W end, Anacapa I, 41 fms (1:1.7 cm) (*Velero* 1937-50); 3.5 mi NE of San Pedro

Pt, Santa Cruz I, 46 fms (4:1.1-1.4 cm) (*Velero* 1418-41); W of Dutch Harbor, San Nicolas I, 8-9 fms (23:0.5-3.1 cm) (*Velero* 1204-40); 3 mi E of South Pt, Santa Rosa I, 18 fms (2:1.7, 2.9 cm) (*Velero* 1410-41); 1.5 mi NW Cavern Pt, Santa Cruz I, 55 fms (42) (*Velero* 1300-41); 3.6 mi off East Pt, Santa Rosa I, 53 fms (2:2.0, 2.1 cm) (*Velero* 1388-41); 2 mi S of Crook Pt, San Miguel I, 42 fms (3:1.3-1.9 cm) (*Velero* 1412-41); 9.5 mi SW of Tanner Bank, 72 fms (1:1.0 cm) (*Velero* 1346-41); 3 mi N of Arch Rock, Santa Cruz I, 55-60 fms (3:0.3-0.7 cm) (*Velero* 1304-41); USNM BRC-002; SBMNH BRA-016.—Puget Sound, Washington (2:2.3, 3.2 cm) (syntypes, MCZ 202);—Oregon: Middle Bay, Cape Arago State Park, (2:2.3, 2.8 cm) (*Velero* 1487-42);

Description. Medium-sized, cylindrical, blunt on both ends, up to 4 cm long. Tube feet retractile, not restricted to ambulacra. Single stone canal and polian vessel present. Ossicles mostly round, mounded, knobbed plates and buttons, smallest with 4 symmetrically placed holes. Some larger plates with one end drawn out into handle.

Biology. From the specimens examined, *Pseudocnus lubricus* apparently lives in both hard- and soft-bottom habitats. In hard-bottom habitats, *P. lubricus* broods its eggs under the ventral surface of the body. When spawning, the female folds the anterior end under the body to release the eggs. While the females were sedentary, the males were apparantly errant during the spawning season. In Puget Sound, spawning occurred in winter (McEuen, 1988).

Remarks. After viewing the type specimens of *Cucumaria fisheri* Wells 1924, Lambert (1990) recognized that the specimens described as *C. fisheri fisheri* and *C. fisheri astigmata* were distinct species, belonging, respectively, to the genera *Cucumaria* and *Pseudocnus*. *Cucumaria fisheri fisheri* was synonymized with *Cucumaria piperata* and *C. fisheri astigmata* was referred to the genus *Pseudonus*.

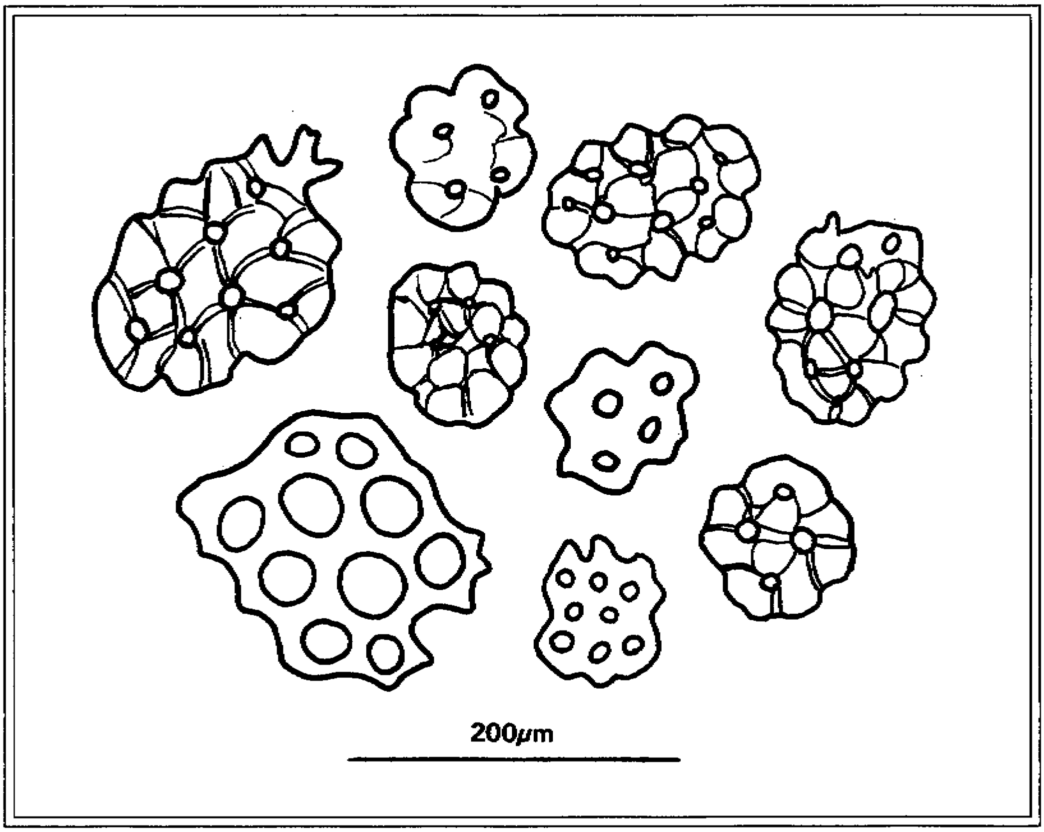

Figure 9.18. *Pseudocnus lubricus*: ossicles from body wall.

Lambert (1990) noted that *Pseudocnus astigmatus* was similar to *Cucumaria curata* and *C. lubrica*, inasmuch as the shape of the ossicles was similar to some degree and also because these species brooded their eggs under the ventral surface of the body. *Cucmaria curata* and *Pseudocnus astigmatus*, however, are quite distinct in terms of size (3 versus 5 cm maximum length), color (black versus white or white with brown spots) and habitat (intertidal versus subtidal). On the other hand, *P. astigmatus* and *C. lubrica* are quite similar. When I examined the type specimens of *C. piperata astigmata* and *C. lubrica*, I found them to be identical. For this reason, I consider *P. lubricus* a junior synonym of *P. lubricus*.

Type Locality and Type Specimens. *Cucumaria lubrica*: Washington, Puget Sound, syntypes (MCZ 202); *C. fisheri astigmata*: California, Monterey Bay, 12 fms, (USNM E1196).

Distribution. British Columbia, Queen Charlotte Sound, Alert Bay south to Cortez Bank, southern California, 1.5-72 fms.

Family Sclerodactylidae Panning, 1949

emend. Pawson and Fell, 1965

Diagnosis. Body wall not enclosed in a test of imbricating plates. Calcareous ring complex with single or paired processes; processes entire, not divided into pieces.

Genus *Eupentacta* Deichmann, 1938

Type Species. Cucumaria quinquesemita Selenka, 1867, by original designation.

Diagnosis. Ten tentacles, 2 ventral tentacles smaller. Body wall cylindrical. Tube feet non-retractile, restricted to ambulacra. Ossicles knobbed buttons or plates and cups or baskets or reticulated bodies.

***Eupentacta quinquesemita* (Selenka, 1867)**

Figure 9.19

Cucumaria quinquesemita Selenka, 1867:351, pl. 20, fig. 107a,b.

Cucumaria chronhjelmi Theél, 1886:105.—H.L. Clark, 1924:55.

Eupentacta quinquesemita Deichmann, 1938:109.

Material Examined. California: off Ford Pt., Santa Rosa I, 92 ft (1) (USNM Acc. 205678); Talcott Shoals, Santa Rosa I, (1:5.2 cm) (MB); SE of Carrington Pt, Santa Rosa I, (1:6.0 cm) (MB); W of pier, Johnson's Lee, Santa Rosa I, (1:2.8 cm) (MB); Puget Sound, Washington (1:4 cm) (USNM 33091); Mendocino, (1) (cotype, MCZ 217).

Description. Medium-sized, up to 10 cm long. Body wall cylindrical with broad interambulacra; numerous tube feet in ambulacra. Ossicles as knobbed plates and cups.

Biology. *Eupentacta quinquesemita* occurs on top of rocks and boulders in rocky habitats. In Puget Sound *E. quinquesemita* spawns in spring (McEuen, 1988).

Type Locality and Type Specimens. California, Mendocino, cotype (MCZ 217).

Distribution. Alaska south to Santa Rosa Island, California, intertidal to 30 m, rocky habitats.

Genus *Pachythyone* Deichmann, 1941

Type Species. Thyone rubra H.L. Clark, 1901, by orginal designation.

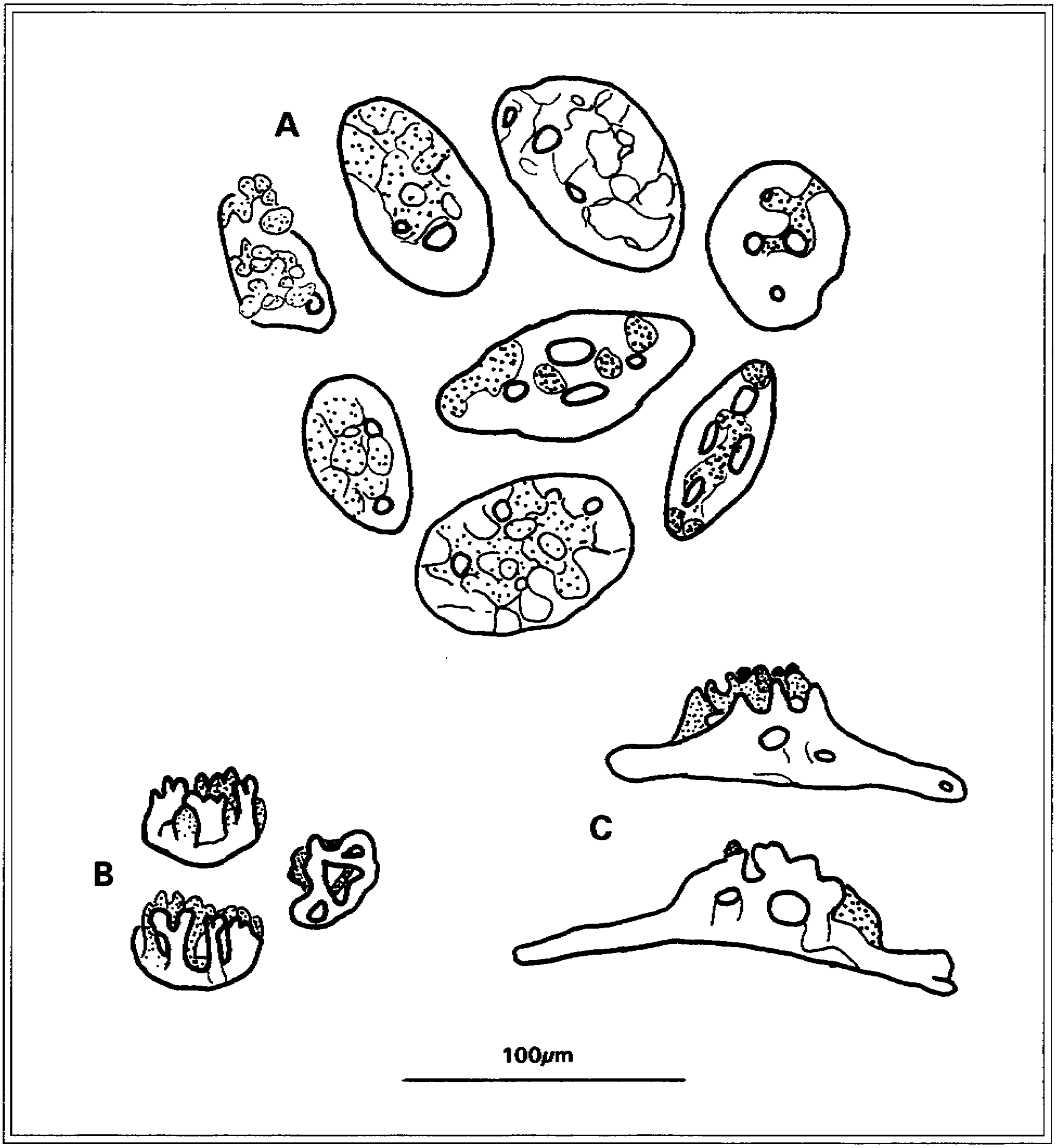

Figure 9.19. *Eupentacta quinquesemita*: ossicles from body wall, A, plates; B, cups; C, supporting tables from tube feet.

Diagnosis. Small form, up to 3 cm long, with numerous interambulacral feet. Ossicles as oval buttons or plates with external side reticulated and regularly-knobbed 4-holed buttons.

Pachythyone rubra (H.L. Clark, 1901)

Figure 9.20

Thyone rubra H.L. Clark, 1901a:494, 1901b:166, figs. 1-5.—Deichmann, 1939:5, fig. 3.

Pachythyone rubra Deichmann, 1941:115, pl. 23, figs. 10-12.

Material Examined. California: S 6°W 2.5 miles north of anchorage, East Point, San Nicolas I, 291-298 fms, gray mud, rock (23) (*Albatross* 4421); Santa Cruz I, intertidal (23)(AHF 294.18); Santa Rosa I, mussel bed No. 5B (1) (BLM); Pelican Cove, Santa Cruz I, 20-40 ft (1) (SBMNH 48848m); reef midway between Twin and Platts Harbors, Santa Cruz I, (1) (SBMNH 48845m); Chinese Harbor, Santa Cruz I, 25 ft (1) (SBNMH 49004m); Los Angeles Harbor, (2:1.5, 1.9 cm) (USNM 261891); Monterey Bay, (1) (cotype, MCZ 244).

Description. Small form, up to 2 cm in long. Dorsal body wall orange red; ventral body wall white. Tube feet scattered in interambulacra. Ossicles in body wall as oval reticulated plates and regular 4-holed buttons.

Biology. This species may be locally very abundant in rocky habitats. It broods it eggs internally, producing fully-formed juveniles.

Type Locality and Type Specimens. California, Monterey Bay, cotype (MCZ 244).

Distribution. California, Monterey Bay south to Los Angeles Harbor, intertidal to 300 fms (548 m), rocky habitats.

Family Phyllophoridae Ostergren, 1907

(emended Pawson and Fell, 1965)

Subfamily Thyoninae Panning, 1949

Diagnosis. Small to medium-sized forms, often U-shaped. Ten tentacles, 2 ventral tentacles smaller. Tube feet non-retractile, restricted to the ambulacra. Calcareous ring with long processes divided into pieces.

Remarks. In Panning's classification, the presence or absence of tables and plates in the body wall was used to divide the genera of Thyoninae. Accordingly, the genus *Stolus* has only plates, *Pentamera* and *Thorsonia* have tables and plates, and *Allothyone*, *Havelockia*, *Thyone* and *Hemiathyone* have only tables in the body wall. *Thorsonia* and *Allothyone* are distinguished by having 4-pillared tables while *Pentamera* and *Havelockia* have two-pillared tables. *Thyone* is distinguished by having rosettes and no tables in the introvert while *Havelockia* has tables and no rosettes.

In his classification, Panning (1949) did not use the presence or absence of interambulacral tube feet as a generic character. Therefore, species in the genus *Thyone sensu* Panning may or may not have interambulacral feet. In addition, many former members of the genus *Thyone*, e.g., *Thyone benti*, were moved into other genera.

It is not clear at present that Panning's classification really works. Tables commonly degenerate with growth in this group, making practical application of the classification difficult. It is often not clear if a ossicle is a plate or a degenerate table.

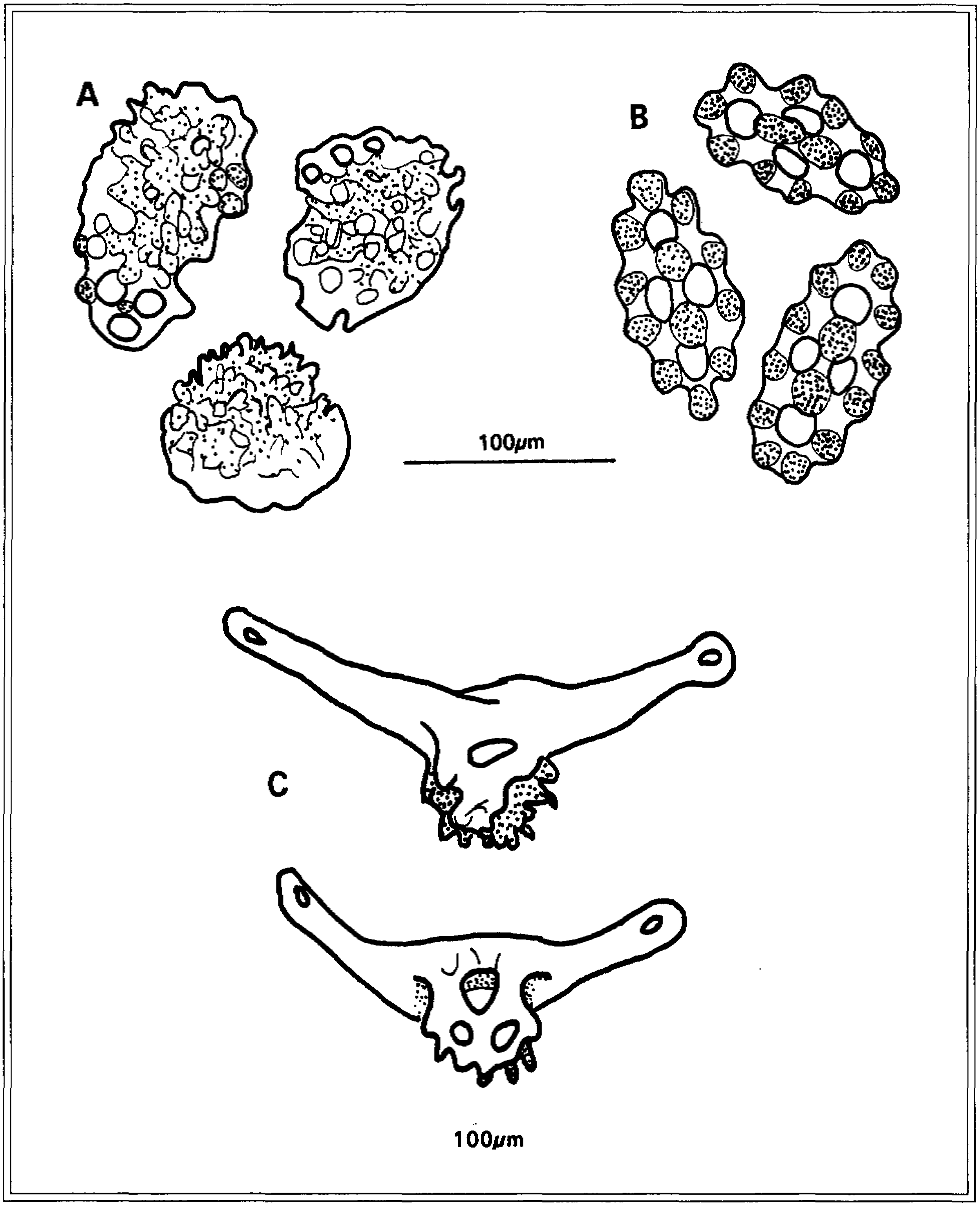

Figure 9.20. *Pachythyone rubra*: ossicles from body wall, A, reticulated plates; B, 4-holed buttons; C, supporting tables from tube feet.

To some degree Panning's classification does seem to work for California species. Species in the genus *Pentamera* generally have tables and plates in the body wall and only have plates in the introvert. Species in the genus *Havelockia* seem to have either tables or ossicles derived from tables in the body wall and introvert. However, there is considerable uncertainty about the placement of some species. In addition, the importance of interambulacral feet as a character is uncertain. Pawson and Miller (1981) use the presence of interambulacral feet in their definition of the genus *Thyone*. Species in *Thyone sensu* Pawson and Miller may have rosettes only, tables only, or rosettes and tables in the introvert.

It is clear that this group is in need of revision. For the purposes of this chapter, I have followed Panning's (1949) classification and allocated the species to the genera to the best of my ability. Since it is difficult to apply the generic definitions to individual specimens, I have not included the genera in the key.

Genus *Havelockia* Pearson, 1903

Type Species. *Havelockia herdmani* Pearson, 1903, by original designation.

Diagnosis. Ossicles in body wall and introvert tables with 2 pillars. Tables may become reduced with age.

***Havelockia benti* (Deichmann, 1937)**

Figure 9.21

Thyone benti Deichmann, 1937:170, fig 2, 1-11.

Havelockia benti Panning, 1949:466.

Thyone benti var. *zacae* Deichmann, 1938a:376, fig. 10.

Havelockia benti var. *zacae* Panning, 1949:466.

Material Examined. *Havelockia benti*: California: 1.8 mi 299° to South Pt, Santa Rosa I, 22 fms, sand, shell,(2: 1.1, 4.2 cm) (BLM 23192); 1 mi 329° to South Pt, Santa Rosa I, 30 fms, sand, shell (2) (BLM 23045); 3.55 mi 359.5° to East Pt, Santa Rosa I, 36 fms, sand, gravel, shell (1) (BLM 23205); 4.8 mi 349° to East Pt, Santa Rosa I, 48 fms, sand, rocks (1) (BLM 22952); 46.3 mi 71° to China Pt, San Clemente I, 46 fms, sand, gravel, shell (1:0.7 cm) (BLM 24382); 4.25 mi 313° to South Pt, Santa Rosa I, 44 fms, sand, gravel, shell (2) (BLM 22976); 2.6 mi 360° to East Pt, Santa Rosa I, 28 fms, sand, shell (2) (BLM 23206); S side of Santa Cruz I, 39-40 fms, sand (6: 0.8-3.4 cm) (*Velero* 1191-40); off Redondo Beach, 11-20 fms, gravel (1:1.0 cm (*Velero* 1139-40); 11.5 mi SE of Long Beach, 32-52 fms, mud, sand, shell (1:1.1 cm) (*Velero* 1160-40); Santa Cruz Channel, 32-34 fms, sand, shell (1:1.9 cm) (*Velero* 1005-39); 3.5 mi S of Frasier Pt, Santa Cruz I, 25-28 fms, sand, shell (1:1.9 cm) (*Velero* 1287-41); off Gull I, S side of Santa Cruz I, 39-43 fms, sand, mud (4:0.6-0.8 cm) (*Velero* 1194-40); off San Nicolas I, 29-30 fms, sand, shell (1:1.5 cm) (*Velero* 1120-40); 2 mi SW of Cardwell Pt, Santa Miguel I, 34-35 fms, mud (3:0.8-1.1 cm) (*Velero* 1413-41); 0.5 mi E of San Pedro Pt, Santa Cruz I, 26-40 fms, rocky (1:2.3 cm) (*Velero* 1297-41); off Bluff Cove, 50-75 fms (1:0.9 cm) (Burch 4085); 1 mi E of Empire Landing, Santa Catalina I, 22 fms, sand, shell (1:0.8 cm) (*Velero* 1374-41); 4.5 mi SE of East Pt, Santa Rosa I, 52 fms, mud (4) (*Velero* 1387-41); 3 mi N of Arch Rock, Santa Cruz I, 55-60 fms, mud, shell (1:1.2 cm) (*Velero* 1304-41); 6 mi E of South Pt, Santa Rosa I, 28-30 fms, rock (7:1.2-4.2 cm) (*Velero* 1292-41); 2.5 mi SE of Bennett Pt, San Miguel I, 57 fms (1:0.7 cm) (*Velero* 1396-41); 10.75 mi W of Pt Dume, 47-48 fms, rocky (1:2 cm) (*Velero* 1276-41); 1 mi N of San Pedro Pt, Santa Cruz I, 45-46 fms, sand, shell (4:0.8-1.0 cm) (*Velero* 1298-41); 1.5 mi NW of Cavern Pt, Santa Cruz I, 55 fms, mud, sand, shell (6) (*Velero* 1300-41); 0.5 mi S of Gull I, Santa Cruz I, 34-41 fms, sand, shell (21:0.4-1.7 cm) (*Velero* 1294-41; 1 mi E of Smugglers Cove, Santa Cruz I, 15-21 fms, sand, pebbles (2:0.5, 1.4 cm) (*Velero* 1295-41); 1.5 mi SW of Gull I, Santa Cruz I, 48 fms, mud (1:1.4 cm) (*Velero* 1435-41); 0.35 mi SW of Ship Rock, Santa Catalina I, 34-43 fms, sand, rock (1:1.3 cm) (*Velero* 2955-54); 1.5 mi SW of Judith Rock, San Miguel I, 45-48 fms, sand, shell (4) (*Velero* 1411-41); 3.5 mi NE of San Pedro Pt, Santa Cruz I, 46 fms, sand (1:1.5 cm) (*Velero* 1418-41); Monterey Bay, 25 fms (1) (Burch 3711); 0.5 mi N of Platt Pt, Santa Cruz I, 36-47 fms, shell (6:0.3-2.2 cm) (*Velero* 1303-41); off Abalone Pt, Laguna Beach, 54-57 fms, mud (9:0.9-4.2 cm) (*Velero* 1131-40); USNM BSS-058.

Havelockia benti var. *zacae*: California: 20.3 mi S of East Pt, Santa Rosa I, 71 fms, sand, gravel, rock (1) (BLM 23071); 7.2 mi SSW of East Pt, Santa Rosa I, 33 fms, sand, shell (1) (BLM 22960); 6.2 mi SSW of East Pt, Santa Rosa I, 37 fms, sand, shell, rock (1) (BLM 22958); off Abalone Pt, Laguna Beach, 54-57 fms, mud (1:4.4 cm) (*Velero* 1131-40); S side of Santa Cruz I, 37-40 fms, sand (1:4.1 cm) (*Velero* 1191-40); off Pt Piños, Monterey Bay, 36 fms, shell (1:3.7 cm) (*Velero* 889-38); W side of Santa Barbara I, , 100 fms, sand (2:2.4, 2.7 cm) (*Velero* 1176-40); 2.5 mi NW of Anacapa Light, 48-51 fms, sand (2:3.1, 4.0 cm) (*Velero* 1268-41); off Bowen Pt, Santa Cruz I, 58-90 fms, sand, shell (5:3.1-4.5 cm) (*Velero* 1192-40); 4.5 mi NNW of buoy, Cortez Bank, 60-61 fms, sand, rock (1:6.2 cm) (*Velero* 1341-41); 3 mi NW of Anacapa Light, 47-52 fms, sand (2:4.0, 5.2 cm) (*Velero* 1267-41); 1.5 mi off Dutch Harbor, San Nicolas I, 63-83 fms, sand, mud, shell (2:4.1, 5.6 cm) (*Velero* 1220-40); 0.5 mi N of Platt Pt, Santa Cruz I, 36-47 fms, shell (2:0.8, 0.9 cm) (*Velero* 1303-41); 3 mi SE of Ship Rock, Santa Catalina I, 52-65 fms, sand, shell (4:1.4-2.9 cm) (*Velero* 2953-54); 4.5 mi SW of East Pt, Santa Rosa I, 43-45 fms, mud (2:2.5, 2.7 cm) (*Velero* 1390-41); 0.35 mi SW of Ship Rock, Santa Catalina I, 34-43 fms, sand, rock (1:1.1 cm) (*Velero* 2955-54); 1.5 mi SW of Judith Rock, San Miguel I, 45-48 fms, sand, shell (1:2.9 cm) (*Velero* 1411-41); 1.5 mi S of Crook Pt, San Miguel I, 41-43 fms, sand, shell (1:4.8 cm) (*Velero* 1412-41); 1.5 mi SW of Gull I, Santa Cruz I, 48 fms, mud (2:2.4, 2.8 cm) (*Velero* 1435-41); 6 mi E of South Pt, Santa Rosa I, 28-30 fms, rock (1:2.2 cm) (*Velero* 1292-41); 2.6 mi E of East Pt, Santa Rosa I, 47-49 fms, mud (1:1.7 cm) (*Velero* 1289-41); 0.5 mi S of Gull I, Santa Cruz I, 34-41 fms, sand, shell (1:2.5 cm) (*Velero* 1294-41); off Abalone Pt, Laguna Beach, 25-27 fms, mud (1:1.9 cm) (*Velero* 1130-40); Pt Arguello, 450 ft (1:3.1 cm) (MEC Sta B2); Pt Arguello, (1) (Chambers sta 5); Pt Arguello, (4) (Chambers sta 1); Pt Arguello, (1:6.3 cm) (Chambers sta 4); 4.5 mi SE of East Pt, Santa Rosa I, 52 fms, sandy mud (2:0.7, 1.0 cm) (*Velero* 1387-41); 6.5 ESE of South Pt, Santa Rosa I, 57 fms (1:1.6 cm) (*Velero* 1392-41); 6.1 mi 344° to East Pt, Santa Rosa I, 56 fms, coarse sand, shell (10).—Mexico: 5 mi S of San Benito I, Baja California, 87-95 fms, sand (2:3.8, 3.9 cm) (*Velero* 1119-40); off San Benito I, Baja California, 92-95 fms, fine sand (8:1.5-5.2 cm) (*Velero* 1010-39).

