OCS Report
MMS 94-0025

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

FINAL REPORT
Volume 4 of 14

The Annelida Part 1 Oligochaeta and Polychaeta: Phyllodocida
(Phyllodocidae to Paralacydoniidae)

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

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FINAL REPORT
Volume 4 of 14

The Annelida Part 1 — Oligochaeta and Polychaeta: Phyllodocida (Phyllodocidae to Paralacydoniidae)

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Pacific OCS Region
770 Paseo Camarillo
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DISCLAIMER

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TAXONOMIC DISCLAIMER

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

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

OBJECTIVES: The objectives of Volume 4 are to introduce the Phylum Annelida. Included in this volume is a chapter on the Oligochaeta, an Introduction to the Polychaeta, and taxonomic treatments of 11 polychaete families: Phyllodocidae, Lacydoniidae, Pilargidae, Nautiliniellidae, Hesionidae, Glyceridae, Goniadidae, Nereididae, Nephtyidae, Paralacydoniidae, and Sphaerodoridae. The remaining polychaete families will be treated in Volumes 5-7.

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DESCRIPTION: The first annelid volume includes an annelid introduction, an oligochaete chapter, a polychaete introduction, and 11 chapters that deal with individual polychaete families. Additional polychaete families will be treated in three subsequent volumes. The oligochaete chapter is intended to introduce readers to methods of collection and study of this interesting group of marine organisms in addition to providing keys and description for 11 species. The introductory polychaete chapter provides a detailed review of polychaete morphology and biology as well as an illustrated key to the benthic polychaete families found in the waters off California. The 11 individual chapters dealing with different polychaete families provide descriptions, illustrations, and keys. In addition, taxonomic problems and comparisons with related species are presented.

SIGNIFICANT CONCLUSIONS: The chapter on oligochaetes represents the first to deal with offshore species in California. The study methods and keys will permit users to identify these difficult organisms for the first time. Five of the oligochaetes were new to science and described in a separate paper. The introductory polychaete chapter includes considerable detail on the morphology, biology, and classification of polychaetes that will be important in orienting users to the complexity of this taxon. The key to the families is an essential starting point for students interested in learning about polychaetes. Six new species of Phyllodocidae were discovered in the collections and described in a separate paper. One new species of *Lacydonia* is described and represents the first published record of the family Lacydoniidae from California. The chapters on the Glyceridae and Goniadidae include detailed descriptions and illustrations for 11 species. Among the five species of Sphaerodoridae, one was found to be new to science and described separately. Of nine species of Hesionidae, two were new to science and described separately. Nine species of Pilargidae were described and illustrated. The first nautiliniellid polychaete to be discovered from California came from the Santa Maria Basin. This new species and new genus were described in a separate publication. Seven species of the Nereididae in four genera are treated, one of species of which was new to science and described in a separate paper. Among the Nephtyidae, 13 species in three genera are treated, one species of which was new to science and described separately. A brief description of the widespread *Paralacydonia paradoxa* is presented.

STUDY RESULTS: The annelids treated in this volume include 11 species of oligochaetes and 81 species of polychaetes distributed over 11 families. Five of the oligochaetes were new to science and were described in three separate papers. The introductory chapter on polychaetes includes a summary of polychaete morphology, a review of the classification of polychaetes, an overview of polychaete reproduction and development, biology and ecology, methods of collection and preservation, laboratory methods, a glossary of technical terms, and key to the families of polychaetes that occur off California. Twenty-seven species of Phyllodocidae are treated. Of these, six were new to science and were described in a separate paper. Several other rare or poorly known species were redescribed and newly illustrated. The eight polychaete families treated in this volume all belong to the Order Phyllodocida. Many of the treatments of individual species include updated descriptions, new illustrations, and clarification of taxonomic issues. The chapter on the Phyllodocidae includes keys to most of the species known from California. Six new species encountered as part of this study were previously described in a separate paper. The small chapter on the Lacydoniidae provides a review of the global distribution of approximately nine species in this poorly known and obscure family. A new species from the northern California continental slope is described, and represents the first record of the genus *Lacydonia* for California. The family Glyceridae includes descriptions and keys to five species of *Glycera* and one species of *Hemipodus*. The chapter on the Goniadidae includes four species of *Goniada* and one of *Glycinde*. The Sphaerodoridae are represented by five species in three genera. *Sphaerodoropsis sexantennella* was a new species that was described in a separate paper by Dr. Jerry Kudenov. The chapter on the Hesionidae includes nine species in four

genera. Two of these species, *Gyptis plurisetis* and *Podarkeopsis perkinsi* were described by Dr. Brigitte Hilbig in a separate paper. The chapter on the Pilargidae includes descriptions and keys to nine species from three genera. In addition, other genera that are likely to be found in California are discussed. The small chapter on the Nautiliniellidae includes a review of the known species and a description of *Miura spinosa*, a new genus and species from the Santa Maria Basin that had been described by Dr. James Blake in a separate paper. Seven species of Nereididae are distributed among four genera. Among the species treated, *Nereis ligulata*, described by Dr. Hilbig in a separate paper, comes from relatively deep upper slope depths. This species is part of characteristic deep-sea species group having elongated notopodial ligules in posterior parapodia. The coverage of the nephtyids includes most of the species known to occur off California. The new species, *Nephtys signifera* Hilbig appears to be widespread throughout the Santa Maria Basin.

STUDY PRODUCT: Blake, J.A. and B. Hilbig (Editors). 1994. Taxonomic Atlas of the Santa Maria Basin and Western Santa Barbara Channel. Volume 4. The Annelida Part 1—Oligochaeta and Polychaeta: Phyllodocida (Phyllodocidae to Paralacydoniidae). 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 93-0030. Contract No. 14-35-0001-30484.

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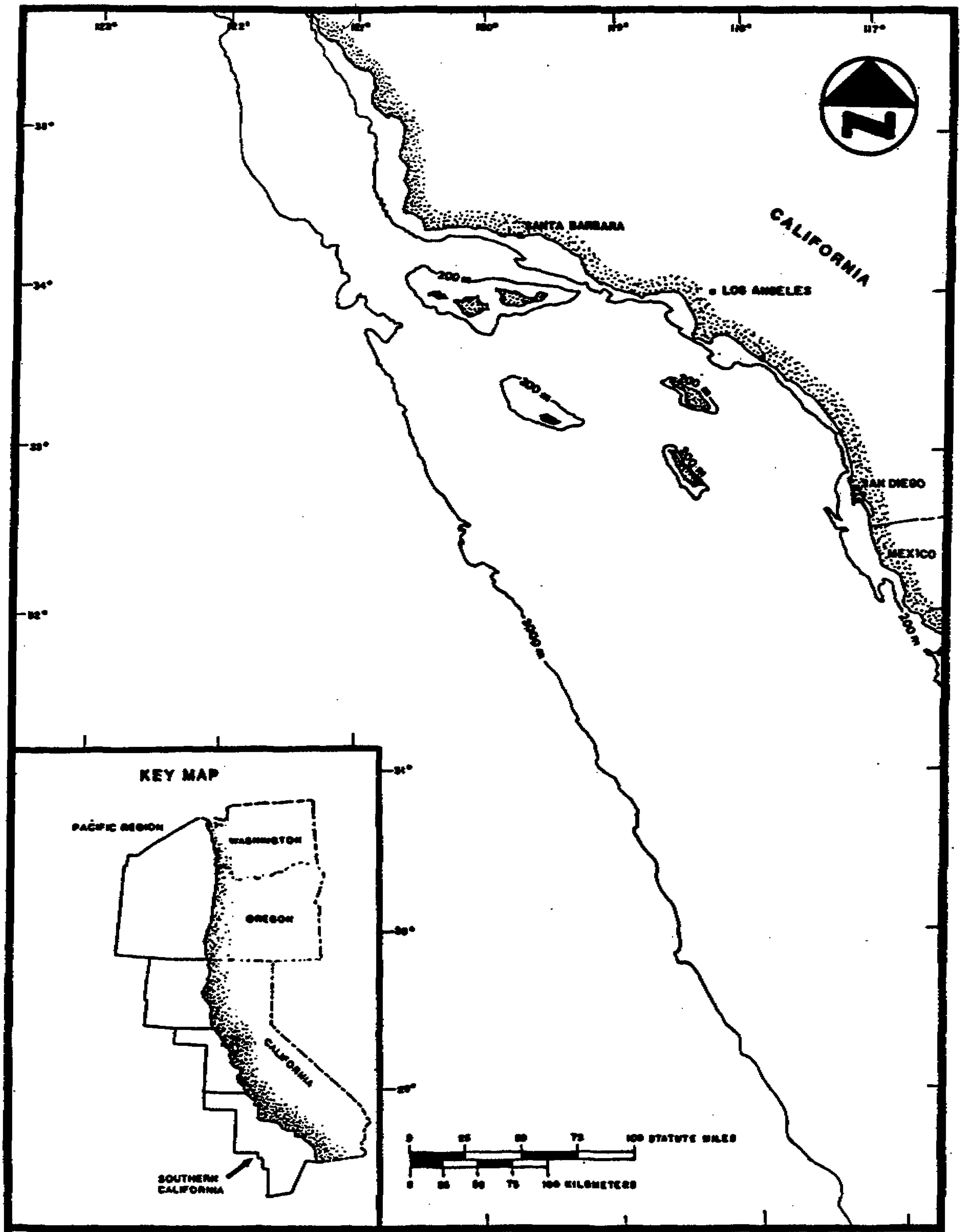

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16. Abstract (Limit: 200 words)

The first annelid volume includes an annelid introduction, an oligochaete chapter, an introductory polychaete chapter, and 11 chapters that deal with individual polychaete families. The chapter on oligochaetes represents the first to deal with offshore species in California. The study methods and keys will permit users to identify these difficult organisms for the first time. Five of the 11 oligochaetes treated were new to science and described in separate papers. The introductory polychaete chapter includes detail on the morphology, biology, and classification of polychaetes that will be important in orienting users to their complexity. In addition, the key to the families is an essential starting point for students interested in learning to identify polychaetes. Eighty-one species of polychaetes are treated in the 11 chapters dealing with individual families. Twenty-seven species of Phyllodocidae were treated in the study. Six of these were determined to be new species and described in a separate paper. One new species of *Lacydonia* is described in the Atlas and represents the first published record of the family Lacydoniidae from California. The chapters on the Glyceridae and Goniadidae include detailed descriptions and illustrations for 11 species. Among the five species of Sphaerodoridae, one was found to be new to science and described separately. Of nine species of Hesionidae, two were new to science and described separately. Nine species of Pilargidae were described and illustrated. The first nautiliniellid polychaete to be discovered from California came from the Santa Maria Basin. This new species and new genus were described in a separate publication. Two new species were also described separately for the Nereididae and Nephytidae, respectively.

17. Document Analysis a. Descriptors

Marine invertebrates, Annelida, Oligochaeta, Tubificidae, Enchytraeidae, Polychaeta, Phyllodocidae, Lacydoniidae, Pilargidae, Nautiliniellidae, Hesionidae, Glyceridae, Goniadidae, Sphaerodoridae, Nereididae, Nephytidae, Paralacydoniidae, taxonomy, California, Santa Maria Basin, Santa Barbara Channel, continental shelf.

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Some previously unpublished illustrations prepared by Ms. Marie Litterer for Dr. Marian H. Pettibone have been included to help illustrate the family key. Dr. Pettibone had originally donated these illustrations for a key to east coast polychaetes. Many of the illustrations used in this volume were borrowed or altered from a variety of original sources. These sources have been acknowledged at the end of each figure legend. Figures which are not acknowledged are original illustrations prepared by the authors.

In addition to collections gathered as part of the MMS Phase I and II programs, additional relevant and comparative materials were made available to the authors for study. These included specimens from other MMS programs such as the Southern California BLM Benchmark Program, the Georges Bank Benthic Infauna Monitoring Program, and the U.S. Atlantic Slope and Rise Program and a recently completed continental slope survey off northern California in the Gulf of the Farallones that was sponsored by the U.S Navy. In addition, numerous collections gathered by Drs. James A. Blake and Keith Woodwick in the 1960's and 1970's from along the central California coast were made available for study. Many of these latter collections will eventually be deposited at the Los Angeles County Museum of Natural History. Mr. Ron Velarde provided some important phyllodocids from off San Diego. Mr. T. Parker provided oligochaetes from off Los Angeles. Finally, curators at numerous museums have generously loaned relevant type and non-type specimens from their collections. The authors wish to thank these individuals and institutions for their assistance.

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LIST OF ACRONYMS

AMNH	American Museum of Natural History (New York).
ANSP	Academy of Natural Sciences, Philadelphia.
BMNH	The Natural History Museum (London).
CAS	California Academy of Sciences (San Francisco).
FSBC	Florida Department of Natural Resources Marine Research Laboratory, Invertebrate Reference Collections.
LACM	Los Angeles County Museum of Natural History. Includes the type collections formerly lodged at the Allan Hancock Foundation (AHF).
MMS	Minerals Management Service
NMC	National Museum of Canada (Ottawa).
OCS	Outer Continental Shelf.
RPD	Redox Potential Discontinuity.
SBMNH	Santa Barbara Museum of Natural History.
SMNH	Swedish Museum of Natural History (Stockholm).
USNM	United States National Museum. A historical designation for the National Museum of Natural History (NMNH) Smithsonian Institution (Washington, D.C.).
ZMH	Zoologisches Museum Hamburg.

1. INTRODUCTION TO THE ANNELIDA

by

James A. Blake[1] and Christer Erséus[2]

General Account

The Annelida, or segmented worms, represent a major phylum of the Animal Kingdom with over 22,000 described species. Annelids include the familiar earthworms, leeches, and polychaetes. Included among the annelids, however, are a great number of marine and freshwater species having diverse morphologies and habitats that are unfamiliar to the casual observer. A sediment sample from a mud flat or a sample of the fauna associated with mussel byssal threads on a rocky shore usually reveals a rich and spectacular assemblage of annelid worms.

As a general rule, annelids include the largest of any of the wormlike invertebrates and display the greatest structural differentiation. Annelids range in size from microscopic interstitial polychaetes to giant tropical earthworms that may attain lengths of 3 m or more. Some marine nereidid polychaetes have been recorded up to 1 m in length (e.g., *Neanthes brandti* in tidepools in California). The bodies of annelids are divided into segments that are arranged in a linear series along an anterior-posterior axis. Segments are always limited to the trunk of the body. The anterior end or head is called the prostomium and usually contains the brain and associated sensory organs. The prostomium is not a segment, nor is the pygidium or terminal part of the body that carries the anus. The peristomium is an achaetous segment that contains the mouth and sometimes tentacular structures (in polychaetes). In oligochaetes the peristomium contains the brain. New segments are formed anterior to the pygidium. The oldest body segments are therefore anterior, and the youngest are posterior. Growth includes enlargement and elaboration of body segments after they are formed. The body wall encloses a spacious body cavity (coelom) that is lined with mesodermal peritoneum. Segments are internally separated to varying degrees by transverse septa. Each septum is composed of two layers of peritoneum, one derived from the segment in front and the other from the segment following. Lateral nerves that branch off the ventral nerve cord, blood vessels branching off dorsal and ventral blood vessels, and excretory organs are also segmentally arranged. The digestive tract is an internal tube, suspended within the coelom by the septal muscles and other mesenteries.

The structure of the digestive tract is highly diverse, depending upon the mode of life and feeding mode. Generally, there is a foregut formed from stomodeal ectoderm, a midgut formed from endoderm, and a hindgut formed from proctodeal ectoderm. From this basic embryonic structure, the digestive tract becomes highly modified. The foregut includes the mouth, buccal cavity, pharynx, and esophagus. In some polychaetes this region becomes modified as an eversible proboscis, which may be soft in the case of deposit feeders, or bear complex jaws or teeth in the case of carnivores or omnivores. In some filter-feeding polychaetes, a branchial crown of ciliated radioles carries particles that are filtered from the water to the vicinity of the mouth where they are sorted for food and tube-building materials. Leeches have biting jaws in the pharynx. Blood sucking species use these structures to pierce the tissue of prey to which they attach. The midgut of leeches is modified into a large crop with paired diverticula for storage of blood. Jaws are lacking in oligochaetes, and they are mostly deposit feeders. Some oligochaetes are known to lack

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digestive tracts entirely, and they are nutritionally dependent on symbiotic bacteria that live in the body wall.

Oligochaetes and polychaetes are characterized by having segmental bristles or setae. In oligochaetes there are two basic kinds of setae: hair setae and crotchets. In polychaetes there are numerous types of setae from simple pointed ones to complex compound setae with elaborate ornamentation. The hair setae of oligochaetes resemble the capillary setae of polychaetes, and the crotchets of oligochaetes also occur in polychaetes, but are usually called hooks. Leeches do not have setae. Setae are important taxonomic characters in polychaetes, yet are relatively unimportant in oligochaetes. The morphology of the reproductive system represents the most important source of taxonomic characters in oligochaetes.

The coelom is filled with coelomic fluid that serves as a hydraulic skeleton working with the muscles to change body shape during locomotion and other body functions. When changes in body shape caused by changes in coelomic pressure are restricted to certain parts of the body, waves of peristaltic contraction pass along the body resulting in lengthening and shortening of the segments. These body movements are powerful forces that can be used in burrowing and sometimes rapid crawling or swimming. Paired setae on each segment increase traction with surrounding surface areas, permitting more control of movements.

All three classes are represented in the marine environment. The polychaetes are the most common and conspicuous of the marine annelids, with more than 80 families represented worldwide. Marine oligochaetes are common, but generally much smaller than their terrestrial relatives (earthworms) and less well known. Leeches (Hirudinea) are typically ectoparasitic on fish. Important general accounts that provide comprehensive overviews of annelid morphology, physiology, biology, and systematics include: Brinkhurst and Jamieson (1971), Brinkhurst and Cook (1980), Clark (1965), Dales (1963), Florkin and Scheer (1969), Giere and Pfannkuche (1982), Grassé (1959), Mill (1978), Pettibone (1982), and Schroeder and Hermans (1975).

Both oligochaetes and polychaetes are well represented in the Santa Maria Basin and Western Santa Barbara Channel. The oligochaetes are presented in the following section of this volume. An introduction to the polychaetes that includes a family key is included in this volume, along with detailed accounts of the families Phyllodocidae, Lacydoniidae, Pilargidae, Nautiliniellidae, Neredidae, Hesionidae, Glyceridae, Goniadidae, Nephtyidae, Paralacydoniidae, and Sphaerodoridae. The remaining polychaete families are treated in volumes 5-7.

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2. THE OLIGOCHAETA

by

Christer Erséus[1]

Introduction

The Oligochaeta are a large class within the Annelida, with over 6,000 known species classified in about 25 different families. The known species are nearly equally divided between the terrestrial earthworms and the aquatic oligochaetes. The ecological importance of oligochaetes in ponds, lakes, and rivers has long been known to freshwater biologists, but the marine species have been neglected and are still poorly known to most marine ecologists. There are several reasons for this.

Most marine oligochaetes are small, with bodies that border between the macrofauna and meiofauna in size. In terms of density, oligochaetes are generally numerically important constituents of benthic communities, but are likely to pass through the sieves normally used in many ecological studies. For example, if a 1-mm sieve is used, the oligochaetes are greatly underestimated, and this has certainly been true for many surveys in the past. On the other hand, in meiofauna studies, although the sieves are fine enough for retaining the oligochaetes, the sample size is usually too small to generate any substantial numbers of specimens.

Furthermore, as marine oligochaetes are morphologically homogeneous externally, and with few conspicuous features, the real diversity may not be revealed even if they have been sampled in a representative way. The whole group is often regarded as a single taxon, "Oligochaeta," with the justification that the species are too difficult to identify.

As a result, few taxonomists have been attracted by the group, and until the early 1970s only about 100 species were known world-wide. Since then, however, due to collecting efforts and taxonomic studies in several parts of the world, many new species have been described, and today more than 500 species of marine oligochaetes are known. Although this is still only a fraction of the actual number of species believed to exist worldwide, the rate at which new genera and families are being described has begun to slow down, at least for the Northern Hemisphere.

The majority of marine oligochaete taxa belong to the Tubificidae. This family includes the two large, almost exclusively marine subfamilies Phallodrilinae and Limnodriloidinae, the former with about 250 species. Members of the Enchytraeidae constitute the second largest group of marine oligochaetes. There are also some marine or brackish-water species of the Naididae, but in cladistic terms this (largely limnic) family appears to be merely a group within the Tubificidae. In recent years two new families, the Capilloventridae and Randiellidae, have been established for a few aberrant marine species (Harman and Loden, 1984; Erséus and Strehlow, 1986).

Marine Oligochaeta do not exhibit many external features and it is seldom possible to identify species by using only the stereomicroscope. However, sectioning of the specimens is not necessary in order to identify them. With some practice, and perhaps guidance, it is rather easy to see the taxonomically important internal structures in cleared specimens that are mounted on slides and examined under a light microscope. The well-developed coelomic cavity and the small size of the worms make whole-mount studies possible.

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The oligochaete fauna of the continental shelf off the Pacific coast of North America is less well known than that of the Atlantic coast. Some previous reports contain taxonomic information about Pacific offshore taxa (Brinkhurst, 1985, 1986; Brinkhurst and Baker, 1979; Coates and Erséus, 1980; Cook, 1974; Erséus, 1982; Milligan, 1991), but although three species have been recorded from off Santa Barbara (Coates and Erséus, 1980; Erséus, 1982) and Los Angeles (Brinkhurst, 1985), there are no reports of oligochaetes specifically from the Santa Maria Basin and Western Santa Barbara Channel.

For the preparation of this chapter, a large collection of oligochaetes from the California Phase II Monitoring Program (CAMP, supported by the Minerals Management Service, Pacific OCS Office) was placed at the author's disposal. This material contained only five species. Two of these species were already known from the adjacent areas in southern California (*Tectidrilus diversus, Tubificoides bakeri*), two others from Baja California (*Limnodriloides monothecus; L. barnardi*), and one species was new to science (*Tectidrilus probus*). However, as the CAMP stations only represent three transects (off Pt. San Luis, Pt. Sal and Purisima Pt., respectively) in the northern part of Santa Maria Basin, it is likely that additional taxa occur in the whole study area of this Atlas. No specimens were available from the Phase I study.

Material from two other sources was therefore studied and included: specimens from (1) the Bureau of Land Management Outer Continental Shelf Project in the Southern California Bight (courtesy of Dr. Jerry D. Kudenov, formerly of the Allan Hancock Foundation, University of Southern California, Los Angeles), and (2) the Los Angeles County Sanitation District's benthic sampling off Los Angeles (courtesy of Dr. T. Parker, Joint Water Pollution Control Plant, L.A. County Sanitation Districts). These collections provided five additional species: *Bathydrilus litoreus, B. rusticus,* and *Olavius tannerensis* (of which the two latter are new taxa) from the Southern California Bight; and two, *Bathydrilus parkeri* and *Tectidrilus profusus* (both new species), from off Los Angeles. Including *Grania incerta,* described from off Santa Barbara (Coates and Erséus, 1980), this makes a total of 11 species of oligochaetes that either are known to occur or can be expected to occur in the Santa Maria Basin and Western Santa Barbara Channel. This chapter provides descriptions of all these species and a key to families, genera, and species. The new taxa are established in separate taxonomic publications (Erséus, 1991a, b, c). Of the 11 species, *G. incerta* belongs to the Enchytraeidae, the others are all Tubificidae.

Specimens are deposited in the following museums: Los Angeles County Museum of Natural History (LACM); National Museum of Canada, Ottawa (NMC); and the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). Voucher collections of the Santa Maria Basin material are deposited at the Santa Barbara Museum of Natural History (SBMNH).

Morphology of Marine Tubificidae and Enchytraeidae (Oligochaeta)

Marine oligochaetes are slender annelids, the majority between 5 and 15 mm long, and between 0.1 and about 0.3 mm wide. The worms are very elastic and are able to stretch their bodies considerably when alive. Contractions in the musculature shorten the worms at fixation; more so in the Tubificidae than in the Enchytraeidae because the cuticle is thicker and more resistant in the enchytraeids. Most taxonomic descriptions are based on fixed material. Therefore, body measurements generally refer to more or less contracted specimens.

An oligochaete (Fig. 2.1A) consists of a presegmental **prostomium**, a number of serially arranged **segments**, and a postsegmental **pygidium**. The segments are referred to by Roman numerals. Segment I, the **peristomium**, contains the mouth. Segment II is generally the first segment with **setae**. In small oligochaetes the septa between the segments are often incomplete, and the annulation of the body wall does not always reflect the repetition of segments. Thus, counting the segments is facilitated by checking the

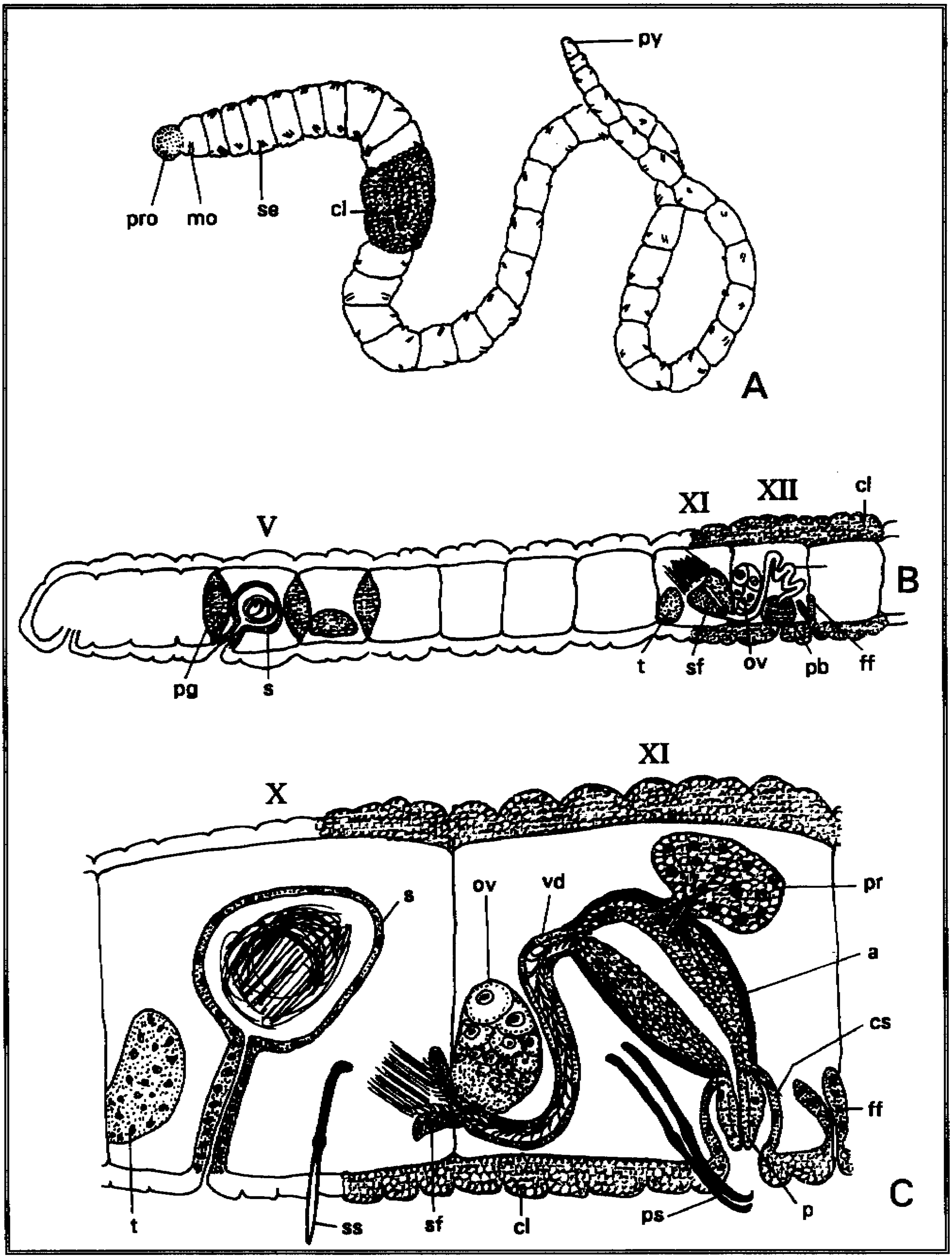

Figure 2.1. A, general appearance of a marine (tubificid) oligochaete; B, lateral view of an enchytraeid (schematic), anterior end; C, lateral view of segments X and XI of a tubificid (schematic), showing genitalia. (A, after Erséus, 1983; B and C after Erséus, 1980).

bundles of setae. In a similar way the characteristic ganglia (one major node per segment) on the nerve cord are used as "markers" of the segments, especially in stained specimens.

The external features are few. There are no appendages of the kinds (tentacles, palps, gills, etc.) that are taxonomically so useful in polychaetes. Setae are present in virtually all species, but their numbers are few and morphological variations are slight. Maximally, and generally, there are four bundles of setae in each body segment, two ventrolateral, and two dorsolateral (lateral in enchytraeids). Although the setae are partly protruded from the body surface, they are always easiest to examine in cleared, mounted specimens. In these preparations, one is able to see through the body and clearly observe the setal bundles as well as the details of individual setae.

A few species of Enchytraeidae lack setae completely. In the other members of the family the setae are rather stout, either straight or sigmoid, and always have single-pointed tips.

In the Tubificidae, two basic kinds of setae occur (see Fig. 2.11A), the long **hair setae** and the shorter **crotchets**. When present, hair setae alternate with crotchets within some or all dorsal bundles. Crotchets normally have bifurcate tips and are called **bifid setae**, but reduction of the upper tooth is common, sometimes producing a sharply single-pointed seta. In a few species within *Tubificoides* and *Heterochaeta*, fine pectinations occur between the primary teeth of the bifid setae, but this phenomenon is more common among freshwater tubificids. In *Heterodrilus*, the anterior setae are normally trifid, with three distinct teeth instead of two.

Many Tubificidae bear modified setae (Fig. 2.1C: ps, ss) near their male and/or spermathecal pores (see **genital setae** in Glossary). These setae supposedly aid in the mutual holding of mating individuals or facilitate the transfer of sperm at copulation.

In mature oligochaetes, certain adjacent segments become thickened and swollen by glands that secrete mucus for copulation and also secrete the cocoon. This glandular area is collectively called the **clitellum**, and forms a conspicuous girdle around the body (Fig. 2.1A).

The alimentary system is simple in marine oligochaetes. The mouth leads into a **pharyngeal cavity**, which has a dorsal **pharyngeal pad**. The **pharyngeal glands** (see Glossary) have narrow connections with this pad and form lumps of chromophilic cells in a few segments further down the esophageal tube from about segment IV (Figs. 2.1B, 2.2C, 2.6D: pg). In the tubificid genus *Bathydrilus*, these glands often extend as far back as VIII or IX (Fig. 2.2C). In most members of the Limnodriloidinae (also Tubificidae), the esophagus is modified in segment IX, and either bears a pair of anteriorly directed blind sacs (diverticula) (Figs. 2.9C, 2.10C: ed) or is inflated and enclosed in a reticulate blood plexus. The remaining alimentary tube is a long simple intestine that terminates in the anus on the pygidium. Two aberrant tubificid genera, *Olavius* and *Inanidrilus*, lack an intestinal system completely. These worms are nutritionally dependent on symbiotic bacteria that live in the body wall.

The morphology of the circulatory, excretory and nervous systems is often treated in descriptions of Enchytraeidae, but it plays a minor role in the taxonomy of the Tubificidae.

The genital organs (Figs. 2.1B-C) are taxonomically important in all marine oligochaetes. The worms are hermaphroditic with one pair of **testes** (in segment X in Tubificidae, segment XI in Enchytraeidae) and one pair of **ovaries** (XI in Tubificidae, XII in Enchytraeidae). The gonadal products ripen and are stored in coelomic fluid, partly confined in particular outpocketings of septa, the sperm sacs or **seminal vesicles**, and the **ovisacs**.

The male efferent ducts consist of inner ciliated sperm funnels that open into the posterior part of the coelom of the testicular segment. These are followed by ciliated and convoluted sperm ducts called **vasa deferentia** that open into some kind of (primary) invaginations of the body wall in the following segment. In the Tubificidae, such an invagination is called an **atrium**, a glandular, sometimes complex organ surrounded by a lining of muscles (Fig. 2.1C: a). Parts of the glandular tissue generally penetrate the lining of the atrium to form more or less discrete **prostate glands**. The two atria may open directly to the exterior through the male pores, or they terminate in more-or-less developed copulatory organs formed by secondary invaginations of the body wall (see **copulatory sac** in Glossary). In the Enchytraeidae, the equivalent of the atria are the **penial bulbs**. These are glandular and often muscular bodies associated with the terminal ends of the sperm ducts (Fig. 2.12E).

The **spermathecae** are paired or unpaired female organs that receive sperm from the mate during copulation (Figs. 2.1B-C: s). They are normally located in segment X of the Tubificidae and in segment V of the Enchytraeidae (see **spermatheca** in Glossary).

The female efferent ducts (Figs. 2.1B-C: ff) are short, virtually consisting only of simple, hardly detectable female funnels followed directly by the inconspicuous female pores. The latter are located near the intersegmental furrow at the posterior end of the ovarian segment. During egg-laying, the large, yolky eggs are squeezed out through these pores, or they simply rupture the body wall in this region. Most oligochaetes lay their eggs in a cocoon formed by mucus from the clitellum, fertilizing them with spermatozoa (originating from another individual) that are ejected from the spermathecae.

Collection and Preservation

Oligochaetes can be satisfactorily collected by the standard methods used for benthic infauna. Carefully taken grab or core samples are needed for quantitative studies, whereas dredged or scooped samples may be sufficient for qualitative work. Most marine oligochaetes are members of the interstitial fauna, and they may penetrate deep into coarse, well-oxygenated sediments. All samples should therefore be taken at least to the redox potential discontinuity (RPD) level. Some species, e.g., the gutless tubificids, are tolerant of low-oxygen environments, and may occur below the RPD layer.

On average, oligochaetes appear less vulnerable to damage during washing and sieving than polychaetes. A large proportion of the specimens will be intact and complete after sieving. For coarse sediments, elutriation (repeated stirring of the sediment in seawater followed by decantation of the suspended organics into a sieve) is necessary, because too much sediment would stay in the sieve if the whole sample were poured into it at once. To retain all juveniles and cocoons, one would probably have to use a 100-mm-mesh screen, but this is hardly feasible with larger macrofaunal samples, considering how time-consuming the subsequent sorting would be. A mesh size of 250-300 mm is therefore recommended for oligochaetes. Even a 500-mm screen will give a substantial representation of the specimens present in the sample, but it certainly would not retain all individuals.

Marine oligochaetes move in a characteristic manner. They exhibit a rapid alternation between stretching and shortening, and show in fact little of the peristaltic movements that otherwise characterize annelids. For this reason, it is easy to detect the worms in a sieved fraction of a sample, if one has the opportunity to sort it while the animals are still alive. Normally, however, in larger benthic surveys, the oligochaetes are killed during the standard formalin fixation. Anesthesia (e.g., magnesium chloride) may be used, but is not really needed as the contraction effect of the fixation seldom causes serious distortion of the bodies of marine oligochaetes. Moreover, most taxonomic descriptions have been based on unanesthetized worms. One problem that may occur, however, is that specimens fixed without anesthesia may curl to such an extent that mounting on a slide is hindered unless the worms are cut into several pieces.

Although facilitating the sorting of fixed oligochaetes from extraction residues, the use of Rose Bengal is disadvantageous, as it is an indiscriminate (protein) stain that will dominate over any nuclear stain that one may wish to apply during the identification process (see Laboratory Methods).

If live specimens have been extracted from a sample, and they are to be fixed for advanced taxonomic work, or simply for a better fixation result, histological methods should be used. If the individuals are put into the fixative one by one, it is worthwhile to use a pair of soft forceps and, to prevent curling, gently shake the animals back and forth when they hit the surface of the fixative. Fixation in Bouin's solution (mixture of formaldehyde, picric acid and acetic acid) is good for sections, dissections and whole mounts, but it is essential that the specimens be transferred into ethyl alcohol (70-80%) after a maximum of a 3-4 (minimum 2-3 hours). If the worms are retained in Bouin's for a longer period, they will harden and eventually become brittle. If properly fixed, oligochaetes can be preserved in alcohol for many years.

Laboratory Methods

General Methods of Observation

Marine oligochaetes can seldom be identified without using a compound microscope. Only in cases when an externally recognizable species is known to occur in a particular sample, or at a particular sampling station, is one able to identify species directly under the stereomicroscope.

Generally, the most essential part of the identification is the examination of genitalia and a few other internal features. The modified genital setae are more useful than the somatic setae. Unfortunately, sexually mature specimens constitute only a small part of the population at most times. However, by identifying the mature worms first it is often possible to match them with the corresponding immatures, using the subtle non-genital traits (general body appearance, etc.) that do exist, but are difficult to represent in a taxonomic key.

Virtually all offshore Tubificidae and Enchytraeidae are small enough to be studied as whole mounts, provided the specimens are cleared (see below). Some of the intertidal species, however, are too thick for whole-mount examination. For these species, it is useful to cut the anterior end, including the genital region, into two lateral halves with a razor blade or a pair of very small iris scissors. If possible, the intestinal parts should be separated from the male genital ducts and the spermathecae using needles or fine forceps. The two sides of the worm can then be mounted separately. Alternatively, or as a complement, the genital region of a few properly fixed specimens can be longitudinally sectioned and stained according to standard histological techniques.

Staining and mounting of whole specimens

If the worms have not been stained in Rose Bengal (see Collection and Preservation), the possibility of discriminating among different internal structures is enhanced if the cell nuclei are stained prior to mounting. Although staining in borax carmine and haematoxylin are fully acceptable, the prefered stain is alcoholic paracarmine, which has two important advantages. First, both staining and destaining is performed in 70% ethyl alcohol (ethanol), not in water, precluding the need for extra hydration and dehydration steps. Second, the staining and differentiation (in acid alcohol) is quick, taking only a matter of minutes.

The paracarmine solution is prepared as follows:

1. Dissolve 1 g carmine acid, 0.5 g aluminum chloride, and 4 g calcium chloride in 100 ml 70% ethanol (under slight and cautious heating).

2. Let cool and settle.

3. Filter. The solution can be used over and over again, and it can be kept for several years. It may have to be refiltered periodically.

The staining procedure with paracarmine is as follows:

1. After fixation (in formalin, Bouin's, etc.) specimens are preserved in 70% ethanol.

2. Specimens are placed in the alcoholic paracarmine solution for 5-10 minutes, possibly somewhat longer. The smaller the worms, the shorter the times.

3. Specimens are transferred back into a small amount (2-3 ml) of 70% ethanol. Add 2-3 drops (or more) of acid alcohol to this. [The acid alcohol is a mixture of 70% ethanol and concentrated hydrochloric acid (HCl) in the proportions of 20:1.]. Differentiate for 1-10 minutes, or proceed until excess stain has disappeared from the specimens. For large, overstained worms, the differentiation may have to continue for some hours, or even overnight.

4. Return specimens to "ordinary" 70% ethanol. Keep them there until they are mounted.

When the worms have been stained, they may be either dehydrated and cleared through an alcohol-xylene or alcohol-toluene series and mounted permanently in balsam (e.g., Canada balsam[2]), or both cleared and temporarily mounted in glycerin, clove oil, or a similar substance. Mounting in glycerin does not always result in specimens as transparent as those mounted in xylene-Canada balsam (see below), but the procedure is quick and allows for easy retrieval of the specimens (for biomass measurements, etc.) after the microscope examination. It also allows for manipulation of the specimen for better observation of the genitalia.

One procedure for making permanent mounts is as follows:

1. Specimens are transferred from 70% into 96% ethanol for 10-20 minutes. The smaller the worms, the shorter the times.

2. Specimens are transferred to 100% ethanol for 10-20 minutes.

3. Specimens are placed in a mixture of 100% ethanol and xylene (1:1) for 10-20 minutes.

4. Specimens are then transferred to xylene for 10-20 minutes. After this, the worms should be cleared and transparent.

5. Specimens are then transferred from the clearing agent into a drop of the mounting medium (Canada balsam or similar) on a microscope slide. If the material is to be used for routine identifications only, it is economical to place several specimens on

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[2] Permount® or other brands of synthetic mounting media available through scientific suppliers are also fully acceptable.

each slide. The balsam should be slightly thicker than syrup. A cover slip is placed on top of the drop and a gentle pressure is applied by pressing a firm, but still somewhat elastic surface down onto the cover slip; the basal ring of a rubber bulb used for small, disposable glass pipettes is excellent for this purpose. The amount of pressure is a matter of experience, but it is important that the specimens are compressed under the cover slip, otherwise the preparation will be too thick for microscopic examination. If the worm is so thick that the cover slip does not stay down, then air may be sucked in under it. In this case, additional balsam can be added at the edge of the cover slip. Finally, balsam squeezed out around the edges of the cover slip may be scraped off.

6. It is advisable to dry the slides for several days in an oven or on a warming tray at about 37°C before they are examined in order to avoid having wet mounting medium smear the objectives.

Because the most important taxonomic features are found in the anterior and clitellar parts of the worms it is essential that no other part of the body crosses over this region. Therefore, it may be necessary to cut curled specimens into two or more pieces before they are mounted.

Glossary

The following terms and expressions are used in the key and descriptions. They are explained here with reference to their application to the taxonomy of aquatic oligochaetes.

Anterior segments/setae. Refers to segments/setae in front of the clitellum.

Atrium. A thickened, basically glandular, part of the male efferent duct in a tubificid worm. It is ontogenically regarded as a primary epidermal invagination of the body wall at the male pore, the space formed by the invagination being termed the lumen of the atrium, and it is communicates with the sperm duct (see **Vas deferens**). The inner end of the atrium is the apex or apical end. In many species the atrium is divided into one inner (ental) part, the atrial ampulla, and one outer (ectal) part, the atrial duct. The wall of the atrium bascially consists of two layers. The inner epithelium is ectodermal, often storing the secretory products of the prostate glands (see **Prostate gland**). The outer layer is mesodermal and generally contains muscle fibers. The thickness of the muscular layer, however, varies considerably among taxa.

Bifid setae. Setae with bifurcated tips, i.e. each with two small teeth (Fig. 2.2B). As the tip is somewhat curved, one tooth becomes distal to the other. The distal tooth is referred to as the upper tooth, the proximal one as the lower tooth.

Clitellum. [In earthworms often referred to as the "girdle."] A glandular thickened part of the epidermis that secretes the cocoon at egg-laying. In small aquatic oligochaetes it is only one cell layer thick, and is therefore not always easy to distinguish. The clitellum is developed when the worm becomes sexually mature. It extends over one or a few specific segments. In Tubificidae and Enchytraeidae, the male pores are always within the clitellar region.

Copulatory sac. A secondary invagination of the body wall at the male pore, in which the atrium [the primary invagination] terminates. The sac is often called penial sac if it encloses a permanently pendent papilla acting as a penis (see also **Pseudopenis**).

Cuticular papillae. In some Tubificidae the cuticle is covered by numerous fine particles giving it a dusty appearance. Sometimes these particles are aggregated on small cuticular projections forming leaf-shaped papillae. When present, the papillae tend to form a dense opaque layer, which makes the worm rather stiff and greyish or blackish in color.

Epidermal glands. Some cells of the body surface other than those of the clitellum may act as adhesive glands. Sometimes, especially in *Bathydrilus*, these glandular cells form discrete patches in particular areas of the segments. Whether they are visible or not in fixed, mounted specimens may depend on their state of activity at the time of fixation, or the kind of chemicals used for the preservation and staining.

Esophageal diverticula. Permanent paired outpocketings of the esophagus. Those commonly occurring in the tubificid subfamily Limnodriloidinae are located in segment IX. They are generally cylindrical with rounded tips, originate near the middle of the segment and are directed toward the anterior, almost reaching the septum VIII/IX. The lumen of a diverticulum often has a characteristic "wavy" outline.

Genital setae. Setae associated with the genital pores. They are generally morphologically different from the ordinary (somatic) setae. If located near the male pores (in segment XI in Tubificidae), they are referred to as penial setae, if near the spermathecal pores (in IX or X in Tubificidae) as spermathecal setae.

Hair setae. Thin, smooth setae, occurring in dorsal bundles of some Tubificidae. They are longer than the accompanying bifid or single-pointed crotchets. The hair setae alternate with the crotchets within the bundles (see Fig. 2.11A).

Male pore. Opening on the body wall through which sperm exit during copulation. It is either the direct opening of the atrium (see Atrium), or the opening of a copulatory sac (see **Copulatory sac**). Unless a penis is protruded or a pseudopenis is everted, the pore is often inconspicuous.

Ovisac. Posterior outpocketing of the septum of an ovarian segment. It may extend through several segments posteriorly. The wall of the sac may be thin and difficult to see, but the extension backwards is indicated by the position of ripening or mature eggs.

Penial bulb (in Enchytraeidae). A glandular body associated with the outermost end of the vas deferens (see **Vas deferens**), near the male pore. Functionally, it may be the equivalent of the tubificid atrium (see **Atrium**), but it is unclear whether the organs are homologous.

Penial setae. See **Genital setae**.

Penis. See **Copulatory sac** and **Pseudopenis**.

Pharyngeal glands. Groups of chromophilic cells located along the esophagus in a number of anterior segments, all with narrow connections to the dorsal pharyngeal pad of the pharynx. In Enchytraeidae, these glands form discrete, roundish bodies, sometimes referred to as "septal glands".

Postclitellar. Posterior to the clitellum.

Prostate gland. A group of glandular cell extensions growing out from the inner epithelium of the atrium, which produce the secretion that later is stored and discharged in the atrium (see **Atrium**). The prostate cells are either lumped into discrete (round or lobed) bodies communicating with the atrial epithelium by narrow or broad "stalks", or they form a diffuse layer outside the atrium with numerous points of communication with the atrial epithelium; the latter situation does not, however, occur in species included in this Atlas.

Prostatic pad. A limited, discrete area in the inner epithelium of the atrial ampulla (see **Atrium**) storing the products of the prostate (see **Prostate gland**). The term is used only for the atria of members of the tubificid subfamily Limnodriloidinae.

Prostomium. The most anterior, pre-segmental part of the worm, separated from the first proper segment (the peristomium) by a thin septum. In oligochaetes, the prostomium is usually simple and lacks appendages.

Pseudopenis. A copulatory organ that will alter its shape when used. Most often it refers to a copulatory sac (see **Copulatory sac**), with or without a pseudopenial papilla inside, which will be turned inside out during copulation (an eversible pseudopenis). If the "papilla" inside has a fixed shape and is more or less pendent within the sac, the copulatory organ is called a penis. There is no clear-cut distinction between a penis and a pseudopenis.

Pygidium. The most posterior, post-segmental difference part of the worm. In species with a gut it bears the anus.

Secondary annulation of body wall. More or less distinct rings within the rings corresponding to the body segments.

Seminal vesicle. Outpocketing of a posterior or anterior septum of a testicular segment. It may extend through several segments. The wall of the sac is thin and difficult to see, but the extension is indicated by the position of ripening or mature spermatozoa inside the sac.

Somatic setae. Setae not associated with genital openings (see **Genital setae**).

Spermatheca. Ectodermal, usually pedunculate, invagination that receives sperm during copulation and stores them, until the eggs are laid and fertilized. It consists of an outer duct and an inner ampulla. The outermost part of the duct is sometimes modified into a hollow chamber called a spermathecal vestibule.

Spermathecal pore. Opening on the body wall that receives sperm during copulation. It is either the direct opening of the spermathecal duct or the opening of a spermathecal vestibule leading into this duct (see **Spermathecae**). The pore may be inconspicuous.

Spermathecal setae. See **Genital setae**.

Spermatozeugma (pl. **spermatozeugmata**). Sperm aggregate implanted in the spermatheca by the mate, characterized by repetitive order of the spermatozoa and the presence of some sort of cementing agent, but lacking a proper capsule (Ferraguti *et al.*, 1989). Such aggregates appear to have evolved independently in different groups of Tubificidae. The shape varies considerably among species, from spherical to very slender.

Sperm funnel. A ciliated funnel at the posterior septum of a testicular segment. It opens into the coelom and generally "attracts" a large bundle of ripe spermatozoa. It is drained by the vas deferens (see below). In Enchytraeidae the funnel is long, cylindrical and heavily granulated.

Subdental ligament (on bifid setae in some Tubificidae). Thin structure connecting the tip of the lower tooth with the setal shaft (see Fig. 2.5B).

Vas deferens. The ciliated, tubular, generally long and convoluted, sperm duct. In Tubificidae, it connects the sperm funnel with the atrium. In Enchytraeidae, it often leads directly to the male pore; although it may be in close contact with a penial bulb (see **Penial bulb**).

Vestibule. See **Spermatheca**.

Abbreviations Used in the Figures

a, atrium
aa, atrial ampulla
ad, atrial duct
br, brain
cl, clitellum
cs, copulatory sac
e, esophagus
ed, esophageal diverticulum
eg, egg
ff, female funnel
gps, gland associated with penial setae
gss, gland associated with spermathecal seta
in, intestine
l, subdental ligament
mo, mouth
mp, male pore
nc, nerve cord
ov, ovary
p, penis
pa, papilla on body wall
pb, penial bulb
pg, pharyngeal gland (along esophagus)
ph, pharyngeal pad (in pharynx)
pp, pseudopenis
ppa, prostatic pad
pr, prostate gland
pro, prostomium
pr1, anterior prostate gland
pr2, posterior prostate gland
ps, penial seta
py, pygidium
s, spermatheca
sa, secondary annulation of body wall
se, somatic seta
sf, sperm funnel
ss, spermathecal seta
sv, seminal vesicle
sz, spermatozeugma
t, testis
v, vestibule associated with spermathecal duct
vd, vas deferens

Key to Families, Genera and Species

The following key will work to the species level of all taxa when sexually mature specimens are examined. Immature specimens of *Limnodriloides* and *Bathydrilus* can only be taken to the genus level, and the identification of all three species of *Tectidrilus* will be possible only if the spermathecae are fully developed.

1A. At least some setae bifid; setae of anterior segments at least 2 per bundle.....Family Tubificidae ... 2

1B. All setae single-pointed, 1 per bundle; in anterior segments, only ventral setae present (Fig. 2.12D) .... Family Enchytraeidae: Genus *Grania: Grania incerta*

2A. Hair setae absent 3

2B. Hair setae (together with bifid setae) present in dorsal bundles of anterior segments (Fig. 2.11A) .... Genus *Tubificoides: Tubificoides bakeri*

3A. Body wall smooth throughout, without small papillae 6

3B. Body wall with small leaf-shaped papillae, at least in postclitellar segments (Figs. 2.6B-C) .... Genus *Tectidrilus* 4

4A. Ducts of spermathecae heavily muscular (Fig. 2.8C: s) .... *Tectidrilus profusus*

4B. Ducts of spermathecae not muscular 5

5A. Esophagus lacking diverticula in segment IX; spermathecal vestibules large, round, with distinct lumen (Fig. 2.6E) .... *Tectidrilus diversus*

5B. Esophagus with very small diverticula in segment IX; spermathecal vestibules small, with indistinct lumen (Fig. 2.7B) .... *Tectidrilus probus*

6A. Normal alimentary system present.. 7

6B. Mouth, gut and anus absent; secondary annulation of body wall conspicuous; body wall with thick layer of symbiotic bacteria (Fig. 2.5A) .... Genus *Olavius: Olavius tannerensis*

7A. Pharyngeal glands in segments IV-V. Esophagus with diverticula in anterior part of segment IX (Figs. 2.9C, 4.10C) .... Genus Limnodriloides 8

7B. Pharyngeal glands extending into segment VIII or thereabouts; esophagus without diverticula in segment IX (Fig. 2.2C) .... Genus Bathydrilus 9

8A. Spermathecae paired, with pores in line with ventral setae. Grooved spermathecal setae generally present near these pores in segment X (Figs. 2.10B-C) .... *Limnodriloides barnardi*

8B. Spermatheca unpaired, with mid-dorsal pore (Figs. 2.9B-C). Spermathecal setae (in segment X) absent .... *Limnodriloides monothecus*

9A. All somatic setae with bifid tips; large modified penial setae present in segment XI 10

9B. Some setae in posterior segments single-pointed (Fig. 2.4B); modified penial setae absent .... *Bathydrilus rusticus*

10A. Penial setae (generally) 3 per bundle, closely parallel within bundle (Fig. 2.2A); each bundle enclosed in large, bilobed sac (Fig. 2.2D: gps). Outer muscular lining of atria thin (not more than 1-2 mm thick) .... *Bathydrilus litoreus*

10B. Penial setae (generally) 2 per bundle; within bundle tips much closer to each other than are inner ends (Fig. 2.3C); bundle enclosed in a small (not bilobed) sac (Fig. 2.3D). Outer muscular lining of atria thick (2-3.5 mm) .... *Bathydrilus parkeri*

Descriptions of Species

Family Tubificidae
Subfamily Phallodrilinae

Bathydrilus litoreus Baker, 1983

Figure 2.2

Bathydrilus litoreus Baker, 1983: 2162-2164, figs. 1, 2A.—Erséus, 1990a: 68-69, fig. 13; Erséus, 1991a: 622-621.

Material examined. California: Southern California Bight, Santa Cruz Island (slope of Santa Cruz Basin), 260 m, medium to coarse sand, 1 specimen (USNM 136578); same area, 271 m, 1 specimen (USNM 136579); same area, 257 m, medium sand with small pebbles, 1 specimen (USNM 136580); Tanner Bank, 96 m, fine sand, 1 specimen (LACM); same area, 203 m, coarse sand with shell, 1 specimen (LACM); San Nicholas Island, 279 m, coarse sand with small rocks, 1 specimen (LACM).