Other Material. California: 0.5 mi S of Gull I, Santa Cruz I, 34-41 fms, sand, shell (4:1.9-2.5 cm) (*Velero* 1294-41); 0.5 mi N of Platt Pt, Santa Cruz I, 36-47 fms, shell (2:3.1, 3.3 cm) (*Velero* 1303-41); E of Bridge Rock, La Jolla, 85 ft, under rocks (1:8.1 cm) (SIO E2657).

Description. Small to medium-sized, up to 8 cm in long, somewhat U-shaped, slightly fusiform, anterior end blunt, posterior end tapering to a tail. Body wall cream, tan, orange, rust brown, grey or black. Tube feet orange, scattered in interambulacra.

In *Havelockia benti*: body wall ossicles tables with round to irregularly-shaped disk, 0.07-0.13 mm in diameter, with 4-18 holes and a short spire (0.02-0.06 mm) ending in a few teeth. Supporting tables with 2-pillared spire. Iintrovert with tables and delicate plates sometimes looking like rosettes. Tentacles delicate rods, plates and occasional tables.

In *Havelockia benti* var. *zacae*: body wall ossicles flat irregularly-shaped plates, 0.01-0.27 mm in diameter, and smaller, more delicate, rectangular plates, 0.10-0.15 mm in length, often with 2 enlarged central holes. Supporting tables with low 2-pillared spire or reduced to simple curved rod. Introvert with delicate plates, sometimes resembling rosettes; tables present, but rare. Tentacles with delicate rods and plates; tables rare.

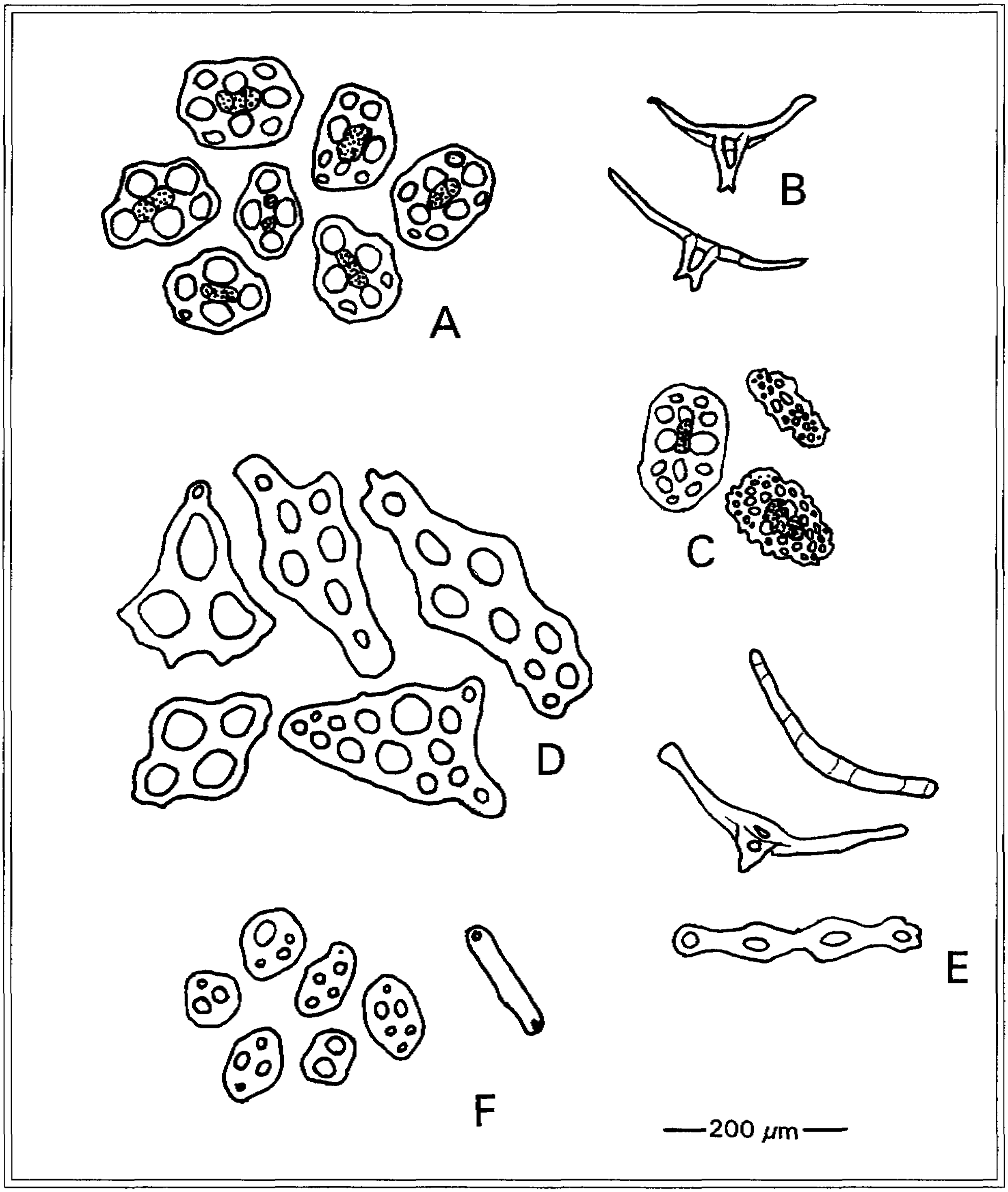

Figure 9.21. *Havelockia benti*: A, tables from body wall; B, supporting tables from tube feet; C, tables from introvert. *Havelockia benti* var. *zacae*: D, tables from body wall; E, supporting tables from tube feet. *Havelockia* variant: F, biscuit-shaped plates and bar-shaped deposit.

In "other" (see Remarks): body wall ossicles small biscuit-shaped plates, 0.04-0.09 mm in diameter, with 2-5 central holes, and bar-shaped ossicles 0.07-0.12 mm long. Occasionally irregular and rectangular plates as in *Havelockia benti* var. *zacae* are present. Supporting tables, when present, curved bars as in *H. benti* var. *zacae*. Introvert with delicate plates that sometimes resemble rosettes. Tentacles with delicate rods, plates and tables.

Biology. This is one of the most common holothurians in soft-bottom habitats on the continental shelf in California.

Remarks. Most specimens of this species fall into one of three distinct groups: *Havelockia benti*, *H. benti* var. *zacae* and those I have allocated to "other". In specimens listed as *H. benti*, tables are abundant in the body wall. In *H. benti* var. *zacae* ossicles are relatively scarce and most of the ossicles are plates. In specimens listed as "other", biscuit-shaped plates are common in the body wall.

There seems to be an association between the size of the specimen and type of ossicles, with *H. benti* tending to be smaller than *H. benti* var. *zacae*, and *H. benti* var. *zacae* tending to be smaller than specimens with biscuit-shaped plates. Deichmann (1937, 1938) believed that body wall tables in *H. benti* degenerated into the typical plates of *H. benti* var. *zacae*. While intermediates between the three forms are rare, there is no reason at present to consider them as separate species. All share a common anatomy and form, including orange pigmentation in the tube feet that persists after treatment with bleach. At the present time, I believe that all the specimens belong to one extremely, variable species. The three groups are differentiated with the hope that someone will study the different forms in greater detail.

Type Locality and Type Specimens. *Havelockia benti*: Washington, Friday Harbor, Rocky Bay, 70 m (Museum of Comparative Zoology, MCZ 1810).

Havelockia benti var. *zacae*: Baja California, East of Cedros Island, 80 m (MCZ 1954).

Distribution. Puget Sound to northern Baja California, 36-200 m.

Havelockia charlottae (Deichmann, 1938)

Figure 9.22

Pentamera charlottae Deichmann, 1938:108.

Havelockia charlottae Panning 1949:466.

Material Examined. California: *Velero* 886-38, S off Pillar Pt, Half Moon Bay, 16 fms, gravel (1:2.1 cm); *Velero* 1004-39, Becher's Bay, 13-16 fms, rock (1:2.5 cm); *Velero* 1856-49, Santa Barbara Basin, 321 fms (1:1.6 cm); MEC 206, Rep A, 49 ft (1); Chambers Station 5, Rep 2 (1); Pacific Biomarine, Long Beach Harbor Breakwater (2:4.9-6.2 cm).

Description. Medium-sized, cylindrical, up to 6.5 cm long. Tube feet crowded in ambulacra. Color of preserved specimens white or light coffee. Body wall ossicles tables with an oblong disk, 0.09-0.11 mm long, and a spire 0.08-0.12 mm long with 3-5 cross beams and a few teeth on the tip. Supporting tables also with a long spire. Tables in introvert round to oblong, with 2 enlarged central holes and 8-16 additional holes, a dentate margin, and low spire. Tentacles with rods, plates and tables.

Type Locality and Type Specimens. California, Pacific Grove, tidepools (USNM E2391 and E2392).

Distribution. California, Monterey Bay to southern California, hard bottom habitats, intertidal to 642 m.

Genus *Pentamera* Ayres, 1852

Type Species. *Pentamera pulcherrima*, 1852, by original designation.

Diagnosis. Ossicles in body wall 2-pillared tables and plates; ossicles in introvert plates.

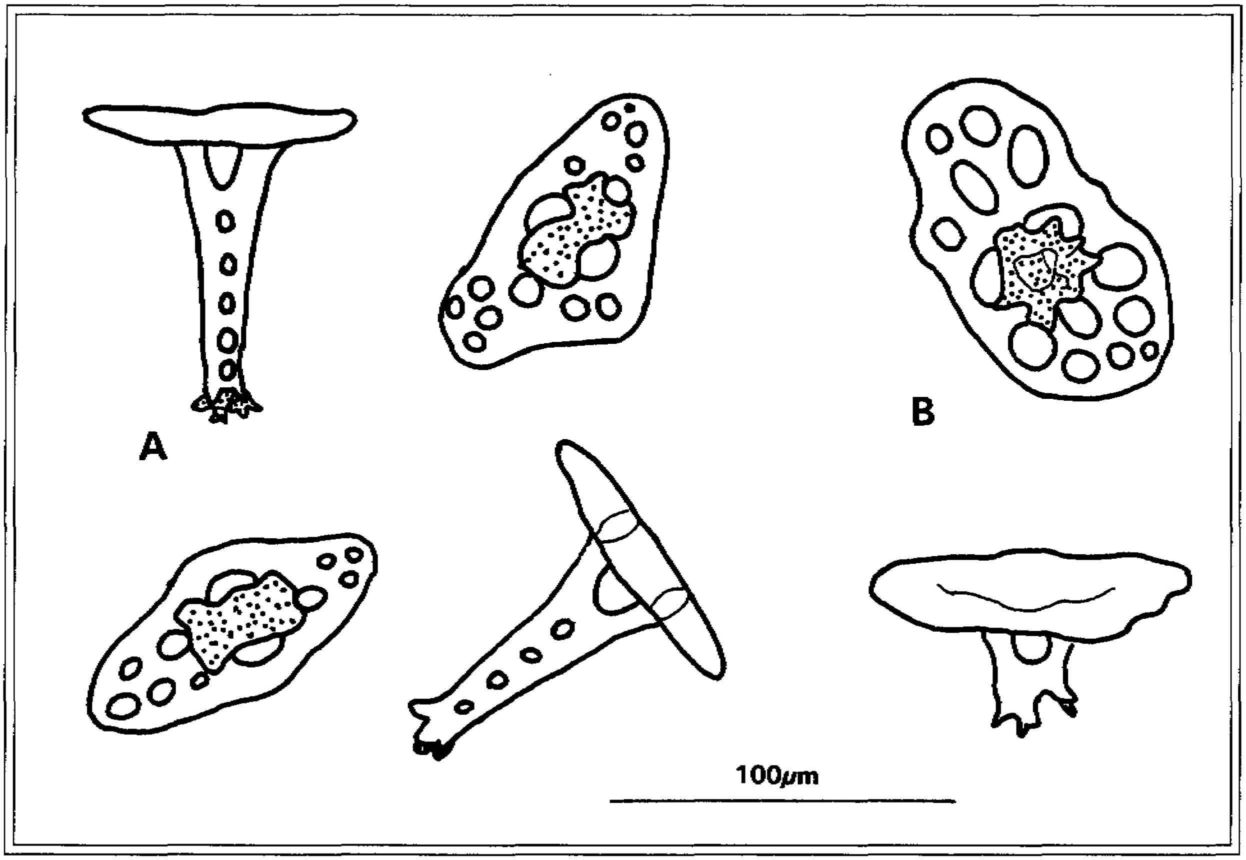

Figure 9.22. *Havelockia charlottae*: A, tables from body wall; B, tables from introvert.

Pentamera lissoplaca (H.L. Clark, 1924)

Figure 9.23

Cucumaria lissoplaca H.L. Clark, 1924:55.—Deichmann, 1937:169.
Pentamera lissoplaca Deichmann, 1938:106 (passim).—Panning, 1949:465.

Material Examined. Specimens with small tables: California: 2.25 mi E of South Pt, Santa Rosa I, 23-28 fms, sand, gravel (1:2.1 cm) (*Velero* 1283-41); Point Loma, (1:3.4 cm) (City of San Diego, E5); off Ford Pt, Santa Rosa I, 92 ft (1:1.2 cm) (USNM Acc. No. 255678); (1:2 cm) (USNM E2293); off San Onofre generating plant (1:1.3 cm) (MB).—Specimens with large tables: California: 10 mi SE of Long Beach, 23-28 fms, mud, sand (1:1.3 cm) (*Velero* 1159-40); White Cove, Santa Catalina I, 36-41 fms, mud, sand (1:0.9 cm) (*Velero* 998-39); 1 mi E of Empire Landing, Santa Catalina I, 22 fms, shell, sand (4:0.7-0.8 cm) (*Velero* 1374-41); off Abalone Pt, Laguna Beach, 54-57 fms, mud (1:2.4 cm) (*Velero* 1131-40); off Huntington Beach, (1) (OCSD S-1-00); 0.75 mi off Mugu Pier, 50-60 ft (1) (SBMNH 48847m); King Harbor, 20 ft (2:6.3, 6.7 cm) (MB); Santa Monica Bay (1:4.7 cm) (Hyperion, IMIV).—Mexico: off Thurloe Head, Baja California, 30 fms, sand (1) (*Velero* 284-34); 4.25 mi of Redondo Pt. light, Magdalena Bay, Mexico, 9 fms, sand (1:1.1 cm) (*Velero* 1717-49); off Thurloe Head, Baja California, 10-20 fms (1:1.2 cm) (*Velero* 285-34).

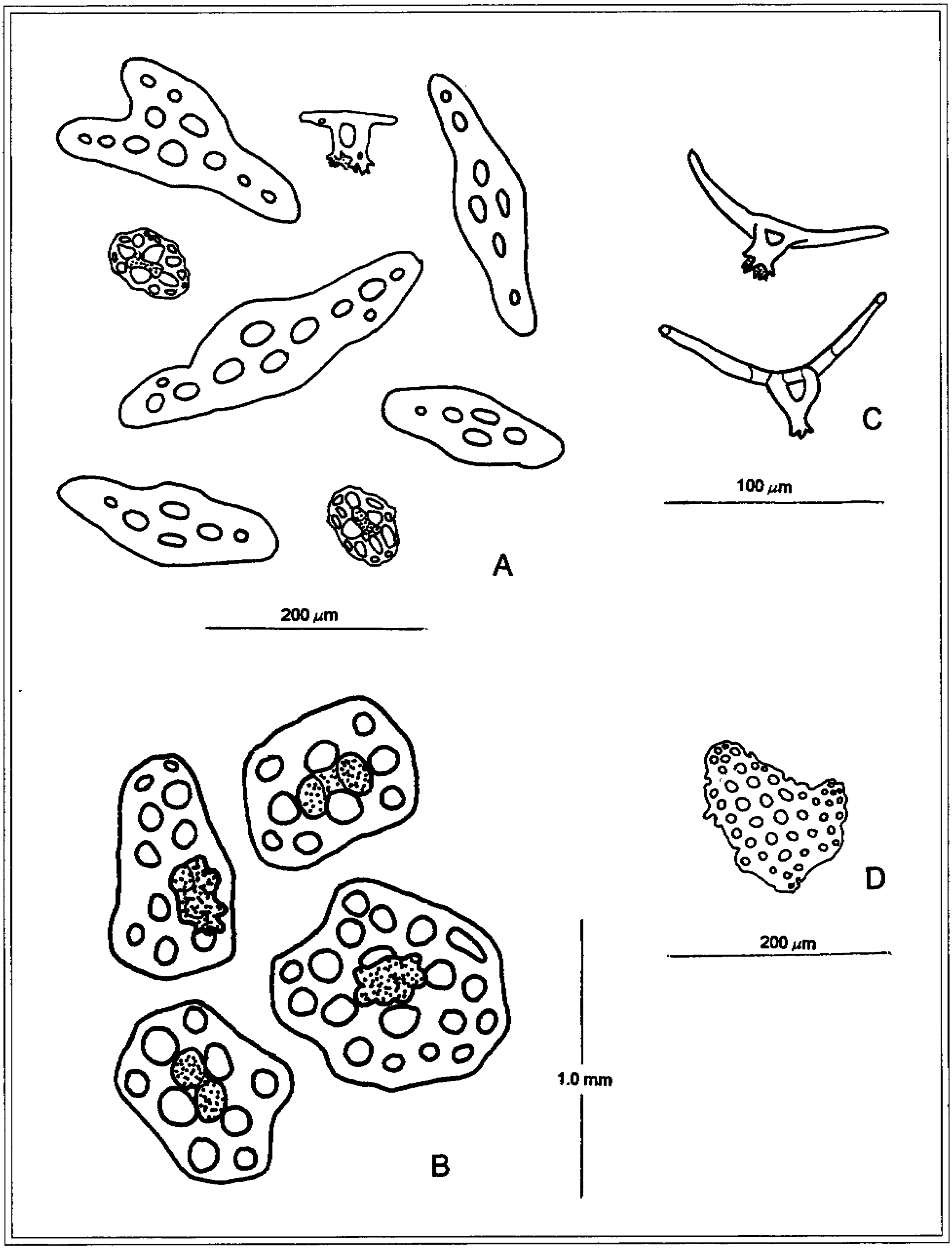

Figure 9.23. *Pentamera lissoplaca*: A, lozenge-shaped plates and small tables, B, large tables, C, supporting tables; D, large plate from specimen from San Clemente.

Description. Medium-sized, up to 7 cm long, U-shaped, fusiform, tapering to a long tail. Body wall ossicles as oblong plates with 4-6 holes and delicate tables 0.03-0.06 mm in diameter; tables sometimes absent; large, round plates occasionally present. Supporting tables with a 2-pillared spire ending in a few blunt teeth. Well developed end plate present.

One group of specimens, listed under "large tables" above, with oblong plates and supporting tables as described but with tables relatively large (0.05-0.16 mm in diameter) and stout. For the purposes of this chapter, these specimens considered *P. lissoplaca* (See Remarks).

Remarks. The specimens listed under "small tables" conform well to Clark's description of *Pentamera lissoplaca*. The specimens listed under "large tables" agree well with the description except that the tables are larger. While these tables are similar to those of *P. pseudopopulifera*, the white color of the body wall, the presence of oblong plates and the shape of the spire on the supporting tables make it clear that these specimens are not *P. pseudopopulifera*. Since the specimens with large tables conform to the description of *P. lissoplaca* in all respects except for the size of the tables, I am considering them herein as a variant of *P. lissoplaca*. Further study is needed to determine if these specimens are *P. lissoplaca* or an undescribed species.

Type Locality and Type Specimens. British Columbia, Queen Charlotte Sound, Alert Bay (Victoria Memorial Museum, No. 583), (Museum of Comparative Zoology, MCZ 1288).

Distribution. Southeastern coast of Alaska to southern Magdalena Bay, Baja California, 18-82 m.

***Pentamera populifera* (Stimpson, 1857)**

Figure 9.24

Pentacta populifera Stimpson, 1857:161.

Cucumaria populifera Theel, 1886:103; H.L. Clark, 1924:56; 1901b:171; Bush, 1921:76, text-figs. 40-41; Deichmann, 1937:170.

Cucumaria tenuicoriata Wells, 1924:121, pl. 3, fig. 4, text-fig. 4.

Pentamera populifera Panning, 1949:465.

Allothyone tenuicoriata Panning, 1949:466.

Material Examined. California: 3.1 mi 106° to Pt Dume, 27 fms, clay (2) (BLM 23981); 1/2 mi SW of Ribbon Rock, Santa Catalina I, 51-56 fms (2:1.9, 2 cm) (*Velero* 51-56); 11 1/2 mi SE of Long Beach, 32-52 fms (1:1.2 cm) (*Velero* 1160-40); 2.6 mi E of East Pt, Santa Rosa I, 47-49 fms (6) (*Velero* 1289-41); off Santa Barbara, 29 fms (1:1.5 cm) (USNM 30638); (1:3.5 cm) (BLM 22966); NE of Anacapa I, 45 fms (4:1.5-2.7 cm) (*Velero* 876-38); 3 mi N of Arch Rock, Santa Cruz I, 55-60 fms, mud (2:3.5, 3.7 cm) (*Velero* 1304-41); off Abalone Pt, Laguna Beach, 28-29 fms, mud (2:1.5, 1.6 cm) (*Velero* 1130-40); off Bluff Cove, 50 fms (3:2.2-3.9 cm) (Burch 40125); 3 mi ESE off Ship Rock, Santa Catalina, 52-65 fms (6:1.1-2.3 cm) (*Velero* 2953-54); 4.5 mi SW X 0.5 mi W of East Pt, Santa Rosa I, 43-45 fms (2:1.8, 4.0 cm) (*Velero* 1390-41); 2 mi W of Church Rock, Santa Catalina I, 45-53 fms (1:1.8 cm) (*Velero* 1321-41); S of Pyramid Cove, San Clemente I, 55-69 fms (1:2.9 cm) (*Velero* 1012-39); 2.5 mi SE of Bennett Pt, San Miguel I, 57 fms (3:1.3-1.9 cm) (*Velero* 1390-41); 3 mi off Seal Beach, 11 fms (2:3.1, 3.3 cm) (*Velero* 1158-40); 2.6 mi E of East Pt, Santa Rosa I, 47-49 fms (1) (*Velero* 1289-41); off Gull Island I, 39-40 fms (3:2.1-2.3 cm) (*Velero* 1194-40); off Abalone Pt, Laguna Beach, 54-57 fms (13:1.2-2.6 cm) (*Velero* 1131-40); S side of Santa Cruz I, 39-40 fms (10:2.3-5.4 cm) (*Velero* 1191-40); 4.5 mi SE of East Pt, Santa Rosa I, 52 fms (9:2.5-5.1 cm) (*Velero* 1387-41); S of San Miguel I, 130-138 fms (2:3.1-3.9 cm) (*Velero* 986-39a); off Redondo Beach, 75 fms (4) (Burch 3856); off Redondo Beach, 96-120 fms (1:3.1 cm) (*Velero* 1137-40); N of west Anacapa I, 44-45 fms (2:2.7, 3.0 cm) (*Velero* 1857-49); Catalina Harbor, Santa Catalina I, intertidal (1:2.4 cm) (*Velero*

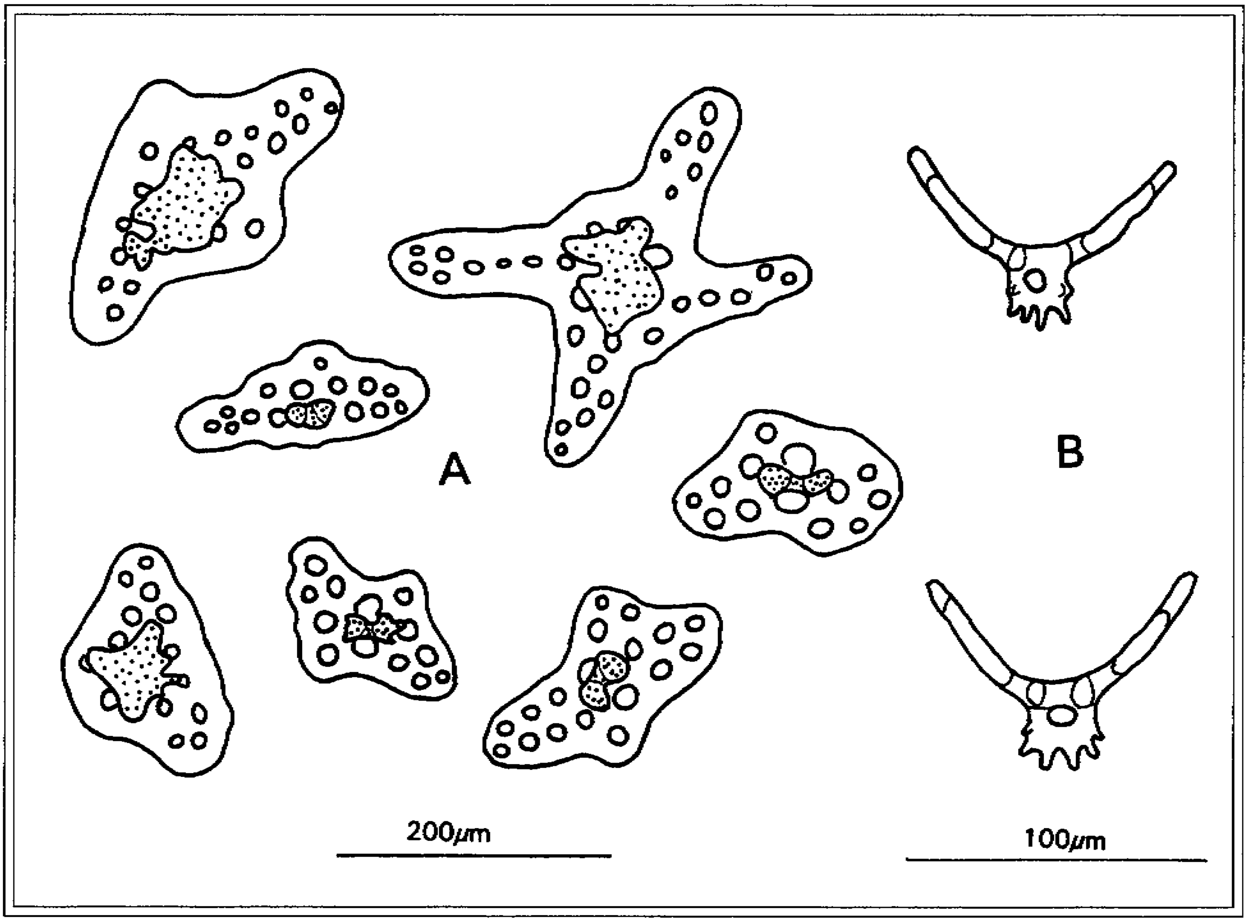

Figure 9.24. *Pentamera populifera*: A, ossicles from body wall; B, supporing tables.