Description. Body length variable, fixed specimens 9-22 mm for 77-115 segments. Body wall smooth, without cuticular papillae. Prostomium bluntly conical or rounded. When fully developed, clitellum extending over segments X-XII and anterior half of segment XIII. Patches of epidermal glands sometimes visible between bundles of dorsal setae from segment VIII posteriorly. All somatic setae bifid, with upper tooth smaller than lower one (Fig. 2.2B); setae generally 3 per bundle in anterior segments, 2 per bundle in postclitellar segments; ventral setae of segment XI modified into single-pointed, straight or somewhat curved penial setae, 3 per bundle (Fig. 2.2A); these setae much larger than somatic setae, closely parallel within bundle, each bundle enclosed in large, glandular, bilobed sac (Fig. 2.2D: gps). Spermathecal pores paired, lateral, in most anterior part of segment X. Male pores paired, in line with ventral somatic setae, on (or inside?) a pair of small epidermal papillae, in posterior part of segment XI. Pharyngeal glands (Fig. 2.2C: pg) in segments IV-VII, or IV-VIII (or even IV-IX). Esophagus unmodified in segment IX (Fig. 2.2C: e). Male ducts paired (Fig. 2.2D); vas deferens narrow, entering anterior face of, and immediately ectal to middle of atrium, but generally difficult to see. Atrium oval to spindle-shaped,

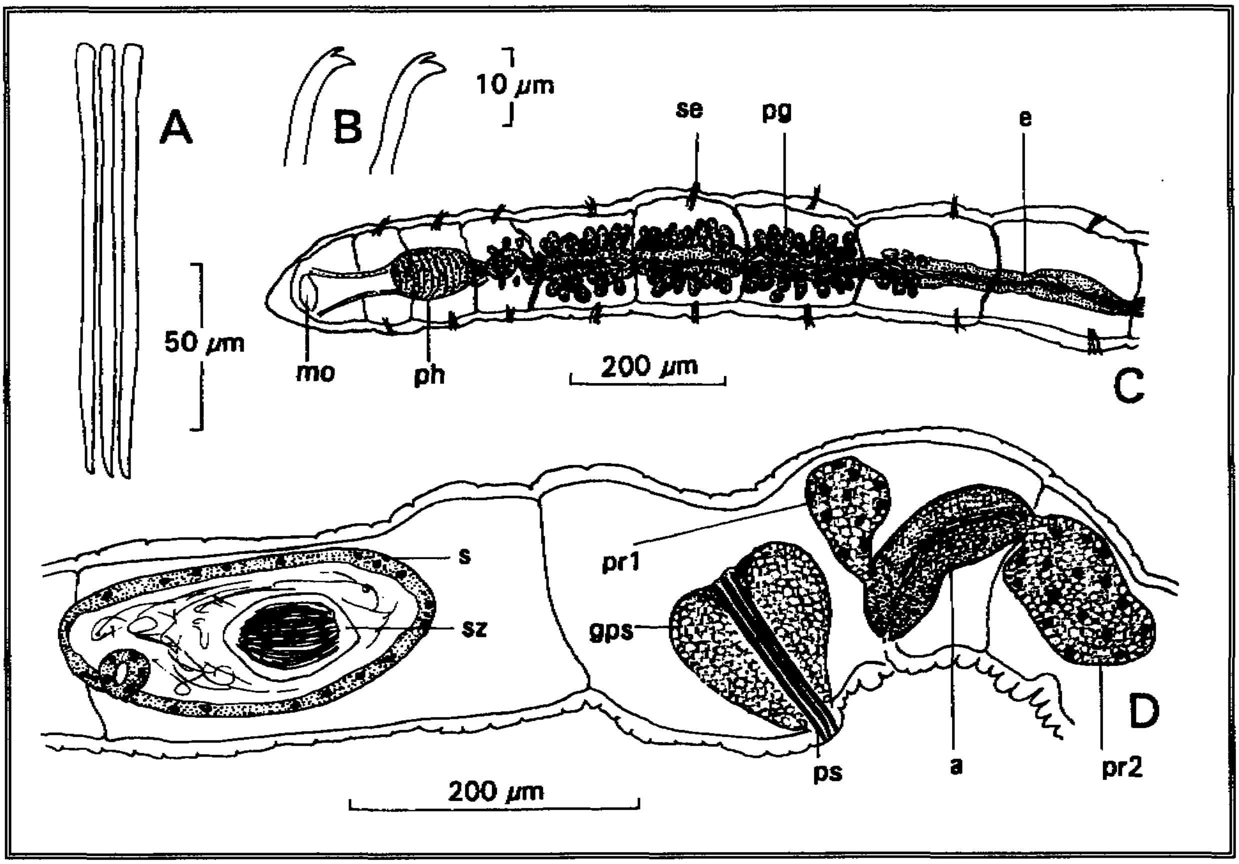

Figure 2.2. *Bathydrilus litoreus*: A, bundle of penial setae; B, somatic setae; C, horizontal view of anterior end; D, lateral view of segments X-XI, showing genitalia.

erect or somewhat tilted over to the posterior, with outer end terminating into narrow, short duct; the latter opening to the exterior on or immediately inside epidermal papilla; atrium with thin outer lining of muscles and thick, ciliated inner epithelium; atrium histologically bipartite, epithelium of outer part less granulated than that of inner part; two large prostate glands per atrium present, anterior one attached to middle of anterior face of atrium, posterior one attached to apex of atrium. Spermathecae (Fig. 2.2D: s) paired; ducts very short; ampullae large, oval, often extending into segment IX. Round or somewhat triangular spermatozeugmata present in postcopulatory specimens.

Biology. This species occurs in sands from the intertidal zone to at least 279 m.

Remarks. Characteristics that are common to all three species of *Bathydrilus* described here include: (1) the lateral spermathecal pores, (2) the extension of the pharyngeal glands into at least segment VII, and (3) the more or less spindle-shaped, erect or tilted-over atria.

In *B. litoreus*, the penial setae are large, straight, and lie closely parallel to one another in bundles of three. Each bundle is enclosed in a large, bilobed, glandular sac. The penial setae are conspicuous in cleared, whole-mounted, sexually mature specimens. There is some variation in this character in related species, and it is possible that specimens with two or four penial setae per bundle will occasionally be encountered. *B. litoreus* is separated from other species occurring in southern California by the characters indicated in the key.

Bathydrilus litoreus, originally described from British Columbia and Washington (Baker, 1983), was recently found in California (Erséus, 1991a). Specimens identified as *B. litoreus* have also been reported from southwestern Australia (Erséus, 1990a). The species belongs to a complex of very similar, tropical/subtropical taxa within the genus. *Bathydrilus litoreus* is most similar to *B. adriaticus* (Hrabe, 1971), which appears to be circumtropical in distribution. In *B. adriaticus*, however, the penial setae are not enclosed in such large, bilobed sacs as those of *B. litoreus* (see Erséus and Davis, 1989).

Type locality and type specimens. British Columbia, Queen Charlotte Islands, Moresby Island, Sperm Bay, Flamingo Inlet, low intertidal. Holotype: (NMC 1983-0206); paratypes (NMC 1983-0207-9 and USNM 80914-80916).

Distribution. West coast of North America: California, British Columbia; intertidal to 279 m.

Bathydrilus parkeri Erséus, 1991

Figure 2.3

Bathydrilus parkeri Erséus, 1991a: 623-624, fig. 1.

Material examined. California: Off Palos Verdes Peninsula, 30 m, holotype (USNM 136573) and 2 paratypes (USNM 136574 and LACM 1533).

Description. Body length (fixed specimens) about 10 mm for about 70-78 segments. Body wall smooth, without cuticular papillae. Prostomium elongate. Large patches of epidermal glands visible between bundles of dorsal setae in many segments. Clitellum extending over posterior half of segment X, and whole segments XI-XII. All somatic setae bifid, with upper tooth shorter and thinner than lower, more pronounced in postclitellar (Fig. 2.3B) than in anterior segments (Fig. 2.3A). Setae 3 per bundle in anterior segments, 2 per bundle in postclitellar segments. Ventral setae of segment XI modified into single-pointed, somewhat curved penial setae, 2 per bundle (Fig. 2.3C). These setae clearly larger than somatic setae, and within bundle inner ends of setae wider apart than tips. Each bundle of penial setae enclosed in narrow sac (Fig. 2.3D). Spermathecal pores paired, lateral, in most anterior part of segment X. Male pores paired, in line with ventral setae, posteriorly in XI. Pharyngeal glands in segments IV-VIII, or IV-IX, well developed (as in *B. litoreus*; Fig. 2.2C). Some anterior septa, in particular 6/7 and 7/8, thickened, conspicuously muscular. Esophagus unmodified in segment IX. Male ducts (Fig. 2.3D) paired; vas deferens inconspicuous, difficult to see, but appear to enter outer end of atrium near attachment of anterior prostate gland. Atrium slender, spindle-shaped; erect or somewhat tilted over to posterior, terminating in bulbous, simple, pseudopenis; atrium with thick outer lining of muscles, and ciliated, granulated inner epithelium; two prostate glands per atrium present, anterior one attached to outer end of anterior face of atrium, posterior one attached to apex of atrium. Spermathecae (Fig. 2.3D: s) paired; ducts very short; ampullae oval. In specimens studied, lumen of spermathecae with some globules of secretion and an amorphous substance, but no sperm observed (specimens precopulatory?).

Remarks. Sexually mature specimens of *Bathydrilus parkeri* are distinguished by the large, conspicuous, somewhat curved penial setae that occur in bundles of two with tips close together. In contrast, the closely related *B. litoreus* has three straight spines per bundle. Similar species within the genus are variable in this character, however, and it is possible that specimens of *B. parkeri* with more than two penial setae per bundle, or worms with a single seta representing any of the two bundles, will be occasionally encountered. *Bathydrilus parkeri* is further distinguished from *B. litoreus* by (1) its

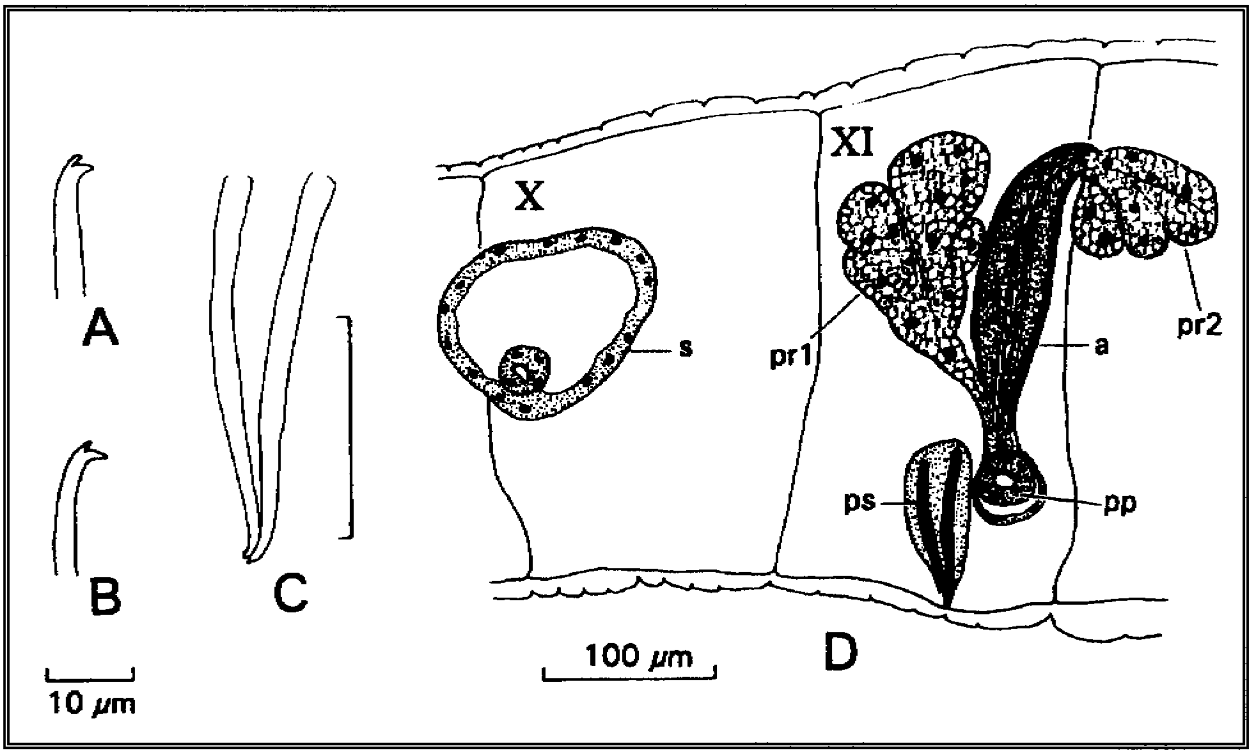

Figure 2.3. *Bathydrilus parkeri*: A, anterior somatic seta; B, postclitellar somatic seta; C, bundle of penial setae; D, lateral view of segments X-XI, showing genitalia. (After Erséus, 1991a).

conspicuously muscular septa in segments VI-VIII, (2) its more slender and more muscular atria, and (3) the small (not glandular and not bilobed) sacs enclosing the penial setae.

Although morphologically similar to *B. litoreus, B. parkeri* appears more closely related to *B. exilis* Erséus and Davis, 1989. The latter, known only from Hawaii, also has somewhat curved penial setae with inner ends wider apart than outer tips, heavily muscular anterior septa, and slender, more or less erect atria (Erséus and Davis, 1989). The posterior setae of *B. exilis,* however, are not bifid as in *B. parkeri* but sharply single-pointed. Moreover, the Hawaiian species is about twice as long (up to at least 26.5 mm, with 149 segments) as *B. parkeri*.

Distribution. Known only from California, in fine sand, 30 m.

***Bathydrilus rusticus* Erséus, 1991**

Figure 2.4

Bathydrilus rusticus Erséus, 1991a:624-625, fig. 2.

Material examined. California: Southern California Bight, Tanner Bank, 113 m, holotype (LACM 1527), paratype (USNM 136575).

Description. Body (fixed specimens) about 10-12 mm long for 44-67 segments. Body wall smooth, without cuticular papillae. Prostomium large, somewhat elongate with rounded tip. Epidermal glands not observed, but may be present (between dorsal bundles of many segments as in other species of the genus). Clitellum extending over posterior half of segment X, and whole segments XI-XII. Anterior setae (Fig. 2.4A) bifid, with upper tooth much shorter and thinner than lower; postclitellar setae with rudimentary upper tooth, or single-pointed with curved tip (Fig. 2.4B); setae 2-3 per bundle in anterior segments, 2 (sometimes 3) per bundle in postclitellar segments; ventral setae of XI (penial setae) absent. Spermathecal pores paired, somewhat ventral to lateral lines, in most anterior part of segment X. Male pores paired, in line with ventral setae, posteriorly in XI. Pharyngeal glands extending into VIII, but poorly developed. Esophagus unmodified in segment IX. Male genitalia paired (Fig. 2.4C); vas deferens inconspicuous, somewhat coiled, appearing to enter outer end of atrium near attachment of anterior prostate gland. Atrium slender, tilted over to posterior, with thick outer lining of muscles, and ciliated, histologically bipartite inner epithelium; inner, longer part of atrium evenly granulated; granules of outer, shorter part aggregated in discrete packages; atrium terminating in hollow copulatory sac, but details not clear in available material; two prostate glands per atrium present, anterior one attached to outer end of anterior face of atrium, posterior one attached to apex of atrium. Spermathecae (Fig. 2.4C: s) paired; ducts distinct, but short; ampullae elongate, with large globules of secretion and an amorphous substance in which bundled sperm appear to be cemented.

Remarks. The many single-pointed setae in posterior segments are highly diagnostic for *Bathydrilus rusticus*. The species is further distinguished from *B. litoreus* and *B. parkeri* by its lack of modified penial setae in segment XI. *B. rusticus* appears closely related to *B. torosus* Baker, 1983, an intertidal species from British Columbia. The latter, however, has spermathecae with ducts that appear to be much longer than the ampullae, which is opposite to the situation in *B. rusticus*.

Distribution. Known only from California in coarse sand, 113 m.

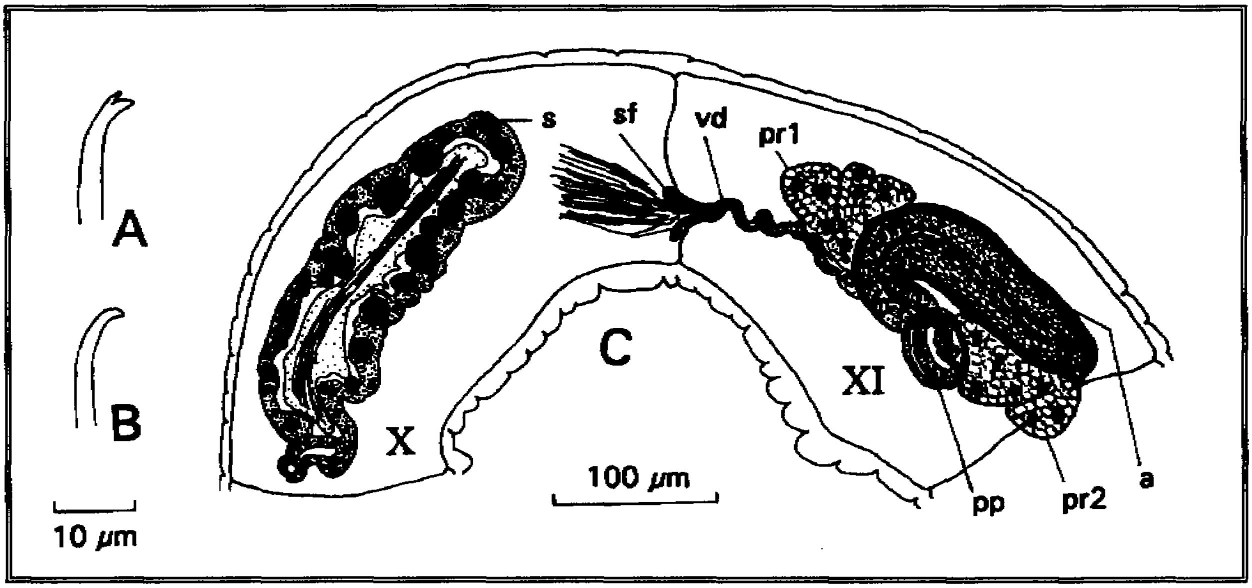

Figure 2.4. *Bathydrilus rusticus*: A, anterior seta; B, postclitellar seta; C, lateral view of segments X-XI, showing genitalia. (After Erséus, 1991a).

***Olavius tannerensis* Erséus, 1991**

Figure 2.5

Olavius tannerensis Erséus, 1991b:627-629, figs. 1A-B.

Material examined. California: Southern California Bight, Tanner Bank, 173 m, holotype (LACM 1528) and paratype (USNM 136576).

Description. Body length (fixed specimens) about 5 mm for about 45 segments. Prostomium and pygidium small, elongate with rounded tips. Body wall thick, opaque and conspicuously white in live worms, due to presence of dense subcuticular layer of symbiotic bacteria. Secondary annulation of body wall conspicuous, 5-7 annules per postclitellar segment (Fig. 2.5A: sa). Clitellum extending over posterior half of segment X, and all of segments XI-XII. Setae (Fig. 2.5B) bifid, with subdental ligaments; with upper teeth variably long but always thinner than lower teeth; 3 setae (occasionally 2) per bundle in anterior segments, 2 per bundle in postclitellar segments; ventral setae of XI (penial setae) absent. Spermathecal pores paired, immediately anteroventral to dorsal setae in segment X. Male pores paired, in line with ventral setae, posteriorly in XI. Mouth, alimentary canal and anus absent (large blood vessel running through whole length of worm, resembling gut). Male genitalia (Fig. 2.5C) paired; vas deferens longer than atrium, but junction with latter not observed. Atrium small, pear-shaped, somewhat curved, with very thin outer lining and thick, granulated (and probably ciliated) inner epithelium opening into inner part of large, folded copulatory sac; two prostate glands present, anterior one located near atrium, posterior one located posterior to copulatory sac. Spermathecae (Fig. 2.5C: s) paired; ducts very short; ampullae elongate, thin-walled, containing large random masses of sperm.

Biology. Two marine genera of Tubificidae, *Olavius* and *Inanidrilus*, lack a normal alimentary system and are nutritionally dependent upon symbiotic bacteria that occur in high numbers under the cuticle of the worms. The bacteria absorb the nutrients through the body wall of the worms directly from the interstitial water of the sediment (Giere *et al.*, 1984). Most gutless species occur in reduced carbonate sands of coral reef areas, i.e., in shallow depths (see, e.g., Erséus, 1990b). *Olavius tannerensis*, however, is only known from a coarse sand bottom at 173 m.

Remarks. The most striking feature of this species is its lack of a normal alimentary system. The worms are not transparent when alive, but the gutless condition is obvious in fixed and cleared specimens mounted on slides. Unlike the majority of species within the gutless genera *Olavius* Erséus and *Inanidrilus* Erséus (see Erséus, 1984), *O. tannerensis* lacks penial setae. *Olavius tannerensis* appears closely related to the northwest Atlantic *O. tenuissimus* (Erséus, 1979) and *O. finitimus* Erséus, 1990 (both treated by Erséus 1990b), which however both have penial setae.

Distribution. Known only from the southern California Bight, the type locality on the Tanner Bank.

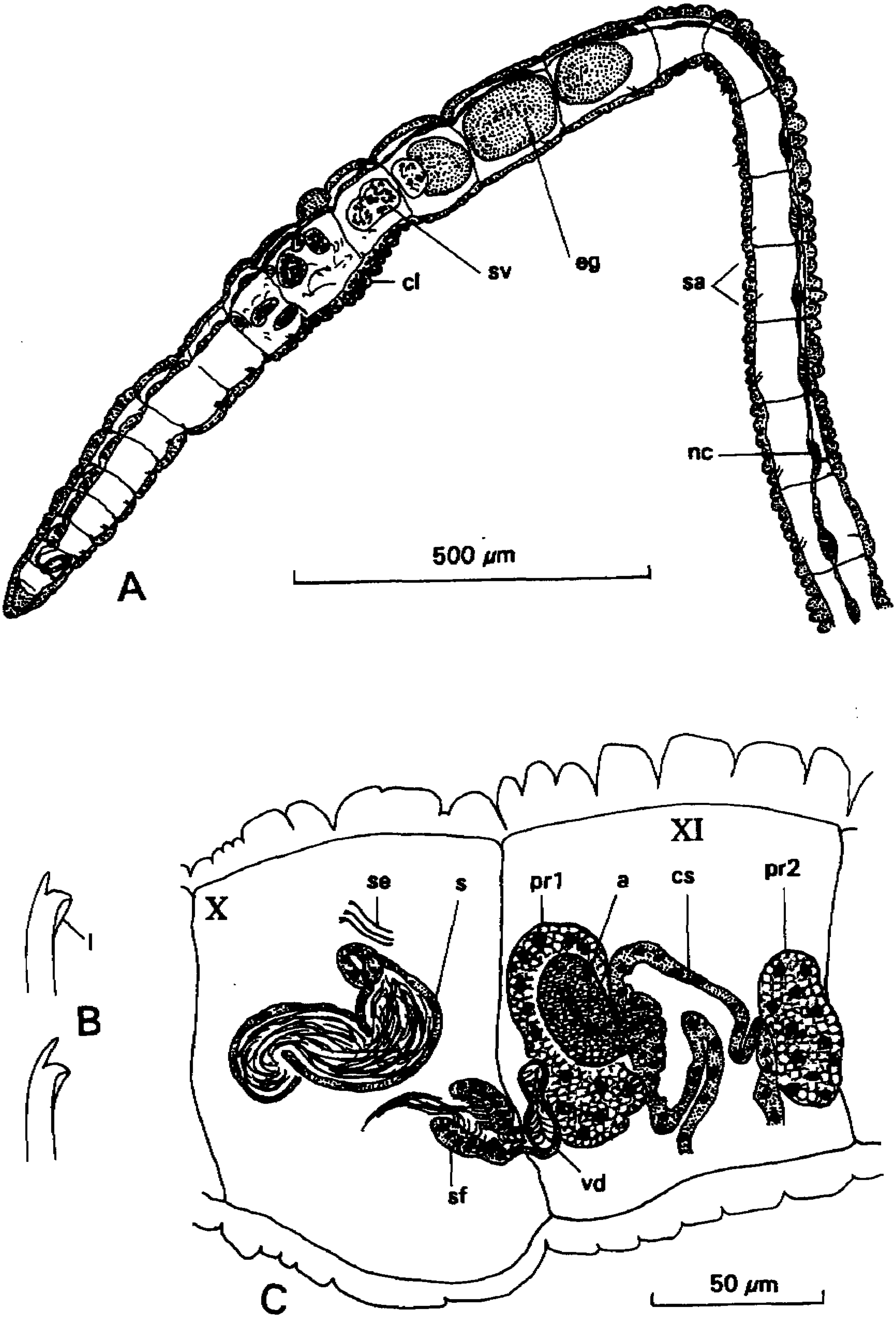

Figure 2.5. *Olavius tannerensis*: A, anterior end of whole specimen; B, setae (free-hand drawings); C, lateral view of segments X-XI, showing genitalia. (B-C after Erséus, 1991b).

Subfamily Limnodriloidinae

Tectidrilus diversus Erséus, 1982

Figure 2.6

Tectidrilus diversus Erséus, 1982:261-262, fig. 35.

Material examined. California: Santa Maria Basin, Sta. R-1, (5), Sta. R-2 (6), Sta. R-3 (2), Sta. R-4 (5), Sta. R-5 (5), Sta. R-7 (1), Sta. PJ-1 (3); Sta. PJ-6 (1), Sta. PJ-7 (7), Sta. PJ-9 (5), Sta. 1/2 (3) (total: 43 specimens).

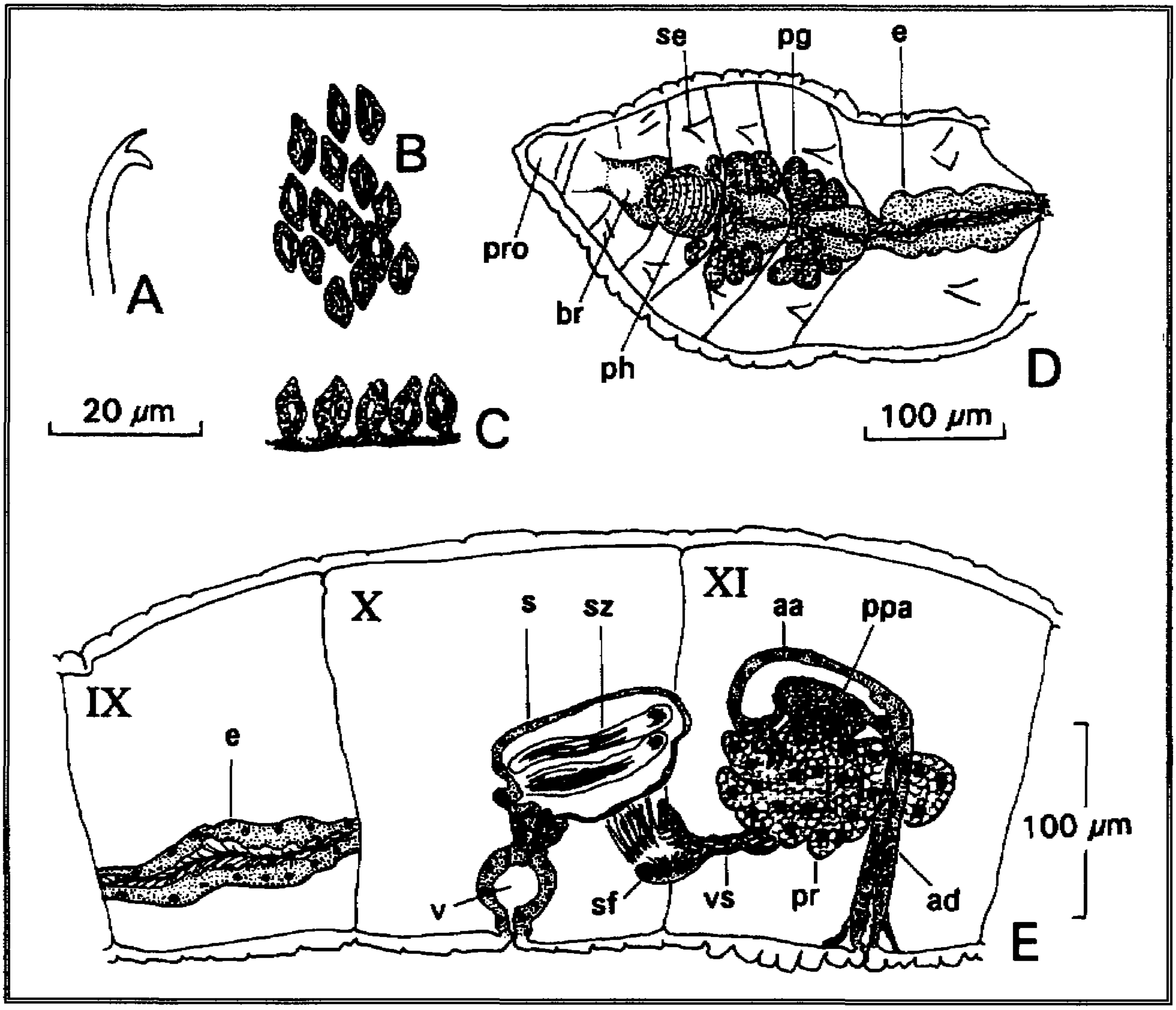

Figure 2.6. *Tectidrilus diversus*: A, seta; B, body wall papillae viewed from above; C, body wall papillae viewed from the side; D, horizontal view of first six segments; E, lateral view of segments IX-XI, showing esophagus (IX only) and genitalia.