1368-41); Avalon Bay, Catalina I, 98-116 fms (1:0.7 cm) (*Velero* 1149-40); 1.5 mi NW of Cavern Pt, Santa Cruz I, 54-56 fms (16:0.9-3.2 cm) (*Velero* 1300-41c); off W end of Santa Catalina I, 134-150 fms (1:4.6 cm) (*Velero* 1201-40); 3 mi NW of Anacapa I light, 47 fms (6:0.8-3.5 cm) (*Velero* 1267-41); 4.2 mi SE of East Pt, Santa Rosa I, 46 fms (2:3.0, 4.5 cm) (*Velero* 1290-41); 4.5 mi W of Church Rock, Santa Catalina I, 51 fms (1:3.9 cm) (*Velero* 1318-41); off White Cove, Santa Catalina I, 105 fms (2:1.4, 3.4 cm) (*Velero* 1373-41a); 1.5 mi SW of Gull I, Santa Cruz I, 48 fms (1:4.8 cm) (*Velero* 1435-41); 6.5 mi ESE of South Pt, Santa Rosa I, 57 fms (1:3.9 cm) (*Velero* 1392-41); SW of Castle Rock, San Clemente I, 40-46 fms (1:3.1 cm) (*Velero* 1328-41); 10 mi SE of Long Beach, 22-25 fms (1) (*Velero* 1159-40); off Bluff Cove, 50-75 fms (1) (Burch 40118); 1.5 mi S of Cron Pt, San Miguel I, 41-43 fms (6:2.3-5.3 cm) (*Velero* 1412-41); off Bluff Cove, 35 fms (4:2.0-2.6 cm) (Burch 40129); 1.5 mi SE of west end, Santa Catalina I, 40-50 fms (1:2.3 cm) (*Velero* 1311-41); 2.5 mi NW of Anacapa I light, 48-51 fms (4:3.1-5.4 cm) (*Velero* 1268-41); 2.75 N of West Pt, Santa Cruz I, 55 fms (1:4.0 cm) (*Velero* 1436-41); N of Anacapa I, 15 fms (2:2.3, 3.1 cm) (*Velero* 878-38a); 2 mi SW of Cardwell Pt, San Miguel I, 34-35 fms (3:1.3-2.1 cm) (*Velero* 1413-41); 10 mi S of San Pedro breakwater, 81-83 fms (1:2.0 cm) (*Velero* 1229-41); 3.5 mi S of Hueneme, 29-30 fms (1: 2.4 cm) (*Velero* 1274-41a); off Ten Mile Creek, Or, 20-40 fms (4) (*Velero* 1471-42); San Miguel Passage, 37-39 fms (10:1.5-6.0 cm) (*Velero* 990-39b); 0.5 mi N of Platt Pt, Santa Cruz I, 36-47 fms (1) (*Velero* 1303-41a); 1.5 mi SE of Point Mugu, 26-30 fms (8) (*Velero* 1275-41); (2) (BCPM FRB 63-204); sandy bay behind Rugged Pt, Kyuquot Channel, 5 fms (1) (BCPM 980-344-1); Haul 2, San Pedro, Ca (1:1.5 cm) (CAS Station

XIV); off San Onofre, 91 m (1:1.6 cm) (SIO E2679); off Morro Bay, 99 m (1) (SIO E 2686); Pt Sal, 132 m (2) (SIO E 2687); MMS CAMP 3-4, R-2.—Mexico: off San Benito I, Baja California, 92-95 fms (2:2.4, 5.7 cm) (*Velero* 1010-39); 8.5 mi S of San Benito I, Baja California, 71-72 fms (1:4.6 cm) (*Velero* 1252-41).

Description. Medium-sized, up to 6 cm long, body shape variable, often fusiform, tapering to pointed ends; body wall thin, so packed with ossicles as to be rough to the touch. Podia cylindrical. Ossicles in body wall mostly tables with round to star-shaped disk, 0.10-0.42 mm in diameter, with stout spire with numerous teeth on top; occasional plates present. Supporting tables with low 2-pillared spire, either blunt or pointed, never flattened as in *P. pseudocalcigera*. Well-developed end plate present. Introvert with oblong to round perforated plates. Tentacles with plates and rods, sometimes absent.

Biology. This species is common in soft-bottom habitats, intertidally to 150 fms. In Puget Sound *Pentamera populifera* spawns in spring (McEuen, 1988).

Remarks. Small specimens (< 1.5 cm) of *Pentamera populifera* and *P. pseudocalcigera* are difficult to differentiate. However the spires on the supporting tables are usually much longer and flattened in *P. pseudocalcigera* than in *P. populifera.*

Type Locality and Type Specimens. Washington, Puget Sound, holotype, lost; *C. tenuicoriata*: California, Monterey Bay (USNM E1201).

Distribution. West coast of North America: Puget Sound to San Benito Island, Baja California.

Pentamera pseudocalcigera Deichmann, 1938

Figure 9.25

Pentamera pseudocalcigera Deichmann, 1938:106.—Panning, 1949:465.

Cucumaria calcigera H.L. Clark, 1901b:165, 1901c:492.—Edwards, 1907:54, text-fig. 5-11. Not *Pentamera calcigera* (Stimpson).

Material Examined. Oregon: USNM Acc. No. 108-05, 7 fms (2:4.1, 5.0 cm); USNM Oregon coll, AD27 (1:5.0 cm); USNM Oregon coll, AD70, 200 m (1:7.0 cm); *Velero* 1471-42, off Ten Mile Creek, 20-40 fms, sand (2:5.1, 5.5 cm).—Alaska: *Albatross* 4240, (1).—California: USNM 30581, off San Luis Obispo Bay, 252 fms (1:3.0 cm); USNM E2294 (1:2.0 cm); *Albatross* 4457, 6 mi 21° W Pt Piños lighthouse, 40-46 fms (2:2.0, 5.0 cm); *Albatross* 4558, 2 mi 79° W Pt Piños lighthouse, 28-40 fms (1); *Albatross* 4464, Monterey, 21-31 fms (1); USNM BCF, 46°08'N, 124°13'W, 50 fms (1:4.2 cm); USNM BCF, 45°60'N, 124°44'W, 200 fm (1:5.5 cm); USNM BCF, 46°02.4'N, 124°37.8'W, 100 fms (1:4.2 cm); USNM Acc. No. 152709, Monterey Bay, 50-60 fms (1:6.4 cm); *Velero* 992-39, off Santa Rosa I, 130-230 fms, mud, gravel (3:3.3-4.5 cm); MCZ 2080, 34°09'30"N, 120°40'00"W, 150 fms (1); BCPM 167-1, 8°41'N 123°29.1'W, 38-40 ft (1); CS DOC Deep, G-16 (1); OCSD B41 (1); OCSD B27 (1); ACE dumpsite, BD2-4IA, 307 m; MEC 123a, 526 ft (1); MBC 081-BSS-01-TX, 34°21.263'N, 120°28.827'W, 980 ft (1); CAS, off Trinidad Head, 65 fms (1:3.0 cm); BLM 24018CH (2:2.2, 5.0 cm); BLM 23283 (1:4.2 cm); USNM BSS-038; SBNMH BSS-081.—Mexico: SIO E2586, between San Benitos and Cedros I, Baja California, 170-180 fms (4:1.5-4.2 cm);

Description. Medium-sized, globose, U-shaped form, tapering to blunt ends, up to 10 cm long. Base of tube feet conical. Body wall rigid, packed with ossicles. Ossicles in body wall of small specimens mostly round to star-shaped tables, 0.15-0.48 mm in diameter, similar to those of *Pentamera populifera.* With growth, number of tables decreases and large, irregularly shaped plates, 0.13-0.72 mm in diameter, predominate. Spire of supporting tables sometimes elongate, flattened. Introvert with open, spiny plates, 0.20-0.40 in diameter. Tentacles with spiny rods.

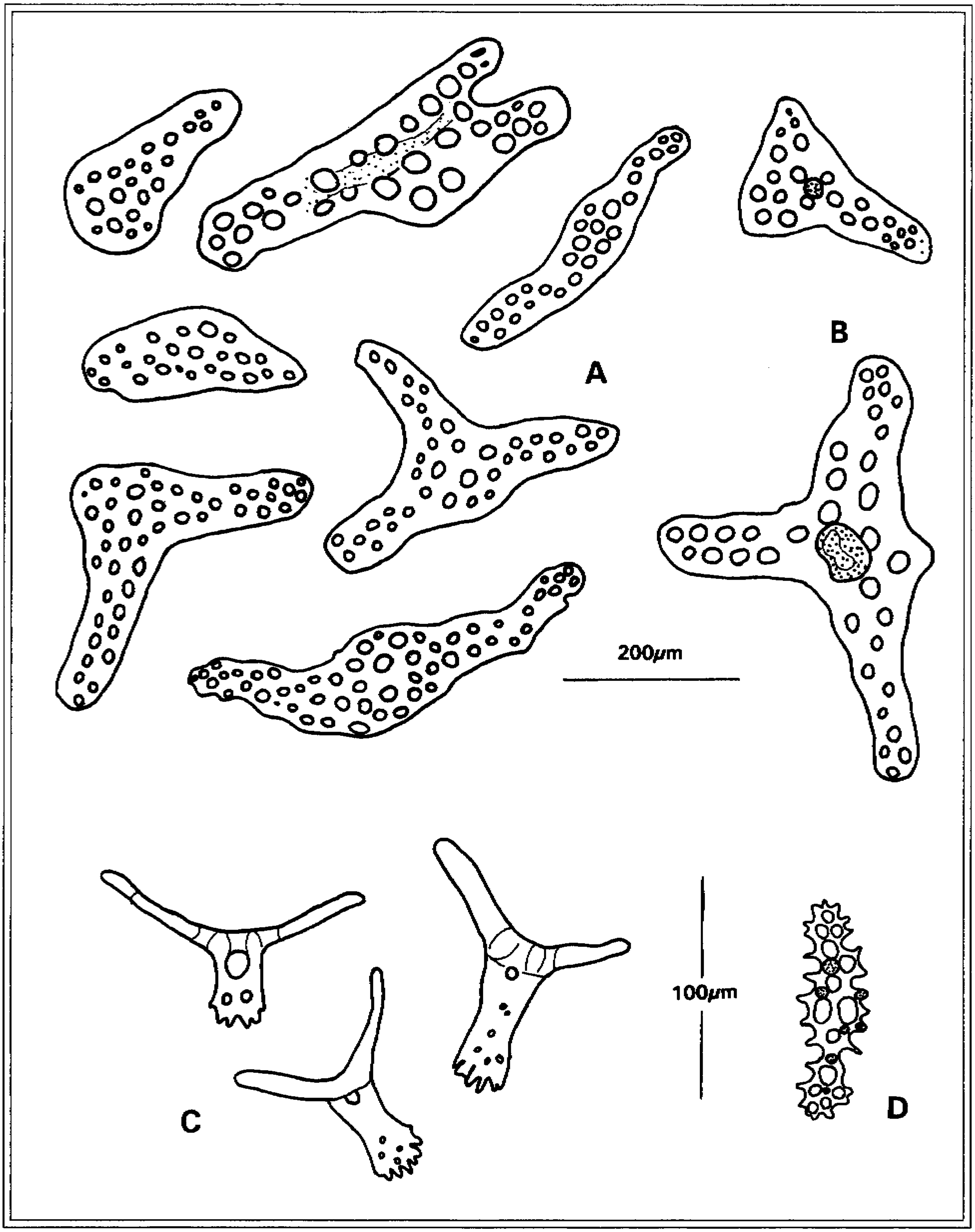

Figure 9.25. *Pentamera psuedocalcigera*: A, plates from body wall; B, tables from body wall; C, supporting tables; D, plate from introvert.

Remarks. The ossicles in small *Pentamera pseudocalcigera* and *P. populifera* are similar, but *P. pseudocalcigera* can usually be differentiated by the globose body form, conical tube feet, and the flattened spire on the supporting tables. The plates in the introvert are generally larger (0.20-0.40 vs. 0.08-0.29 mm) in *P. pseudocalcigera* than in *P. populifera*. In two lots from Baja California in the Scripps Institute of Oceanography, tables predominated in large as well as small specimens. In a few large specimens, tables predominated in the dorsal body wall but plates predominated in the ventral body wall. In two lots from Southern California, the dorsal and ventral body were fused so that the anus and mouth were contiguous. These specimens were typical of *P. pseudocalcigera* in every other respect and are considered a variant of *P. pseudocalcigera*.

Type Locality and Type Specimens. off California, syntypes (USNM 16411, 30568, 30569, 30572, 30573, 30578, 30580, 30581, 30585, 30669, 30681, E2294, E2386, E2387).

Distribution. Southeast Alaska to San Benitos Island, Baja California, from 7 to 250 fms (12 to 450 m).

Pentamera pseudopopulifera Deichmann, 1938

Figure 9.26

Pentamera pseudopopulifera Deichmann, 1938:107.—Panning, 1949:465.

Material Examined. California: *Velero* 1131-40, off Abalone Pt, Laguna Beach, 54-57 fms, mud (10:2.8-5.2 cm); *Velero* 1130-40, off Abalone Pt, Laguna Beach, 25-27 fms, mud (8:0.8-3.9 cm); *Velero* 897-38, off Point Santa Barbara, 33 fms, mud (3:4.5-6.3 cm); *Velero* 1292-41, 6 mi E of East Pt, Santa Rosa I, 28-30 fms, rock (3:1.8-3.1 cm); *Velero* 1142-40, off Pt Vicente lighthouse, 17-41 fms, mud, sand (1:4.5 cm); *Velero* 1191-40, S side of Santa Cruz I, 39-40 fms, sand (2:4.7, 5.5 cm); *Velero* 1281-41, 3 mi E of South Pt, Santa Rosa I, 23-26 fms, sand (1:1.0 cm); *Velero* 1160-40, 11.5 mi SE of Long Beach, 32-52 fms, mud, sand shell (3:1.1-2.5 cm); *Velero* 1205-40, S side of San Nicolas I, 20-23 fms, sand (1:4.3 cm); *Velero* 1143-40, off Portuguese Pt, 16-20 fms, sand (1:2.0 cm); *Velero* 1619-48, White Cove, Santa Catalina I, 26 fms (1:4.1 cm); *Velero* 1275-41, 1.5 mi SE of Pt Mugu, 26-30 fms, mud (4:3.2-3.8 cm); MEC 313A, 72 ft (1:4.7 cm); MCZ 473, Corona del Mar, 77 fms (1:2.5 cm).

Description. Medium-sized, up to 6.5 cm long. Body shape variable, often fusiform, curved, sometimes U-shaped. Preserved specimens often purplish brown. Body wall ossicles mostly small roundish tables, 0.04-0.17 mm in diameter, with stout spire tipped with bifurcate teeth; plates rare. Supporting tables with 2 pillars, also with bifurcate teeth. Well-developed end plate present. Introvert with delicate plates, approaching rosettes. Tentacles with oblong plates and rods.

Biology. This species is common in soft-bottom habitats in the Southern California Bight, in shallow water to 114 m.

Remarks. *Pentamera pseudopopulifera* differs from *P. populifera* in that the disk of the tables is smaller, more regularly shaped and never star-shaped. The bifurcate teeth on the body wall tables and the supporting tables are also diagnostic.

Type Locality and Type Specimens. California, Point Dume, holotype (USNM 39159)

Distribution. Southern California, shallow water to 57 fms.

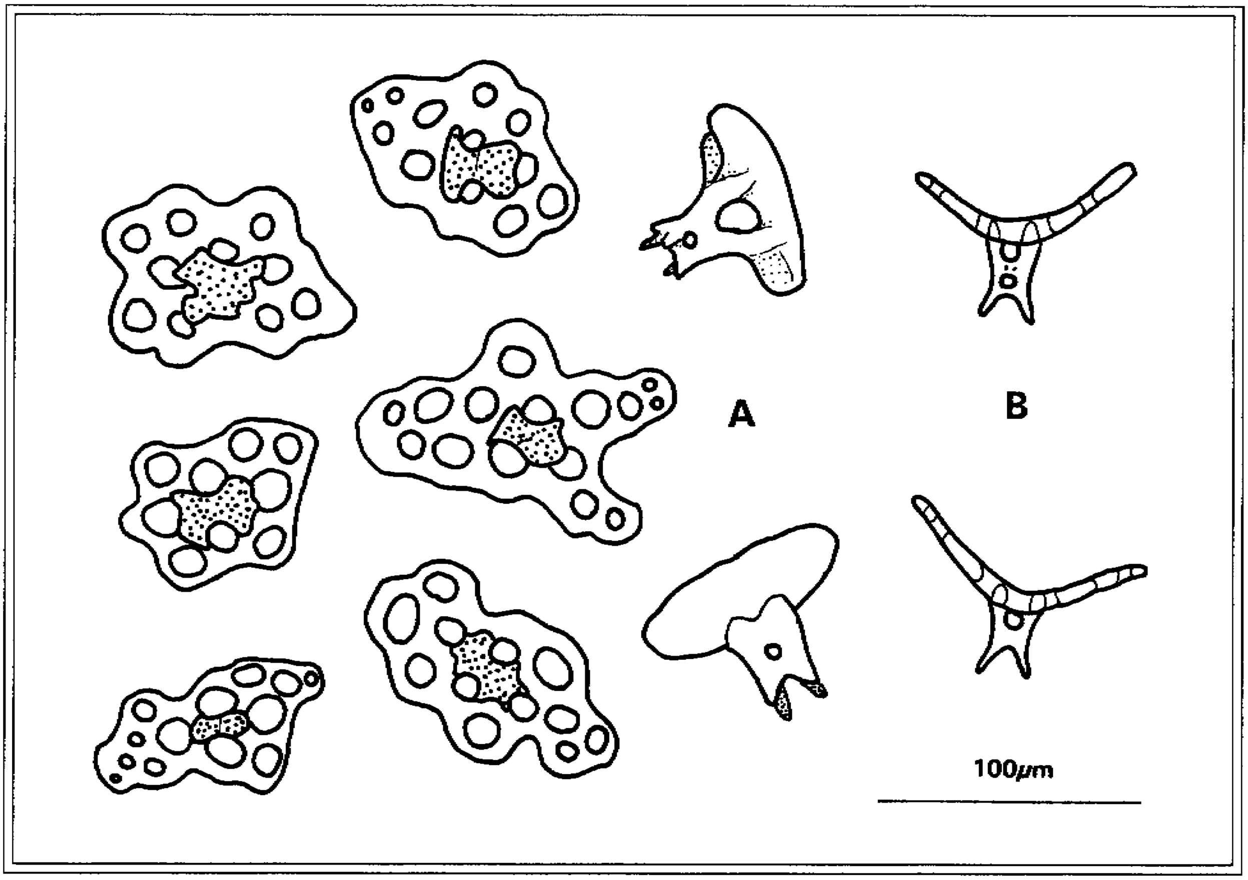

Figure 9.26. *Pentamera pseudopopulifera*: A, ossicles from body wall; B, supporting tables.

Genus *Stolus* Selenka, 1867

Type Species. *Thyone buccalis* Stimpson, 1856, by subsequent designation in Panning (1949).

Diagnosis. Ossicles in body wall plates, tables absent.

Stolus trachyplaca (H.L. Clark, 1924)

Figure 9.27

Cucumaria trachyplaca H.L. Clark, 1924:56.

Cucumaria cosmotyrsitus Wells, 1924:119, text fig. 3, pl. 3, fig. 3.

Pseudothyone trachyplaca Panning, 1949:456.

Material Examined. California: SBMNH, Pelican Cove, Santa Cruz I, 20-60 ft (1); SBMNH 488, 45m, reef midway between Twin and Platts Harbor, Santa Cruz I, 10-50 ft; USNM E2276, Monterey Bay (1:2 cm); USNM Acc. 205678, off Ford Pt, Santa Rosa I, 92 ft (1:2.1 cm); USNM BRA-002.—Canada: BCPM FRB63-204; BCPM 978-199-4, Possession Pt, near Sooke, 48°20.4' N, 42.8° W, < 30 ft (1).

Description. Small, cylindrical form, up to 3 cm long, with stout tube feet. Body wall ossicles plates, usually oblong, sometimes irregularly shaped, 0.1-0.2 mm long; undeveloped plates with 2 enlarged central holes and 3-5 smaller holes in either end. More developed plates with varying numbers of spines and knobs, sometimes built into a mass resembling a spire. Supporting tables with 4 pillars ending in spiny mass. Well-developed end plate present. Introvert with oblong reticulated plates. Tentacles with various sized plates often with 2 enlarged central holes.

Remarks. The type specimens of *Cucumaria trachyplaca* and *C. cosmotyrsitus* are synonyms. Clark's (1924) description antedates Well's (1924) description by several months. Since the ossicles in the body wall are derived from plates, I have placed this species in the genus *Stolus*.

Type Locality and Type Specimens. *Cucumaria trachyplaca*: British Columbia, Queen Charlotte Sound, Alert Bay, 20 m (National Museum of Canada, Acc. 85-4, cat. No. 272); *C. cosmotyrsitus*: California, off Monterey, shale, 24 m (National Museum of Natural History, USNM E 1200).

Distribution. North Pacific Ocean, at least from British Columbia to Santa Cruz Island, California, intertidal to 100 ft (30 m), rocky habitats.

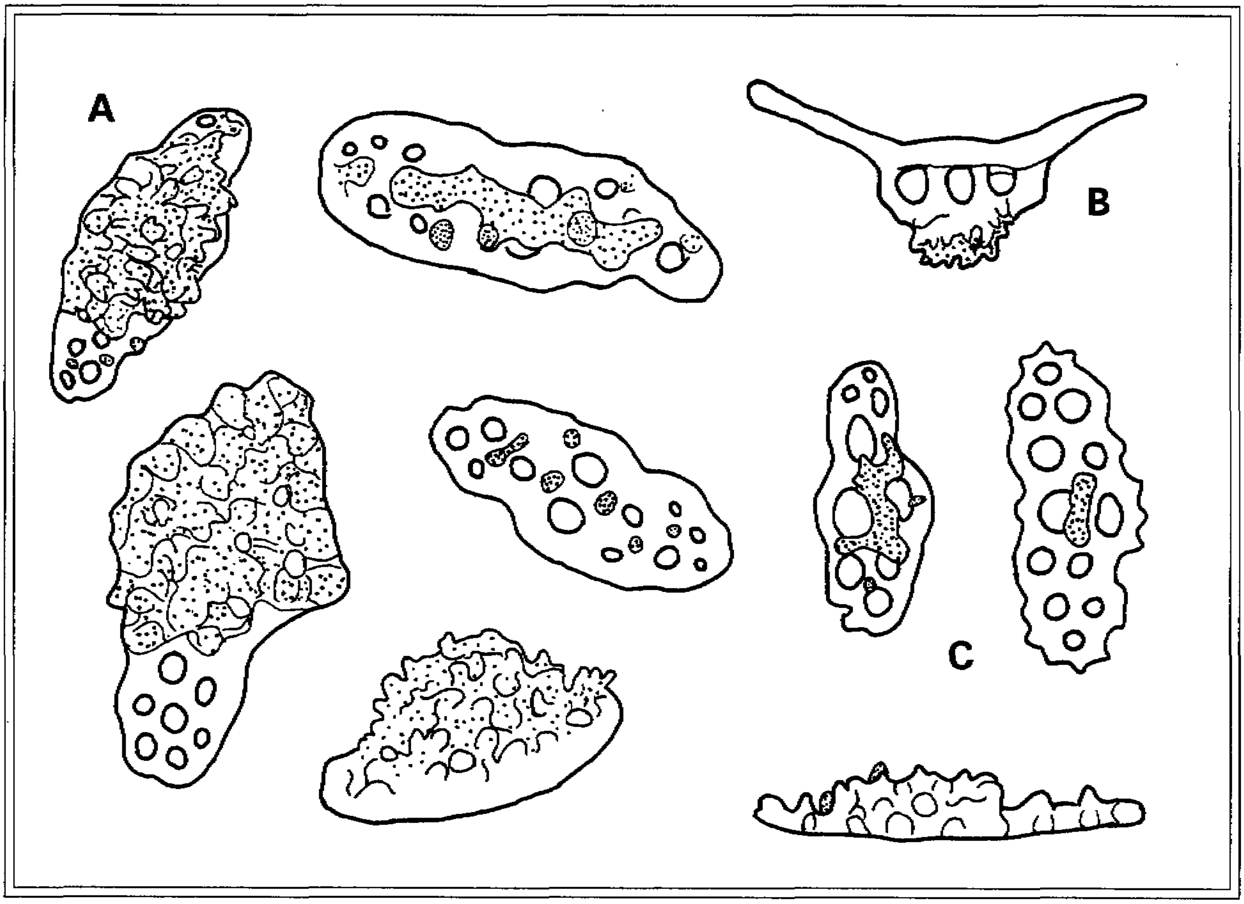

Figure 9.27. *Stolus trachyplaca*: A, plates from body wall; B, supporting table; C, plates from introvert.

Genus *Thyone* Jaegger, 1833

Type Species. *Thyone fusus* (O.F. Müller, 1766), by subsequent designation.

Diagnosis. Ossicles in body wall tables, sometimes reduced. Ossicles in introvert rosettes, tables absent.

***Thyone montereyensis* (Deichmann, 1938)**

Figure 9.28

Pentamera montereyensis Deichmann, 1938a, p. 108, text-fig.

Thyone montereyensis Panning, 1949, p. 467.

Material Examined. California: Long Beach breakwater, Ca (2:4.3, 4.8 cm) (PBM); E of pier, Johnson's Lee, Santa Rosa I, 20-40 ft (1:2.2 cm) (MB).

Description. Medium-sized cylindrical form, up to 5 cm long; interambulacral feet absent. Ossicles small oval buttons, 0.025-0.055 mm long, with 2 central and up to 8 marginal knobs. Supporting tables with marginal knobs, spire reduced to knobs. Well-developed end plates and perforated rods present. Introvert with round to oblong perforated plates often with 2 enlarged central holes and 6-20 additional holes. Two central knobs often present, additional knobs sometimes present. Tentacles with plates and rods.

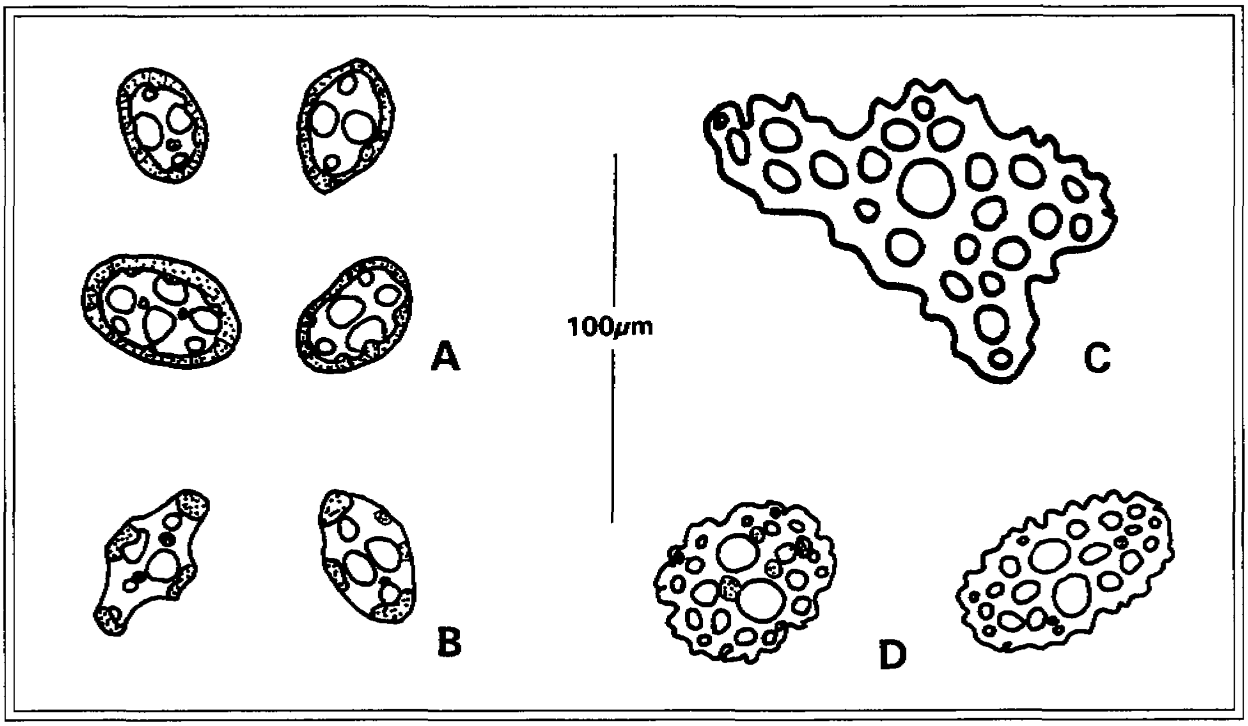

Figure 9.28. *Thyone montereyensis*: A, buttons from body wall; B, supporting tables; C, irregular plate from specimen from Long Beach; D, plates from introvert.

Remarks. The generic placement of this species is uncertain. Since interambulacral feet are lacking, this species does not belong in the genus *Thyone sensu* Pawson and Miller (1981). The presence of two central knobs on the plates in the body wall and the introvert suggest that this species is a member of the genus *Havelockia* with the spire on the tables reduced. However, because it is not clear that this species belongs in the genus *Havelockia*, I am retaining Panning's (1949) designation. Irregularly shaped plates, 0.06-0.15 mm in diameter, were present in a large specimen taken from Long Beach breakwater.

Type Locality and Type Specimens. California, Pacific Grove, intertidal (Museum of Comparative Zoology, MCZ 1840), ossicles dissolved.

Distribution. California, from Pacific Grove to southern California, hard-bottom habitats, intertidal to at least 14 m.

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10. HEMICHORDATA: ENTEROPNEUSTA

by

Keith H. Woodwick[1]

Introduction

Enteropneusts (acorn worms) are soft bodied marine worms of the Phylum Hemichordata. Most species have been described as burrowers in sand and mud of the intertidal and subtidal. They average 10 to 50 cm in length and are about the diameter of a pencil. The first species, *Ptychodera flava,* was described by Eschscholtz (1825) and there are now more than 70 known species in 13 genera and 4 families.

Morphology

Enteropneusts are fragile burrowing animals often collected as incomplete specimens. Complete specimens have three main divisions of the body, an anterior muscular proboscis, a central cuff-like collar, and a posterior elongate trunk including branchial, esophageal, hepatic, and intestinal regions. Collections usually contain specimens with only proboscis, collar, and the branchial region of the trunk. External features used in placing specimens in families and genera include the shape and size of the proboscis, shape and size of the collar and its ratio to that of the proboscis, presence or absence of genital wings in the anterior trunk and hepatic caeca in the mid-trunk area. Presence of branchial slits externally versus small branchial pores as well as gonad positioning are other useful characteristics. Histological features and internal structures, their presence or absence, and variations, are important in placing specimens in family, genus, and species. Proboscis muscle pattern, glomerulus, proboscis skeleton and crura, buccal diverticulum, neurocord and epidermal zones of the collar, shape and size of gill bars and presence or absence of synapticules as well as epithelial variations throughout the gut of the trunk, all provide information and suites of characteristics important to classification.

Taxonomic History

Ptychodera flava, the first known enteropneust, was described by Eschscholtz (1825) as a new species of sea cucumber from the Marshall Islands. In the next 30 years only two more species were described, *Balanoglossus clavigerus* Delle Chiaje (1829) from Naples and *Stimpsonia aurantiacus* by Girard (1853) from the Carolina coast. The latter was described as a nemertean and later transferred to *Balanoglossus.* After Kowalevsky (1866) described the gill slits in *B. clavigerus*, Gegenbaur (1870) used this characteristic in establishing Enteropneusti (Enteropneusta). Bateston (1885) proposed using Hemichordata for Enteropneusti and placed it in Chordata. Most present day workers consider Hemichordata to be a separate phylum (Hyman, 1959).

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A period of intensive systematic investigation of enteropneusts occurred between 1891 and 1901; eight new genera and 36 new species were described. They comprise about 75% of the presently known genera and 50% of the known species. Spengel (1893, 1901) was the dominant worker of that period. Since 1901 systematic research has been meager and sporadic. Classification now includes 73 species in 13 genera and the following families: Ptychoderidae, Spengeliidae, Harrimaniidae, and Saxipendiidae (Hyman, 1959; Woodwick and Sensenbaugh, 1985). In the last 30 years there have been a number of special subject studies, for example, histology and cytology (Norrevang, 1965; Welsch and Storch,1970; Saita *et al.*, 1978), development (Hadfield, 1975), larval dispersal (Scheltema, 1987), ecology (Thistle, 1980), and presence of organohalogens (Higa *et al.*, 1980; King, 1986; Corgiat *et al.*, 1993).

Biology

Nearly all known species of enteropneusts are found in the intertidal zone or in shallow waters. Generally they inhabit burrows in sand and/or mud, although a few species occur under rocks or are associated with marine plants. They feed upon the sediment using cilia and mucus to move materials into and through the gut as they extract items of food. Undigested materials are deposited at the surface as piles of castings and in quiet waters are useful indicators of enteropneust populations. Sexes are separate and gametes are released into the environment; development may be indirect with tornaria larvae or direct, as it is in all members of Harrimaniidae.

Only four species have been reported from depths greater than those of the immediate subtidal. They are *Spengelia sibogae* (275 m: Spengel, 1907), *Glandiceps talaboti* Marion (30-350 m), *Saxipendium coronatum* (2478 m: Woodwick and Sensenbaugh, 1985), and *Glandiceps abyssicola* (4500 m: Spengel, 1893).

Methods

Many genera can be identified using external characteristics but identification of other genera and all species is dependent on individual and suites of characteristics of the internal anatomy. The internal anatomy is revealed through study of serial cross and sagittal sections. For this reason, straight, clean, well-preserved complete specimens are desirable. Hyman (1959) summarized the usual situation in enteropneusts wherein most species are known only by the original description which in addition was usually based on one or a few and often imperfect specimens. Imperfection results from a number of enteropneust features. They are fragile and likely to be within the sediment so that whole specimens are rarely taken; it is also likely that even if many parts of specimens are collected they will not include all trunk regions. Enteropneusts are ordinarily covered with mucus and sediment which remain attached to their bodies on fixation. Sediment moving through the gut is also retained on fixation. These features limit the taking of clean complete specimens when collections are made individually in the field and they may be magnified during benthic surveys.

When possible, live specimens should be sorted from the sediment. Sometimes breaking the sediment into large pieces will reveal the burrow and the organism and further careful breaking will free the specimen. Live specimens should then be placed in large containers of clean sea water to permit evacuation of the gut. Several changes of the sea water may be needed and surface sediment may be released with their movement or assisted utilizing a camel's hair brush. Clean specimens should then be fixed by holding them at the posterior end with a pair of forceps and dipping them in a tall jar of fixative (e.g., Bouin's fluid). Gravity will assist in straightening the specimen as fixative is added to the posterior end and allowed to flow down into the jar. When fixation is complete release the specimen into the jar and store on its side for several days. Transfer specimen to 50% alcohol, and then wash several times in 70% alcohol (not water) to clear the picric acid (Galigher and Kozloff, 1971). Specimens can then proceed through an alcohol, toluene, paraffin series for embedding. Prepared paraffin blocks are then serially sectioned at 10-15 μm and slide sections stained with Harris' Hematoxylin and Eosin Y. The anatomy is reconstructed from microscopic study of the serial cross and sagittal sections. Most published descriptions have included labelled drawings of critical diagnostic features and areas.

Systematic Account

Specimens from the benthic survey of the Santa Maria Basin and the Western Santa Barbara Channel include members of four genera and three families. It is likely that they represent four new species. Genera represented include *Saccoglossus* and *Stereobalanus* in Harrimaniidae, *Schizocardium* in Spengeliidae, and *Glossobalanus* in Ptychoderidae. Woodwick (1955) found representatives of the same four genera in samples of the benthos of San Pedro Basin.

A total of 54 identifiable specimens were taken at 8 of the 28 MMS Phase II soft-substrate stations. (A unit which included proboscis, collar, and some part of the trunk was considered a specimen. Parts of the trunk, collar, or proboscis were considered fragments.) *Stereobalanus* sp. was the dominant form. It was taken at Stations R-1, R-4, R-7, and R-8. Seventeen of the 28 specimens came from a depth of 565 m at Sta. R-7. *Balanoglossus* sp. was represented by 19 specimens and 17 of these were from 90 m at Sta. R-8. *Schizocardium* sp. was the largest form but was represented by only a total of 4 specimens at 3 stations (R-8, R-1, and R-4 at 90, 91, and 92 m, respectively). *Saccoglossus* sp. was the smallest form. The 3 specimens were collected at 3 different stations (R-1, PJ-1, and PJ-11 at 91, 145, and 136 m, respectively). There were 3 unidentifiable specimens and many fragments.

For purposes of survey work, specimens of the four genera can be sorted on the basis of external morphology. They will either have or lack genital wings or lappets, long or short probosces, and large or small eggs (KEY I). Because the muscular proboscis is the most easily recognized and regularly collected part of an enteropneust, its muscle pattern was chosen as the most diagnostic internal characteristic manifested in serial cross sections (KEY II). In addition to the two keys, a list is provided which includes many positive family characteristics, as well as, characteristics specific for each genus. The selected family characteristics are useful in further separating the four genera of this study and will be helpful in identification of specimens taken in other surveys or present in existing collections.

Family Ptychoderidae Spengel, 1893

Diagnosis. Proboscis short,conical; longitudinal muscle,radial pattern of many thin bands. Collar as long as broad. Trunk with pronounced external regionation; short curved gill bars; synapticules; parabranchial ridges;ventral digestive area in pharynx; wide long genital wings; plate-shaped hepatic caeca; ciliated intestinal grooves (ridges). Development indirect, with tornaria larvae.

Genus *Balanoglossus* Delle Chiaje, 1829

Diagnosis. Cauliflower organ lacking; lateral septa extend only half way into genital wings; small external branchial pores; gonads dorsal and lateral.

Remarks. There are no described species of *Balanoglossus* from the west coast of North America. Representatives of the genus have been found in the intertidal at several localities and at about 50m in the San Pedro Basin. Comparison of the Santa Maria form with the 22 described species of the genus is in progress.

Family Spengeliidae Willey, 1899

Diagnosis. Proboscis short, ovate; longitudinal muscle, homogeneously arranged; circular muscle, thick layer; vermiform process; chondroid tissue well-developed. Collar shorter then broad. Trunk with circular muscle, internal and well developed. Development indirect, with tornaria larvae.

Genus *Schizocardium* Spengel, 1893

Diagnosis. Vermiform process long; gill bars long; hypobranchial area narrow; gonads lateral only; esophageal pores present, single and paired; hepatic caeca present and finger-shaped.

Remarks. There are two species of *Schizocardium, S. brasiliense*, and *S. peruvianum*, described by Spengel in 1893. The species from Peru is represented by a single incomplete specimen. The Santa Maria form fits the characteristics of the genus but preliminary observations suggest that it has a suite of characteristics different from the described species. In comparison to *S. brasiliense* its proboscis is more elongate in shape (less pyramidal), circular muscle layer of the proboscis is thinner, vermiform process begins in the posterior one-third of the proboscis, auricles are longer than the vermiform process, and the proboscis skeleton has a high sharp keel. In comparison to *S. peruvianum* its proboscis is longer, the vermiform process begins in the posterior one-third of the proboscis, and the auricles are longer than the vermiform process. Presence of the Santa Maria Basin form at a depth of 91m and in the northeast Pacific are additional important factors.

Family Harrimaniidae Spengel, 1901

Diagnosis. Proboscis lacks cauliflower organ and vermiform processes. Collar lacks neurocord nerve roots and peripharyngeal cavities. Trunk lacks genital wings, hepatic caeca, parabranchial ridges, and synapticules. Eggs large (150-400 m); development, direct.

Genus *Saccoglossus* Schimkewitsch, 1892

Diagnosis. Proboscis long, cylindroid; longitudinal muscle of proboscis in concentric rings; collar broad as long; gonads simple.

Remarks. One species of *Saccoglossus, S. pusillus*, has been described from intertidal areas in California. Specimens of the genus were reported from 40-50 m in the San Pedro Basin. The Santa Maria form is very small. The proboscis, collar and branchio-genital region of an incomplete specimen measured 1.05 cm; total length is estimated to be 2.0-3.0 cm. The number of concentric rings (3) of longitudinal muscle in the proboscis is smaller than that of most species and most similar to *S. otagoensis* (3-4) and *S. cambrensis* (4-6). The Santa Maria form is different in being taken at a depth of 91 m and in having small ova (160 µm). The most similar species is *S. horsti* with ova measuring 230 x 70 µm. Other species have ova of 250, 310, 375, and 400 µm. Additional morphological comparisons are underway.

Genus *Stereobalanus* Spengel 1901

Diagnosis. Proboscis short, conical, and ringed anteriorly; longitudinal muscles, radial pattern (heavier bands); collar shorter than broad; elongate dorso-ventral gill slits open directly to the exterior; two pairs of genital lappets; gonads lateral and dorsal.

Remarks. *Stereobalanus* was established in 1901 by Spengel for a species he described as *Balanoglossus canadensis* in 1893. The specimens from Sta. R-7 in the Santa Maria Basin fit the characteristics for *Stereobalanus* listed above; however, they do not fully match the geographic distribution, habitat, and morphological features of *S. canadensis* of this monotypic genus.

Characteristics found in preliminary studies which suggest that the Santa Maria Basin form is a new species include the following: thick layer of circular muscle in the proboscis, heavy central area of radial pattern of longitudinal muscle, glomerulus poorly developed, appearing as a series of isolated islands surrounding the buccal diverticulum, well-developed chondroid tissue sheath encases the buccal diverticulum and the sinus organ in the peduncle, longer peduncle, skeletal crura develop in the peduncle, connective tissue and muscle well-developed in the collar coelom, ova about 500 μm but nucleus and nucleolus larger at 200 and 100 μm, respectively, nucleolus lunate. In addition, the Santa Maria form was found in the Pacific, at 565 m, and in a very fine silty sediment with high clay density.

Keys to Enteropneusts

I. Key Based on External Characteristics

Figure 10.1

1A. Genital wings or enlarged genital lappets absent 3

1B. Genital wings or enlarged genital lappets present 2

2A. Lateral genital wings (A) in the branchial and esophageal region .... *Balanoglossus*

2B. Four enlarged genital lappets (B), not present in esophageal region; lappets present below and above branchial openings .... *Stereobalanus*

3A. Elongate cylindroid proboscis (C); small with large eggs (150 μm) visible externally .... *Saccoglossus*

3B. Proboscis not elongate, generally ovate (D); large with small eggs (<100 μm); proboscis 3 x length, 5 x width of *Saccoglossus* .... *Schizocardium*

II. Key Based on Internal Characteristics

Figure 10.2

1A. Longitudinal muscles of proboscis arranged in definite patterns; thin layer of external circular muscle 2

1B. Longitudinal muscle of proboscis not in patterns but is homogeneously arranged; thick layer of external circular muscle (E) .... *Schizocardium*

2A. Muscle arranged in radial pattern 3

2B. Muscle not arranged in radial pattern; concentric rings common (F) .... *Saccoglossus*

3A. Many (>100) thin radial bands closely packed and concentrated peripherally; large central proboscis coelom (G) .... *Balanoglossus*

3B. Less than 50 bands, narrow peripherally with much open space between bands, thicker and more concentrated near the center where the proboscis coelom is small (H) .... *Stereobalanus*

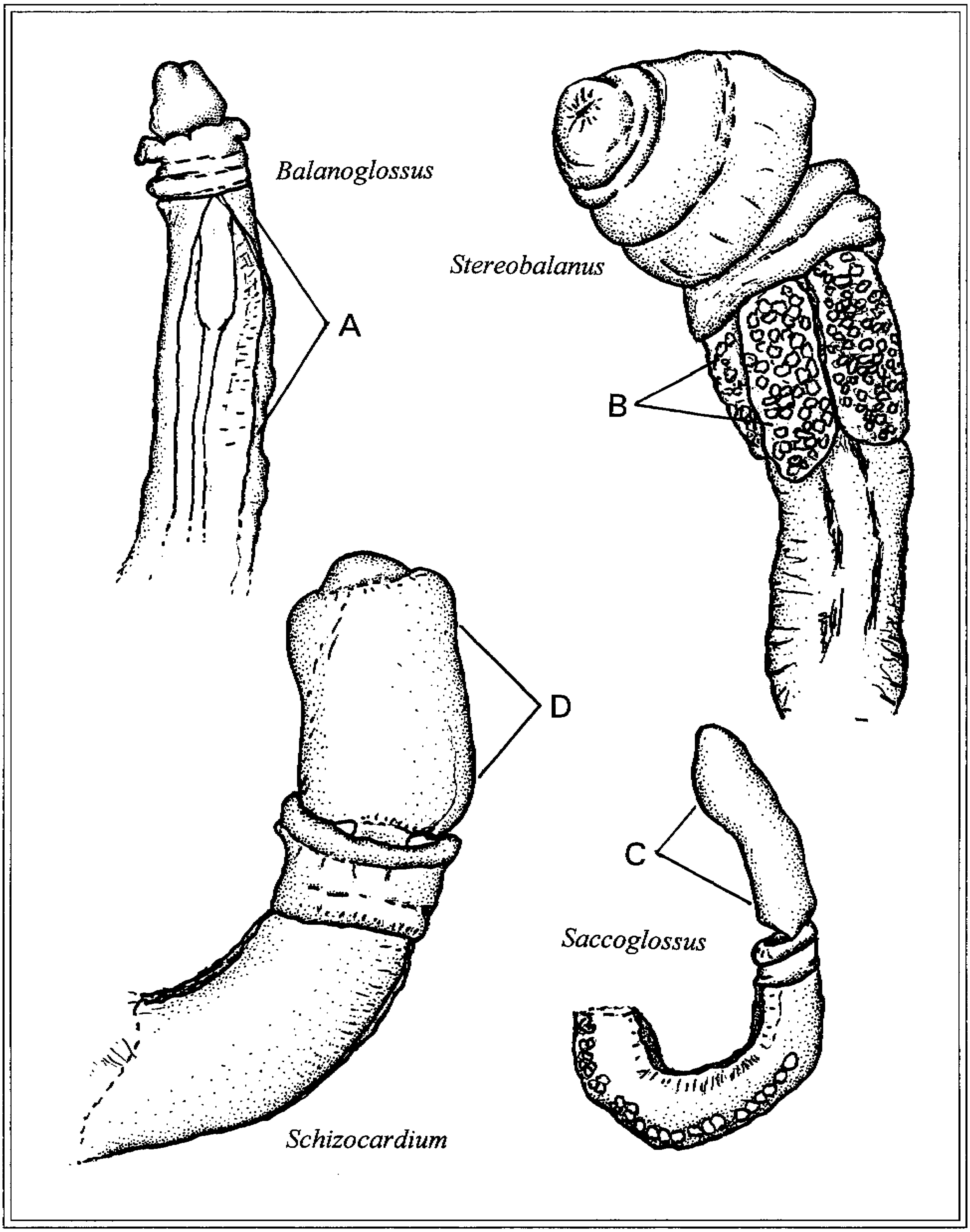
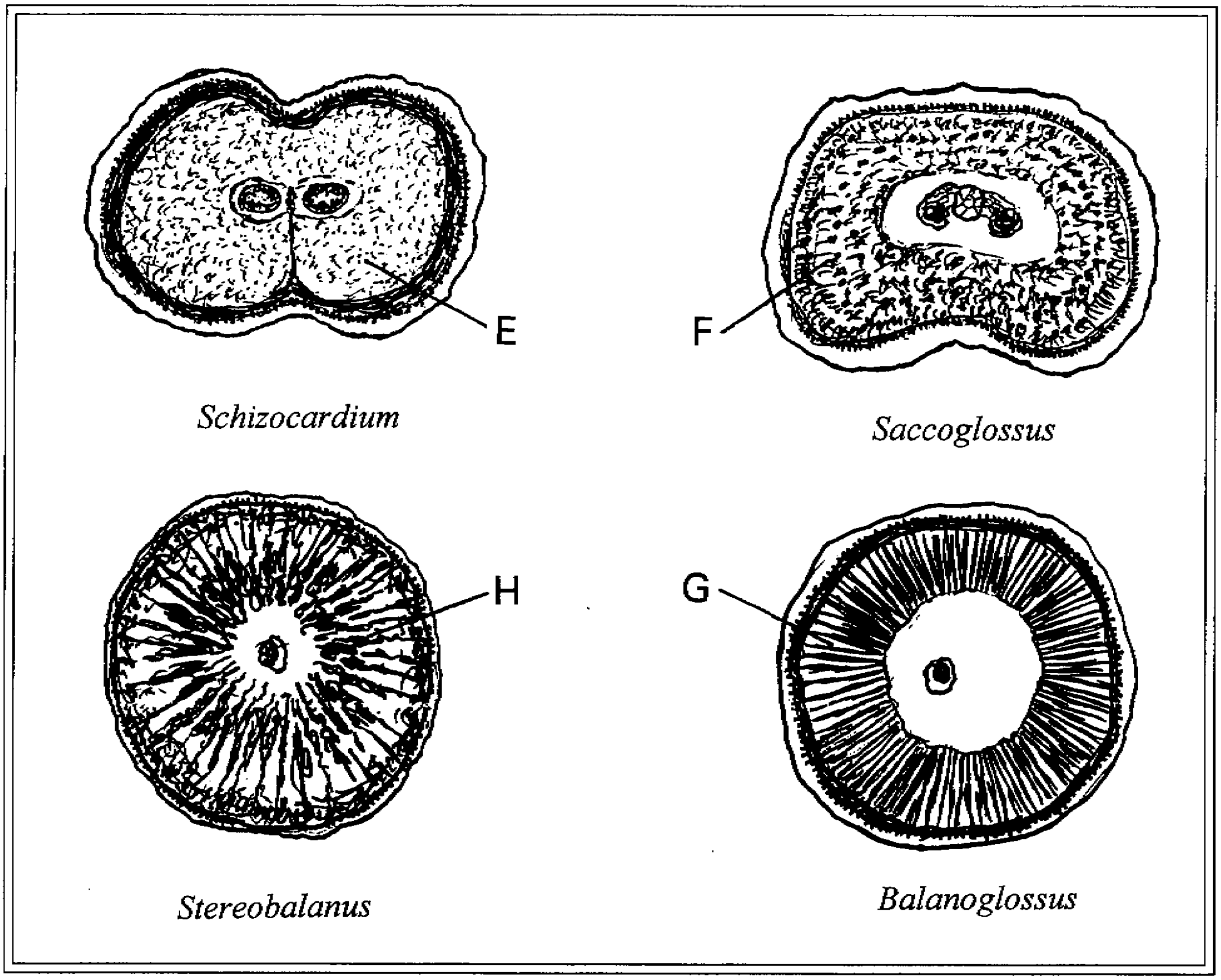


Figure 10.1. Plate showing anterior ends of four different genera of enteropneusts. Letters explained in key.



Schizocardium

Saccoglossus

Stereobalanus

Balanoglossus

Figure 10.2. Plate showing cross sections of the proboscis in four different genera of enteropneusts. Letters explained in Key.

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11. PHYLUM CHORDATA:
SUBPHYLUM UROCHORDATA, CLASS ASCIDIACEA

by

Gretchen Lambert[1]

Introduction

The ascidians, or tunicates, are a group of exclusively marine invertebrate chordates whose chordate affinities are expressed primarily in the larval stage. The early development of the egg shares many similarities with vertebrate early development. The larva is a tiny (< 1mm long) short-lived, non-feeding tadpole (Fig. 11.1A) with a notochord, dorsal tubular nerve cord, and the non-functioning rudiments of pharyngeal gill slits that become greatly proliferated in the adult branchial sac that is used for filter feeding. The notochord is lost when the swimming tadpole settles and undergoes metamorphosis into the sessile saclike adult form; all that remains of the nerve cord in the adult is a dorsal ganglion. Another chordate feature is the endostyle, considered to be an evolutionary forerunner of the thyroid gland, which produces a thyroxin-like hormone. Detailed overviews of the ascidians are well presented by Van Name (1945), Abbott (1975, 1980), and Monniot *et al.* (1991).

Morphology and General Biology

Adult ascidians are sessile filter feeders (Figs. 11.1B, 11.2). Each animal has two siphons, incurrent and excurrent, for the passage of water through the pharynx or branchial sac. At the base of the incurrent oral siphon are a number of oral tentacles that sort the incoming food particles and may reject large ones. The oral siphon opens into the branchial sac which is pierced by a number of rows of ciliated gill slits. A mucous sheet is formed by the ventral endostyle during feeding and spreads across the inner surface of the branchial sac, covering the gill slits and catching filtered particles down to the size of bacteria. When the mucous sheet reaches the dorsal side of the sac, a longitudinal series of curved dorsal languets form the mucus into a string which moves by ciliary action into the esophagus and stomach. Fecal pellets accumulate in the rectum and are expelled periodically through the excurrent siphon.

The ascidian body is covered by a mantle or body wall which contains longitudinal and circular muscle bands. The mantle is loosely attached to a tough outer covering, called the tunic, composed of a cellulose-like material; ascidians are often referred to as tunicates because of their tunic.

All ascidians are hermaphroditic, possessing both ovaries and testes. Although a few species routinely self-fertilize their own eggs, most species do not. The eggs and sperm are usually spawned into the sea, or fertilization may be internal with the larvae being incubated until they reach the swimming tadpole stage (Fig. 11.1A). A few species breed all year, but most have a definite breeding season, usually in the summer. Ascidians may be either solitary or colonial. Solitary, or simple, forms reproduce sexually; they may reach several centimeters in length, though the smallest species are interstitial and just a few mm in length. Some

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solitary forms are stalked, although the majority of solitary species attach directly to the substrate by their posterior end or left side. Colonial forms are composed of many small zooids a few mm in length embedded in a common tunic which in some species, may spread out in a sheet to cover considerable space. Each colony arises from the settlement of a single tadpole which then buds asexually to form a clone of zooids. There are two types of colonial species: (1) social ascidians in which the zooids are attached to one another only by their base, with the rest of the body independent and covered by its own tunic (Fig. 11.6), and (2) compound ascidians in which the zooids are completely contained within the common tunic with only one or both siphonal openings visible on the tunic surface.

Ascidians can be found in almost every marine habitat: interstitially in mud and sand, attached to rocks on exposed coasts, epibiotic on molluscs or other ascidians, and as common fouling organisms on floats, pilings and boat hulls. They occur from the intertidal to abyssal depths, and in the warmest and coldest waters of the planet. In the tropics some compound ascidians contain symbiotic algae, primarily the unicellular *Prochloron* (Lewin and Chang 1989). A newly discovered family of abyssal ascidians do not filter-feed; their pharynx is modified to catch large prey such as crustaceans. Another recently discovered group of benthic deep-sea tunicates (not covered in this chapter) is so different from the Ascidiacea that they have been placed in their own class, the Sorberacea (Monniot *et al.* 1975). Undoubtedly there are still many undescribed species yet to be collected, especially from deeper waters; this Atlas contains three new ascidian species, described separately (Lambert, 1993).

Commensals and parasites are common in ascidians. The clam *Mytilimeria* is never found living freely but only embedded in the tunic of certain compound or solitary ascidians. Certain species of burrowing amphipods are sheltered in the tunic. Free living amphipods are found in the branchial sac of most solitary species, apparently feeding on the nutritiously rich mucous sheet. Ascidians are frequently parasitized by specially adapted copepods called ascidicoles (Ooishi, 1991). Although predation on ascidians does occur, it is not common because the ascidian tunic appears to be a deterrent. The tunic is often highly acidic, and in some species contains large numbers of calcareous spicules (Lambert, 1979). A number of solitary forms also have spicules in their body tissues (Lambert, 1992). Nevertheless, flatworms, fish, various echinoderms, and molluscs have been observed feeding on both solitary and colonial forms.

The ascidians collected as part of this study come mostly from collections made along hard bottom transects that were surveyed with a submersible. Specimens were taken as part of these surveys and were collected with the aid of manipulator arms on the submersible. The coordinates of each transect are provided in the Appendix (Table A.3) at the end of this volume. A list of ascidian species found at each station is provided in Table 11.1.