Description. Body length (fixed specimens) 6-11 mm, for about 40-60 segments. Body wall with dense cover of fine particles, generally forming small, leaflike papillae (Figs. 2.6B-C), at least in postclitellar segments. Prostomium (Fig. 2.6D: pro) small, triangular. First 5 segments short (Fig. 2.6D). Clitellum extending over segment XI and anteriormost part of segment XII. Setae (Fig. 2.6A) bifid, with upper tooth as long as, but thinner than, lower tooth; 2 setae per bundle in segments II-VI or II-VII(VIII), 1 per bundle thereafter; ventral setae of segments X-XI absent. Spermathecal pores paired, in line with ventral setae, in middle of segment X. Male pores paired, in line with ventral setae, posteriorly in segment XI. Pharyngeal glands (Fig. 2.6D: pg) well developed in segments IV-V. Esophagus unmodified in segment IX (Fig. 2.6E: e). Male genitalia (Fig. 2.6E) paired; vas deferens about as long as atrium, entering atrium subapically. Atrium cylindrical, consisting of ampulla and duct; duct about as long as, or slightly longer than ampulla; outer end of atrial ampulla with conspicuous prostatic pad; lobes of prostate gland communicating with pad through bulging wall of atrial ampulla; atrial duct opening directly to exterior, but outer end of duct somewhat hollow and supported by a few thin muscle fibers indicating that it acts as a simple pseudopenis. Spermathecae (Fig. 2.6E: s) paired; ducts discrete, generally short, but sometimes appearing stretched, each with conspicuous, spherical vestibule near pore; ampullae oval, thin-walled. Sperm arranged in torch-shaped spermatozeugmata inside ampullae.

Biology. *Tectidrilus diversus* is the most common oligochaete in the Santa Maria Basin. The species occurs in fine sands and silts over the entire depth range included in the samples from the Phase II monitoring program (91-565 m). The closely related *T. probus* occurs only at the deeper locations (see below).

Remarks. All three species of *Tectidrilus* included in this atlas generally have discrete body wall papillae in postclitellar segments. Of these, *T. diversus* is the only species that lacks esophageal diverticula (in segment IX), a feature that generally can be checked in cleared, mounted specimens. However, the diverticula are very small, almost rudimentary, and sometimes difficult to see in the closely related *T. probus* (described below). Thus it may be insufficient to use the absence of esophageal diverticula to separate *T. diversus* from *T. probus*. Fortunately, the large, spherical spermathecal vestibules of *T. diversus,* as opposed to the small, indistinct ones of *T. probus,* facilitate the distinction of the two species.

Type locality and type specimens. Southern California, off Santa Barbara, Coal Oil Point, Isla Vista Seep (a natural oil seep), 16 m, holotype (USNM 72977) and 3 paratypes (USNM 73978-73980).

Distribution. California and British Columbia, 91-565 m.

Tectidrilus probus Erséus, 1991

Figure 2.7

Tectidrilus probus Erséus, 1991c: 334-335, fig. 1.

Material examined. California: Santa Maria Basin, off Purisima Point, holotype (USNM 136561), 5 paratypes (USNM 136562-6), and 2 additional paratypes (LACM 1531-2).

Description. Body length (fixed specimens) variable, range at least 7-15 mm for 35-60 segments. Body wall with dense cover of fine particles, generally forming small, leaflike papillae (as in *T. diversus*; Figs. 2.6B-C), at least in postclitellar segments. Prostomium small, triangular. First 5 segments short. Clitellum extending over segment XI and anteriormost part of segment XII. Setae (Fig. 2.7A) bifid, with

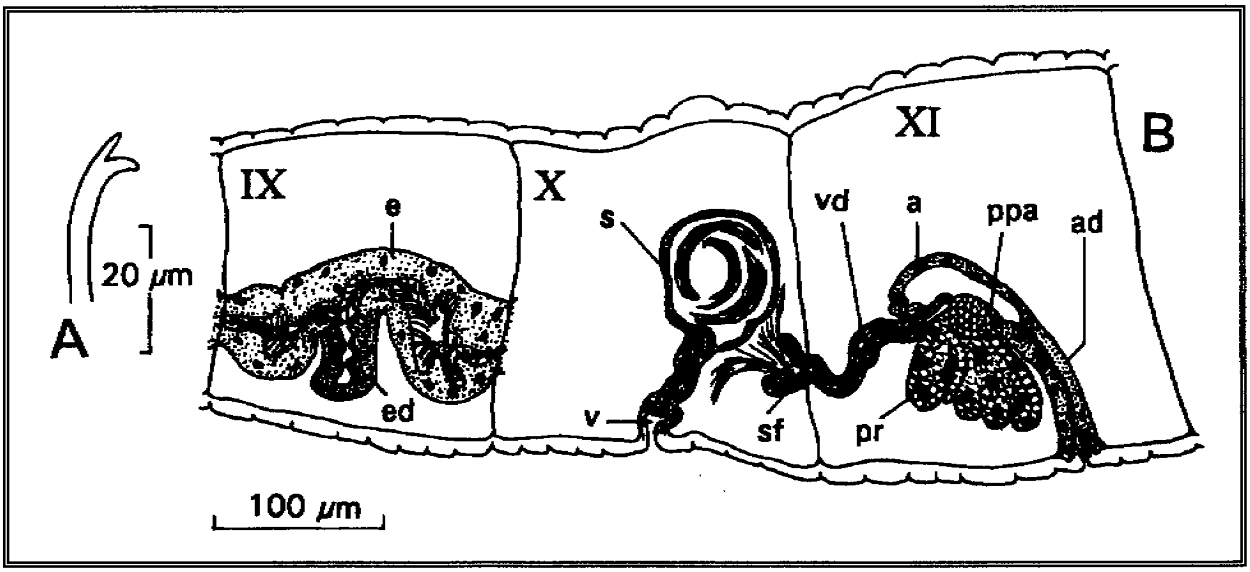

Figure 2.7. *Tectidrilus probus*: A, seta; B, lateral view of segments IX-XI, showing esophagus (IX only) and genitalia. (After Erséus, 1991c).

upper tooth slightly shorter and thinner than lower; 2 setae per bundle in segments II-VI or II-VII, 1 per bundle thereafter; but totally absent from X-XI. Spermathecal pores paired, in line with ventral setae, in middle of segment X. Male pores paired, in line with ventral setae, slightly posterior to middle of segment XI. Pharyngeal glands in segments IV-V. Esophageal diverticula (Fig. 2.7B: ed) present in middle of segment IX, but very small. Male genitalia (Fig. 2.7B) paired; vas deferens slightly shorter than atrium, entering atrium more or less apically; apical end of atrium generally somewhat curved. Atrium cylindrical, consisting of ampulla and duct, latter about as long as ampulla; outer end of ampulla with conspicuous prostatic pad; lobed prostate gland communicating with pad through bulging wall of atrial ampulla; atrial duct opening directly to exterior, but outer end of duct supported by a few thin muscles fibers indicating that it acts as a simple pseudopenis. Spermathecae (Fig. 2.7B: s) paired; ducts discrete, slender, each with small vestibule near pore; ampullae round to oval, thin-walled. Sperm arranged in spindle-shaped spermatozeugmata inside ampullae.

Biology. This species appears to be restricted to deeper upper slope depths having silty sediments having high clay inventories, whereas its congener, *T. diversus*, is common over a wider depth range and greater diversity sediment types (see above).

Remarks. *Tectidrilus probus* is similar to *T. diversus* (see above), but possesses small esophageal diverticula in segment IX (diverticula absent in *T. diversus*) and its spermathecal vestibules are not as large and distinct as those of the latter species.

Distribution. California, Santa Maria Basin, 410-565 m.

Tectidrilus profusus Erséus, 1991

Figure 2.8

Tectidrilus profusus Erséus, 1991c: 335-336, fig. 2.

Material examined. California: Off Long Point, Palos Verdes Peninsula, 61 m, holotype (USNM 136567) and 5 paratypes (USNM 136568-72), 2 additional paratypes (LACM 1529-30).

Description. Body length (fixed specimens) about 10-12 mm for 40-57 segments. Body wall with dense cover of fine particles, generally forming small, leaflike papillae (as in *T. diversus*; Figs. 2.6B-C), at least in postclitellar segments. Prostomium small, rounded or triangular. First 5 segments short. Clitellum extending over a small, posterior portion of segment X, all of segment XI, and a small, anterior portion of segment XII. Setae (Fig. 2.8A) bifid, with upper tooth thinner and slightly shorter than lower; 2 setae per bundle in segments II-VI, or II-VII, or II-VIII, 1 per bundle thereafter, but totally absent from segments X-XI. Spermathecal pores paired, somewhat ventral to lines of ventral setae, anterior to middle of segment X.

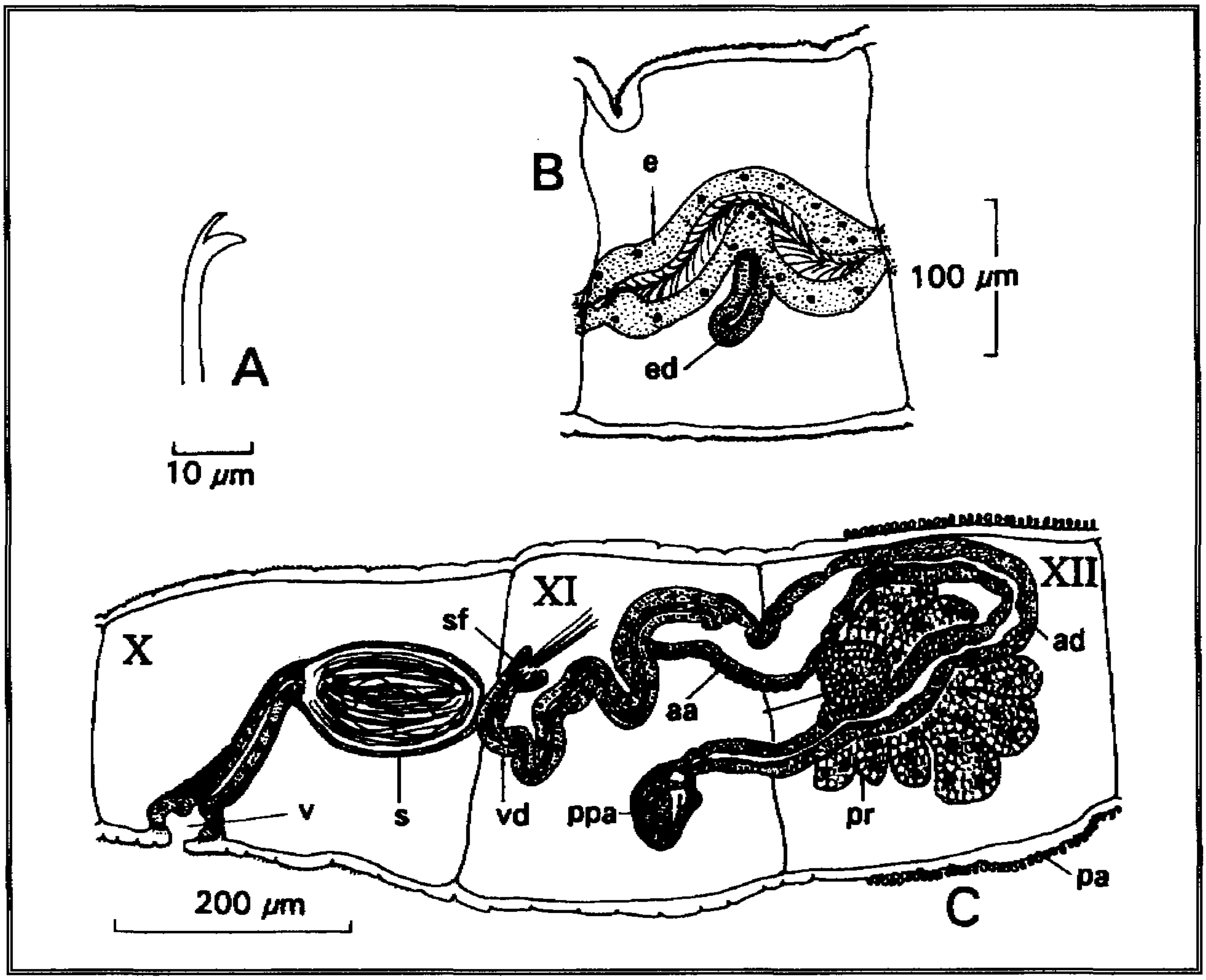

Figure 2.8. *Tectidrilus profusus*: A, seta; B, lateral view of segment IX, showing esophagus; C, lateral view of segments X-XII, showing genitalia. (A and C after Erséus, 1991c).

Male pores paired, somewhat ventral to lines of ventral setae, posterior to middle of segment XI. Pharyngeal glands in segments IV-V. One pair of small, slender esophageal diverticula present in middle of segment IX (Fig. 2.8B). Male genitalia (Fig. 2.8C) paired, elaborate, often extending into segment XII; vas deferens shorter than atrium, entering atrium subapically; outer part of vas deferens generally wider than inner part. Atrium cylindrical, consisting of heavily muscularized (and often twisted and distorted) ampulla and very long, granulated duct; outer end of atrial ampulla with round diverticulum containing prostatic pad; lobes of large prostate gland communicating with this diverticulum; atrial duct opening directly to exterior, but outer end enclosed in simple somewhat muscular sac and thus probably acting as eversible pseudopenis. Spermathecae (Fig. 2.8C: s) paired; ducts distinct, long, heavily muscular, each with large vestibule near pore; ampullae oval, thin-walled. Sperm as compact, random masses inside ampullae.

Biology. Shallow subtidal in silt and sand.

Remarks. *Tectidrilus profusus* is easily distinguished from the other two congeners by its elaborate, partly muscular, male ducts and spermathecae (see Fig. 2.8C), and from *T. diversus* by its possession of esophageal diverticula in segment IX.

Distribution. Known only from off Palos Verdes, California, 3-61 m.

Limnodriloides monothecus Cook, 1974

Figure 2.9

Limnodriloides monothecus Cook, 1974:131-132, fig. 3.—Brinkhurst and Baker, 1979:1564.—Erséus, 1988:67; Erséus, 1990b:280-282, figs. 26A-H.
Bohadschia monotheca Hrabe, 1975:112-114, figs. 1-3 (but status uncertain; see Remarks).
Limnodriloides monothecus (part); Erséus, 1982: 250-253, figs. 28-29; Erséus, 1986: 309.
Not *Limnodriloides monothecus*; Erséus, 1987:274 (=*L. anxius* Erséus, 1990b).

Material examined. California: Santa Maria Basin, Sta. R-1, (2), Sta. R-2 (1); off Palos Verdes Peninsula, 30 m (1).

Description. Body size variable, fixed specimens 3-13 mm long for 40-78 segments. Body wall smooth, without cuticular papillae. Prostomium rounded. Clitellum weakly developed. Setae (Fig. 2.9A) bifid, with upper tooth shorter and thinner than lower, 2-3(4) setae per bundle in anterior segments, (1)2 per bundle in postclitellar segments; modified genital setae absent. Spermathecal pore unpaired, mid-dorsal, situated somewhat anterior to middle of segment X. Male pores paired, in line with ventral setae, in posterior of segment XI. Pharyngeal glands in segments IV-V. One pair of slender esophageal diverticula present in anterior part of IX (Fig. 2.9C: ed). Male ducts (Fig. 2.9C) paired; sperm funnel small; entrance of vas deferens somewhat subapical on atrium. Atrium consisting of ampulla and duct, latter narrower and much longer than former; inner epithelium of atrial ampulla with small, glandular prostatic pad; lobes of prostate gland communicating with pad through wall of atrial ampulla; inner part of atrial duct generally granulated, outer part often much coiled, terminating in small pseudopenial papilla located in deep copulatory sac. Spermatheca (Figs. 2.9B-C: s) unpaired, virtually without proper duct, but with outer end of ampulla often thick-walled; ampulla slender, sometimes reaching into (even throughout) segment XI (Fig. 2.9B). Sperm arranged in very slender spermatozeugmata inside spermatheca.

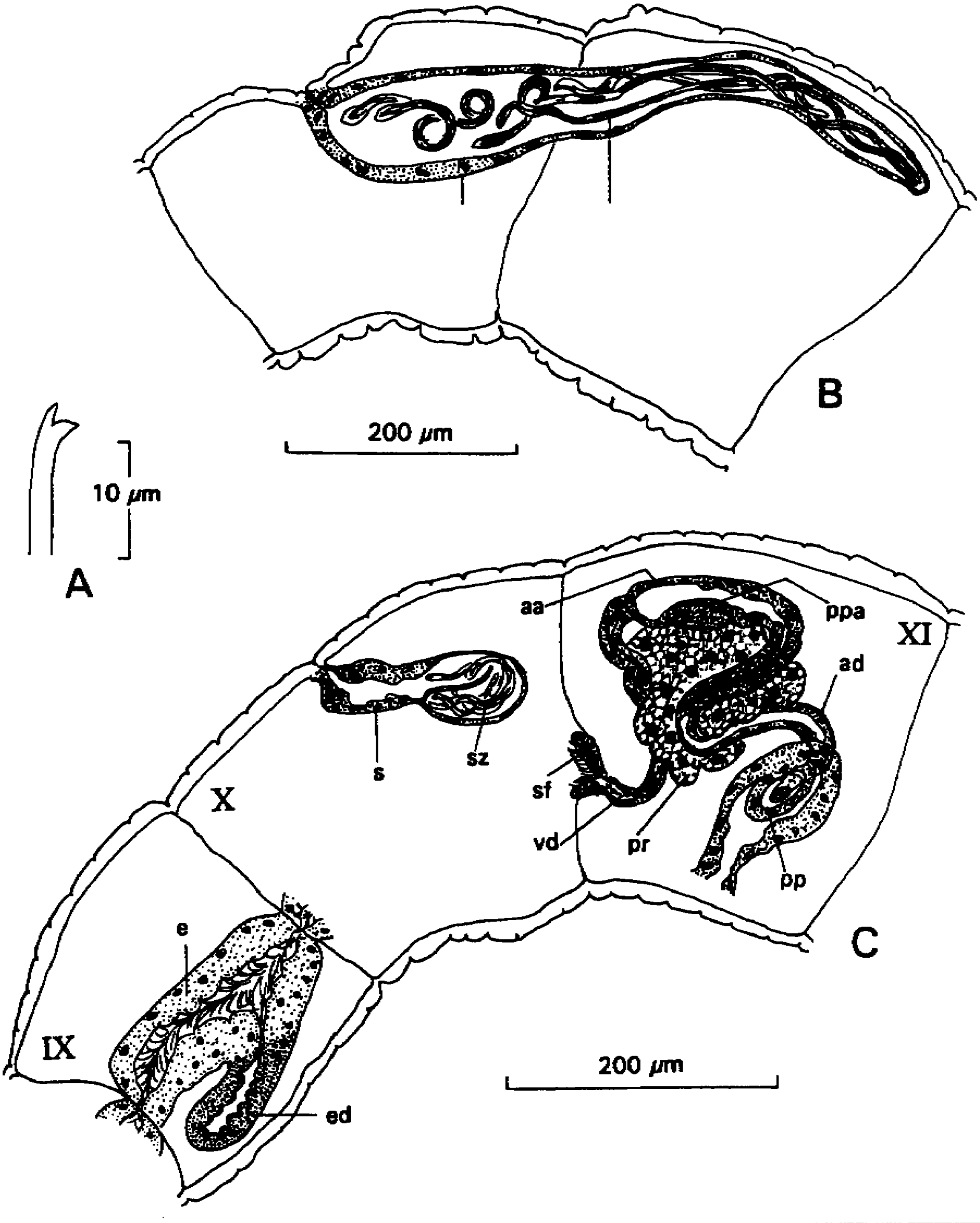

Figure 2.9. *Limnodriloides monothecus*: A, seta; B, lateral view of segments X-XI, showing spermatheca only (specimen from Santa Maria Basin); C, Lateral view of segments IX-XI, showing esophagus (IX only) and genitalia (specimen from off Los Angeles).

Biology. *Limnodriloides monothecus* is common in marine sands and muds, to at least 583 m but has also been reported from brackish water.

Remarks. *Limnodriloides monothecus* is readily recognized by the unpaired, slender spermatheca, with characteristic spermatozeugmata (Figs. 2.9B-C: sz), as well as the long atrial ducts, that are generally easy to see in cleared, whole-mounted, sexually mature specimens. Originally described from the Pacific coast of Mexico (Cook, 1974), *L. monothecus* has been recorded from many areas in the Caribbean and along both sides of North America (Brinkhurst and Baker, 1979; Erséus, 1982, 1986, 1988, 1990b). The Mediterranean taxon *Bohadschia monotheca* Hrabe is a possible synonym (and homonym) for *L. monothecus* (see Erséus, 1990b). These forms belong to a complex within *Limnodriloides* that is characterized by unpaired, mid-dorsal spermatheca, and long, convoluted atrial ducts. In Belize on the Caribbean side of Central America, no less than five species within this complex have been reported (Erséus, 1990b), but *L. monothecus* is the only one known from the eastern Pacific to date. It is distinguished from the other taxa by its slender spermatheca (spermatheca oval or spherical in the other species).

Type locality and type specimens. Mexico, Baja California, Bahía de San Quintin, subtidal, less than 2 m, holotype (USNM 45285) and 7 paratypes (USNM 45286), 1 additional paratype (NMC 3478).

Distribution. West coast of Mexico and North America (California through British Columbia); Gulf of Mexico; East coast of United States (Florida through New Jersey); Belize; Bermuda; Yugoslavia(?).

Limnodriloides barnardi Cook, 1974

Figure 2.10

Limnodriloides barnardi Cook, 1974:134-135, fig. 5.—Erséus, 1982:232-234, fig. 13.—Davis, 1985: 171-172.—Erséus, 1990b:287-288, fig. 30.

Limnodriloides barnardi (part); Erséus, 1976:32-22, not fig. 3.

Limnodriloides winckelmanni Michaelsen, 1914 (part) .—Jamieson, 1977: 338, not fig. 2.—Brinkhurst and Baker, 1979: 1564.

Material examined. California: Santa Maria Basin, Sta. R-1; (3); Sta. R-2 (31); Sta. R-3 (3); Sta. R-4 (25), Sta. R-5 (14), Sta. R-6 (9), Sta. R-7 (11); Sta. PJ-1 (9), Sta. PJ-7 (10), Sta. PJ-9 (8). (total: 123 specimens).

Description. Body size variable, fixed specimens 4-16 mm long for 31-66 segments. Body wall smooth, without cuticular papillae. Prostomium small, somewhat triangular. When developed, clitellum extending over posterior half of segment X and all of whole segments XI-XII. Somatic setae (Fig. 2.10A) bifid, with subequal teeth, 2-4 per bundle in anterior segments; bundles of postclitellar segments often unisetal (at least in specimens from Santa Maria Basin), or with 2 setae; ventral setae of segment X modified into slender, walking-stick-shaped spermathecal setae (Fig. 2.10B); these setae straight or curved, single-pointed, but with hollow groove from node to outer ends; inner end generally somewhat hooked, outer part enclosed in glandular sac (this sac also bearing outer glandular body similar to prostate gland; Fig. 2.10C: gss); spermathecal setae either situated posterior to, or anterior to spermathecal pores; occasionally lacking at one or both sides of worm. Spermathecal pores paired, more or less in line with segment XI. Pharyngeal glands in segments IV-V. One pair of esophageal diverticula present in

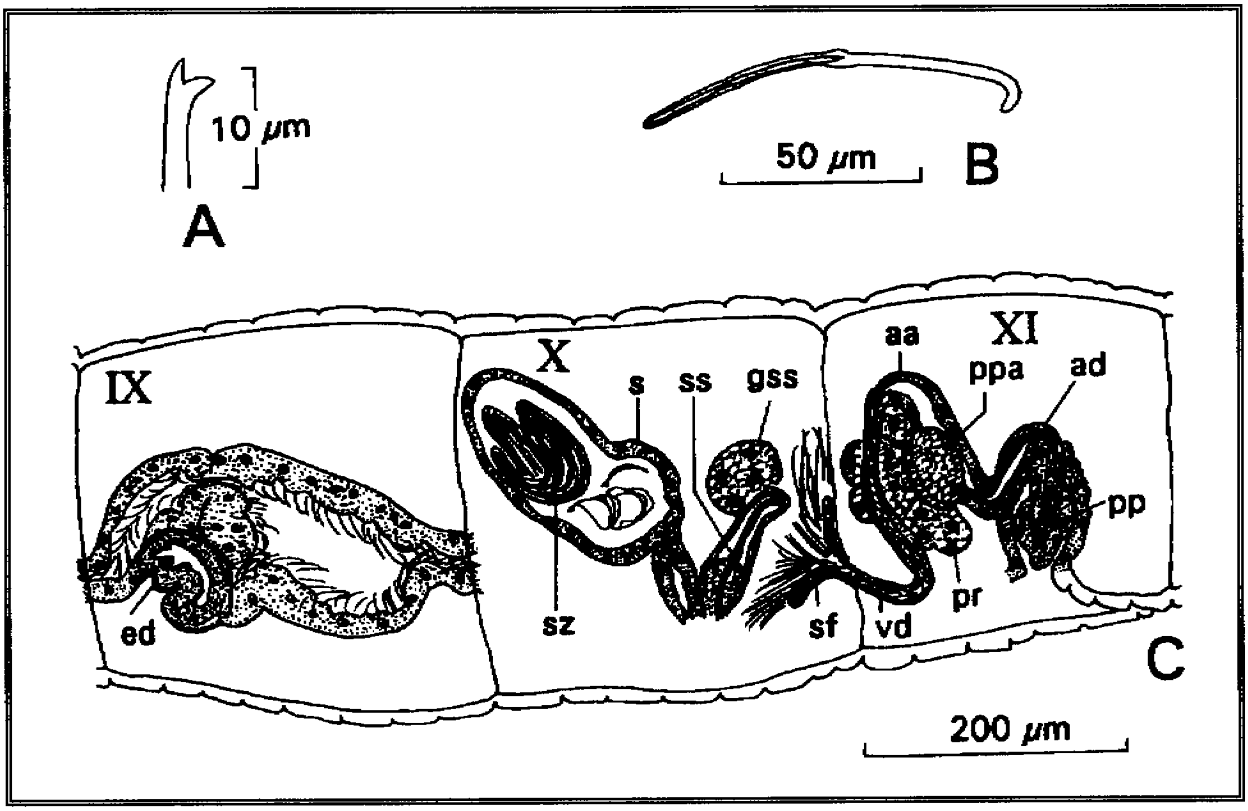

Figure 2.10. *Limnodriloides barnardi*: A, somatic seta; B, spermathecal seta; C, lateral view of segments IX-XI, showing esophagus (IX only) and genitalia. (B after Cook, 1974).

ventral setae, in middle of segment X. Male pores paired, in line with ventral setae, in posterior portion of anterior part of segment IX (Fig. 2.10C: ed). Male ducts (Fig. 2.10C) paired; sperm funnel large; vas deferens opening into apical, somewhat curved end of atrium. Atrium cylindrical, consisting of ampulla and duct, latter generally slightly longer than former; outer end of atrial ampulla with large glandular prostatic pad, filling most of atrial lumen in this part; lobes of prostate gland communicating with pad through bulging wall of atrial ampulla. A great part of atrial duct heavily granulated, but outer end narrow, terminating in somewhat conical pseudopenial papilla located in large copulatory sac. Spermathecae (Fig. 2.10C: s) paired; duct short, outer part generally hollow, with somewhat glandular wall; ampulla oval, pear-shaped, or slender, often with glandular wall. Sperm arranged in slender spermatozeugmata inside spermatheca.