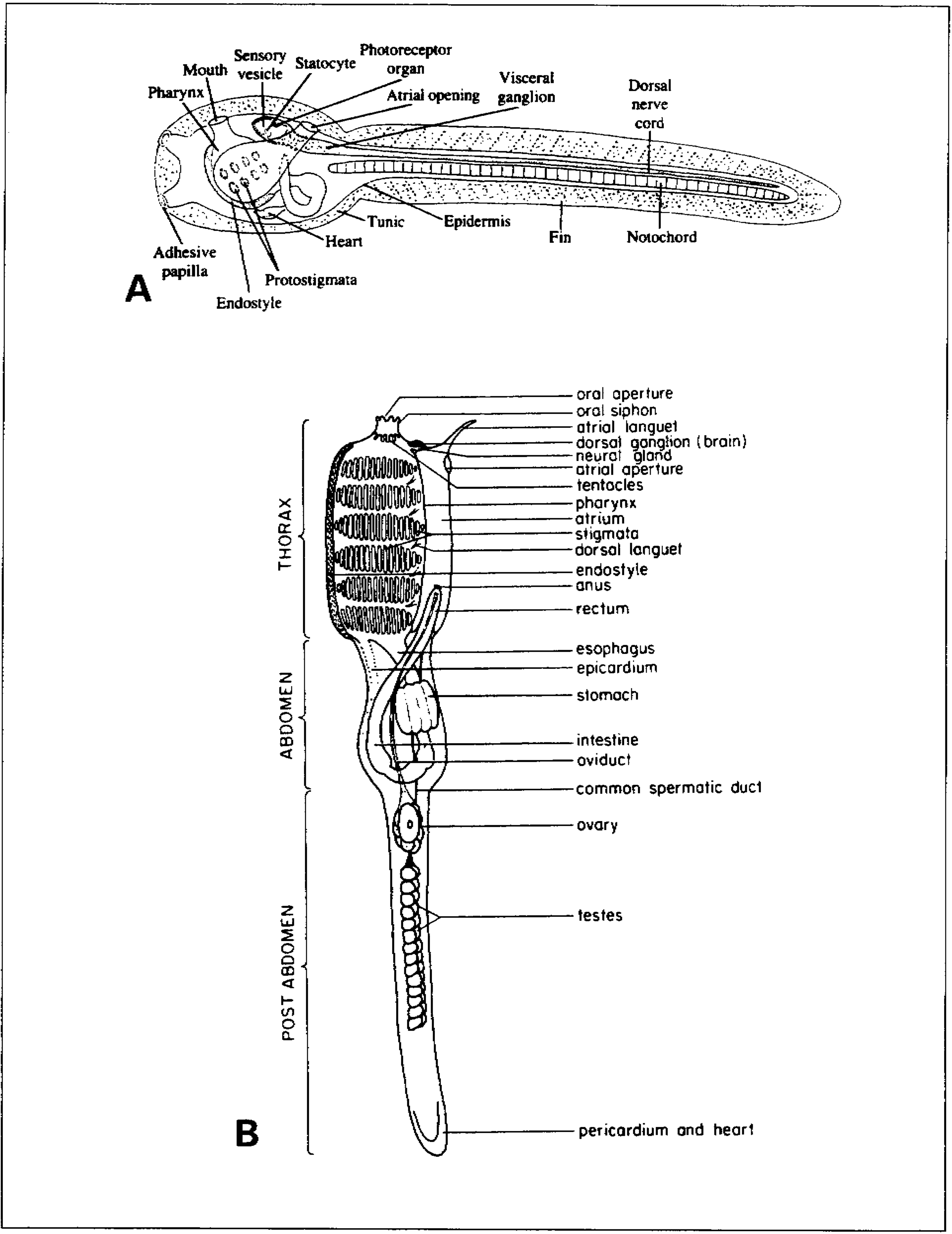

Figure 11.1. A, ascidian tadpole larva greatly enlarged (from Kozloff, 1990); B, a typical compound ascidian zooid with postabdomen, ×16. (from Abbott, 1975).

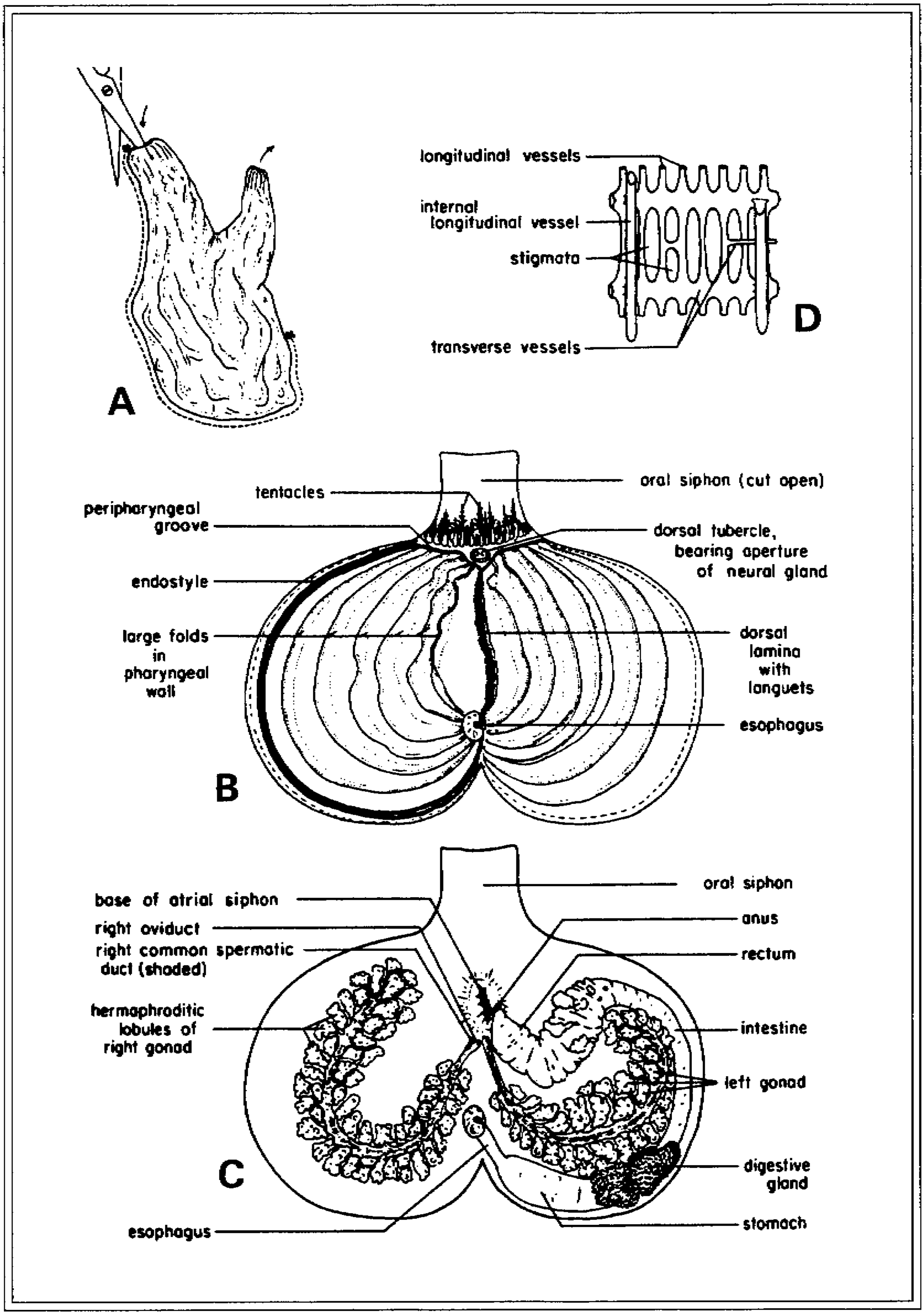

Figure 11.2. *Pyura haustor*, an example of a typical solitary ascidian (approximately life size) showing major body parts. A, method of dissection; B, animal spread open to show inner surfaces of oral siphon and branchial sac (pharynx); C, same view as in B but with branchial sac removed, oral tentacles not shown; D, a small part of branchial sac, enlarged. (from Abbott, 1975).

Taxonomy

The class Ascidiacea is divided into three orders based on the structure of the branchial sac. The Aplousobranchia are all compound species with small zooids possessing a simple branchial sac with no transverse and longitudinal internal blood vessels. The Phlebobranchia includes both social and solitary forms; the pharynx contains internal vessels. In the Stolidobranchia the inner surface of the branchial sac, besides containing vessels, is greatly expanded into longitudinal folds. Identifications are based on the presence or absence, and number, of branchial folds, and number of longitudinal vessels, as well as the structure of the stomach, number and arrangement of the ovaries and testes, and a host of other details. The relevant differences are listed in the Key to Species. Figs. 11.1B and 11.2 show the general anatomy of compound and solitary ascidians.

Table 11.1. Assemblages of Ascidian Species on Hard Substrate Stations in the Santa Maria Basin and Western Santa Barbara Channel. Listed by Hardbottom Transect Number (See Appendix A.3).

Transect No.	Species assemblages
1	*Chelyosoma columbianum, Styela milleri, Didemnum carnulentum* var. *lacteolum, Styela* sp.
2	*Boltenia polyplacoderma, Chelyosoma columbianum*
4	*Chelyosoma columbianum, Halocynthia igaboja, Corella* sp., *Pyura haustor*
6	*Aplidium californicum, Pyura* sp., *Chelyosoma columbianum, Styela gibbsii, Didemnum carnulentum* var. *lacteolum, Styela tesseris, Halocynthia igaboja, Trididemnum opacum*
13	*Aplidium* sp., *Halocynthia igaboja, Ascidia* sp., *Pyura haustor, Boltenia polyplacoderma,Pyura* sp., *Chelyosoma columbianum, Styela milleri, Eudistoma carolinense* (?)
14	*Boltenia polyplacoderma, Pyura haustor, Chelyosoma columbianum, Styela milleri, Molgula regularis*
16	*Aplidium spauldingi, Chelyosoma columbianum, Ascidia* sp., *Halocynthia igaboja,Boltenia polyplacoderma, Pyura haustor*
20	*Chelyosoma columbianum, Pyura haustor, Halocynthia igaboja, Styela milleri*
21	*Chelyosoma columbianum, Halocynthia igaboja, Distaplia occidentalis, Styela tesseris, Eudistoma carolinense* (?)
25	*Chelyosoma columbianum, Styela milleri, Corella* sp.
27	*Aplidium californicum, Halocynthia igaboja, Chelyosoma columbianum, Pyura haustor, Euherdmania claviformis*

Methods of Preservation and Dissection

Ascidians should be relaxed and narcotized before fixation to best observe the anatomical details necessary for taxonomic identification. However, this is often a problem because these organisms are extremely difficult to relax. A common method involves leaving the animals in a bowl of ambient temperature sea water until they are fully expanded. Then a few drops of a concentrated solution of menthol in 95% ethanol is added and gently stirred in; a solution of 7% magnesium chloride in diluted sea water can also be gradually added to the bowl. Alternatively, the chemical MS-222 will quickly anesthetize most compound species and solitary phlebobranchs when a few milligrams are sprinkled on the surface of the dish in which the ascidians have already relaxed; it does not seem to work well on stolidobranchs.

When the animals do not contract their siphons in response to prodding (after 4-12 hours or more), they are then transferred to a solution of 10% buffered sea water formalin. One animal should be transferred first; if it contracts in the fixative, then add about two drops of 10% formalin to the bowl of sea water and wait until the animals are dead before transferring them to the fixative. They can be stored in the formalin, or if they have calcareous spicules, they should be transferred after a few hours to permanent storage in 70% ethanol.

In order to observe the zooids in a compound species, thin slices of the colony can be made with a razor blade, or if the tunic is not too tough, it can be torn with forceps to release the zooids. Certain details of the branchial sac may require cutting this tiny structure open with small iridectomy scissors or a scalpel. Some zooids are opaque and must be cleared in glycerin for several hours before observation. Sometimes staining the zooids in a very dilute solution of methylene blue or toluidine blue will enhance the outlines of difficult-to-see structures such as the branchial stigmata.

Solitary ascidians are opened by cutting posteriorly from the oral siphon along the ventral side through the tunic, body wall and branchial sac to the posterior end of the animal (Fig. 11.2). The animal is then laid out in a dish of water with its two halves still connected dorsally.

Key to Genera and Species of Ascidians

This key includes those species collected to date from the Santa Maria Basin, and is not meant to be used as a general key for ascidians. For more comprehensive keys to American Pacific coast species the reader is directed to Van Name (1945), Abbott (1975), or Lambert *et al.* (1987).

1A. Solitary; not attached to other individuals by a common tunic or by stolons 8

1B. Social (zooids connected at their base by stolons or a sheet of tunic, their bodies separate and contained within their own tunic) or compound (zooids contained within a common tunic) 2

2A. Social, zooids attached by stolons at their base; body very slender, about 2 mm wide and 20-35 mm in length .... *Euherdmania claviformis*

2B. Compound, zooids embedded in a common tunic; zooids never more than 10 mm in length 3

3A. Tunic with stellate calcareous spicules .... Didemnidae 4

3B. Tunic without calcareous spicules 5

4A. Zoids with 3 rows of branchial stigmata .... *Trididemnum opacum*

4B. Zooids with 4 rows of branchial stigmata .... *Didemnum carnulentum* var. *lacteolum*

5A. Zooids with 3 rows of stigmata .... *Eudistoma carolinense*(?)

5B. Zooids with more than 3 rows of stigmata 6

6A. Zooids with 4 rows of stigmata .... *Distaplia occidentalis*

6B. Zooids with 8 or more rows of stigmata 7

7A. Zooids with 8-12 rows of stigmata; stomach with 12-23 longitudinal folds ....*Aplidium californicum*

7B. Zooids with 18 rows of stigmata; stomach with 3 or 4 longitudinal folds .... *Aplidium spauldingi*

8A. Branchial sac without longitudinal folds 9

8B. Branchial sac with 4 or more longitudinal folds on each side 11

9A. Branchial stigmata straight ....*Ascidia* sp.

9B. Branchial stigmata coiled 10

10A. Oral and atrial apertures surrounded by horny disk composed of variable number of plates arranged in definite pattern .... *Chelyosoma columbianum*

10B. Tunic relatively smooth, without plates ....*Corella* sp.

11A. Branchial sac with 4 longitudinal folds on each side; oral tentacles not branched .... Styelidae 16

11B. Branchial sac with more than 4 longitudinal folds per side; oral tentacles branched 12

12A. Stigmata straight, both oral and atrial apertures 4-lobed; without renal sac (="kidney") .... Pyuridae 14

12B. Stigmata coiled, oral aperture 6-lobed, atrial aperture 4-lobed, with renal sac (="kidney") on right side of body below gonad .... Molgulidae 13

13A. Ovaries very long, sinuous tubes; animal with only short rootlet hairs, attached primarily by posterior region of tunic .... *Molgula regularis*

13B. Ovaries compact, oval; tunic covered with short hairs plus a very long branched rootlike process that projects from posterior end; siphons widely separated, the atrial anteriormost and the branchial about halfway back .... *Molgula napiformis*

14A. Stigmata with long diameter transverse to body axis, each crossed by narrow longitudinal vessel; tunic rather thin but composed of flat irregular polygonal plates; animal flattened anteroposteriorly .... *Boltenia polyplacoderma*

14B. Stigmata with long axis arranged anteroposteriorly in branchial sac 15

15A. Tunic thick, ridged, without obvious spines; siphons long, reddish; gonads one on each side .... *Pyura haustor*

15B. Tunic densely covered with long fleshy thorn-like spines, branched at their tips and with recurved spinelets along the sides; spines may obscure short siphons; several gonads on each side .... *Halocynthia igaboja*

16A. One ovary on each side of animal, attached to body wall .... *Styela milleri*

16B. Two ovaries on each side of animal, attached to body wall 17

17A. Tunic irregularly thickened into flattened polygonal tessellations with groove separating each one; 5-6 longitudinal vessels on each branchial fold .... *Styela tesseris*

17B. Tunic with numerous longitudinal or oblique wrinkles, may also be warty or bumpy but not tessellated; 5-15 longitudinal vessels on each branchial fold .... *Styela gibbsii*

Additional species not in the key, but which are known from the area are listed below:

Family Polycitoridae

Cystodytes lobatus (Ritter, 1900); 79-203 m

Family Ascidiidae

Ascidia clementea Ritter 1907; 1196-2012 m
Benthascidia michaelseni Ritter 1907; 3990 m
Ciona mollis Ritter 1907; 2012 m

Family Pyuridae

Bathypera feminalba Young and Vazquez, 1995; 60-100 m off Santa Catalina Island
Bathypera ovoida (Ritter, 1907); 1829 m
Boltenia villosa (Stimpson, 1864); 38-88 m
Culeolus pyramidalis Ritter, 1907; 4131 m
Pyura millari Rodrigues, 1966; 91 m
Pyura mirabilis (von Drasche, 1884); 60 m

With two exceptions, all the above species were collected by Ritter in 1904 off the coast of California and described in his 1907 paper. See Young and Vazquez (1995) concerning *Bathypera feminalba*. *Pyura millari* (?) was collected by Dr. Richard Emlet and myself by dredging at 91 m off Santa Catalina Island, April 1992. The species was abundant and was provisionally identified by Dr. Claude Monniot, Museum Nationale d'Histoire Naturelle, Paris. This species has previously been recorded only from the Atlantic, near Sao Paulo, Brazil, its type locality, at 140 m.

Description of Species

Order Aplousobranchia

Family Didemnidae

Didemnum carnulentum var. *lacteolum* Ritter and Forsyth, 1917

Figure 11.3 A-B

Didemnum carnulentum Ritter and Forsyth, 1917:470, pl. 39, fig. 11, pl. 44, figs. 57-59.—Johnson and Snook, 1927:596, fig. 696.—Abbott, 1975:649.—Abbott and Newberry, 1980:187, fig. 12.11.

Didemnum carnulentum var. *lacteolum* Ritter and Forsyth, 1917:471, pl. 40, fig. 23, pl. 44, fig. 60.—Van Name, 1945:94-95.

Material Examined. California, off Point Arguello, Sta. BRA-6, 61 m, sample 2 (3 pieces, SBMNH).—Western Santa Barbara Channel, Stat BRA-1, sample 4, 69-73.5 m (1 colony piece, USNM).

Description. From Ritter and Forsyth (1917). Colony encrusting, 1 mm or less in thickness; color pure white due to numerous calcareous spicules in test, 0.015-0.065 mm in diameter (stated incorrectly as 0.15-0.065 mm). Spicules in both upper and lower strata of colony. Bladder cells not conspicuous but present around closely packed zooids, which extend into both upper and lower strata. Zooids only about 1 mm long, with 4 rows of stigmata. Zooids similar to *D. carnulentum* but smaller, with atrial opening proportionately much larger, extending over half length of branchial sac and sometimes even larger than depicted by Ritter and Forsyth (1917). Testis almost spherical when fully ripe and half as large as branchial sac. Coil of vas deferens with seven turns. Ripe ova gigantic, larger proportionately than in *D. carnulentum*. Breeding season in June.

Remarks. This variety differs by enough characters from *D. carnulentum* that it may be a separate species. In the USNM colony, one zooid had a testis cleft into 2 halves and the vas deferens with 9-10 coils, while others had fewer turns and an undivided testis. In the SBMNH colonies all the zooids had a testis with 2 large lobes and the vas deferens with 7 coils. Van Name (1945, p. 80 under the genus description) states that "neither is the number of parts into which the testis is cleft always constant within the same species."

Distribution. Southern California, on under sides of rocks and in kelp holdfasts, from the zero tide level to a few meters; Santa Barbara Channel, 69-73.5 m; Santa Maria Basin, 61 m.

Trididemnum opacum (Ritter, 1907)

Figure 11.3 C-D

Didemnum opacum Ritter, 1907:42, pl. 3, figs. 40, 41.

Trididemnum opacum Van Name, 1945:106-107, text fig. 49 (synonymy).—Abbott, 1975:649.—Abbott and Newberry, 1980:187-188, fig. 12.12.—Lambert *et al.*, 1987:473.

Material Examined. California, off Point Arguello, Sta. BRA-6, sample 2, 61 m (several pieces of probable single colony, USNM).

Description. From Van Name (1945). Colonies encrusting; may reach 15 cm or more across and 10-15 mm thick, opaque pale flesh color or white, with the stellate calcium carbonate spicules showing through as dense white specks. Test tough and firm. Spicules abundant throughout the test but especially in superficial region, 0.03-0.035 mm in diameter, with spines greater than half spicule diameter, their points

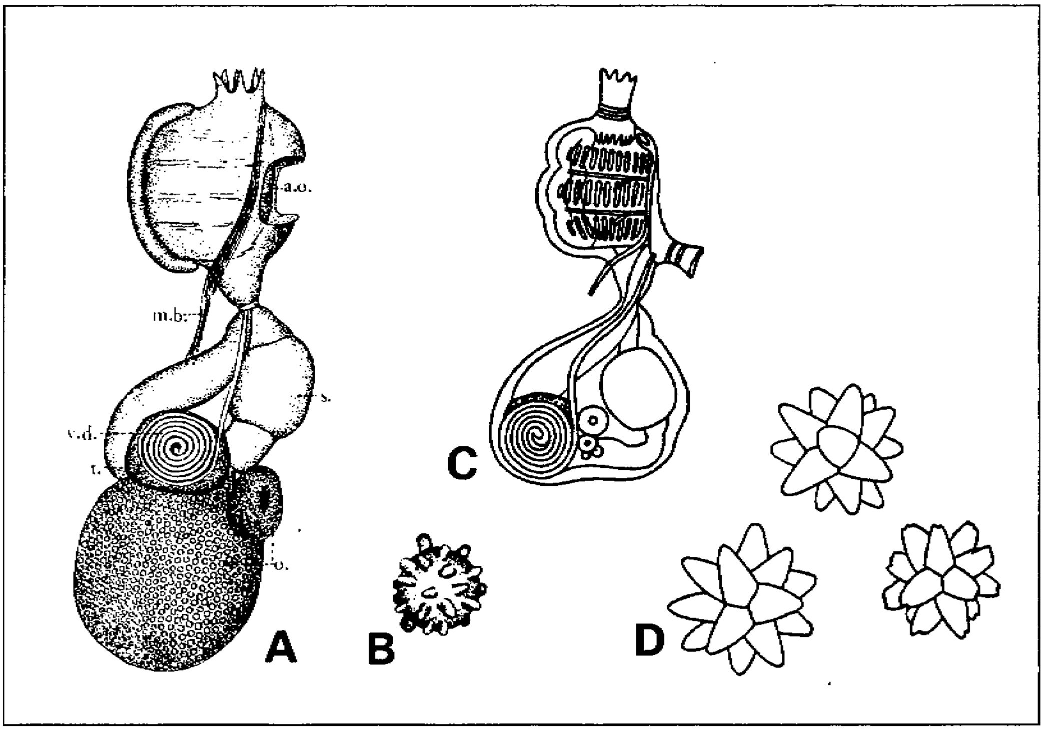

Figure 11.3. *Didemnum carnulentum* var. *lacteolum*. A, zooid, ×50 (a.o.: atrial opening; m.b.: muscle band; o.: ovary; s.: stomach; t.: testis; v.d.: vas deferens); B, spicule, ×650 (from Ritter and Forsyth, 1917). C-D, *Trididemnum opacum*. C, zooid, X30; D, spicules, ×900. (from Van Name, 1945).

long but often truncated at tips. Zooids 2 mm or less in length in contracted specimens. Both branchial and atrial tubes well developed, atrial far back on thorax, slightly funnel-shaped and commonly directed obliquely backward. Three rows of stigmata. Stomach large and globular. Testis round and undivided; vas deferens with about 6 coils on surface but may be fewer in young zooids.

Remarks. The colony in this collection has zooids that are brownish, visible through the tunic which is not as opaque as Van Name (1945) indicates, but he does state that the zooids become a dull brownish or grayish white after preservation. The vas deferens has eight coils. The atrial siphon is not quite as far back as stated by Ritter (1907), but it is tubular and flared like a funnel as stated by Van Name.

Distribution. Common in central California intertidally on overhanging rocks, and dredged off San Nicolas Island, California, from 61 m. Also recorded from southern California; Santa Maria Basin, 61 m.

Family Polycitoridae

Distaplia occidentalis Bancroft, 1899

Figure 11.4 A

Distaplia occidentalis Bancroft, 1899:59-112, pls. 1-6.—Ritter and Forsyth, 1917:464-467, pl. 45, figs. 64, 65.—Van Name, 1945: 149-150 (synonymy).—Abbott, 1975:650.—Abbott and Newberry, 1980:194-195, fig. 12.21.—Lambert *et al.*, 1987:473.

Material Examined. California, Santa Maria Basin, off Purisima Point, Sta. BRA-21, sample 2, 87 m (1 small colony, USNM).

Description. From Van Name (1945). Colony form variable; may be flat and encrusting or, more usually, pedunculate or mushroom shaped with heads up to 1 cm or more across. Several systems in head, zooids closely arranged around a large cylindrical common atrial opening extending above test surface as delicate-walled short pipe. Color of heads highly variable, from dirty white to yellow, light green, lavender, brown or reddish, due to pigment cells in test; peduncle often grey. Test with thin, very tough outer layer. Zooids 2-3 mm long due to contraction, but if expanded, may be much longer. Body with an expanded thorax; abdomen connected by very narrow neck. Four rows of stigmata present, each row crossed at its middle by slender parastigmatic transverse vessel; 12-14 stigmata per row on each side. Stomach wall smooth externally but with irregular internal ridges giving it a reticulated appearance.

Ovary posterior to intestinal loop and partially to testis; incubatory pouch rarely containing up to 4 embryos, extending into test from posterior end of thorax by long slender, easily breakable neck.

Remarks. This species is most easily identified by the pedunculate shape of the colonies with their flattened upper surface, the incubatory pouch, and the parastigmatic transverse vessels in the branchial basket. The species occurs in quiet waters on marina floats, and may be very abundant during summer months in Washington.

Distribution. Puget Sound, San Juan Archipelago, on rocks usually in shallow water; southern California (San Diego); Santa Maria Basin, 87 m; ? British Columbia.

Eudistoma carolinense (?) Van Name, 1945

Figure 11.4 B-C

Eudistoma carolinense Van Name 1945:123-124, fig. 58.—Plough 1978:59, 61, fig. 26e.

Material Examined. California, Santa Maria Basin, off Purisima Point, Sta. BRA-13, 86-98 m, sample 4 (1 small colony, USNM).

Description. From Van Name (1945). Colony composed of irregularly tapering clavate heads over a narrowed neck region, arising from an expanded, encrusting base; 20-30 mm in height, 3-10 mm wide at top; specimens may be flattened laterally, usually curved and crooked. The heads not all arising from expanded base of the colony, but in many cases from lower part of another head or neck. Test densely impregnated with sand. Contracted zooids only about 2 mm long, with anterior ends withdrawn 4-5 mm below colony surface. Each separate head in colony narrow, small, containing from 1-6 zooids, each with its oral and atrial siphons opening separately to surface, as typical for genus. Three rows of stigmata, about 10 stigmata per row on each side of branchial sac. Oral tentacles numerous, of 2 sizes. Stomach rounded, smooth walled; with gland surrounding intestine consisting of very few tubules swollen at ends. Testes pyriform, 6-7. Strong longitudinal muscle bands extend from thorax far down sides of abdomen.

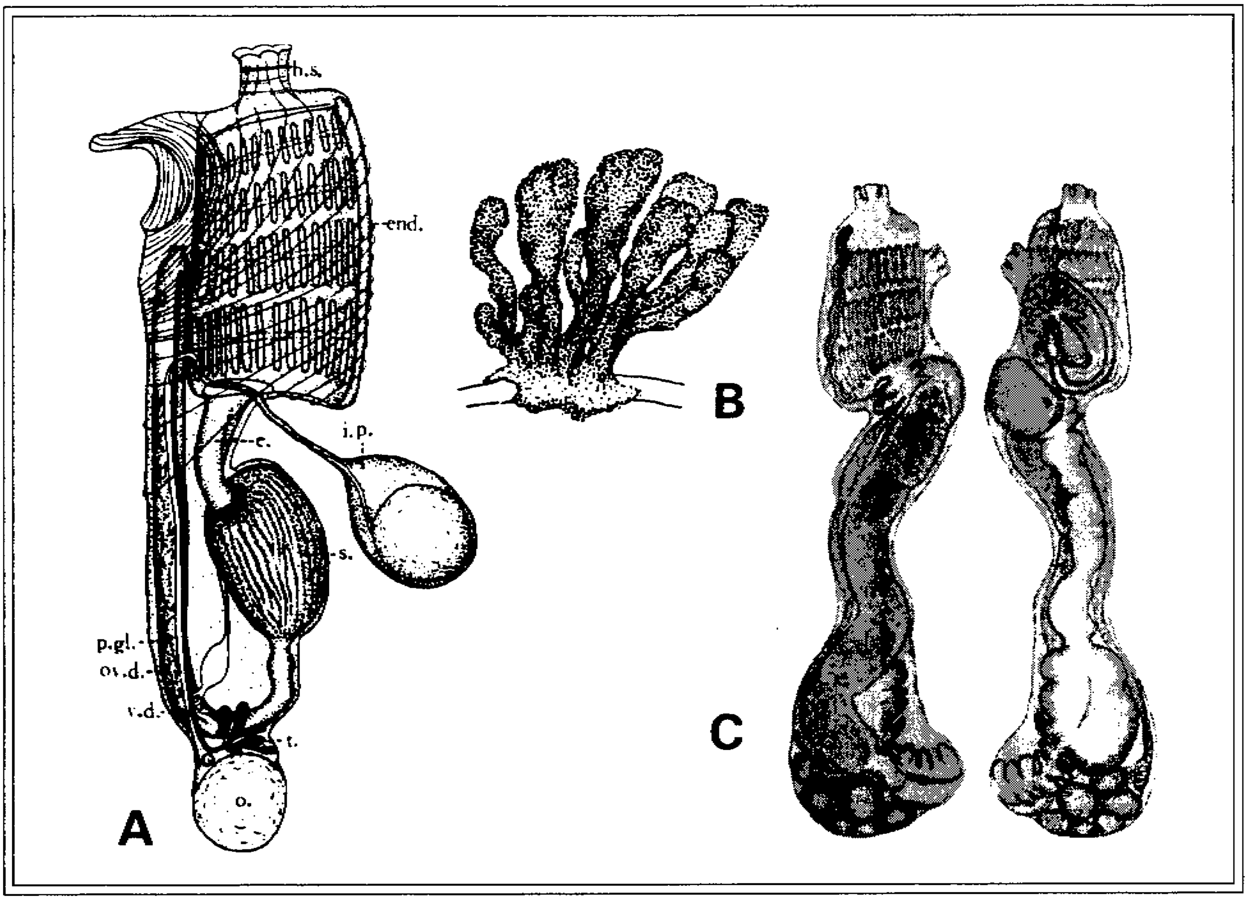

Figure 11.4. *Distaplia occidentalis,* A, zooid, ×42 (b.s. - branchial siphon, e - esophagus, end. - endostyle, i.p. - incubatory pouch, o. - ovary, ov.d. - oviduct, p.gl. - pyloric gland, s. - stomach, t. - testis, v.d. - vas deferens) (from Ritter and Forsyth, 1917); *Eudistoma carolinense,* B, colony, ×1.3 (from Van Name, 1945); C, zooid, left and right sides of body, ×3.2 (from Plough, 1978).

Remarks. The two small colonies in this collection resemble in almost every respect *E. carolinense* Van Name, 1945, but that species has been recorded only from the Atlantic, in warm shallow water from the southeast U. S. coast. Thus, it may not be appropriate to establish a new species name for these colonies when they agree so closely with Van Name's description. The colonies in this collection are about 10 mm tall. The distal and basal portions of the voucher specimen are expanded and about 5 mm wide, the middle portion a constricted neck; the zooids are 5-6 mm long. The zooids are slightly longer than indicated by Van Name (1945) and Plough (1978), but the species in this genus are all capable of extreme contraction, so lengths of preserved specimens can be very variable.

Distribution. Coastal SE United States, down to 30 m; California, Santa Maria Basin. 86-98 m.

Family Synoicidae

Aplidium californicum (Ritter and Forsyth, 1917)

Figure 11.5 A

Amaroucium californicum Ritter and Forsyth, 1917:483, pl. 46, fig. 72.—Van Name, 1945:47-48, fig. 12.

Aplidium (=*Amaroucium*) *californicum* Abbott, 1975:648, 650.—Abbott and Newberry, 1980:182-183, fig. 12.1.—Lambert *et al.*, 1987:473, fig. 23.3.

Material Examined. California, off Point Arguello, Sta. BRA-6, sample 2, 61 m (1 small colony, USNM).

Description. From Van Name (1945). Colonies extremely variable in size, shape and color. Often flat and cake-like; sometimes attaining large size. Surface usually smooth, without embedded sand grains; test gelatinous, somewhat translucent, zooids visible within. Surface of test may be tougher than interior softer regions. Color of test ranges from opalescent white to yellowish, yellowish-brown or reddish brown, or mottled. Zooids also variable in color, from yellow or orange in some colonies to bright red in others. Zooids usually 6 mm or less in length. Branchial aperture with 6 lobes, atrial smooth and with long undivided atrial languet. Eight to 12 rows of stigmata, with about 12 stigmata per row on each side.

Stomach short, rounded, with about 15-20 regular longitudinal folds (the number varies from 12-23). Ovary located in anterior region of post-abdomen; double row of testes occupy most of post-abdomen, this variable in length.

Remarks. The genus *Amaroucium* was formally synonymized with *Aplidium* by Nishikawa (1991), thus making official a long-standing informal lumping of these two genera. *Aplidium californicum* is probably the most common compound ascidian on the California coast, especially in shallow waters. The great variability between colonies can make this species difficult to identify, however. The zooids can be removed very easily from preserved colonies; they may in fact fall out when the colony is dissected. Zooids in this collection about 2 mm long, bright orange-red, with 10 rows of stigmata. Tokioka (1967) tentatively grouped this species with the apparently identical *A. multiplicatum* from Palau and the Gilbert Islands, though he remarked that the localities are very far apart.

Distribution. Pacific coast of North and South America from British Columbia to Gulf of California, on rocks and man-made pilings and floats; rare in waters below 85 m. Santa Maria Basin, 61 m.

Aplidium spauldingi (Ritter, 1907)

Figure 11.5 B

Psammaplidium spauldingi Ritter 1907:41, pl. 3, fig. 39.

Amaroucium spauldingi Hartmeyer, 1909-1911:1471.—Van Name, 1945:53.

Material Examined. California, Santa Maria Basin, off Purisima Point, Sta. BRA-16, sample 4, 96 m (1 piece of colony, USNM).

Description. From Ritter (1907). Top of colony smooth, hard from great quantity of sand uniformly distributed through test. Numerous small zooids evenly distributed, systems not obvious. Each branchial opening marked on colony surface by small papilla. Color uniform grey due to embedded sand. Zooids long, slender, nearly straight; thorax about equal in diameter to abdomen and post-abdomen. Thorax about 3 mm long, abdomen about 2 mm long, and post-abdomen several times as long as thorax and abdomen combined. Mantle with few slender longitudinal muscle bands, extending far down into post-abdomen.

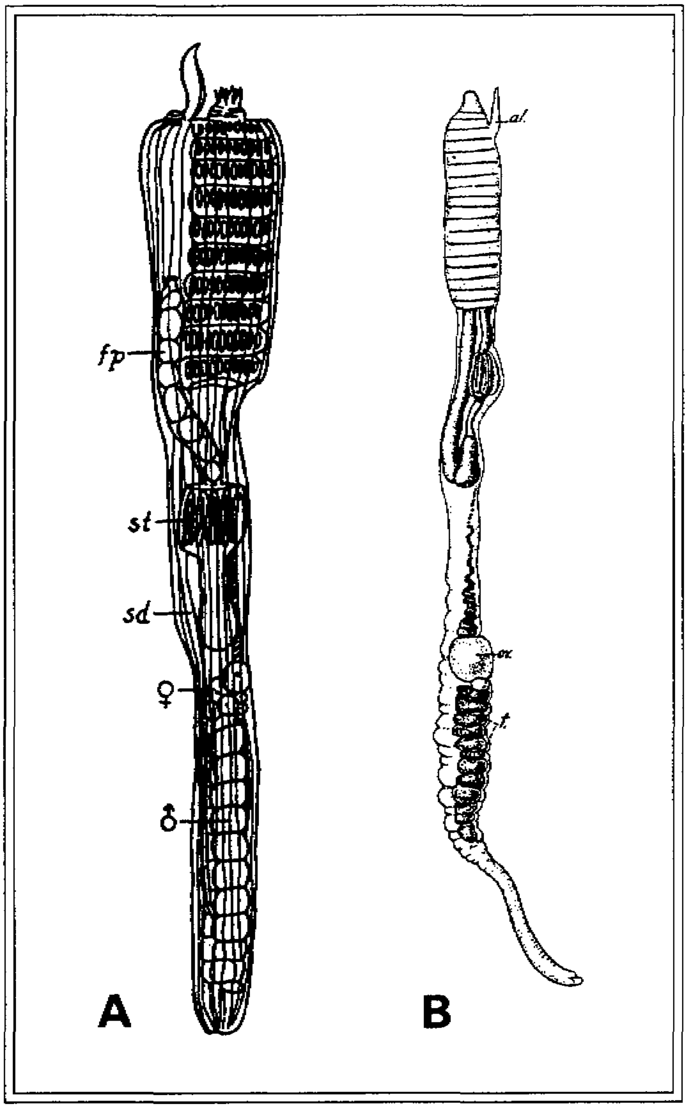

Figure 11.5. *Aplidium californicum,* A, zooid, ×22 (fp - fecal pellet, sd - sperm duct, st - stomach) (from Van Name, 1945, adapted from Ritter and Forsyth, 1917); *Aplidium spauldingi,* B, zooid, ×8 (al. - atrial languet, ov. - ovary, t. - testis) (from Ritter, 1907).

Branchial opening on prominent 6-lobed siphon, atrial siphon situated well back from end of branchial siphon about equal in thickness to thorax. Atrial languet long, and either undivided or bifid at tip. About 18 rows of stigmata. Endostyle large and tortuous. Branchial tentacles about 10, of unequal length. Esophagus about equal in length to stomach, this with 3-4 large longitudinal folds or lobes. A distinctly set off enlarged section of intestine follows pyloric section. Gonads in post-abdomen, testes a number of spherical lobes.

Remarks. The zooids in this collection are from a very small torn piece of colony, and their post-abdomens are entirely or partially missing. Nevertheless, because their morphology agrees in all respects with the characters listed by Ritter (1907), they are referred to this species with confidence. These characters include the unusual placement and bifurcated atrial languet, coupled with the large number of stigmatal rows, very few longitudinal stomach folds, heavily sand-encrusted test, and location of collection.

Distribution. Type locality, 61 m, 3.8 miles off the east point of San Nicolas Island, California, in fine grey sand; Santa Maria Basin, 96 m.

***Euherdmania claviformis* (Ritter, 1903)**

Figure 11.6

Herdmania claviformis Ritter, 1903:239-261, pls. 18, 19.

Euherdmania claviformis Ritter, 1904:650.—Johnson and Snook, 1927:597, fig. 698.—Van Name, 1945:76-78, fig. 32 (synonymy).—Abbott, 1975:647.—Abbott and Newberry, 1980:186-187, fig. 12.10.

Material Examined. California, Santa Maria Basin, north of Point Buchon, sample 1, 116 m (1 colony, USNM).

Description. From Van Name (1945). Zooids in a group, slender, club-shaped, each with its own covering of test for entire length, arising from an interwoven mass of branching stolons. Zooids often thickly encrusted with firmly adhering sand except at or near anterior end; test where free of sand translucent, slightly greenish in life, and tough. Zooids 2-5 cm in length (occasionally longer), 2-4 mm in greatest diameter, at the level of thorax. Thorax short in proportion to rest of body, separated from stomach and gonads by very long slender neck. Gonads posterior to stomach, but without clearly defined post-abdomen. About 12 rows of stigmata preseent, with about 40 stigmata per row on each side of thorax. Thirty to 40 simple branchial tentacles and additional smaller ones. The transverse vessels each with membrane projecting prominently into branchial cavity, and with dorsal languet present where each vessel crosses median dorsal vessel.

Stomach small, with 6 unequal longitudinal plications and a longitudinally furrowed typhlosole. Numerous small oval testes present; ovary usually small because eggs pass into oviduct when still small and develop in anterior region of oviduct. Developing embryos form longitudinal series in oviduct, with most advanced being closest to anterior end. Larvae may be 1-1.2 mm in body length.

Remarks. The zooids in the colony examined are 15 mm long, a little shorter than Van Name (1945) lists; this may be a young colony, although Ritter and Forsyth (1917) state that "zooids are somewhat smaller in southern than in northern colonies." It is not as sand-encrusted in the posterior portion as is usual. This species is distinguished from *Clavelina huntsmani* by the zooids being smaller, more slender, often bent or crooked and sand-encrusted.

Distribution. North American Pacific coast from San Juan Archipelago in Puget Sound (rare) to southern California (common), on rocks and among algal holdfasts intertidally and in shallow subtidal; Santa Maria Basin, 116 m.

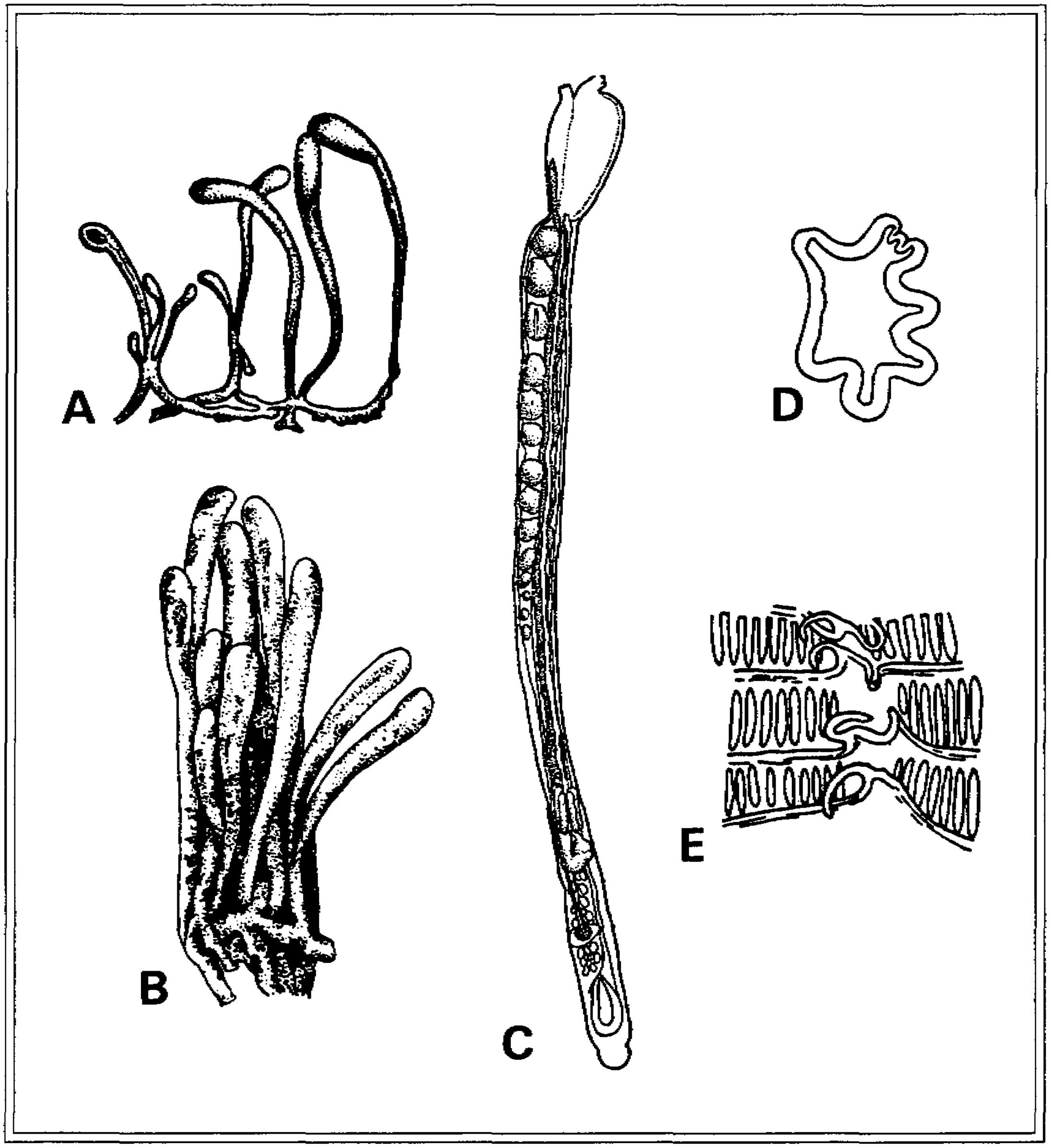

Figure 11.6. *Euherdmania claviformis.* A, young colony; B, older colony, ×2; C, zooid with embryos and larvae in oviduct, ×9; D, cross section of stomach; E, part of branchial sac with dorsal languets and adjacent stigmata, greatly enlarged. (A, C, D, E from Van Name, 1945, after Ritter, 1903; B from Johnson and Snook, 1927).

Order Phlebobranchia

Family Rhodosomatidae

Chelyosoma columbianum Huntsman, 1912

Figure 11.7 A-C

Chelyosoma columbianum Huntsman, 1912:114, 124; 1912a:126, pl. 11, figs. 2,3, pl. 16, figs. 3,5,6.—Van Name, 1945:208-209, fig. 121 (synonymy).—Lambert *et al.*, 1987:468, fig. 23.9.

Material Examined. California, Santa Maria Basin, north of Point Buchon, Sta. BRA-27, sample 1, 96-126 m, (1); off Port San Luis, Sta. BRA-25, sample 2, 64.5-72 m (3, SBMNH voucher); off Purisima Point, Sta. BRA-21, sample 1, 75-90 m (1); same transect, sample 2 (1); Sta. BRA-20, sample 2, 90-13-0. 5 m (1); Sta. BRA-16, sample 2, 91.5-123 m (2); same station, sample 4 (4); Sta. BRC-14, sample 1, 105-117 m (6); same station, sample 2 (1); same station, sample 3 (2); Sta. BRA-13, sample 1, 92-100 m (3); same station, sample 4 (1); Sta. BRC-13, sample 1, 88.5-100.5 m (2); same station, sample 2 (1); same station, sample 3 (2); off Point Arguello, Sta. BRA-6, sample 2, 54-63 m (5); same station, sample 4 (1); Sta. BRA-4, sample 2, 168-237 (4, USNM voucher); same station, sample 4 (1).—Off Point Conception, Sta. BRA-2, sample 2, 110-126 m (2).—Western Santa Barbara Channel, Sta. BRA-1, sample 2, 69-73.5 m (2); Sta. BRC-1, sample 2, 73.5-78 m (1).

Description. Adapted from Huntsman (1912a). Surface of test smooth, yellowish-brown or occasionally clear and transparent. Branchial and atrial apertures situated in a horny disk up to 15 mm in largest diameter and composed of a number of plates. Body usually much flattened and depressed, elongated in direction of about 45° with disk, and attached by broad area on side opposite disk.

Margin of disk sharper than in *Chelyosoma productum*, not raised above level of disk in contracted individuals. Disk somewhat elliptical, usually broader behind atrial opening. Apertures nearer to right side of disk than left. Plates typically with 2 ventral, 2 intermediate on left side, and 12 marginal; sometimes with additional central plate, 1 or several intermediate plates on right side, and a larger or smaller number of marginal plates; plates not showing growth lines in this species. Siphonal and marginal muscles as in *C. productum*, but with additional short thick strands crossing lines located at some distance from margin.

Usually with 2 stigmata coiled together forming each small infundibulum, but these sometimes broken into many short ones. Fifty to 100 oral tentacles, 12-22 languets. Stomach narrow, with diameter slightly greater than that of intestine; stomach wall with irregular longitudinal folds. Gonads typical for genus: ovary branched, located in intestinal loop; testes extensive, spreading over part of intestine anterior and ventral to stomach.

Remarks. *Chelyosoma columbianum* does not attain the size of *C. productum*. It reaches maturity at a smaller size, is more flattened, the surface is smoother, the margin of the disk is not definitely raised, and the disk is not symmetrical. It can also be distinguished from *C. productum* by the presence of numerous short muscle strands, usually visible through the transparent plates, connecting the two central plates as well as most of the other plates, the presence of two intermediate plates on the left side and differently arranged marginal plates, and the absence of growth lines on the plates. In Station BRA-25 (SBMNH, voucher), one specimen has a third central plate and the largest specimen has no intermediate plates but, nonetheless, appears to belong to this species.

Type Locality. Stony and shelly bottoms in 18-37 m off British Columbia (Departure Bay, Northumberland Straits, and Burrard Inlet).

Distribution. Washington, near entrance of Strait of Juan de Fuca: *Albatross* Station 2876, off Cape Flattery, 108 m, and Station 2866, 313 m (Ritter, 1913).— California, numerous stations from western Santa Barbara Channel north to Point Buchon in Santa Maria Basin, on rocks, 54-237 m.

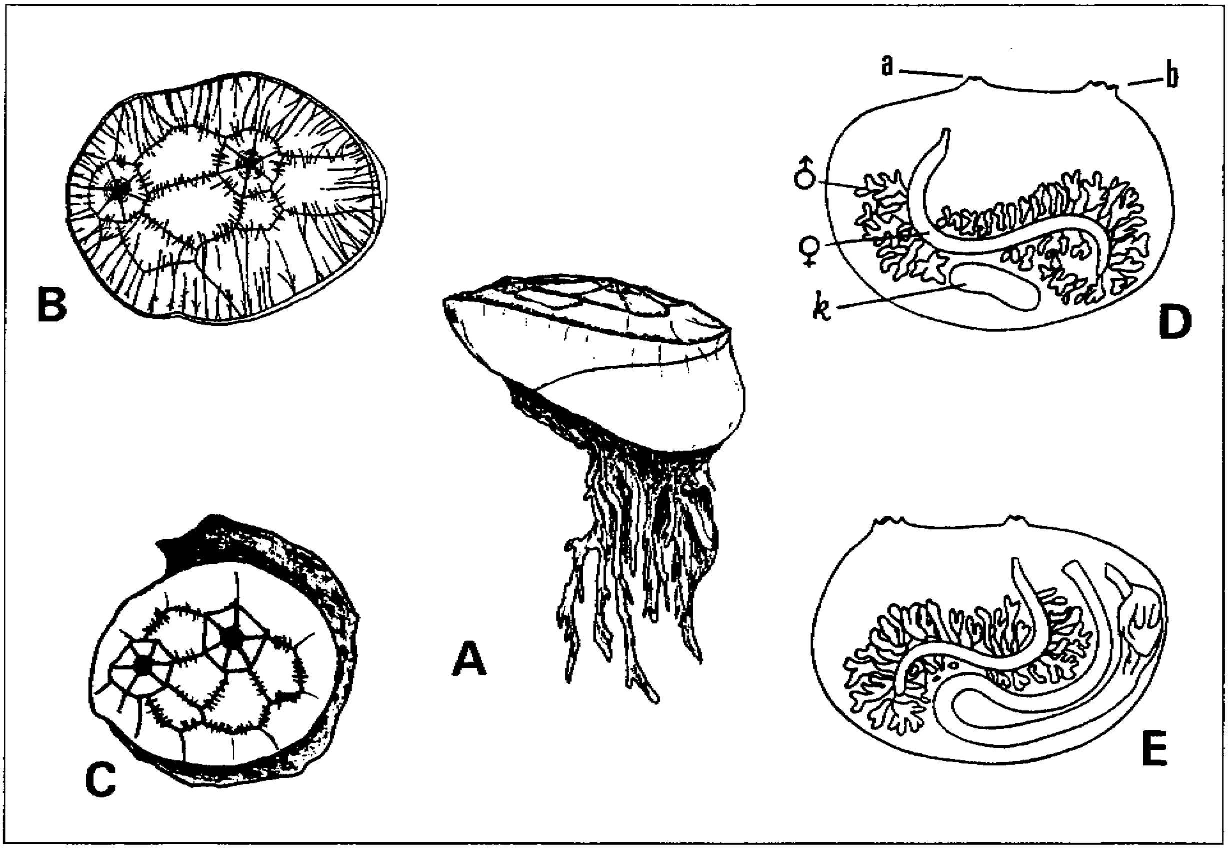

Figure 11.7. *Chelyosoma columbianum.* A, whole animal, ×2.4 (redrawn from Huntsman, 1912a); B, plates of disk surrounding apertures, showing connecting muscles, ×3 (from Van Name, 1945, after Huntsman, 1912a); C, plates of disk from another animal, with a slightly different pattern of plates, ×2.2 (redrawn from Huntsman, 1912a); *Molgula regularis.* D, left side of body; E, right side; ×5. (a - atrial siphon, b - branchial siphon, k - kidney) (from Van Name, 1945).

Order Stolidobranchia

Family Molgulidae

Molgula regularis **Ritter, 1907**

Figure 11.7 D-E

Molgula regularis Ritter, 1907:8, pl. 1, figs. 7,8.—Huntsman, 1912a:135-136.—Van Name, 1945:415-416, fig. 305.

Material Examined. California, Santa Maria Basin, off Purisima Point, Sta. BRA-14, sample 2, 105-117 m (1 voucher, SBMNH).

Description. From Ritter (1907). Body ellipsoid, very regular in outline, surface entirely covered with foraminiferous shells and sand particles clinging to numerous filiform processes of test. No definite area of attachment. Test thin and leathery, semi-transparent; no siphons visible externally. Up to 4 cm long by 2-3 cm wide. Large muscle bands of uniform length on mantle, terminating abruptly, extending longitudinally, radiating from apertures; also with a narrow zone of circular muscles around each aperture. Rest of mantle with meshwork of fine fibers.

Branchial opening far forward and 6-lobed; atrial opening 4-lobed near middle of body; branchial tentacles about 10, very branched, with smaller, simpler tentacles between larger ones. Dorsal lamina a plain-edged rather broad membrane. Branchial sac with 6 prominent folds, 5-7 longitudinal vessels on each side of each fold and about equally spaced. Infundibula large, extending full size to edge of folds; stigmata large, little curved except extending around infundibula.

Stomach on left side at extreme posterior end of animal; nearly twice as long as broad, smooth-walled or with few slight folds, bearing dark hepatic organ proximally. Intestine very long, thin, of uniform diameter throughout; rectal half forming wide semi-circle; anus without lobes. Kidney a large, brown, regular elongate central part surrounded by larger clear part and located on right side of body, close to posterior end of endostyle. Ovaries S-shaped, one on each side, long, thin, sinuously curved tubes extending along dorsal to, and bending down in front of intestinal loop on left side and kidney on right. Posterior ends bending dorsally, ending near atrial aperture. Testes lobed or branched, may be voluminously developed.

Remarks. The single specimen in this collection is small, measuring 8 mm dorsoventrally, but has a long slender ovary on each side. There is no indication that this species is viviparous.

Distribution. California: Corona Del Mar, about 10 m; off Point Loma, 122-134 m; Santa Cruz Island, 37 m; Santa Maria Basin, 105-117 m, apparently adhering to a rock; usual habitat, soft substrate.

Molgula napiformis Lambert, 1993

Figures 11.8, 11.9

Molgula napiformis Lambert, 1993:111-113, figs. 1-2.

Material Examined. California, Santa Maria Basin, MMS Phase II Program: Off Point San Luis, Sta. R-1, Jan 1988, 91 m (3 **paratypes**, USNM 35608); off Point Sal, Sta. R-8, June 1987, 90 m (paratype, CASIZ 086764); off Purisima Point, Sta. R-4, May 1988, 92 m (**holotype**, USNM 20008) and (5 **paratypes**, USNM). Sta. R-1 (3); Sta. R-4 (6); Sta. R-8 (1).

Description. Animals 2-3 mm in size, with length and width about equal. Tunic clear, transparent, covered with short hairs to which numerous sand grains firmly adhere. An extremely long branched rootlike posterior process with long hairs projecting from posterior end of tunic; additional long hairs present or absent around main process. One specimen with process or stolon about 4 times longer than animal and greatly branched, gradually tapering to very fine hair at apex.