Biology. *Limnodriloides barnardi* occurs in subtidal (often silty) sands, to at least 565 m.

Remarks. The characteristic spermathecal setae and the large copulatory sacs are generally easy to see in cleared, whole-mounted, sexually mature specimens of *Limnodriloides barnardi* and readily distinguish the species from *L. monothecus*. Spermathecal setae may, however, be absent in some individuals.

Originally described from the Pacific coast of Mexico (Cook, 1974), *L. barnardi* has been recorded from many areas in the Caribbean and along both sides of North America (Erséus, 1982, 1990b; Davis, 1985; Brinkhurst, 1987). Because there is great variation in the overall size, as well as in the extension of the pseudopenis and the atrial ducts, it is possible that the taxon in fact represents a complex of very similar species. Several other members of the subfamily Limnodriloidinae possess modified spermathecal setae similar to those of *L. barnardi*. Most of these species are located in the genus

Limnodriloides. One such species is *L. victoriensis* (Brinkhurst and Baker, 1979), which occurs in more northern parts of the Pacific Ocean, including northern China (Erséus *et al.*, 1990). *Limnodriloides barnardi* and *L. victoriensis* appear to overlap (at least) in British Columbia (see Brinkhurst, 1987), but *L. victoriensis* is distinguished from the former by its unpaired pseudopenis.

Type locality and type specimens. Mexico, Baja California, Bahía de San Quintin, subtidal, less than 2 m, holotype (USNM 48730) and 14 paratypes (USNM 48731), 1 additional paratype (NMC 3480).

Distribution. Eastern Pacific, including Mexico, California, and British Columbia; East and Gulf coasts of United States (Massachusetts to Florida); throughout Caribbean.

Subfamily Tubificinae

Tubificoides bakeri Brinkhurst, 1985

Figure 2.11

Tubificoides bakeri Brinkhurst, 1985:407-408, figs 7B, 8i; Milligan, 1991:344-345, fig. 5.

Material examined. California: Santa Maria Basin, Sta. R-5, (9, all sexually immature).

Description. Body length (fixed specimens) about 5-7 mm for up to 60 segments. Anterior region of worm inflated, posterior segments elongate. Body wall often "dusty" in postclitellar region due to presence of scattered fine particles on cuticle; occasionally these particles aggregated into small papillae (similar to those of *Tectidrilus diversus*; see Figs. 2.6B-C). Prostomium pointed, triangular. Clitellum not apparent in sexually immature specimens, but reported as poorly developed in previously descriptions. Dorsal bundles of anterior segments (Fig. 2.11A) with 2-4 bifid and 3-5 hair setae; bifid setae (Fig. 2.11B) with upper tooth about as long as, but thinner than, lower; hair setae absent posterior to segment X or thereabouts; dorsal bundles of postclitellar segments with 1-2 bifid setae (1 per bundle common near posterior end of worm), with upper tooth slightly shorter and thinner than lower (Fig. 2.11C). Ventral setae (Figs. 2.11D-E) all bifid, with upper tooth thinner, and about as long as or slightly shorter than lower; in anterior segments, ventral setae 2-5 per bundle; in postclitellar segments, ventral setae 1-2 per bundle; setae totally absent from segment XI. Spermathecal pores paired, somewhat anterolateral to ventral setae in segment X. Male pores paired, in line with ventral setae in segment XI. Pharyngeal glands in segments IV-V. Esophagus unmodified in segment IX. Male genitalia (Fig. 2.11G) paired; vas deferens thin-walled, slightly longer than atrium, entering latter subapically, somewhat opposite to attachment of prostate gland; but entrance of vas deferens is closer to apical end of atrium than is attachment of prostate gland. Atrium cylindrical, curved, histologically divided into three regions: (1) inner caplike region with large epithelial cells, (2) elongate middle region within thickened inner epithelium, and (3) outer bulbous part at basis of penis. One prostate gland communicating with inner epithelium of atrium through narrow entrance, located between (caplike) inner and (elongate) middle regions of atrium; atrium terminating in cylindrical penis, latter about twice as long as wide and covered with thin cuticular sheath. Spermathecae (Fig. 2.11F) paired; ducts discrete, slender, each with small vestibule near pore; ampullae oval to roundish, thin-walled. Sperm as vermiform spermatozeugmata inside ampullae.

Biology. A subtidal species occurring in silty sediments.

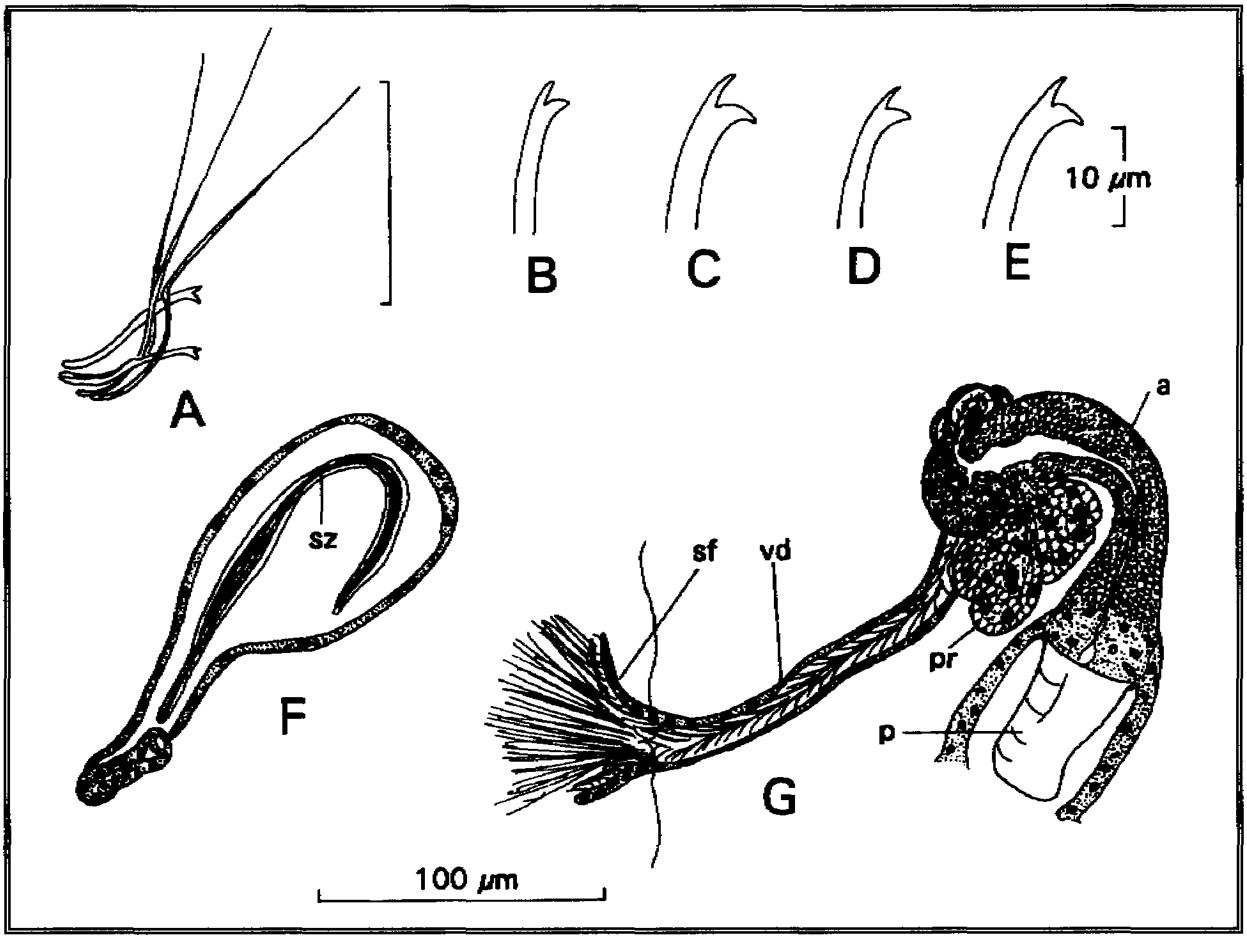

Figure 2.11. *Tubificoides bakeri*: A, anterior dorsal bundle of setae, containing both hair setae and bifid crotchets; B, anterior dorsal, bifid, seta; C, posterior dorsal seta. D. anterior ventral seta. E. posterior ventral seta. F. spermatheca. G. male genitalia. (F and G after Milligan, 1991).

Remarks. *Tubificoides bakeri* is the only tubificid with hair setae known from the Santa Maria Basin area. The hairs can be seen under a stereomicroscope, and they occur in immature as well as sexually mature specimens. The characteristic cuticular penis sheaths are generally easy to observe in mature specimens that have been cleared, and then mounted on a slide.

Tubificoides is a large, but relatively uniform genus of marine tubificids (see Brinkhurst, 1985, 1986), many of the species occurring in offshore sediments having high silt content. In the available material from the Santa Maria Basin, only nine specimens belonging to this genus were found, none of which were sexually mature; their identity as *T. bakeri* is confirmed by their setal characteristics. *Tubificoides bakeri* was originally recorded from the Palos Verdes Peninsula, Los Angeles (Brinkhurst, 1985; see also Milligan, 1991), an area that is not far from the Santa Maria Basin.

Type locality and type specimens. Canada, British Columbia, Mackenzie Bight, Saanich Inlet, near Victoria, 10 m, holotype (USNM 97294) and four paratypes (USNM 97295-97298).

Distribution. British Columbia and California, 10-154 m.

Family Enchytraeidae

Grania incerta Coates and Erséus, 1980

Figure 2.12

Grania incerta Coates and Erséus, 1980:1038-1040, fig. 2.—Coates, 1984:fig. 4.

Material examined. California: Off Santa Barbara, Isla Vista Seep (a natural oil seep east of Coal Oil Point), 16 m, well-sorted fine sand, holotype (USNM 58908) and 9 paratypes (USNM 58909-58910; 4 of which are from British Columbia).

Description. Body length (fixed specimens) 7-10 mm, for 47-55 segments. Filiform and smooth worms (Fig. 2.12A), transparent and iridescent when alive, somewhat resembling nematodes; body wall with thick cuticula. Prostomium conical or rounded. Clitellum extending more or less completely over segments XII-XIII. Setae (Figs. 2.12B-C) large and straight, always one per bundle, but totally absent from segments II-III (and XII in sexually mature specimens); ventral setae on segment IV, dorsal (or rather lateral) setae in segment XVIII or XIX (Fig. 2.12D). [Due to cephalization of some anterior segments, segmental numbers are difficult to establish in this species unless position of spermathecae is assumed to be in segment V.] Tips of setae sharply single-pointed, inner ends broad and slightly curved; posterior setae (Fig. 2.12C) about twice as long as anterior ones (Fig. 2.12B). Spermathecal pores paired, lateral in most anterior part of segment V. Male pores paired, ventral in segment XII. Pharyngeal glands paired, as two rows of distinct, roundish bodies in segments IV-VI (Fig. 2.12A: pg); three pairs of "primary" glands at septa IV/V, V/VI, and VI/VII, secondary glands especially well developed in segment VI. Esophagus and intestine without diverticula or appendages. Unpaired seminal vesicle extending backwards as far as segment XVII; mature eggs in ovisac extending even further backwards (Fig. 2.12A: eg). Male ducts paired; sperm funnel (Fig. 2.12A: sf) generally located in segment XI, large, cylindrical, glandular, 2-4 times longer than wide; vas deferens thin and coiled, extending into XIV (or thereabouts), then returning into XII, where its opens to exterior through male pore. Penial bulb (Fig. 2.12E) small, glandular, attached medially to male pore; latter also with elongate, aglandular, lateral outpocketing, attached to body wall by muscles. Spermathecae (Fig. 2.12F) paired; ducts narrow, with a few small glands around outer end (near pore); ampullae pear-shaped or ovoid, somewhat incised at junction with ducts and with inner ends attached to (and possibly communicating with) esophagus in posterior part of segment V; with numerous small rings of sperm dispersed within walls of ampullae.

Biology. This species occurs in shallow subtidal sandy bottoms.

Remarks. The species of *Grania* are very slender, somewhat stiff oligochaetes, with stout setae arranged in unisetal bundles, and unless additional species are present in the Santa Maria Basin and Western Santa Barbara Channel, *G. incerta* should be easy to separate from all other oligochaetes included elsewhere in this atlas. The specific features of *G. incerta* are the distribution of setae (Fig. 2.12D), the morphology of the male ducts (especially the structures associated with the male pores; Fig. 2.12E) and the spermathecae (Fig. 2.12F).

This species was originally described by Coates and Erséus (1980). However, the morphology of the terminal portions of its male ducts were studied later by Coates (1984), who pointed out that the various species of *Grania* can be discriminated taxonomically only if the details of these structures are carefully examined.

Distribution. California and British Columbia, 3-16 m.

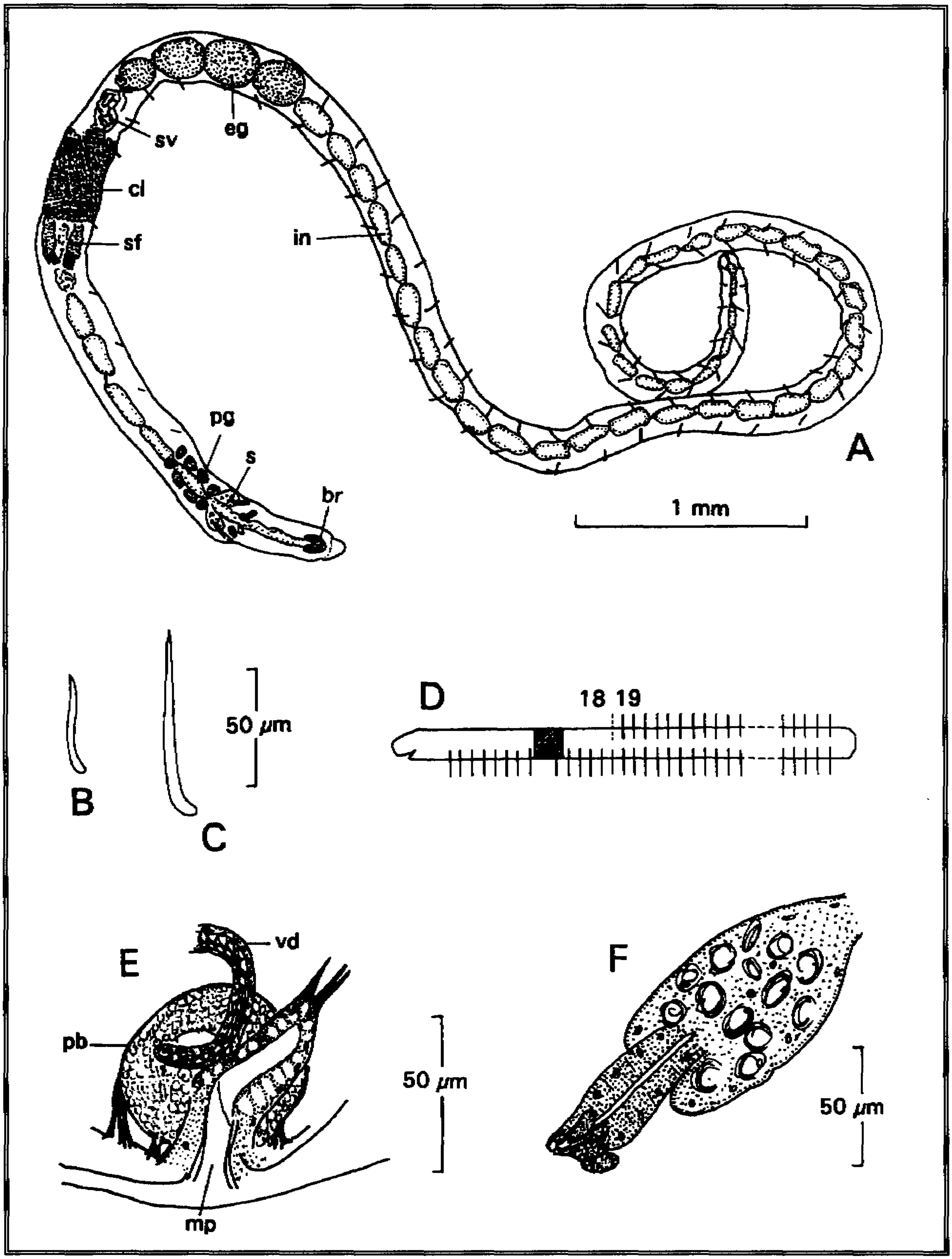

Figure 2.12. *Grania incerta*: A, whole specimen; B, anterior seta; C, posterior seta; D, schematic view of the distribution of seta, numbers indicating segments; E, terminal part of male duct; F, spermatheca. (A-D and F after Coates and Erséus, 1980; E after Coates, 1984).

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3. INTRODUCTION TO THE POLYCHAETA

by

James A. Blake[1]

Introduction

The Class Polychaeta represents a major group of marine invertebrates with more than 16,000 known species. They are the dominant component of the marine benthic infauna, regardless of whether nearshore shallow waters or offshore continental shelf areas are sampled. In early studies, when screens of 1-mm mesh were used to sieve samples, polychaetes comprised about 30% of the fauna collected. In recent years, screens with mesh sizes of 0.5 mm and 0.3 mm have been used more routinely, and polychaetes have been demonstrated to account for as much as 70% of all species and individuals collected.

Use of the fine screens, while rewarding in that the benthic habitats are more adequately sampled and described, has also led to increasing frustration on the part of researchers attempting to identify the polychaetes in these collections. The information necessary to make correct identifications has either been in inadequate local keys, scattered in the literature, taxonomically confused, or non-existent because many of the species collected are in fact undescribed.

In general, the polychaete fauna of the estuarine, open-coast, and near coastal habitats of California is relatively well known largely due to the life-long work of Dr. Olga Hartman. Beginning as a graduate student at the University of California in the 1930s and continuing as a Scientist and Professor at the Allan Hancock Foundation until her death in 1974, Dr. Hartman revised and described most of the families of polychaetes from the eastern Pacific and especially California. This effort culminated in the publication of her 2-volume Atlas of the Polychaetous Annelids from California (Hartman, 1968; 1969). This composite work provides keys, descriptions, and illustrations to 701 species of polychaetes that are distributed in 312 genera and 61 families. Dr. Hartman's Atlas has served as the principle resource for the identification of California polychaetes for two decades. In the years since Dr. Hartman's Atlas was published, research on polychaetes has flourished, and it is apparent that many of the earlier keys are now out of date. The extensive benthic surveys on the California continental shelf and upper slope supported by the U.S. Department of Interior, Minerals Management Service (MMS) has yielded a harvest of polychaetes that are either new records or new to science. In addition, extensive monitoring and reconnaissance programs of nearshore habitats in the vicinity of sewage outfalls and dredged material disposal sites using newer quantitative techniques have yielded new polychaete taxa.

For the most part, the majority of these new taxa have remained undescribed and are reported locally under provisional names such as "sp. A" of various genera. The fauna of the Santa Maria Basin and Western Santa Barbara Channel contains many such species and it is one of the goals of the present study to make these species known to the scientific community. As part of the Phase I reconnaissance and Phase II monitoring programs, approximately 520 species of polychaetes were identified. At least 25% of these species were not included in Hartman's Atlas (Hartman, 1968; 1969).

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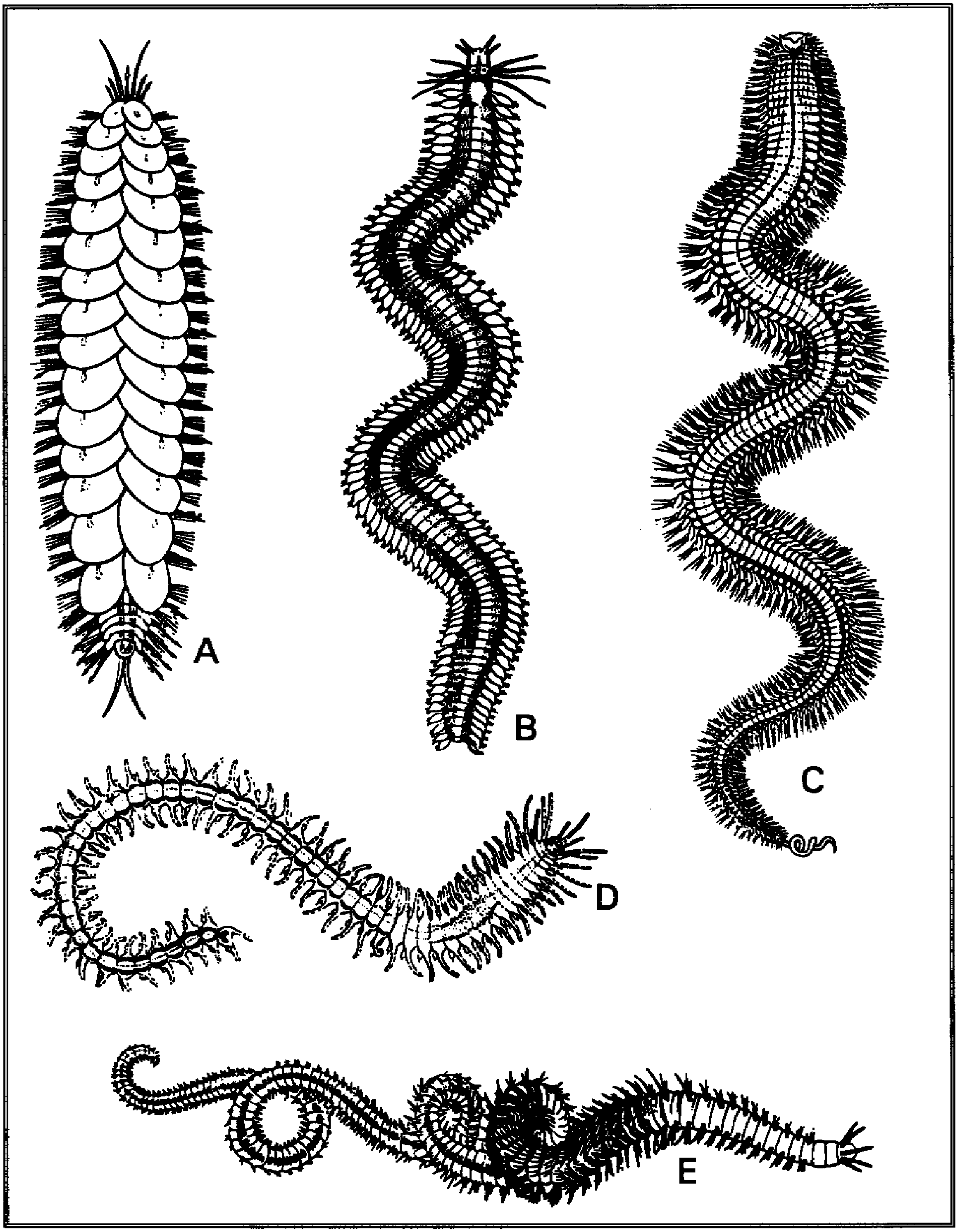

Figure 3.1. Representative Errant Polychaetes: A, Polynoidae (*Harmothoe*); B, Phyllodocidae (*Paranaitis*); C, Nephtyidae (*Nephtys*); D, Syllidae (*Odontosyllis*); E, Eunicidae (*Marphysa*). (all after McIntosh).

The geographic area covered by this Atlas includes the Santa Maria Basin and Western Santa Barbara Channel from approximately 50 to 1000 m. In addition, some species that have been encountered in adjacent areas and are expected to occur in the study area are included as well.

In preparing the polychaete volumes for this Atlas, the authors have been encouraged to re-examine earlier records and type specimens wherever appropriate. Some revisionary work was done by the contributing authors in the preparation for the individual family presentations; new taxa have been described in separate manuscripts and others will be included in the individual chapters. Although this Atlas is not intended as a revision of Hartman's Atlas, it should serve as the framework upon which an updated guide to California polychaetes can be developed.

Polychaete Morphology

In general, the polychaetes, like other members of the phylum Annelida, are distinguished by a metameric body form, in which the body is divided into similar parts or segments arranged in a linear series along the anterior-posterior axis (Fig. 3.1). The segmented portion is limited to the trunk region; the anteriormost cephalic lobe or prostomium and the posteriormost anus-bearing region or pygidium are not true segments. The formation of new segments always takes place just anterior to the pygidium, so the anterior segments are the oldest and the posterior segments are the youngest.

All polychaetes share these basic features, but at this point, the similarity ends. The body varies greatly in form and for the most part is related to whether the species has a crawling, swimming, burrowing, boring, tube-dwelling, or parasitic habit. Individual species range in length from less than 1 mm for meiofaunal forms to more than 1 to 3 m for some nereidids, onuphids, and eunicids. The number of segments may be as few as seven, and may be fixed at some finite number or unlimited. Body forms range from typical crawling errant animals as represented by polynoids, phyllodocids, nephtyids, syllids, and eunicids (Fig. 3.1) to the astonishing array of sedentary forms with different degrees of development of specialized body regions and modifications of the prostomium (Fig. 3.2). Errant polychaetes generally do not have regions defined along their body and exhibit sinuous movements when in motion. Free-living worms, such as polynoids, crawl sluggishly, but still lack defined body regions (Fig. 3.1A-E). Tube-dwelling forms frequently have defined body regions and are able to move in predictable patterns within their burrows assisted by uncini or hooks that grip the walls and provide traction.

In order to present basic polychaete morphology, a comparative approach has been taken here, where no one "typical" polychaete is presented as an example of the structure being discussed. The following provides comments and illustrations on some of the more important structures that are necessary for the use of keys and interpretation of differences among species. With a basic understanding of this morphology, it should be possible to deal with individual families.

The anterior end may be simple or modified in a variety of ways (Fig. 3.3). The prostomium is a preoral lobe that contains the cerebral ganglia and bears most of the sense organs and sometimes two types of appendages, the **antennae** and **palps** (Figs. 3.3A, F, I). The presence or absence of these structures, their number and specific morphology, are of great taxonomic importance. The mouth is located on the ventral side of the body, as an opening in the **peristomium** or buccal segment, which in some forms at least is also presegmental in nature (Åkesson, 1967). The peristomium may sometimes be combined with anterior trunk segments to varying degrees. This region may bear one to eight pairs of **tentacular cirri (=peristomial cirri)** (Figs. 3.3B, E, H, J).

A variety of sense organs are associated with the prostomium and peristomium. Eyes may be present or absent. Eyes may include simple ocelli that include a photoreceptor with an inverted pigment cup imbedded in the brain. More complex eyes consist of a receptor cell and lens that is surrounded by a pigment cell. Although eyes are usually thought of as being photoreceptors on the prostomium, some

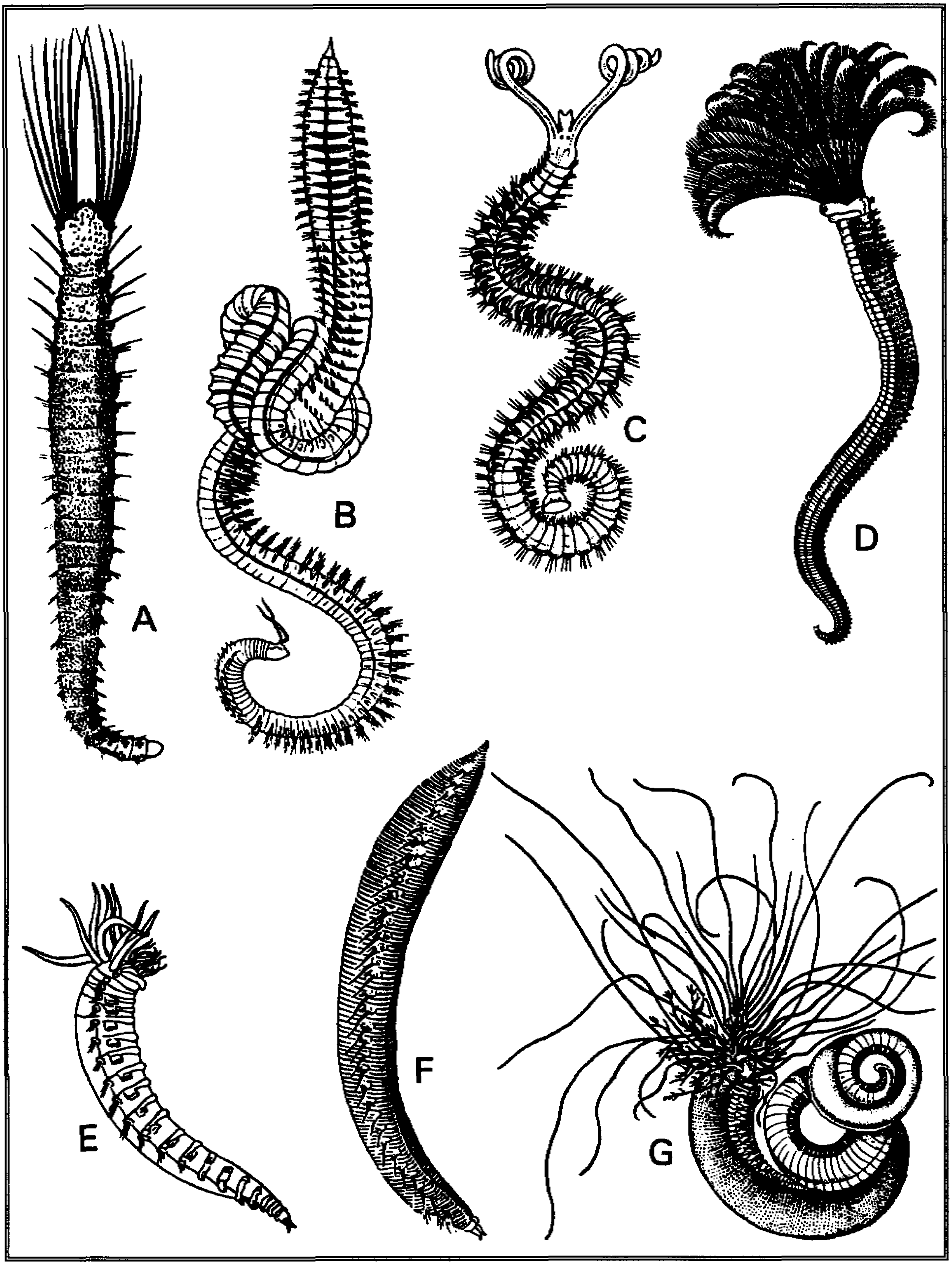

Figure 3.2. Representative Sedentary Polychaetes: A, Flabelligeridae (*Pherusa*); B, Orbiniidae (*Scoloplos*); C, Spionidae (*Polydora*); D, Sabellidae (*Megalomma*); E, Ampharetidae (*Amage*); F, Opheliidae (*Ophelia*); G, Terebellidae (*Amphitrite*). (all after McIntosh).

opheliids have segmental eyes along their body. Some sabellids have compound eyespots on the tentacles of the branchial crown, and some species of *Fabricia* have eyes on the pygidium. Errant polychaetes, such as nereidids, nephtyids, and syllids have evolved more complex eyes in which a group of photoreceptor cells share a common pigment cup. Important references dealing with the structure and function of eyes include: Eakin and Westfall (1964), Hermans and Cloney (1966), Hermans (1969), Hermans and Eakin (1974), and Kernéis (1968). In addition to eyes, a type of chemoreceptor called a **nuchal organ** may be present. Nuchal organs are found in several families including the Glyceridae, Nephtyidae, Opheliidae, Capitellidae, Orbiniidae, and Spionidae. Nuchal organs may be simple sensory pits or more complex, folded lobelike structures. The physiology of these organs is poorly known, but their presence/absence may be diagnostic at the species level. A survey of nuchal organs in polychaetes and considerable histological detail is provided by Rullier (1951).

The use of the terms palp, antenna, tentacle, and cirrus varies greatly in published accounts. **Antennae** are usually dorsal or on the anterior margin of the prostomium (Figs. 3.3A, B, C, E, F, G, H, I), and are always sensory structures. **Palps** are usually associated with the mouth (Figs. 3.3E, F, I, J), and may be used in feeding or may be sensory structures. Palps tend to be ventral or lateral to the prostomium (Figs. 3.3E, F, I, J; 3.4A). In the family Spionidae, however, the large grooved, prehensile dorsolateral structures found at the postectal corners of the prostomium are also called palps (Fig. 3.3M). The term **cirrus** is usually applied to dorsal or ventral structures on the parapodia, but also applies to the elongated **tentacular cirri** on the anterior part of the body. The pygidium often bears **anal** or **pygidial cirri** (Figs. 3.1A, 3.2B). The term **tentacle** tends to be used in a general sense to designate a variety of elongated sensory or feeding structures, usually on the head, except for the cossurids and some cirratulids where they are located on an anterior body segment.

Sedentary polychaetes differ quite obviously from the typical body form characteristic of errant types. In general, body parts such as the prostomium, proboscis, and parapodia are reduced or lost. In some highly specialized forms such as the tube-dwelling sabellids and serpulids, the anterior end is greatly modified into a **branchial crown** or **radiole** used for feeding and respiration (Fig. 3.2D). In other forms such as terebellids, the peristomial tentacles are long, filamentous, and prehensile, serving to carry food along ciliated grooves (Fig. 3.2G). Parapodia in tubiculous polychaetes tend to be small and provided with rows of uncini for gripping the sides of the tubes. The body in tube-dwelling forms is often divisible into two (or sometimes three) regions (Figs. 3.2D,E), including an anterior **thorax**, often the more highly specialized region, and a posterior **abdomen**, which may be followed by a terminal **caudal region**. Some sedentary polychaetes superficially resemble earthworms in their specialization towards a burrowing habit (Fig. 3.3N).

In some polychaetes the anterior region of the digestive tract may be eversible. Dales (1963) distinguished between a ventral plate-muscle pharynx and an axial pharynx. The detailed structure of the pharynx, especially the presence or absence, and structure if present, of **jaws, teeth (paragnaths)** and other chitinized structures or soft **papillae** associated with the anterior end are particularly important taxonomic characters at the generic and specific level. In nereidids, the proboscis bears heavy, curved jaws and sometimes small, horny paragnaths. The nereidid proboscis is divisible into two regions, including (1) the **oral ring**, closest to the mouth when everted and divisible into areas V-VIII, and (2) the **maxillary ring**, located distally and bearing the jaws and divisible into areas I-IV (Figs. 3.4A-B). An understanding of these areas and the form and arrangement of the paragnaths is important at the generic and specific level. The jaw pieces of some polychaetes, particularly the euniciforms, are complex and consist of several parts, each of which may have several teeth (Figs. 3.4C-D). Glycerids have four simple hooked jaws on the tip of their proboscis, each composed of a supporting piece and an **aileron** (Fig. 3.4E). Goniadids have several types of teeth on the tips of their proboscis called **micrognaths** and **macrognaths**. Glycerids and goniadids also have the surface of their proboscis ornamented with **proboscideal organs** (*Glycera*), soft or chitinized

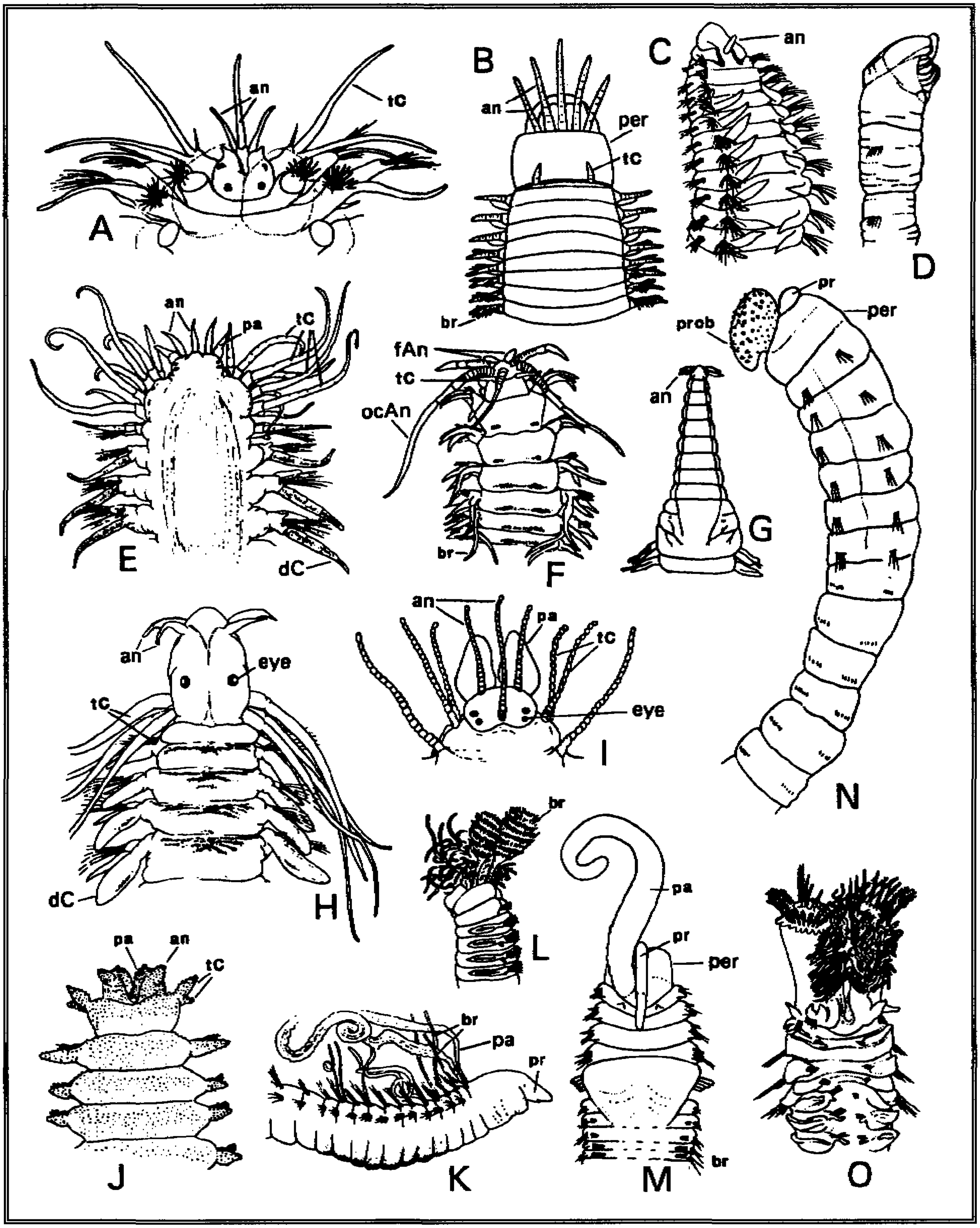

Figure 3.3. Representative Anterior Ends of Polychaetes Showing Diversity of Prostomial and Peristomial Structures: A, Polynoidae (*Harmothoe*); B, Eunicidae (*Eunice*); C, Paraonidae (*Aricidea*); D, Maldanidae (*Axiothella*); E, Hesionidae (*Gyptis*); F, Onuphidae (*Onuphis*); G, Goniadidae (*Glycinde*); H, Phyllodocidae (*Phyllodoce*); I, Syllidae (*Typosyllis*); J, Pilargidae (*Pilargis*); K, Cirratulidae (*Tharyx*); L, Terebellidae (*Pista*); M, Spionidae (*Polydora*); N, Capitellidae (*Neomediomastus*); O, Sabellariidae (*Idanthyrsus*). (most after Hartman, 1968; 1969; others original).

papillae (*Glycinde*), or **chevrons** (*Goniada*). In other polychaetes, such as phyllodocids and capitellids, the proboscis may be smooth or covered with papillae or cirri (Fig. 3.3N).

The metameric body segments bear **parapodia**, which may be **biramous** or **uniramous** (Fig. 3.5). The typical, well-developed biramous parapodium, for example, in nereidids (Fig. 3.5E) consists of a dorsal lobe or **notopodium** and a ventral lobe or **neuropodium**. In species with uniramous parapodia, it is the notopodium that has been secondarily reduced or lost. In some polychaetes, particularly sedentary forms, the parapodia are greatly reduced or absent (Fig. 3.5N); this is termed an **apodous** condition. In many forms, dorsal **gills** or **branchiae** arise from the parapodial bases in certain parts of the body (Figs. 3.5C, J-M). In some families branchiae are elaborate (Fig. 3.5J). Different types of parapodial cirri or lamellae may be variously developed. Dorsal and ventral cirri (Fig. 3.5E) and sometimes interramal cirri (Fig. 3.5L) or papillae (Fig. 3.5I) may be present. Pre- and postsetal lamellae (Fig. 3.5C) or lobes may be developed to varying degrees; in some errant families such as nephtyids and glycerids, for example, they may be critical specific characters (Figs. 3.5C,G).

Each parapodial lobe typically contains a bundle of slender, projecting chitinous **setae** and sometimes a larger, internal supporting rod or **acicula** (Figs. 3.5B-E). The parapodia, aciculae, and setae are very important characters at the familial level. The detailed development of each ramus and the associated lobes and cirri is important at the generic and specific levels, and the shape, size, number, and position of setae are also important taxonomic features, with certain types often associated with particular families or genera. It is especially important to make careful observations of setal structure when attempting to identify polychaetes to species, and a compound microscope equipped with good optics is a basic necessity when doing this work.

Setae vary widely in form and furnish precise characteristics for determination of species. The setae illustrated in Figure 3.6 represent many of the common types. Basic forms include **simple** and **compound (=composite) setae**. Simple setae may be long, thin, and hairlike, in which case they are called **capillary setae**; they may also be thick and similar to the internal supporting rod in each parapodium and are termed **acicular setae**. The tips of simple or compound setae may be **entire, bifid (bidentate), trifid (tridentate)**, or **multidentate**. Certain simple setae with bent tips, often bidentate or multidentate, are called **hooks** or **crotchets**. These setae are usually relatively stout and may be capped with translucent hyaline **hoods** or **half-hoods**. In some families, particularly the sedentary forms, these hooks are modified into short broadened setae called **uncini** that are often set in close rows. Differences in the structure of hooked setae are very important taxonomic characters. However, Ohwada and and Nishimo (1991) have discovered considerable variation in the number of apical teeth of hooded hooks in single individuals of spionids, and it is apparent that the arrangement of apical teeth should be used with caution in distinguishing between species of Spionidae.

Compound setae characteristically have two distinct parts—the proximal **shaft** and distal **blade**—that are joined and articulate. The blade is variously shaped and may be a hook, with or without a hood. It rests in a notch at the distal end of the shaft, and specific terminology is applied in describing the configuration of this notch. If the two sides are equal, and the articulation is at right angles to the long axis of the shaft, it is termed **homogomph** (Fig. 3.6W); if the sides are unequal, with the articulation clearly oblique to the shaft, it is called **heterogomph** (Fig. 3.6V).

The ultrastructure of annelid setae was subject of extensive investigations during the 1960s and 1970s, mainly because it was discovered that annelids share the principal inner structure of their setae with similar derivatives of the integument in other phyla, such as pogonophorans and mollusks. The annelid seta is produced by a basal cell and several accompanying cells that secrete a specific type of collagen through microvilli and push it upward, resulting in a bundle of parallel collagen tubes that are often visible in the light microscope as striations (for example, in hesionid and nereidid setae) or as fine marginal serrations formed by the distal ends of those tubes. The particular shape of a seta is therefore the thickness of the seta. Structures such as hoods and wings develop when there is a more or less complete gap between

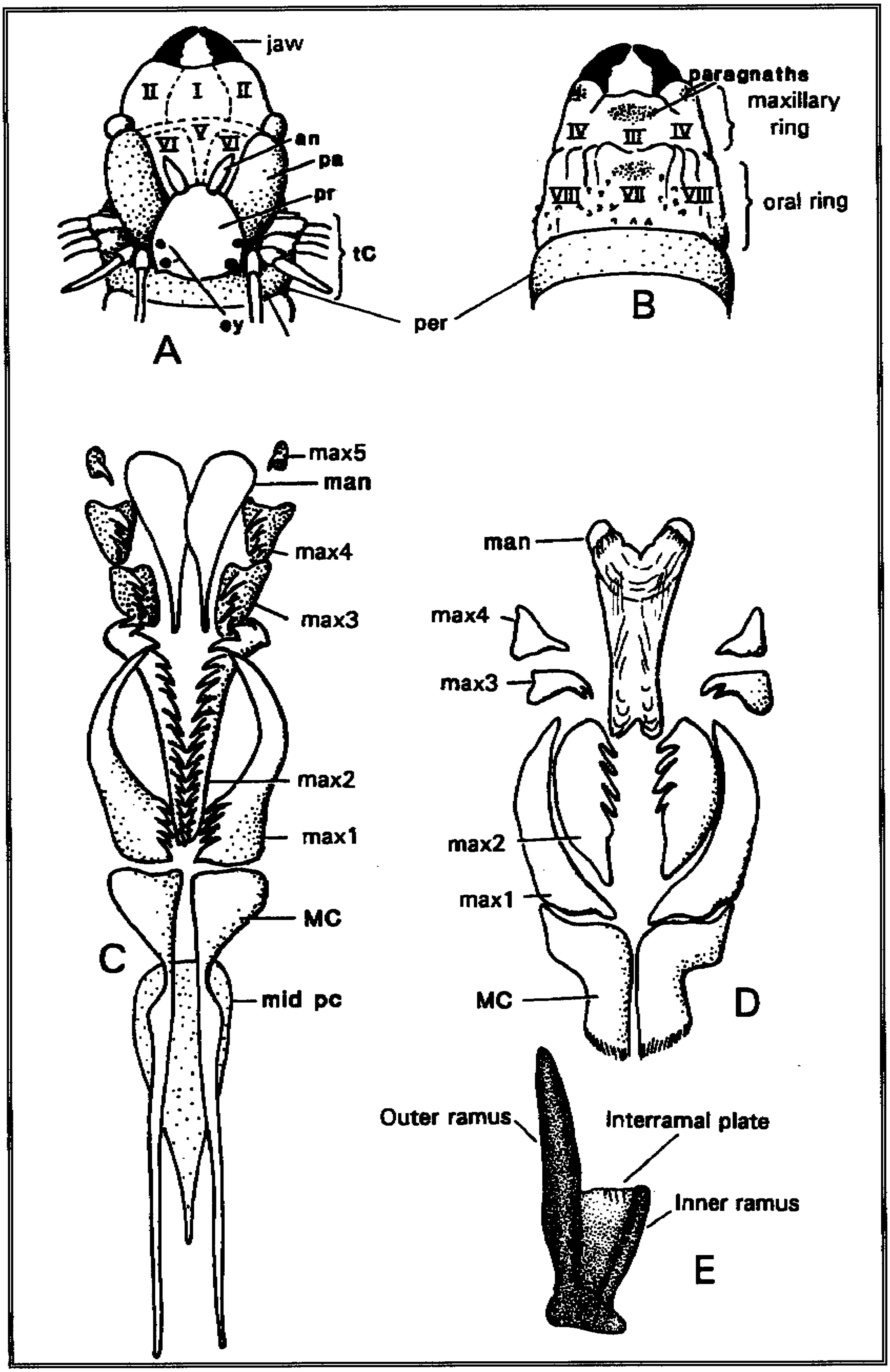

Figure 3.4. Morphology and Armature Associated with the Proboscis of some Errant Polychaetes: A, *Nereis*, anterior end, dorsal view showing prostomial structures and areas of the proboscis; B, Same, ventral view, with paragnaths indicated; C, *Arabella*, maxillary apparatus; D, *Lumbrineris*, maxillary apparatus; E, *Glycera*, aileron. (A-D, after Blake, 1975a; E, original by B. Hilbig).

the inner core of a seta and the outermost layers of collagen tubes (Fig. 3.7A). Hoods of setae are actually sheaths that are inflated extensions of the setal shafts. Important contributions to the knowledge of setal ultrastructures have been provided by Lippert & Gentil (1963), Bouligand (1966; 1967), Foster (1971), Orrhage (1971), Thomassin & Picard (1973), O'Clair & Cloney (1974), Kennedy & Kryvi (1978), Rosenfeld (1978), Hilbig (1989), and Kryvi (1989).

An appreciation of the diversity and beauty of polychaete morphology will be gained only through careful study of representative specimens. The foregoing account has been by necessity an oversimplification of the diversity to be found in polychaete body form. The often elegant specialized structures, with their corresponding specialized terminology, will in many cases be figured throughout the presentations of each family. The glossary contains definitions of these terms. Some excellent published general accounts of polychaete morphology include Barnes (1980), Blake (1975a), Dales (1963), Day (1967), Fauchald (1977), Fauvel (1923, 1927, 1953), Hartmann-Schröder (1971), Pettibone (1963, 1982), Uebelacker and Johnson (1984), and Uschakov (1955). Some important major works that deal with specific families include Arwidsson (1906: Maldanidae), Blake and Kudenov (1978: Spionidae), Fauchald (1968 and 1982: Onuphidae, 1970: Eunicea, except Onuphidae; 1974: Sphaerodoridae; 1992: Eunicidae), Fitzhugh (1989: Sabellidae), Gustafson (1930: Amphinomidae and Euphrosinidae), Hartman (1947a-b: Capitellidae and Pilargidae; 1950: Goniadidae, Glyceridae, and Nephtyidae; 1957: Orbiniidae, and others), Light (1978: Spionidae), Paxton (1986: Onuphidae), Pettibone (1976: Trochochaetidae; 1986: Eulepethidae, 1989: Acoetidae), Söderström (1920: Spionidae), Strelzov (1973: Paraonidae), Uschakov (1972: Phyllodociform families; 1982: Aphroditidae and Polynoidae), and Westheide (1967: Hesionidae, Microphthalminae).

Classification

Annelids are divided into three classes: Polychaeta, Clitellata [Subclasses: Oligochaeta and Hirudinea], and Myzostomata. Older schemes would treat the Oligochaeta and Hirudinea as separate classes. Another old category, the Archiannelida, include several polychaete families that are adapted to the meiofaunal or interstitial habitat.

The family level is the most important category that is required to understand the different and widely varying morphology of polychaetes. No single system for grouping the polychaete families into superfamilies and orders has ever been universally accepted. As knowledge of polychaete morphology and diversity has increased over time, various systems of a higher classification have been presented (Hatschek, 1893; Benham 1896; Dales, 1962; Clark, 1969; Mileikovsky, 1977; Fauchald, 1977; Pettibone, 1982; George and Hartmann-Schröder, 1985). Each of these authors developed systems that attempted to group related families together into superfamilies and/or orders by using a combination of important adult and/or larval morphological characters. To date, no one has conducted a cladistic analysis of polychaetes at the family level.

In an attempt to bring some organization to the presentation of polychaetes in this Atlas, the families are being presented in groups that correspond to the scheme presented by Pettbone (1982). The following classification includes modifications that are necessary based upon recent research on morphology and systematics. Out of approximately 80 families of polychaetes, 53 have been encountered in the benthic samples available for this Atlas or are known previously from the area.

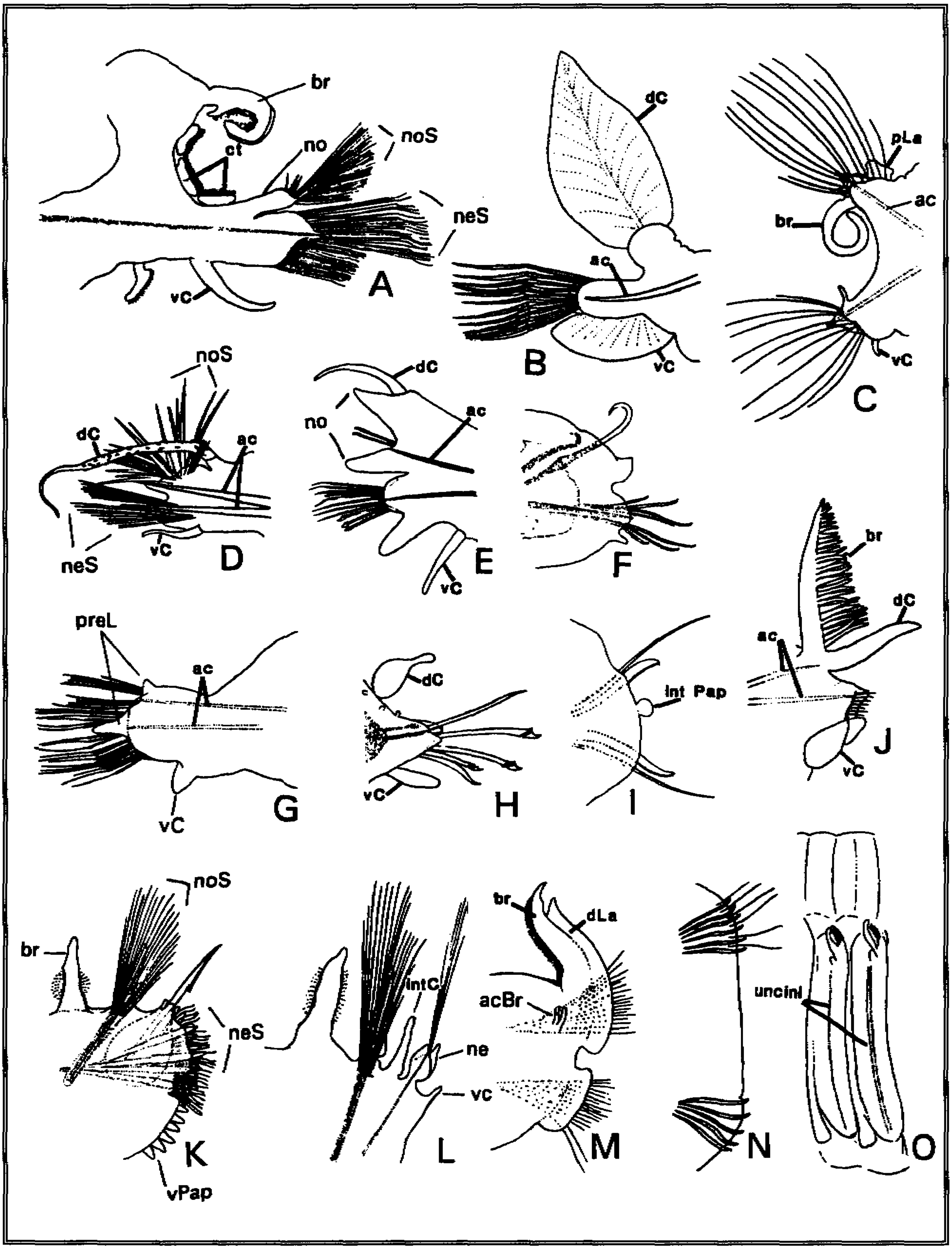

Figure 3.5. Parapodia of Various Polychaetes. A, Sigalionidae (*Laenira*); B, Phyllodocidae (*Phyllodoce*); C, Nepthyidae (*Aglaophamus*); D, Polynoidae (*Harmothoe*); E, Nereididae (*Nereis*); F, Pilargidae (*Ancistrosyllis*); G, Glyceridae (*Glycera*); H, Syllidae (*Sphaerosyllis*); I, Fauveliopsidae (*Fauveliopsis*); J, Euncidae (*Eunice*); K, Orbiniidae (*Phylo*), thoracic; L, same, abdominal; M, Spionidae (*Dispio*); N, Cirratulidae (*Cirriformia*); O, Terebellidae (*Amphitrite*), abdominal. (all after Hartman, 1968; 1969).