Siphons short, widely separated; with branchial siphon more noticeable on tunic surface than atrial siphon, produced into 6 pointed processes; atrial siphon square-shaped. All 12 specimens examined with identical location of siphons; atrial siphon anteriormost, at opposite end of animal from stolon; branchial siphon about halfway back, opening laterally. Dorsal tubercle with narrow oval opening. Largest specimen (3 mm in diameter) with 7 branchial folds on left side of branchial sac, and 6 on right side; some folds not distinct in smallest specimens; with 3 longitudinal vessels per fold. Infundibula large, with only a single row between each rudimentary branchial fold. All specimens examined more or less immature, precluding determination of adult number of infundibular spirals. Dorsal lamina smooth membrane. Largest specimen with 8 large branchial tentacles, each long, slender, variably branched; additional small tentacles of various sizes occur between large ones, these difficult to count.

Mantle with widely spaced longitudinal muscles radiating from siphons over body, overlapping slightly; circular muscles well developed only on siphons. Intestine and lobed stomach located on left side of body. The kidney not developed. Gonads oval in outline, with branched or unbranched testes surrounding each ovary; left gonad secondary in intestinal loop.

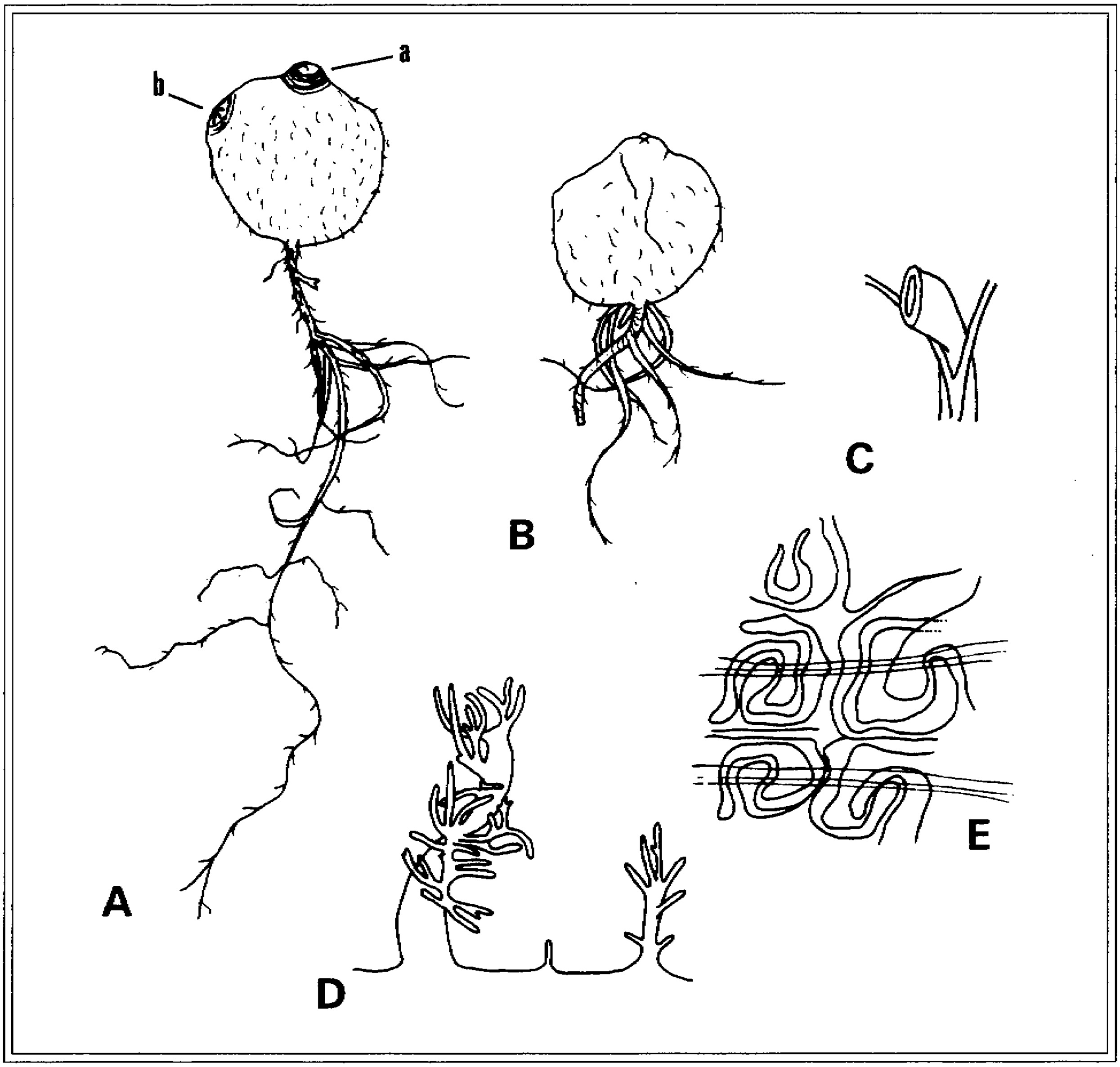

Figure 11.8. *Molgula napiformis.* A-B, whole animals, ×13 (a - atrial siphon, b - branchial siphon); C, dorsal tubercle; D, three branchial tentacles; E, detail of branchial sac. C-E greatly enlarged: (from Lambert, 1993).

Remarks. This species resembles *Molgula pugetiensis* in many of its characteristics but differs, (1) in possessing a very long branched tunic stolon and secondary processes in addition to the numerous short tunic hairs, (2) in the siphons being farther apart and shorter, and (3) in the body being attached ventrally which results in the endostyle appearing to be posterior.

Distribution. California, Santa Maria Basin, soft substrate, 90-92m.

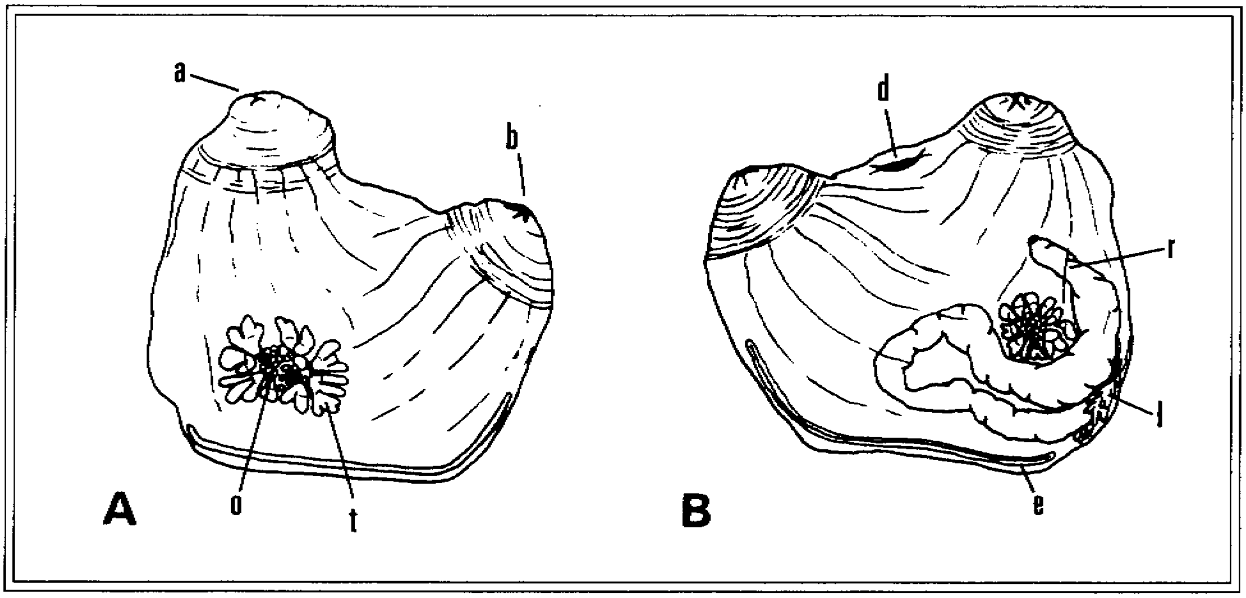

Figure 11.9. *Molgula napiformis.* A, right side of animal removed from tunic; B, left side. (a - atrial siphon, b - branchial siphon, d - dorsal ganglion, e - endostyle, l - liver, o - ovary, r - rectum, t - testis). ×32: (from Lambert, 1993).

Family Pyuridae

Boltenia polyplacoderma **Lambert, 1993**

Figure 11.10

Boltenia polyplacoderma Lambert, 1993:113-116, figs. 3-4.

Material Examined. California, Santa Maria Basin, off Purisima Point, Sta. BRA-16, sample 1, 98 m (2 **paratypes**, USNM 20010); Sta. BRA-14, , sample 2, 104 m (**paratype**, CASIZ 086766); Sta. BRA-13, sample 4, 98 m (2 **paratypes**, CASIZ 086765).—Western Santa Barbara Channel, Sta. BRA-2, sample 1, 116 m (**holotype**, SBMNH 35607).

Description. Body very flattened anteroposteriorly. Tunic thin, composed of thickened, irregular, polygonal flat-topped plates, each with numerous closely spaced annulations. Plates straight-sided, with 3-8 sides of unequal lengths. Each polygon set off from others by narrow groove in tunic; plates abutting closely, especially in contracted specimens. Inner surface of tunic covered by continuous thin sheet of white fibrous material. Apertures 4-sided, formed by 4 main triangular plates; with smaller plates forming between each of these at base of each aperture. Mantle muscles very regular, robust, with longitudinally radiating ones deeper, and circular ones around each aperture more superficial, creating beautiful regular meshwork.

Dorsal tubercle a simple oval tube, opening on right side between peripharyngeal bands. With about 18 branched oral tentacles, mostly of 2 alternating sizes; larger tentacles alternately branched, with branches containing tiny protruberances; additional very small projections occurring on trunk of main tentacles between branches. Tentacles possibly more branched in larger animals.

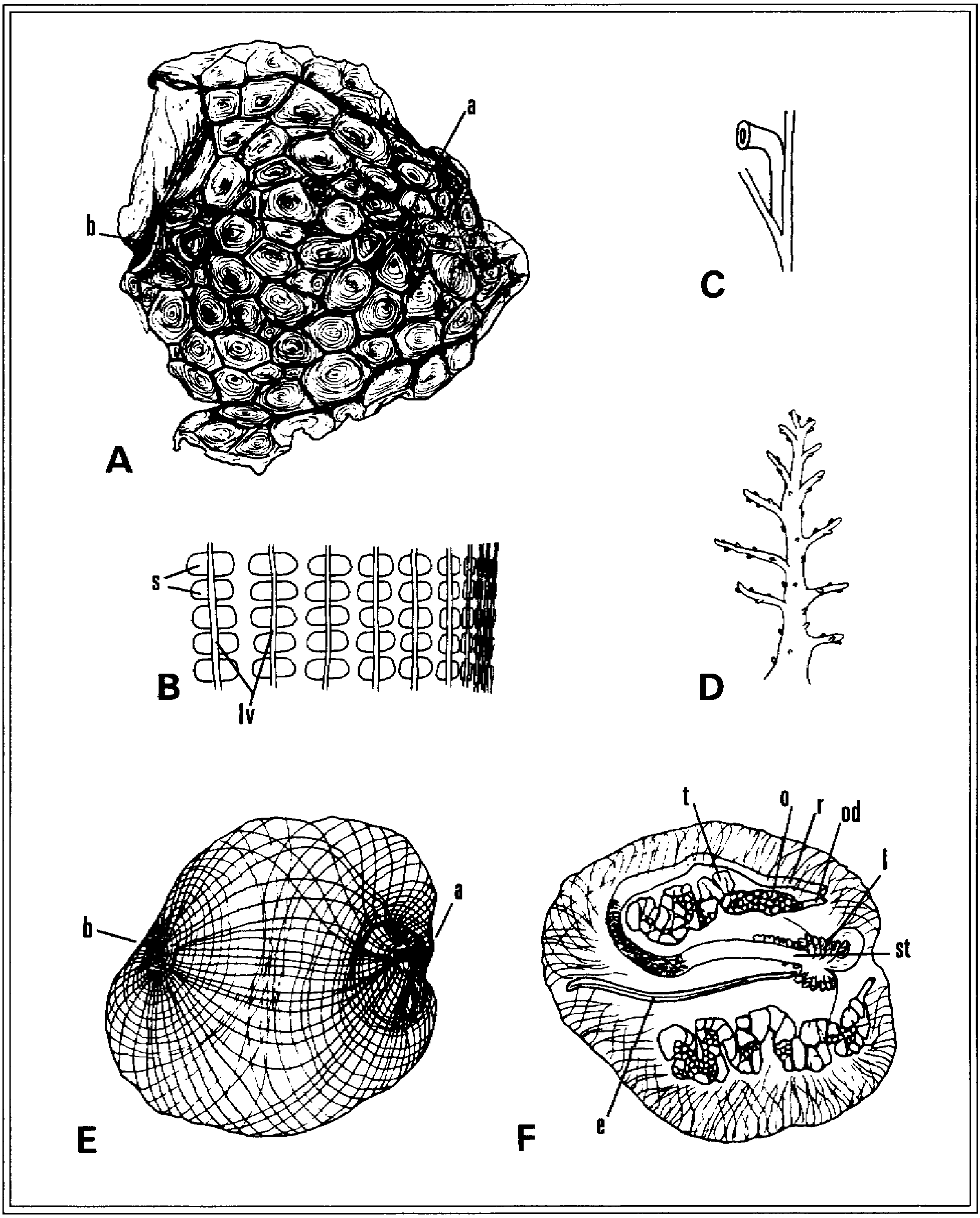

Figure 11.10. *Boltenia polyplacoderma.* A, anterior surface of tunic, ×7.2; B, detail of branchial sac; C, dorsal tubercle; D, branchial tentacle (B-D greatly enlarged); E, anterior surface of mantle showing the siphons and musculature; F, posterior view of body removed from tunic; E-F ×9.7.(a - atrial siphon, b - branchial siphon, e - endostyle, l - liver, lv - longitudinal vessels, o - ovary, od - oviduct, s - stigmata, st - stomach, r - rectum, t - testis): (from Lambert, 1993).

Branchial sac with 6 branchial folds on each side, of unequal size; second (counting from dorsal lamina) rudimentary, visible mainly as region of more closely spaced longitudinal vessels. Longitudinal vessels numerous, with about 5 between branchial folds and about 8-12 on each fold; with about 10-12 rows of stigmata between transverse vessels. Stigmata arranged with long axis running dorso-ventrally in branchial sac, characteristic for genus. Stigmata fairly short, broad, with each crossed at midpoint by very thin parastigmatic internal longitudinal vessel. Dorsal lamina cleft into series of closely spaced languets. An unidentified notodelphyid copepod found in branchial sac.

Stomach long, tubular, smooth without plications. Small lobes of the hepatic gland (liver) visible at anterior end of stomach. Intestine long, tubular, recurved; with margin of anus slightly lobed. One gonad present on each side, with left one completely within gut loop. Each ovary long, slender, with numerous irregularly lobular testes arranged alongside most of length of left ovary and along entire length of right ovary.

Sizes of specimens examined range from 3-10 mm wide as measured across siphons. All specimens very flattened, no more than 4 mm thick. All immature, but with gonads fairly well developed in larger specimens.

Remarks. The most striking difference between *Boltenia polyplacoderma* and the other *Boltenia* species is the large number of plates on the anterior and lateral regions of the tunic. It could be confused with *Chelyosoma* spp. were it not for the square four-sided apertures, branchial folds, branched oral tentacles and dorso-ventrally arranged stigmata. The tunic pattern resembles that of the European ascidian *Pyura tessellata*, so a re-examination was made of several specimens kindly provided by Dr. Ib Svane of the Kristineberg Marine Station in Sweden. The stigmata in *P. tessellata* are oriented longitudinally as in the other *Pyura* spp. *Pyura tessellata* has only four branchial folds per side in the branchial sac, a much thicker tunic, and the body is compressed laterally, while *Boltenia polyplacoderma* has six branchial folds per side and is flattened antero-posteriorly.

Distribution. Canada, Barkley Sound, Vancouver Island, Canada, 61-185 m (C.M. Young, pers. comm.). California, Santa Maria Basin, 98-116 m.

Halocynthia igaboja Oka, 1906

Figure 11.11

Halocynthia igaboja Oka, 1906:45.—Van Name, 1945:362-363 (synonymy).—Abbott, 1975:644.—Abbott and Newberry, 1980:212-213, figs. 12.40a-b.—Lambert *et al.*, 1987:469.

Material Examined. California, Santa Maria Basin, north of Point Buchon, Sta. 6, 109 m, 2 specimens; Sta. BRA-27, sample 2, 96-126 m (1); off Purisima Point, Sta. BRA-21, sample 2, 75-90 m (2); Sta. BRA-20, sample 2, 90-130.5 m (1); Sta. BRA-16, sample 2, 91.5-123 m (2, vouchers, USNM), (3 vouchers, SBMNH); Sta. BRC-13, sample 1, 92-100 m (3); Sta. BRA-13, sample 1 (1); off Point Arguello, Sta. BRA-4, sample 2, 168-237 m (4).

Description. From Van Name (1945). Body oval or globular, attached at posterior end, covered densely with non-calcareous flexible spines 10-12 mm, each long, straight, tapering, and thornlike with recurved branches along sides and circle of obliquely extending straight branches at tips. Between longer spines, many small, more-or-less branched spines extending out from test surface. Body up to 8-10 cm long, 4.5-6 cm wide. Branchial aperture terminal, with atrial openings located dorsally and one third to one half body length back. Apertures reddish during life; rest of body brownish due to adherent mud and other matter.

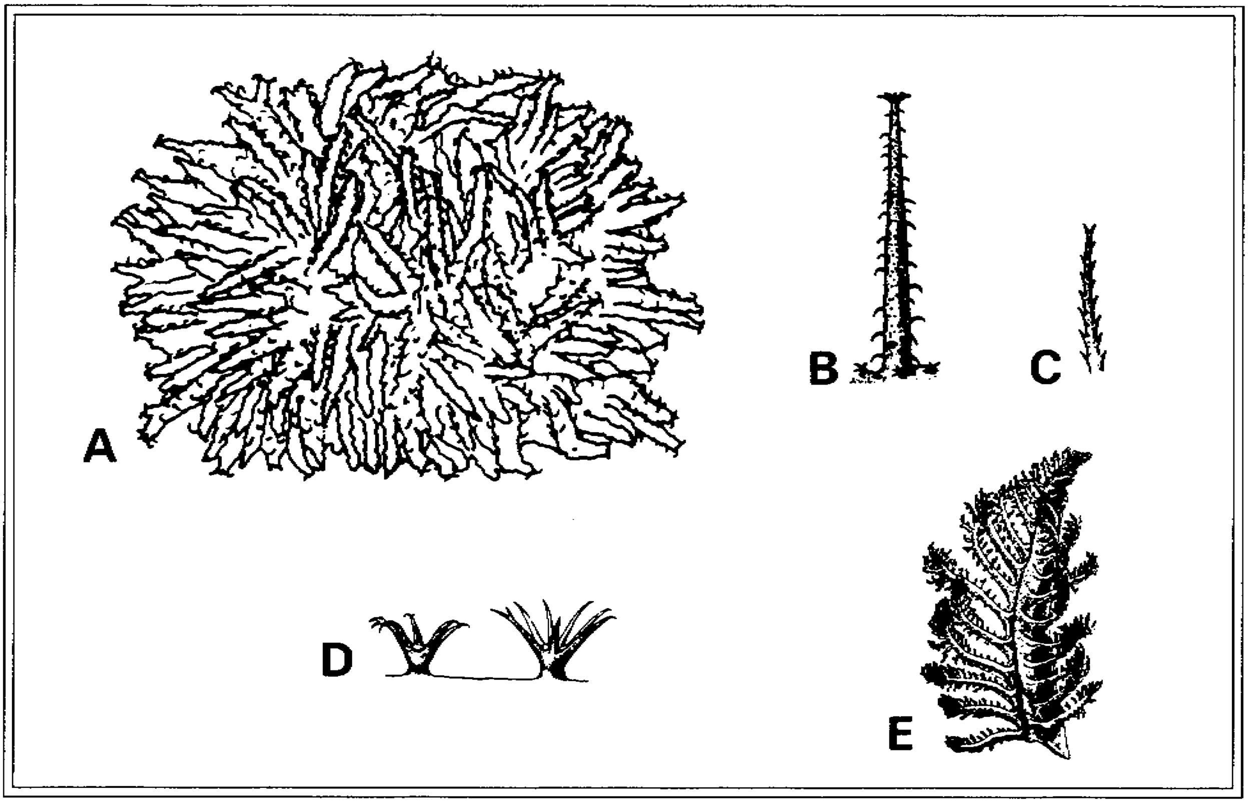

Figure 11.11. *Halocynthia igaboja.* A, whole animal, ×2.3 (redrawn from Abbott and Newberry, 1980); B, a large tunic spine, ×4; C, a smaller spine without terminal whorl of spinelets, ×4; D, two of the short whorled spines, ×27; E, a single branched oral tentacle, greatly enlarged. (B-E from Ritter, 1907).

Mantle thin, transparent, with large muscle bands extending nearly entire body length from bases of siphons and crossing obliquely. Oral tentacles 12-50, with larger ones pinnately branched. Branchial sac with 9-10 folds per side and sometimes with poorly developed eleventh fold on one or both sides. Folds with 20 or more longitudinal vessels, but only 1 vessel on each interval between folds.

Two to 16 gonads on right side, 5-14 on the left, each consisting of an elongate, tubular, sinuous ovary with numerous small testes. Gonads positioned antero-posteriorly, with anterior ends extending across intestinal loop.

Remarks. The test spines form a mat that traps sediment, in some cases so much that the siphonal openings are hidden and the ascidian resembles a fuzzy ball of mud. This species is distinguished from another spiny solitary ascidian, *Boltenia echinata*, by the longitudinal stigmata, the larger number of branchial folds, and the 4-7 gonads per side (*B. echinata* has just one on each side). The species is more common in colder, well-circulated waters.

Distribution. Japan.—North America, Alaska to southern California; low intertidal to 165 m, on rock, shelly and gravelly bottoms; Santa Maria Basin, 75-237 m.

Pyura haustor (Stimpson, 1864)

Figures 11.2, 11.12

Cynthia haustor Stimpson, 1864:159.

Pyura haustor Hartmeyer, 1909-1911:1340.—Van Name, 1945:338-340, pl. 31 figs. 3,4, text fig. 223 (synonymy).—Abbott, 1975:646, 653.—Abbott and Newberry, 1980:210, fig. 12.37a-b.—Lambert *et al.*, 1987:472, fig. 23.5.

Material Examined. California, Santa Maria Basin, north of Point Buchon, Sta. BRA-27, sample 1, 96-126m (1); off Purisima Point, Sta. BRA-20, sample 4, 90-130.5 m (1); Sta. BRA-16, sample 4, 91.5-123 m (2 vouchers, SBMNH), sample 1 (5); Sta. BRA-13, 1 sample, 92-100 m (1); Sta. BRC-13, 88.5-100.5m (voucher, USNM).

Description. From Van Name (1945). Body taller than wide, 5 cm long or more. Siphons usually conspicuous tubes, with branchial tubes larger, longer, directed obliquely forward or upward. Atrial tube arising near anterior end. Tubes vary greatly in length, from very short to longer than body width, sometimes crooked. Test red or reddish orange, tough, leathery, often discolored with mud and completely encrusted with debris or other organisms except near ends of siphons. Test coarsely wrinkled, often elevated into high, sharply defined ridges that meet and cross each other in various directions or sometimes run roughly parallel and which may have irregular tubercles, giving test appearance of coverinig by network of irregular polygonal meshes. Surface smoother near ends of siphons, covered with minute slender spines 0.25-0.5 mm in length, lacking elsewhere on body.

On mantle, prominent muscle bands extend down sides of body from bases of siphons, these irregularly crossed by many narrow, superficial bands; each siphon with strong ring muscles at base.

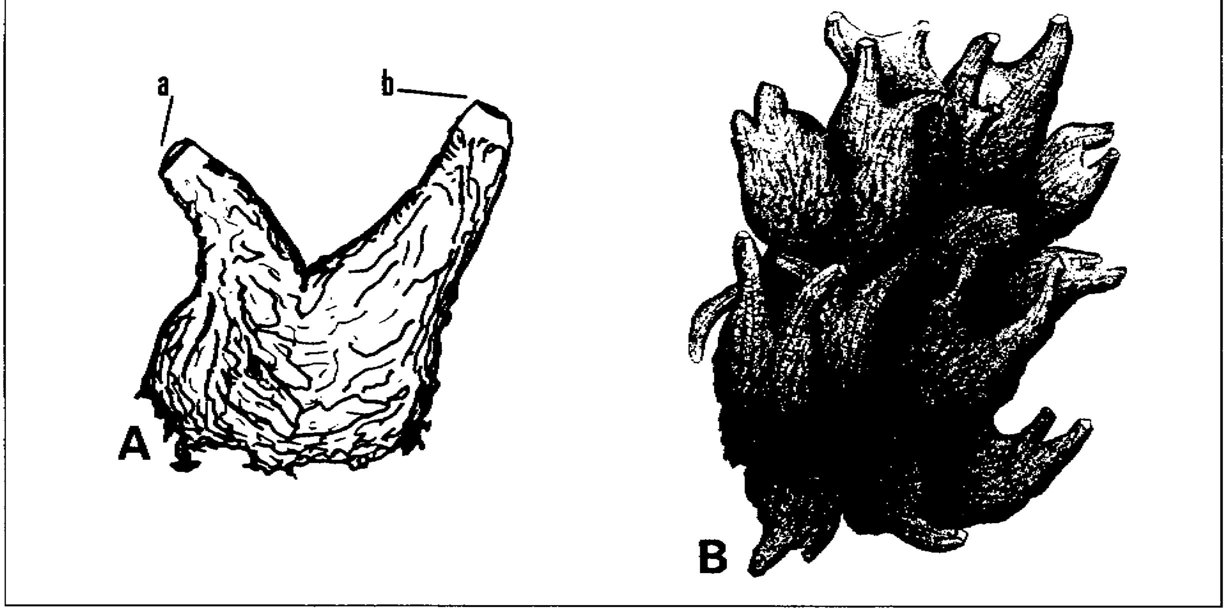

Figure 11.12. *Pyura haustor.* A, whole animal, life size (redrawn from Kozloff, 1990) (a - atrial siphon, b - branchial siphon); B, a clump of animals, ×0.4 (from Herdman, 1898).

Oral tentacles 15-30, typically 21, in species from British Columbia and Puget Sound, 42 in specimens from south of Point Conception, irregular in size and distribution, compound pinnate and sometimes extensively branched. Branchial sac with 6 rather wide folds on each side, each with many closely spaced longitudinal vessels; transverse vessels numerous, of different sizes.

Digestive tract forming an elongate, widely open loop. Hepatic organ or liver large, with several extensively branched glands arising separately from stomach. Individual sacs of gonads irregular in size and shape; when numerous may be crowded out of normal serial position along common duct, forming more than 2 rows or appearing irregularly distributed on inner surface of mantle; large specimens with 50 or more gonads on right side, fewer on left.

Distribution. British Columbia south to the Mexican border. Abundant intertidally and in shallow subtidal, often growing in huge masses on rocks, pilings and floats. Subtidally occurring rarely as deep as 279 m; Santa Maria Basin 88-123 m, on hard substrate.

Family Styelida

***Styela gibbsii* (Stimpson, 1864)**

Figure 11.13 A-C

Cynthia gibbsii Stimpson, 1864:159.

Styela gibbsii Huntsman, 1912a:149, pl. 12, fig. 5, pl. 19, figs. 10, 11.—Van Name, 1945:313-314, fig. 208 (synonymy).—Abbott, 1975:646.—Lambert *et al.*, 1987:472.

Material Examined. California, Santa Maria Basin, off Point Arguello, Sta. BRA-6, sample 2, 61 m (1 voucher, USNM).