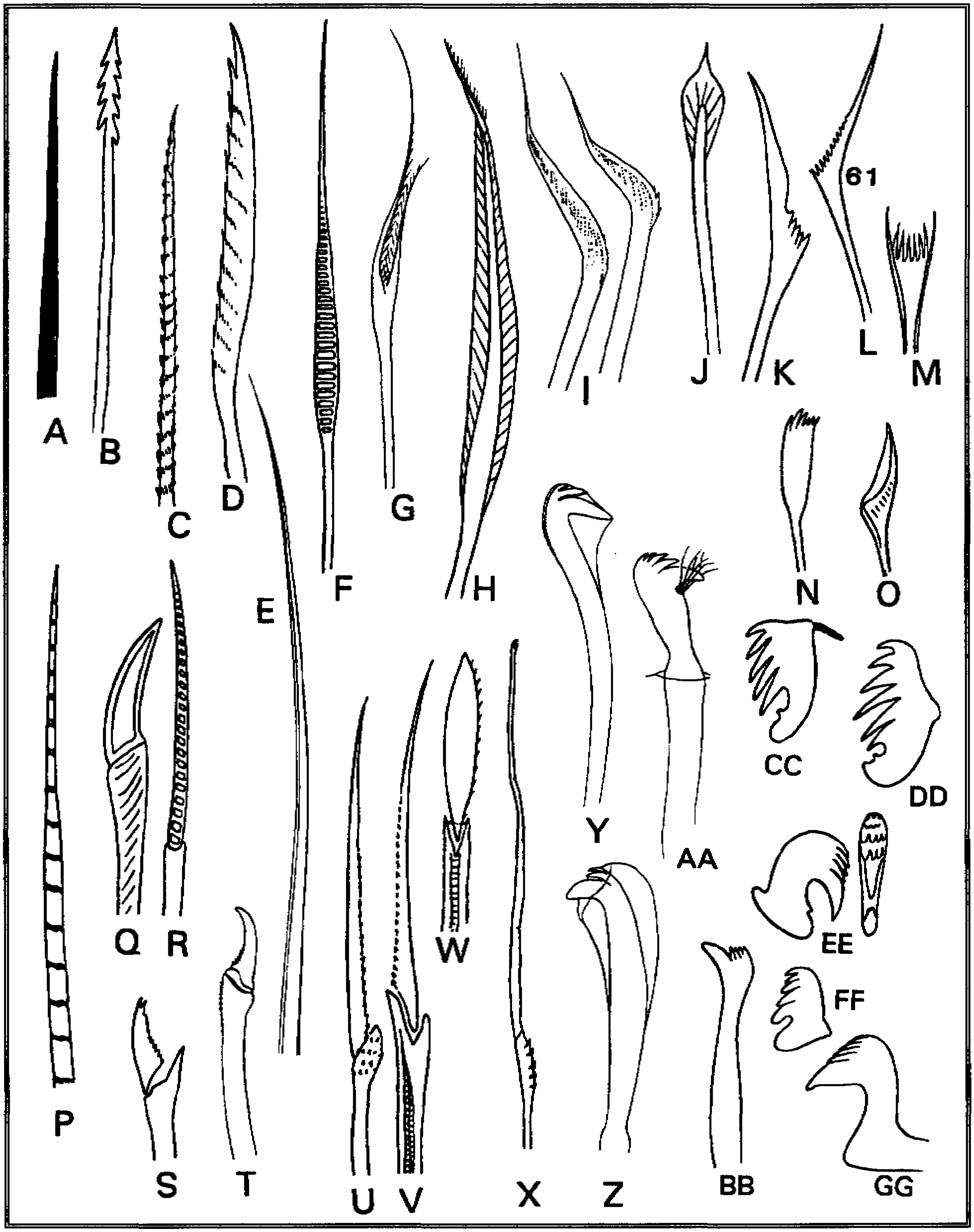

Figure 3.6. Types of Polychaete Setae: A, Acicula; B-M, Simple Setae: B, barbed; C, spinous capillary; D, serrated; E, simple capillary; F, camerated capillary; G, furcate or lyrate; H, bilimbate; I, limbate or winged; J, spatulate; K, bayonet seta (Serpulidae); L, geniculate or bent (Serpulidae); M, pectinate (Eunicidae); N, O, paleae (Sabellariidae).—P, Multiarticulate Seta: Flabelligeridae.—Q-X, Compound Setae: Q, Flabelligeridae; R, Sigalionidae; S, Syllidae; T, Pholoidae; U, Phyllodocidae; V, heterogomph spiniger (Nereidae); W, homogomph falciger (Nereidae); X, Sigalionidae.—Y-GG, Hooks and Uncini: Y, Spionidae; Z, Capitellidae; AA, rostrate hook (Maldanidae); BB, Trichobranchidae, thoracic; CC-DD, Serpulidae; EE, Terebellidae; FF, Serpulidae; GG, Sabellidae. (From various sources, some original).

- Order Phyllodocida
  - Superfamily Phyllodocidae
    - Family Phyllodocidae
    - Family Alciopidae
    - Family Lopadorrhynchidae
    - Family Pontodoridae
    - Family Lacydoniidae
    - Family Tomopteridae
    - Family Typhloscolecidae
  - Superfamily Glycerea
    - Family Glyceridae
    - Family Goniadidae
    - Family Sphaerodoridae
  - Superfamily Nereididacea
    - Family Hesionidae
    - Family Pilargidae
    - Family Nautiliniellidae
    - Family Nereididae
    - Family Syllidae
    - Family Calamyzidae
    - Family Ichthyotomidae
  - Superfamily Nephtyidacea
    - Family Nephtyidae
    - Family Paralacydoniidae
  - Superfamily Aphroditacea
    - Family Aphroditidae
    - Family Polynoidae
    - Family Acoetidae
    - Family Pholoidae
    - Family Sigalionidae
    - Family Eulepethidae
    - Family Chrysopetalidae
  - Superfamily Pisionacea
    - Family Pisonidae
- Order Amphinomida
  - Family Amphinomidae
  - Family Euphrosinidae
  - Family Archinomidae
- Order Spintherida
  - Family Spintheridae
- Order Eunicida
  - Family Onuphidae
  - Family Eunicidae
  - Family Lumbrineridae
  - Family Oenonidae (includes Arabellidae)
  - Family Dorvilleidae
  - Family Hartmaniellidae
  - Family Histriobdellidae
  - Family Iphitimidae
- Order Orbiniida
  - Family Orbiniidae
  - Family Paraonidae
- Order Spionida
  - Family Apistobranchidae
  - Family Spionidae
  - Family Trochochaetidae
  - Family Poecilochaetidae
  - Family Heterospionidae
  - Family Uncispionidae
- Order Chaetopterida
  - Family Chaetopteridae
- Order Magelonida
  - Family Magelonidae
- Order Psammodrilida
  - Family Psammodrilidae
- Order Cirratulida (includes Ctenodrilida)
  - Family Questidae
  - Family Cirratulidae
  - Family Ctenodrilidae
  - Family Parergodrilidae (includes Stygocapitellidae)
- Order Cossurida
  - Family Cossuridae
- Order Flabelligerida
  - Family Flabelligeridae
  - Family Acrocirridae
  - Family Fauveliopsidae
- Order Poeobiida
  - Family Poebiidae
- Order Opheliida
  - Family Opheliidae
  - Family Scalibregmatidae
- Order Sternaspida
  - Family Sternaspidae
- Order Capitellida
  - Family Capitellidae
  - Family Maldanidae (includes Bogueidae)
  - Family Arenicolidae
- Order Oweniida
  - Family Oweniidae
- Order Terebellida
  - Family Pectinariidae
  - Family Sabellariidae
  - Family Ampharetidae
  - Family Trichobranchidae
  - Family Terebellidae

- Order Sabellida
    - Family Sabellidae (includes Sabellongidae)
    - Family Serpulidae
    - Family Spirorbidae
- Order Nerillida
    - Family Nerillidae
- Order Dinophilida
    - Family Dinophilidae
- Order Polygordiida
    - Family Polygordiidae
- Order Protodrilida
    - Familiy Protodrilidae
    - Family Saccocirridae

Reproduction and Development

Polychaetes are known to exhibit more diversity in their modes of reproduction and development than other invertebrate taxa. This reproductive plasticity often manifests itself in the morphology of juveniles and adults. It is essential, therefore, that any serious student of polychaete taxonomy be aware of the modes of polychaete reproduction, how polychaetes develop, and how the morphology of adults and juveniles is influenced by these phenomena. In the paragraphs which follow, the general patterns of polychaete reproductive processes and changes in morphology are outlined, including sexual and asexual life cycles. In addition, some of the diversity in morphology of polychaete larvae are presented, including structures and features that are unique to larvae and juveniles. Important works that summarize and review reproductive processes, reproductive morphology, and larvae of polychaetes include: Clark (1965), Clark and Olive (1973), Schroeder and Hermans (1975), Bhaud and Cazaux (1986), and Strathmann (1986).

Asexual Reproduction

Asexual processes are well-developed in polychaetes. Subdivision of the body and regeneration of missing parts has been reported in several families, although relatively few examples have been studied in the laboratory. For example, the chaetopterid *Phyllochaetopterus prolifica* is a well-known species off our coasts with asexual reproduction that has not been investigated in any detail. There are several different types of asexual reproduction in polychaetes including **architomy**, **paratomy**, **schizometry**, and **stolonization**. Examples of each of these processes are discussed.

Architomy. Architomy is a form of simple fission, where the body of a worm fragments into individual segments or groups of segments. These fragments simply break off and then regenerate new anterior (Fig. 3.7C) and/or posterior ends. Architomy has been reported in several families including chaetopterids (*Phyllochaetopterus*), amphinomids (*Eurythoe*), spionids (*Pygospio*), ctenodrilids (*Raphidrilus* and *Zeppelina*), and sabellids (*Megalomma, Myxicola*, and *Potamilla*) (Schroeder and Hermans, 1975; personal observations).

In California, the spionid *Pygospio elegans* is a well-known species that has architomic asexual reproduction. Although this species also reproduces sexually and produces planktonic larvae, the populations appear to be maintained by asexual reproduction (Armitage, 1979). The individuals that are produced by asexual reproduction tend to be pale and lack pigment on the body, whereas, sexually mature individuals are often heavily pigmented, and the males bear elongated notopodial lobes on setiger 2.

Paratomy. Paratomy involves the subdivision of the body into two halves, with the reconstitution of the missing components made up by regeneration of the remaining segments. Paratomy has been examined extensively in small serpulids of the genera *Salmacina* and *Filograna* and summarized by Schroeder and Hermans (1975). In these animals the body splits into two pieces. The anterior half of the parent animal is called the **stock**. Regeneration of the anterior end of the posterior half is actually

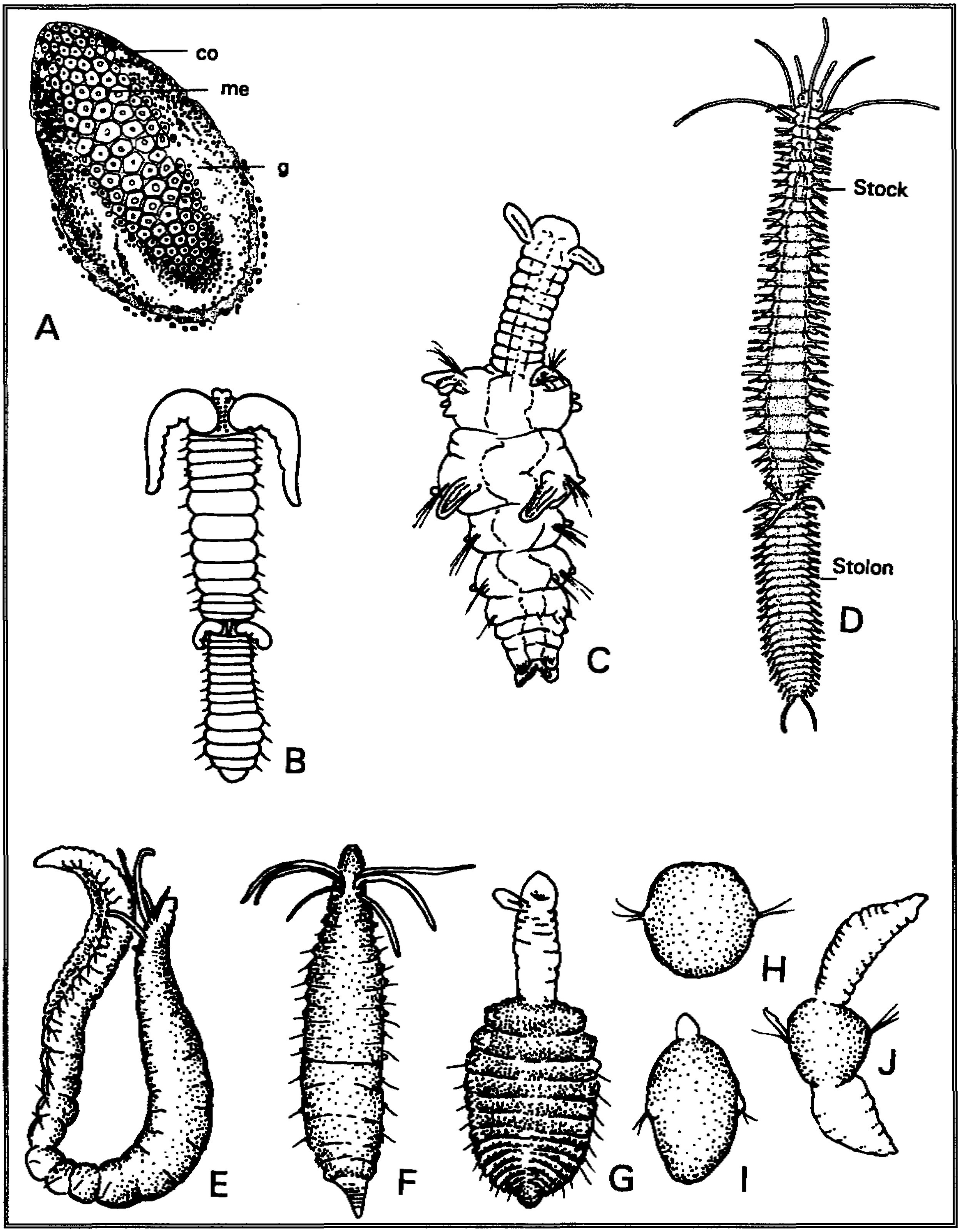

Figure 3.7. A, Setal Ultrastructure: cross section of limbate capillary—B-J: Asexual Reproduction in Polychaetes: B, paratomic regeneration in *Pseudopolydora*; C, architomic regeneration in *Pygospio*; D, stolon formation in *Autolytus*; D-I, asexual budding in *Dodecaceria*. (A, after Hilbig; B, after Tsetlin and Britayev; C, after Rasmussen; D, after Hauenschild; E-J, after Gibson).

reconstituted before it separates from the stock. The stock also regenerates its posterior body parts and the two individuals remain attached by a thin peduncle of tissue.

Paratomy has also been reported in some spionids such as *Polydora tetrabranchia* (Campbell, 1955) and *Pseudopolydora smurovi* (Tzetlin and Britayev, 1985, as *Polydorella*; Fig. 3.7B) and species of the genus *Ctenodrilus* (Reish, 1980). In the case of *Ctenodrilus serratus*, asexual reproduction is the only mode of reproduction that has been reported.

Stolonization. Stolonization is a form of paratomic asexual reproduction where chains of newly regenerated individuals called **zooids** or **stolons** are attached to the original stock animal (Fig. 3.7D). Although reported in the ctenodrilids *Zeppelina* and *Raphidrilus*, the process is elaborate in syllids, especially in the subfamily Autolytinae.

In syllids, asexual and sexual phases alternate in a complex life cycle where benthic males and females produce pelagic sexual stages by asexual stolonization. Zooids or stolons are produced in chains that are attached to the stock animal (Fig. 3.7D). Twenty or more stolons have been observed in some species. Once released, the male **(polybostrichus)** and female **(sacconereis)** stolons mate within ½ to 3 hours. The males die after mating, while the females carry their fertilized eggs in a sac that develops on the ventral side. Larvae develop within in this sac which is carried by the female stolon until they are released, at which time she also dies (Gidholm, 1965). The morphology of the stock, polybostrichus, and sacconereis stages is very different in *Autolytus* and other genera of the Autolytinae, and needs to be understood when encountered. Stolonization also occurs in other subfamilies of the Syllidae, but the modification of the stolons is less extreme.

Schizometry. Schizometry is a specialized form of architomic fission in the cirratulid genus *Dodecaceria* where individual segments from the middle of the body form a beadlike chain. Each of these segments break away on their own and individually begin a regenerative process. During the course of this regeneration, these new individuals may again break apart and repeat the process, sometimes as many as four times (Fig. 3.7E-J). The morphology of the different stages of fission and regeneration have very different appearances and can lead to confusion in the identification of species unless several different stages are present (Gibson, 1977, 1978, 1979; Gibson and Clark, 1976).

Sexual Reproduction

Owing to the wide variety of processes, sexual reproduction in polychaetes has been a subject of considerable interest among biologists. Some species of *Nereis* and *Palola* have become textbook examples of morphological modification and lunar periodicity in the timing of reproduction.

Important reviews of polychaete reproduction have been published by Clark (1965), Clark and Olive (1973), and Schroeder and Hermans (1975). The reader is referred to these references for additional information on the physiology and endocrinology that regulate polychaete reproduction. However, a few salient aspects of polychaete reproduction are relevant to understanding and interpreting polychaete morphology.

Sexes are separate in most species although hermaphroditism is not uncommon (Pfannenstiel, 1976; Holbrook and Grassle, 1984; Westheide, 1990). Gametes are typically proliferated in simple gonads that are attached to the peritoneal wall and released into the coelomic fluid where they are nourished and develop into mature sperm and eggs. Gonads are variously developed in polychaetes and while defined, are sometimes limited to a few cells located beneath the peritoneum. Oocytes are sometimes nourished directly by **nurse cells** (e.g., *Diopatra*) that are more or less permanently attached during development. In other cases nutrients are transferred to the developing oocytes by coelomocytes.

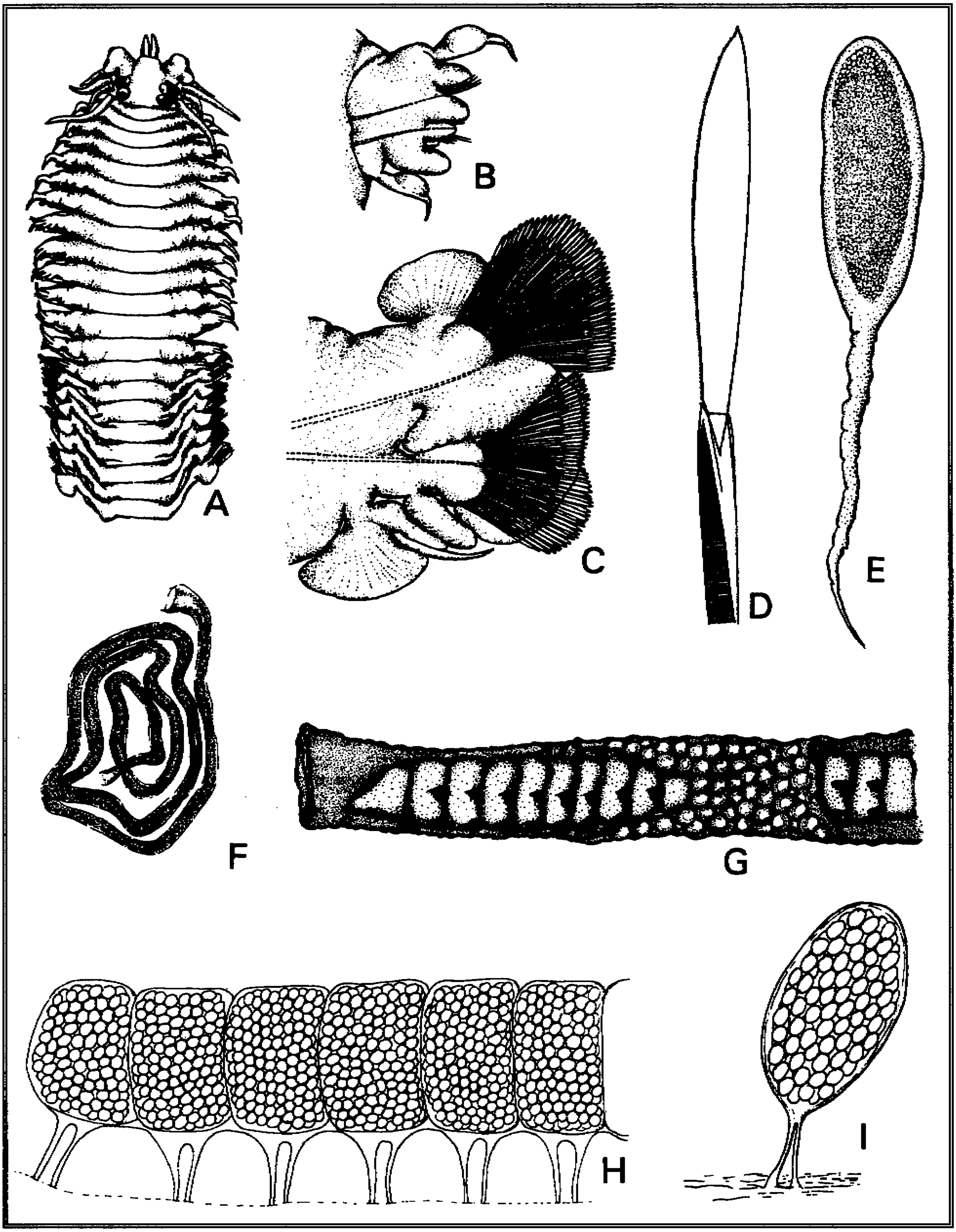

Figure 3.8. A-D, Heteronereid morphology in *Nereis*: A, anterior end; B, anterior parapodium; C, middle parapodium; D, modified falciger.—E-I, Egg Capsules and Egg Masses: E, *Scolelepis*; F, *Phyllodoce*; G, *Capitella*; H, *Polydora*; I, *Boccardia*. (A-D, after Imajima; G, after Reish; others original).

In preparing descriptions of species it is important to observe whether eggs are present or absent and to measure them if present. Eggs can be seen through the body wall of whole mounted specimens or in the parapodia when they are dissected. Eggs come in a variety of forms and shapes. They may be spherical, elliptical, or flattened. They may be colorful, opaque or transparent and may have soft membranes or ones that are thick and highly ornamented. When mature, eggs have been recorded to range in size from 40 mm in opheliids to 1.2 mm in one antarctic onuphid. When recording egg diameter data, investigators should measure both the long and short dimensions of elliptical eggs and take sufficient measurements so that the mean and standard deviation can be calculated.

Sperm are difficult to observe in preserved polychaetes. Typically, sperm occur as masses of opaque tissue in parapodia. Upon close inspection with a high power objective, the heads and tails of individual sperm can sometimes be seen. With oil immersion and phase contrast optics, additional detail can be seen. Franzen (1956) classified sperm into primitive and aberrant based upon their structure and relationship to mode of reproduction. Primitive sperm are found in species that spawn their gametes directly into seawater where external fertilization takes place. Primitive sperm have a small, spherical middle piece and large mitochondria. Aberrant sperm, on the other hand, are not spawned into seawater and are found in species that have a modified form of reproduction where specialized copulatory structures or brooding behaviors are present. Aberrant sperm have an elongated, modified middle piece with modified mitochondria. Spermatogenesis has been reviewed by Olive (1983).

Polychaetes with internal fertilization often exhibit pair formation to increase the chance of successful fertilization. Sperm may be injected directly into the female through a copulatory organ, or a spermatophore may be deposited close to a female and then be actively picked up (Rice, 1978).

There are two basic types of reproduction: **monotelic** and **polytelic**. Species which are monotelic develop only one set of gametes during their life, but they may produce more than one set of eggs. Classic examples of monotelic species include *Platynereis dumerilii* and *Nereis succinea* which become highly modified during gametogenesis, spawn, and die. Polytelic species develop multiple sets of gametes and spawn more than once during their lifetime. Examples include spionids such as *Polydora* which deposit sequential sets of egg capsules during their life.

Frequently, major morphological changes take place during sexual maturation in polychaetes. Changes include the development of **natatory setae**, modified parapodia, enlarged eyes, and considerable vascularization. These types of changes are best developed in the Nereididae (Fig. 3.8A-D). An excellent account of sexual maturation in *Nereis grubei* describes the morphological changes and timing of egg development and spawning (Schroeder, 1967). In nereidids, the modified sexually mature individuals are called **epitokes** or **heteronereids**. A sexually unmodified nereidid can be called an **atoke**. Other polychaetes such as scalibregmatids and cirratulids frequently develop elongated capillary setae at the time of sexual maturity. Recently, a dorvilleid has been found to develop natatory setae (Hilbig and Blake, 1991).

Eggs are either discharged directly into seawater (Blake 1975b-d) or are deposited in some type of **egg mass**, **capsule**, **cocoon**, or other structure that serves to protect the embryos and larvae during their development. In free-spawning species, gametes are shed into the sea through segmental nephridial pores or through ruptures of the body wall. In brooding species, sperm are transferred to the female either directly or via **spermatophores** and stored in **seminal receptacles**. Egg masses and capsules are either deposited on a structure in the habitat such as eelgrass blades, rocks, or piles, are associated with or inside the adult tubes (Fig. 3.8G), or are simply anchored in the mud or sand by a long gelatinous extension (Fig. 3.8E). In the first example, the egg mass is exposed directly to the sea where water movement serves to keep the capsule well-oxygenated while the embryos develop. There are many examples of this type of egg mass or capsule formation in California polychaetes including *Phyllodoce williamsi* (Fig. 3.8F), *Leitoscoloplos pugettensis*, and *Nereis vexillosa* (Blake, 1975d; 1980). Examples of polychaetes that exhibit brooding of egg capsules in tubes of adults include virtually all known spionid species of the genera *Polydora* (Fig. 3.8H), *Boccardia* (Fig. 3.8I), *Pygospio*, and *Spio* (Blake, 1969a; Rasmussen, 1973), many onuphids (Blake 1975c), and some terebellids such as *Ramex californiensis* (Blake, 1991). In these examples, the female usually incubates the capsules by passing ciliated branchiae or some other part of her body over the capsules. This behavior serves to keep the capsules clean and free of bacteria.

Development

Polychaete embryos and larvae have been the subject of many types of research. Embryologists have used polychaetes to answer basic questions about developmental processes; ecologists have used polychaete larvae to address questions about the maintenance of benthic communities; zoologists have studied polychaete larvae to understand recruitment phenomena and life cycles and patterns in the life history; and evolutionary biologists and systematists are interested in larvae to understand relationships among polychaete families and genera.

Fertilized polychaete eggs undergo spiral, holoblastic cleavage and form a ciliated gastrula that eventually differentiates into a **trochophore** larva. The classic **monotrochal** trochophore has a broad anterior end and a defined set of cilia that includes an **apical tuft** of sensory cilia on the dorsal side, a large **prototroch** that encircles the body anterior of the mouth, a **neurotroch** or ventral sensory tract ventral to the mouth, and a **telotroch** that is posteriorly directed. This type of trochophore has been found in the families Phyllodocidae, Hesionidae, Polynoidae, and Serpulidae, among others (Fig. 3.9A-B). These trochophores are **planktotrophic** and have an open digestive tract with mouth, intestine, and anus. They are excellent swimmers and usually have eyespots that assist in orienting their movements in the water column. They feed on small phytoplankton. In the **atrochal** larva, the only visible cilia are the apical tuft and fine cilia that encircle the entire sphere of the larva. These larva lack an open digestive system and are **lecithotrophic** and do not feed in the plankton. Such larvae are found in the families Eunicidae and Lumbrineridae. A **mesotrochal** trochophore is one where both the prototroch and telotroch are lost and occurs in the Chaetopteridae. Different types of trochophore modifications occur in those larvae that are encapsulated such as in the Spionidae. In early larvae of *Polydora*, the apical cilia are lost and although a mouth is present as a large ciliated vestibule, the digestive tract is incomplete with the larva subsisting on its own yolk reserves. Eyes are frequently present, and the trochophore encircles the anterior half of the body. The telotroch is modified into a band of cilia that encircles the posterior end (Blake, 1969a).