Description. From Van Name (1945). Body elongate-cylindrical, both apertures on short siphons located close together on anterior end, atrial aperture slightly posterior to branchial aperture. Attachment at posterior end, somewhat narrow, with few rootlike processes. Test tough, with outer surface bearing numerous wrinkles; wrinkles mainly longitudinal or oblique, generally crossed by less prominent circular wrinkles on some parts of body. At anterior end and on bases of siphons, wrinkles break up into tubercles. Color brown or brownish yellow, more-or-less discolored with mud, becoming reddish around apertures. Size up to 6 cm long, 1.5-2 cm wide; smaller specimens may be proportionately wider. Often grows in clusters.

Mantle thin, with inconspicuous musculature. Branchial tentacles 25-40, unbranched. Branchial sac with 4 well-developed folds on each side, with first (most dorsal) usually highest, third next highest. Internal longitudinal vessels numerous. Transverse vessels quite regular and of about 4 orders.

Stomach elliptical, about twice as long as wide, with up to 30 longitudinal folds. Intestine bending parallel to stomach, then bending forward again forming rectum. Margin of anus lobed.

Two gonads per side; ovaries each long, moderately straight and tubular; testes numerous small, somewhat elongate and irregularly shaped along posterior third or half of ovary; ovaries longer on right side of body, extending for most of body length; on left side, ovaries shorter, more anteriorly located, especially ventral one.

Distribution. British Columbia to southern California, usually in shallow water in northern part of range but deeper in southern part of range, to 91 m, on rocks; Santa Maria Basin, 61 m.

Styela milleri Ritter, 1907

Figure 11.13 D-E

Styela milleri Ritter, 1907:21.—Van Name, 1945:308-309, fig. 204.

Tethyum milleri Hartmeyer, 1912:374, 378.

Material Examined. California, Santa Maria Basin, off Point San Luis, Sta. BRA-25, sample 2, 64-5-72 m (2); off Purisima Point, Sta. BRA-20, sample 3, 90-130.5 m (1, SBMNH); Sta. BRA-14, sample 232, 96-105 m (1 voucher, USNM); Sta. BRC-13, sample 3, 88.5-100.5 m (1).—Western Santa Barbara Channel, Sta. BRC-1, sample 2, 69-73.5 m (2).

Description. From Ritter (1907) and Van Name (1945). Body cylindrical to ovoid or dome-shaped; with surface broken by few irregular low wrinkles anteriorly and large patches of warty thickenings posteriorly; scattered minute spines may be present. Color yellowish brown, warty areas darker. Test very thin, parchment-like, readily detachable from mantle, dull white on inner surface. Posterior anchoring part of test spreading out in thin border onto attaching surface; area of attachment with many short filamentous processes. Mantle thin, with longitudinal and circular muscle fibers uniformly distributed, not in definite bands. Size small: Ritter's single type specimen 22 mm long (incorrectly given as 22 cm), 12 mm wide.

No siphons present, but apertures distinct, both 4-lobed, at anterior end. About 30 oral tentacles present, of several lengths. Four branchial folds per side, all broad, more like undulations except one next to endostyle on right side; 2 folds on each side next to endostyle drawn out anteriorly into long processes. Internal longitudinal vessels numerous, 140 or more per side in adults, closely crowded on and between folds (18-20 vessels on largest folds). Dorsal lamina broad thin membrane; endostyle heavy, irregularly tortuous. Stomach elongate, melon-shaped, with numerous ridges or folds; proximal part of intestine short, bent closely back on stomach; longer rectal section extending forward dorsally, almost to atrial aperture. Ovary a single elongated cylindrical mass on each side, extending anterodorsally to posteroventrally. Testes in crowded group around posterior end of ovaries.

Remarks. Specimens in this collection are all smaller than Ritter's (1907) holotype and differently shaped, being flattened anteroposteriorly, the largest one 13 mm wide and 5 mm tall; they correspond more to Van Name (1945: Fig. 204). No siphons are visible externally, but when removed from the test the body has long siphons; this might indicate that they were retracted when preserved. The test is sand encrusted, although this character was not listed by either Ritter or Van Name. The test is thin and parchment-like, corresponding to the species description. Gonads are very large relative to the small body size, especially the testes.

Distribution. This is an abyssal Pacific species, recorded from red or gray mud in depths of 825-4074 m off southern California, the Bay of Panama, Peru, and possibly southern Chile. In the current survey this species was collected from the Santa Maria Basin and Western Santa Barbara Channel, 64-130 m.

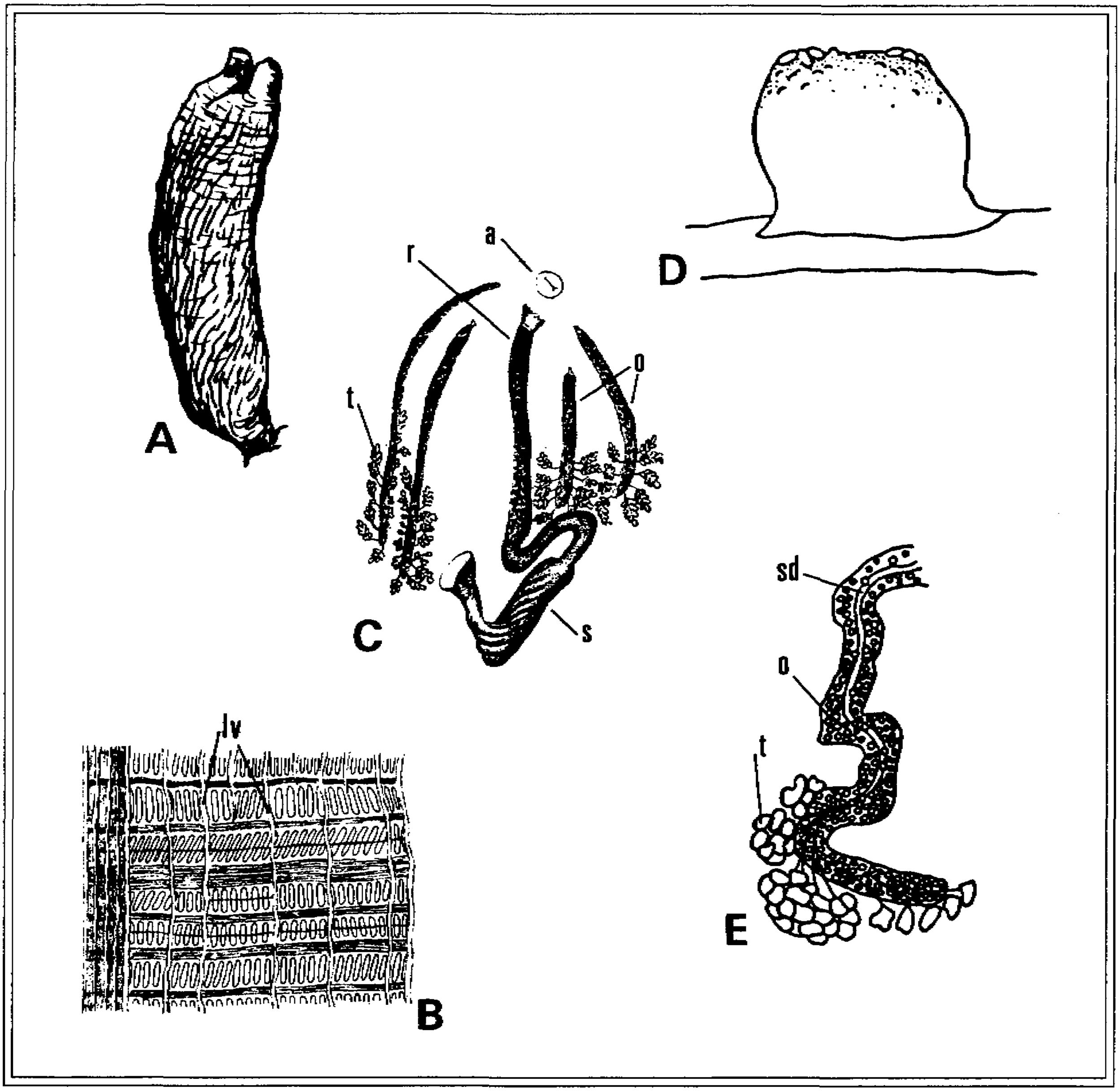

Figure 11.13. *Styela gibbsii*. A, whole animal, ×1.4 (redrawn from Huntsman, 1912a); B, piece of branchial sac, ×31; C, alimentary canal and gonads, ×1.6 (B and C from Herdman 1898); *Styela milleri* (from Van Name, 1945). D, body outline, ×2; E, terminal part of gonad, ×6. (a - atrial siphon, lv - longitudinal vessels, o - ovary, r - rectum, s - stomach, sd - sperm duct, t - testis.

Styela tesseris Lambert, 1993

Figures 11.14, 11.15

Styela tesseris Lambert, 1993:116-118, figs. 5-6.

Material Examined. California, Santa Maria Basin, off Purisima Point, Sta. BRA-21, sample 2, 75-90 m (**holotype**, USNM 20011); off Point Arguello, Sta. BRA-6, sample 2, 54-63 m (**paratype**, USNM 20012).

Description. Holotype and paratype both immature; paratype 2 mm long, holotype 15 mm long, 8 mm wide across siphons. Body flattened laterally; tunic with distinctive, irregularly tessellate pattern, with flat-topped plates raised and separated from one another by furrows over entire tunic except adjacent to siphonal openings, where tunic smooth. Pattern resembles mosaic tilework with narrow groove between tiles. Tunic between tessellations flexible, changing shape as tunic bends or moves. Platelike tunic thickenings may overlap at edges in contracted areas of tunic. Furrow between each raised area presumably allowing for great expansion and contraction. Tunic thick, with smooth inner white layer; with outer tessellations not penetrating to white layer. At posterior end of both animals, tunic forms wide, short, laterally flattened stalk; body parts not extending into this region; with small scattered sand grains embedded superficially in tunic. Tessellations largest, most pronounced anteriorly; posteriorly becoming progressively smaller, flatter, less distinct; absent on stalk region; tesselations running in more-or-less horizontal pattern across tunic dorsoventrally, especially in more posterior region.

Both siphons with square openings, branchial siphon terminal, atrial siphon slightly posterior to branchiae. On mantle, numerous very fine longitudinal muscles extend full length of body, with only few on siphons. Deeper circular muscles predominate on siphons. Opening of dorsal tubercle simple oval slit. With about 40 long slender unbranched oral tentacles, mostly of 2 alternating sizes, and a large number of very tiny simple atrial tentacles. Dorsal lamina a wide flat membrane. Branchial sac with 4 folds per side, with following numbers of longitudinal vessels (numbers in parentheses referring to vessels on folds): Right side, counting from the dorsal lamina to the ventral endostyle: 6 (6) 3 (6) 3 (6) 5 (5) 3; left side, starting from dorsal lamina: 2 (6) 3 (6) 3 (6) 3 (6) 3. On flat areas of sac, 4 stigmata between internal longitudinal vessels; each stigma crossed at mid-point by very thin parastigmatic transverse vessel.

Stomach elongate, with about 23 longitudinal folds or ridges. Proximal part of intestine folding back alongside stomach; distal portion curving anteriorly toward atrial siphon. Hepatic gland absent. In larger animal 2 thin-walled gastro-intestinal connections (pyloric ducts) present within first intestinal curve; one much wider than second. With single pyloric duct in smaller animal.

Holotype with 2 long, tubular ovaries on each side, with few irregularly lobed testes grouped around posterior end of left anterior ovary, which is the most fully developed. Iindividual sperm ducts forming common sperm duct running along surface of ovary to end near mouth of oviduct and base of atrial siphon; right anterior ovary least developed, without eggs. Gonads not developed in smallest specimen. Numerous endocarps of various sizes attached to inner side of body wall around posterior regions of gonads and stomach.

Remarks. The most obvious way in which *Styela tesseris* differs from all the described NE Pacific *Styela* species is the tessellated pattern of the tunic. This species most closely resembles *S. atlantica* , from deeper water, but never recorded from the Pacific. *Styela tesseris* differs from *S. atlantica* in the tessellated pattern on the tunic, the fewer internal longitudinal vessels on and between the folds in the branchial sac, and the rather wide dorsal lamina even in these immature specimens. In addition, the dorsal tubercle is an oval slit without inrolled horns.

Distribution. California, Santa Maria Basin, 54-90 m, hard substrate.

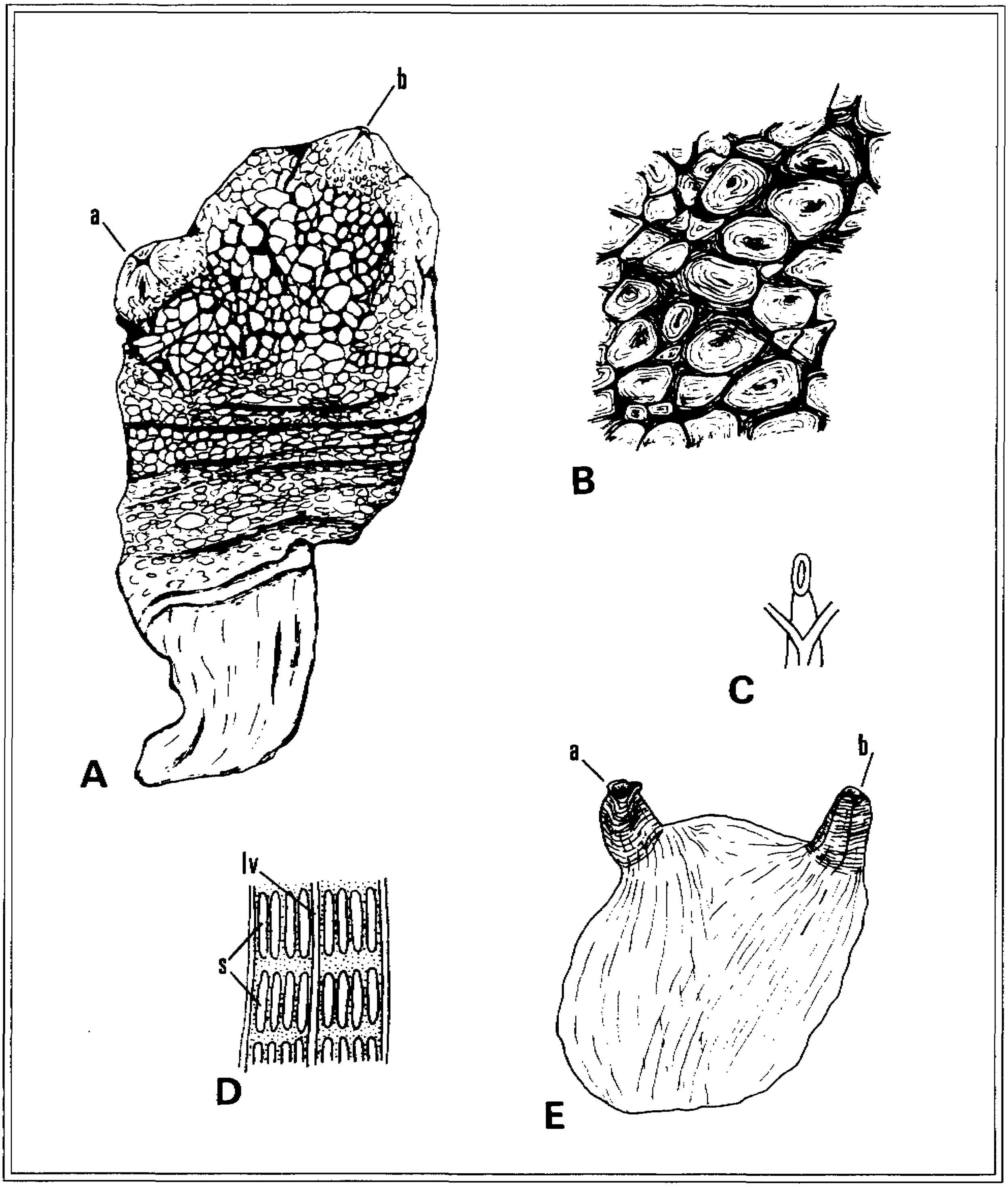

Figure 11.14. *Styela tesseris.* A, whole animal, ×7; B, detail of tunic, ×23; C, dorsal tubercle; D, small piece of branchial sac (C-D greatly enlarged); E, body removed from tunic, right side, ×7. (a - atrial siphon, b - branchial siphon, lv - longitudinal vessel, s - stigmata): (from Lambert, 1993).

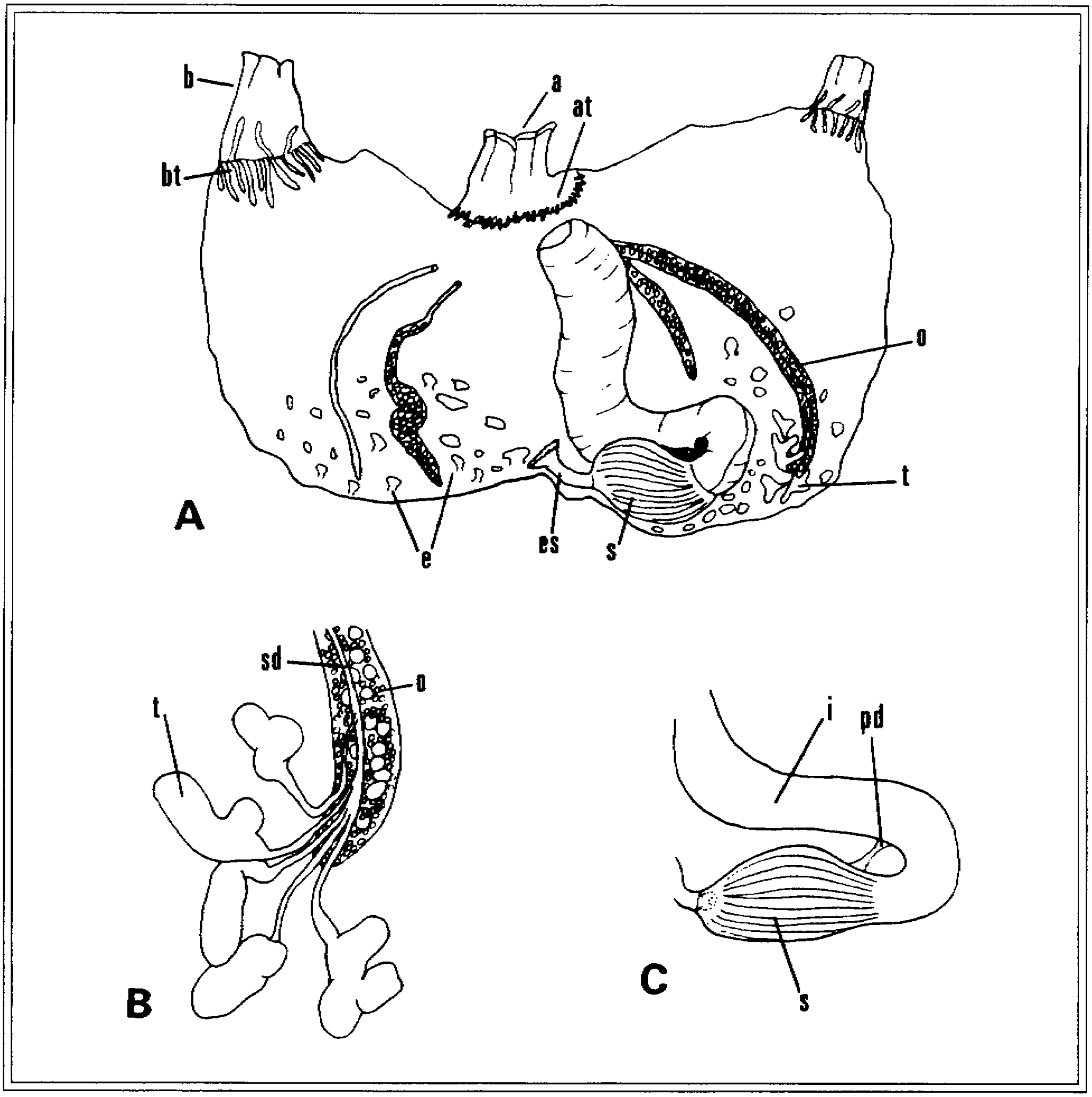

Figure 11.15. *Styela tesseris.* A, animal opened to show internal anatomy, ×9; B, enlarged detail of gonad; C, detail of stomach and anterior intestine showing the delicate connection between them. (a - atrial siphon, at - atrial tentacles, b - branchial siphon, bt - branchial tentacles, e - endocarps, es - esophagus, i - intestine, o - ovary, pd - pyloric duct, s - stomach, sd - sperm duct, t - testis): (from Lambert, 1993).

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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.

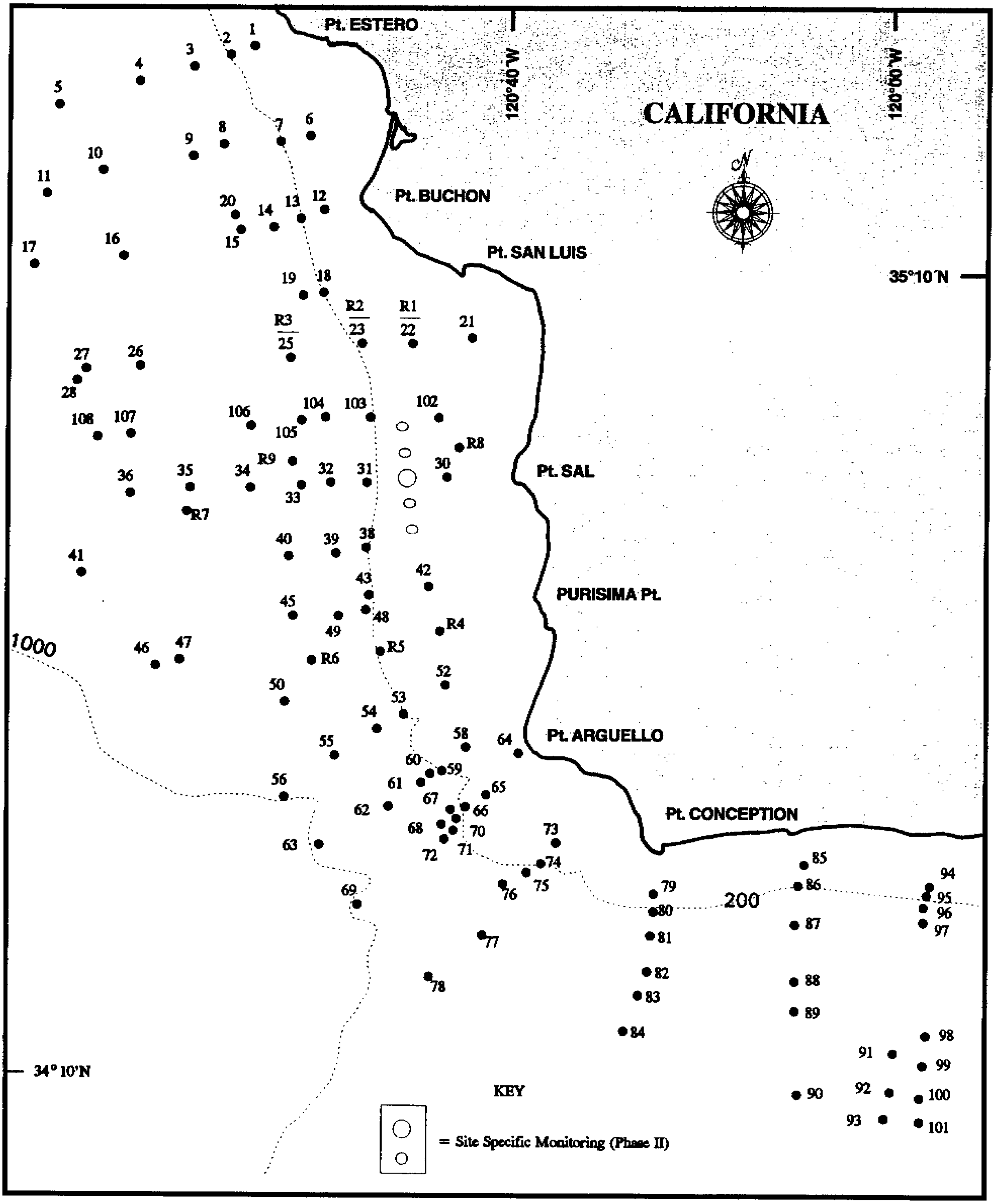

Figure A.1. Map showing location of soft-substrate stations from the Phase I Reconnaissance and Phase II Monitoring Programs.

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 Latitude	Longitude	End Latitude	Longitude	Depth (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

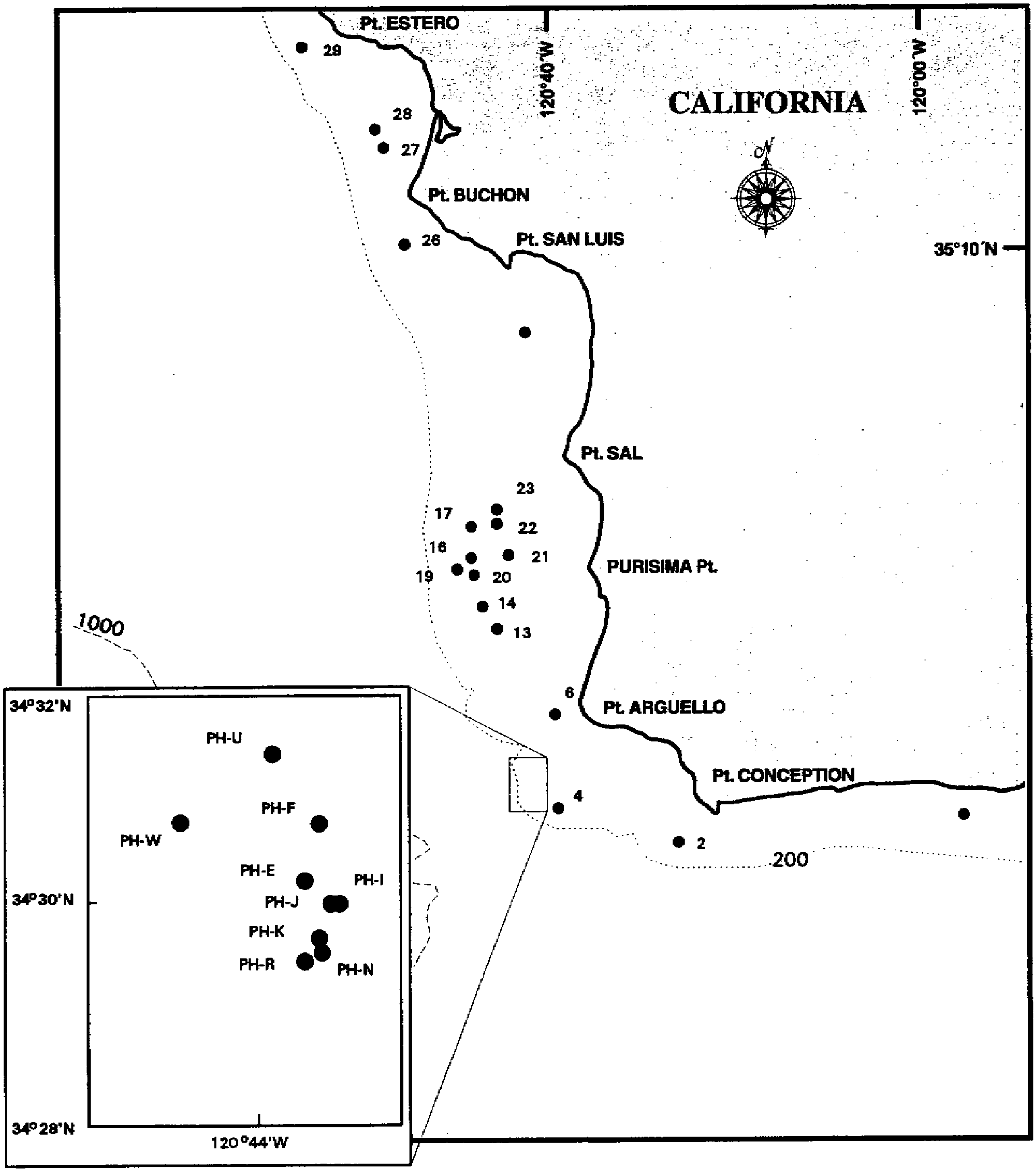

Figure A.2. Map showing location of hard-substrate stations from the Phase I Reconnaissance and Phase II Monitoring Programs. Phase II stations are indicated in the inset.

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.