The **metatrochophore** is produced by growth of the ventral plate and mesodermal bands producing body segments. Segmental ciliary bands, called **metatrochs** have developed. If these bands are broken, the dorsal bands are called **nototrochs** and the ventral bands are called **gastrotrochs**. Larvae with numerous metatrochal cilia are called **polytrochal** larvae. Setae may be present in metatrochophores, and tentacular structures are not developed. Metatrochophores are found in species of Phyllodocidae (Fig. 3.9D), Polynoidae, Chrysopetalidae, Hesionidae, and Capitellidae.

The **nectochaete** is a polychaete larva that has many of the features of the adults. Setae are well developed and tentacular structures are apparent. Nectochaetes represent many of the classic polychaete larvae that have been described from plankton including the **mitraria** of oweniids, **rostraria** of amphinomids, and **chaetospheres** of spionids (Bhaud and Cazaux, 1987).

From a systematic point of view, the morphology of larvae can be used to assist in the interpretation of the interrelationships of genera and species and can supplement traditional alpha characters of adults. Unfortunately, polychaete taxonomists rarely apply these data to systematic interpretations.

Pelagic polychaete larvae are often elegantly pigmented and provided with elaborate ciliary patterns and provisional setae (Figs. 3.12A-C; 3.13A-C). In some families such as the Spionidae, keys have actually been written that enable users to identify genera and local species encountered in plankton tows. Important works that provide descriptions of polychaete larvae include: Bhaud and Cazaux (1987), Blake (1969a, 1975b-d, 1980), Blake and Woodwick (1975), Cazaux (1968, 1969, 1972), Haaland and

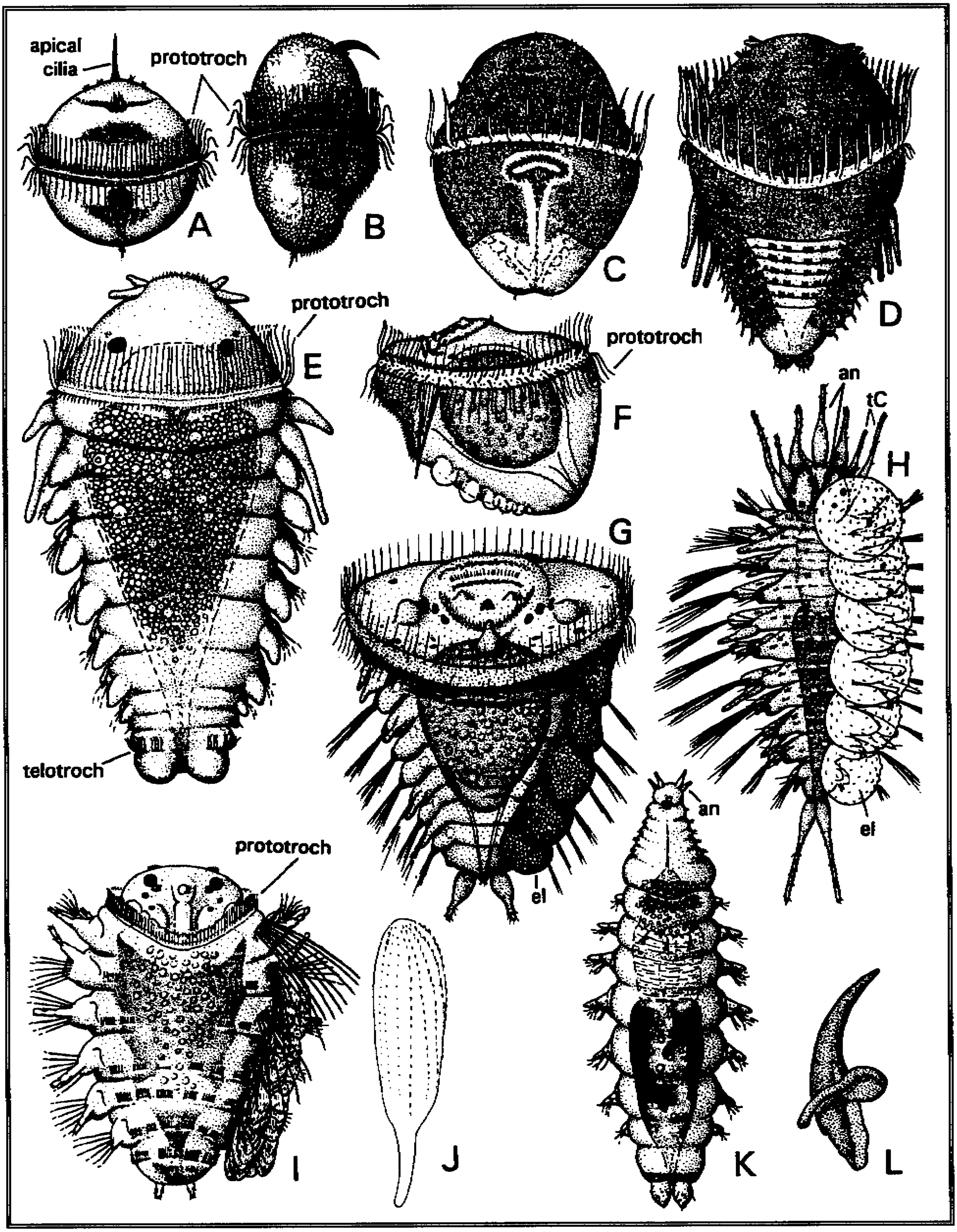

Figure 3.9. Larvae of Polychaetes: A-D, *Phyllodoce williamsi* (trochophores and metatrochophores); E, *Eteone dilatae* (metatrochophore); F-H, *Halosydna brevisetosa* (metatrochophores and nectochaete); I-J *Paleanotus bellis* (nectochaete and palea); K-L, *Glycera tenuis* (nectochaete and jaw piece). (all after Blake, 1975d).

Schram (1982, 1983), Hannerz (1956), Okuda (1946), Rasmussen (1956, 1973), Reish (1957, 1974, 1980), Smith and Chia (1985), Thorson (1946), Ward (1978), Wilson (1928, 1929, 1932a-b, 1936, 1948, 1968a, 1982), and Woodwick (1960, 1977). Some representative polychaete larvae are presented in Figures 3.9 to 3.13.

From a functional point of view, polychaete larvae may be **planktotrophic**, **lecithotrophic**, or **direct** in their development. Planktotrophic larvae feed on phytoplankton; lecithotrophic larvae are able to swim too and use all of their ciliary structure, yet subsist on intrinsic yolk reserves. Direct development usually includes embryos or larvae that develop from very large eggs where body mass would be too large for a planktonic life even when cilia are developed.

Developmental morphology and biology have been recently used to assist in the identification of sibling species. In the Capitellidae, many sibling species have now been separated from the cosmopolitan species, *Capitella capitata* (Grassle and Grassle, 1976; Eckelbarger and Grassle, 1983, 1987a-b). These sibling species exhibit differences in size of the larvae, ciliary patterns, nutritional requirements, and setal distributions as well as ultrastructural differences in ova and in chromosome numbers. Sibling species are also believed to exist in the Spionidae (Blake, 1969a; Simon, 1967, 1968), Opheliidae (Parke, 1973), and the Nereididae (Weinberg *et al.*, 1990). It is likely that additional sibling species complexes will be identified with further studies of reproductive biology and development.

Metamorphosis and Development of the Juvenile

The stage at which settlement occurs varies widely. Some species with pelagic larvae settle with only 3-6 setigerous segments, while others live for months in the plankton and develop elaborate structures. The transition of the planktonic larval form into a crawling, benthic juvenile may be gradual, or rapid and dramatic. Specific biochemical and sediment responses have been identified that serve to induce settlement (Knight-Jones, 1951; Wilson, 1951, 1952, 1954, 1955, 1968b, 1970a-b; Scheltema *et al.*, 1981; Jensen and Morse, 1984).

During settlement, ciliary swimming is replaced by attachment, creeping, crawling, or burrowing in post-larval forms. These behavioral changes accompany the extensive morphological changes that are referred to as **metamorphosis**. The transition from a planktotrophic swimming larva to a benthic juvenile is manifested in the development of adult sensory, tentacular, and parapodial structures as well as changes in the digestive system that permit a change from the larval ciliary feeding method to the adult feeding mode. In pelagic lecithotrophic larvae, metamorphosis is accompanied by ingestion of food soon after settlement. Examples of changes in morphology that accompany metamorphosis of the pelagic larvae to the benthic juvenile are depicted for *Halosydna brevisetosa* (Fig. 3.9G-H), *Platynereis bicanaliculata* (Fig. 3.10), *Onuphis elegans* (Fig. 3.10A-E), *Podarke pugettensis* (Fig. 3.10F-I), and *Phragmatopoma californica* (Fig. 3.13).

There has been little study of the development of the adult morphology that follows settlement. However, juveniles may not necessarily have the same structures as their fully developed, sexually mature adults. For example, Blake (1975c) described types of juvenile setae and jaw structures in the onuphid *Onuphis elegans* (as *Nothria elegans*) that differed from those of the adults and later on determined that the dorvilleid *Apophryotrocha mutabiliseta* was actually a postlarval stage of an onuphid (Blake, 1979). Anterior branchiae are known to develop slowly in spionid and onuphid polychaetes (Dean and Blake, 1966; Simon, 1967; Blake, 1975c) and may confuse generic identifications. The development of pairs of tentacular cirri is sequential with growth in hesionids and because the generic definitions are closely tied to the numbers of pairs of these structures, generic misidentifications are likely (Blake, 1975d, Haaland and Schram, 1982, 1983; Schram and Haaland, 1984).

Detailed investigations into morphological changes that occur at metamorphosis are best documented in the Sabellariidae (Wilson, 1929; Eckelbarger, 1978), Opheliidae (Wilson, 1948; Hermans, 1978), Oweniidae (Wilson, 1932a), and Serpulidae (Potswald, 1978).

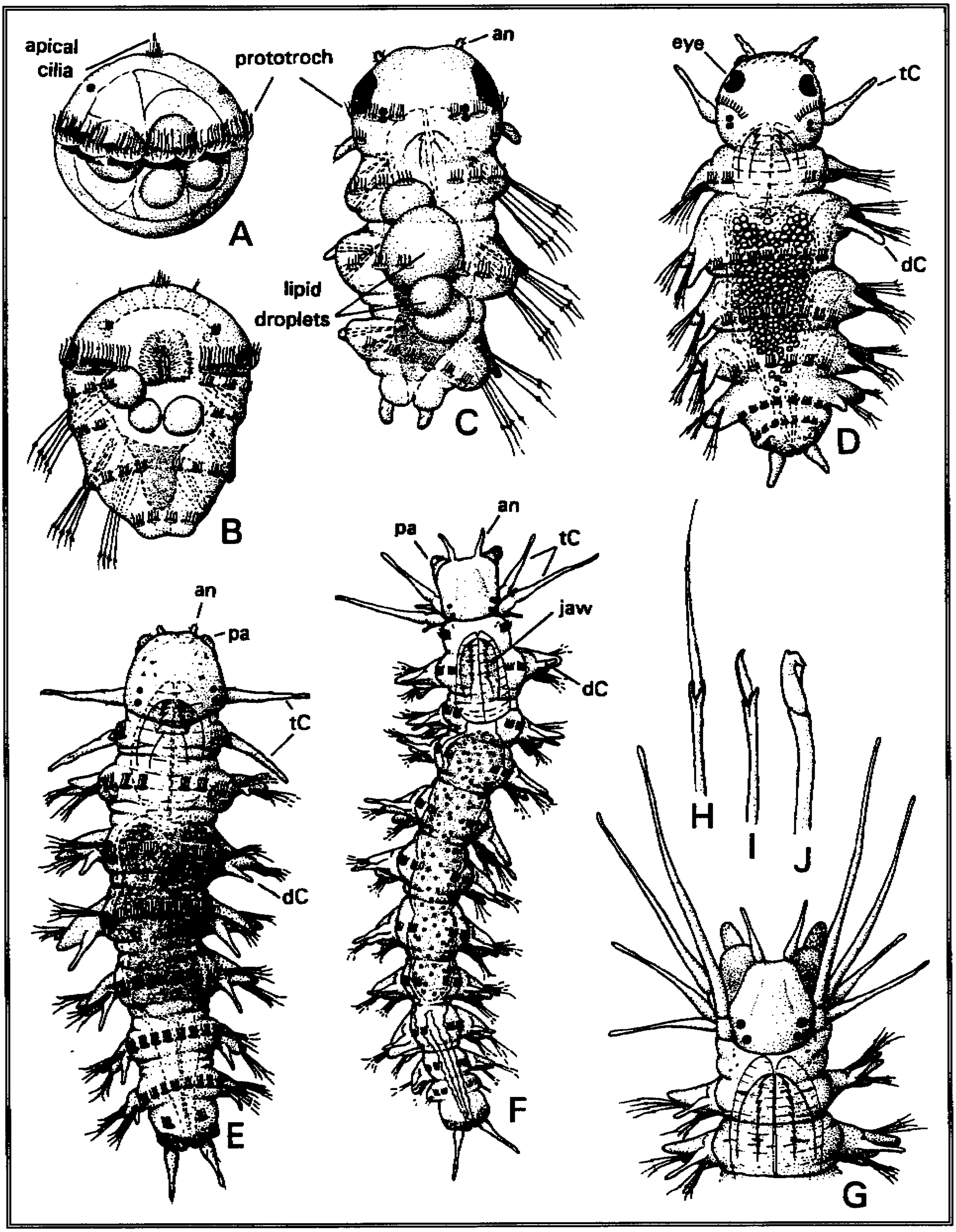

Figure 3.10. Larval Development of *Platynereis bicanaliculata*: A, trochophore; B, metatrochophore; C-D, nectochaetes; F-G, benthic juveniles; H-J, setae. (after Blake, 1975d).

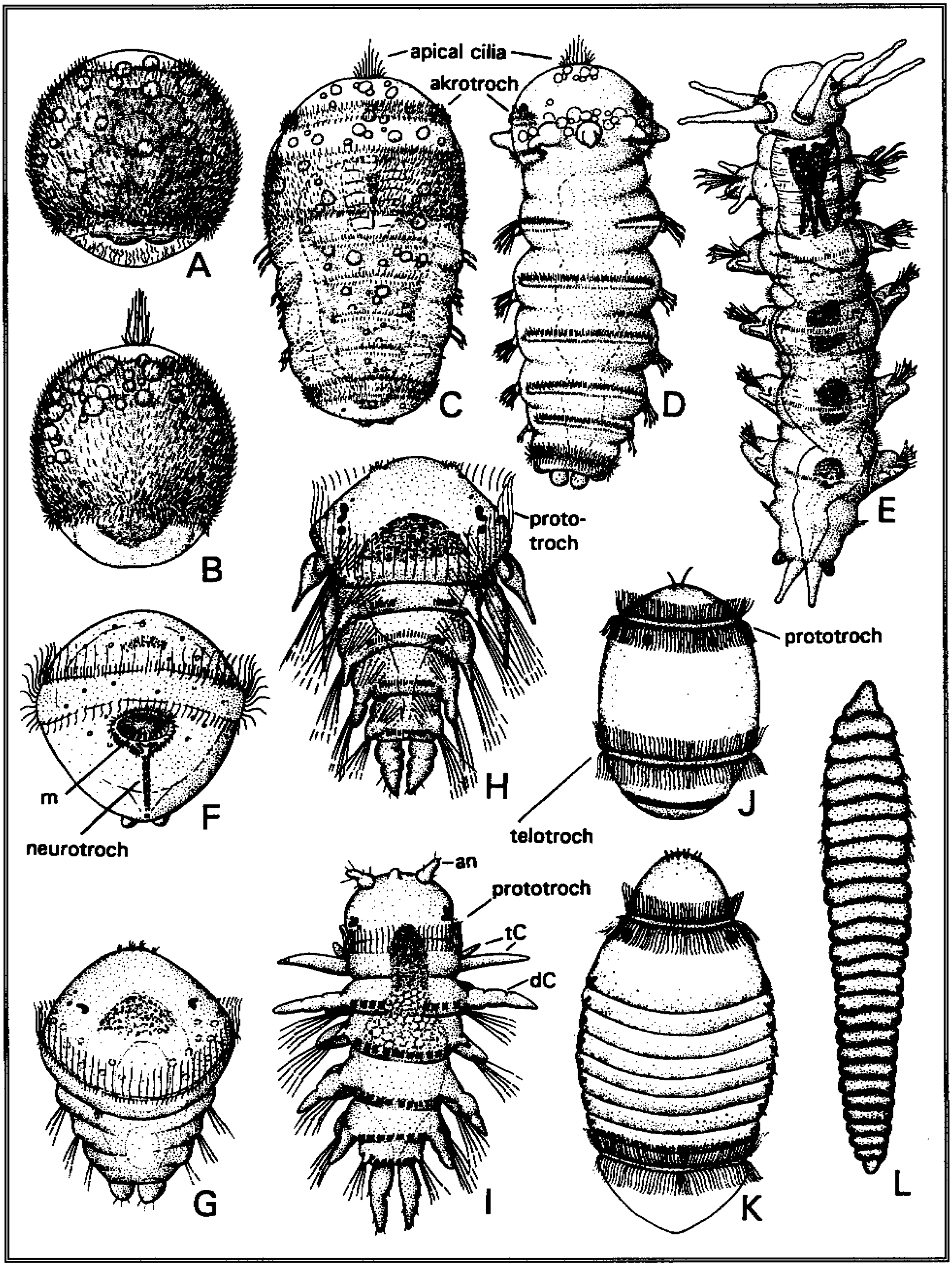

Figure 3.11. Larvae of Polychaetes: A-E, *Onuphis elegans*; F-I, *Podarke pugettensis*; J-L, *Capitella capitata*. (A-I after Blake 1975c, 1975d; Reish, 1972).

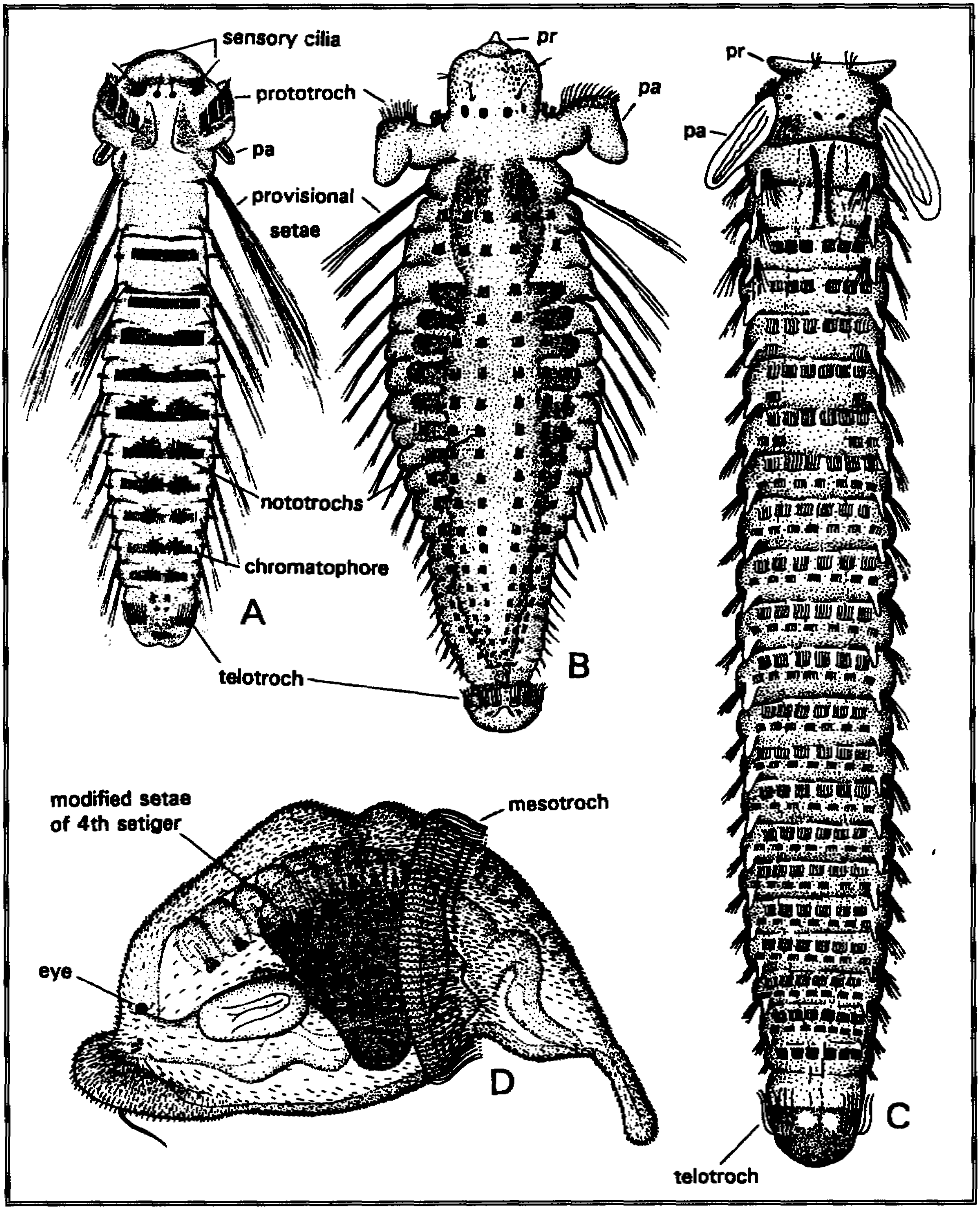

Figure 3.12. Larvae of Polychaetes: A, *Polydora websteri*; B, *Scolelepis*; C, *Spiophanes missionensis*; D, *Spiochaetopterus*. (A, after Blake, 1969; rest original).

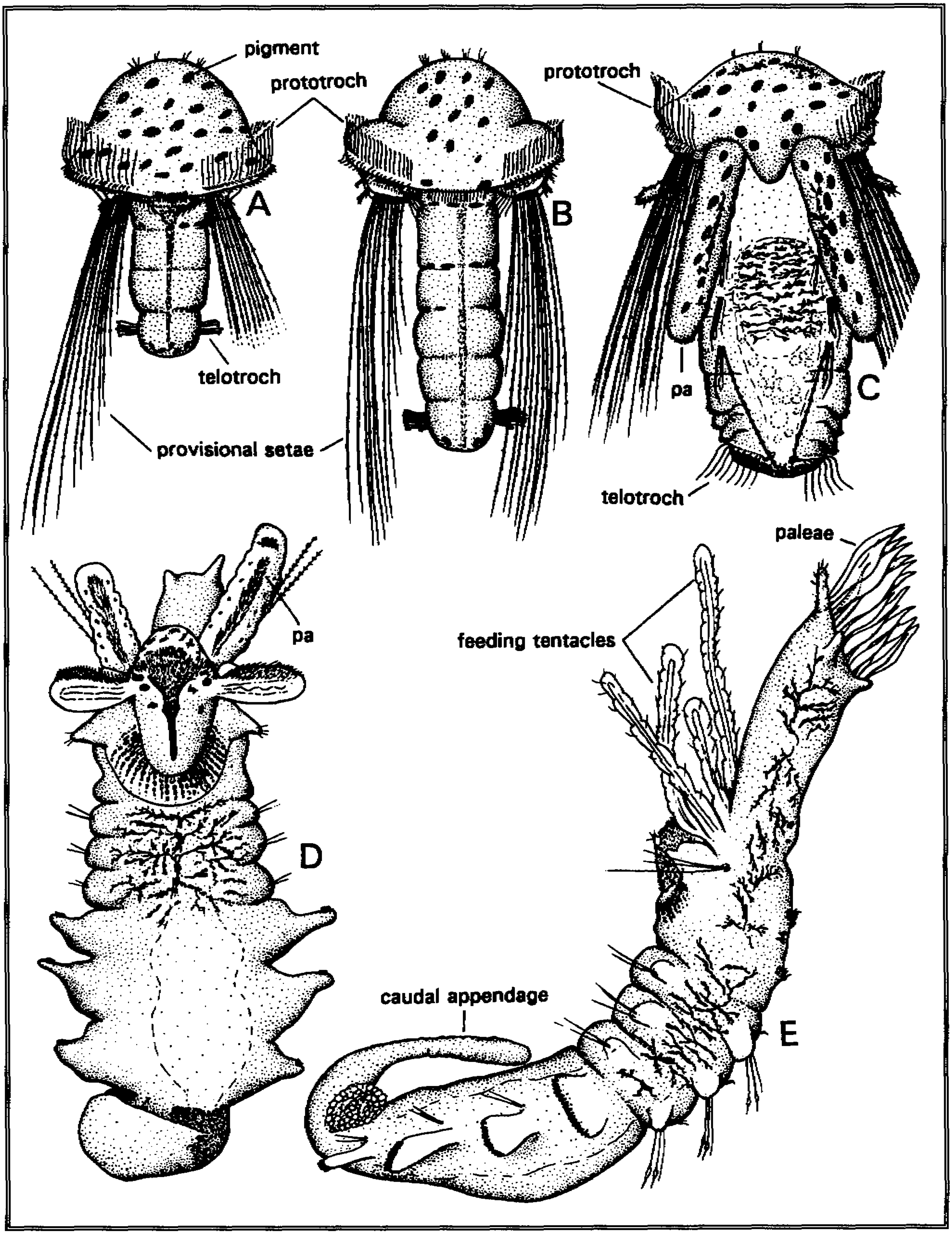

Figure 3.13. Larval Development of *Phragmatopoma californica*: A-C, pelagic nectochaetes; D-E, settling and early benthic stages.

Biology and Ecology

Although a comprehensive review of the biology and ecology of polychaetes is beyond the scope of this article, a few comments and generalizations are required so that the diverse morphology exhibited by polychaetes can be put in a functional perspective. Additional details will be presented for individual families in subsequent volumes.

Habitats

Polychaetes occupy and live in and on a wide variety of substrates including soft sediments, rocks, shells, and plankton. An excellent summary of habitats and morphological adaptations is presented by Barnes (1987). Many of the habitats and associates for California polychaetes are described in Ricketts, Calvin, and Hedgpeth (1985) and MacGinitie and MacGinitie (1968).

Polychaetes that are adapted for burrowing such as glycerids, arabellids, lumbrinerids, opheliids, and capitellids, typically have reduced parapodia and streamlined bodies. Most of these types of polychaetes construct simple burrows that may be lined with mucus. The morphological trends in these groups are similar in that the prostomium is reduced and pointed; eyes, palps, and antennae are reduced or absent, and parapodia are very reduced. Other types of burrowers include magelonids that use a shovel-shaped prostomium to assist in moving through sediment. Some burrowers form U- or J-shaped burrows from which species-specific deposit feeding behaviors are developed. Many of these burrowers tend to be subsurface deposit feeders that are important in aerating sediments by moving oxygenated surface water to feeding voids that are deep in the sediment. The activities of burrowers assist in maintaining a deeper level of the redox potential discontinuity (RPD) of marine sediments.

A tube-dwelling habit has evolved in many families of polychaetes. The tube may be simple or elaborate and serve as a protective retreat from which the worm is able to feed and sometimes brood young. Tubes may be simple, with a mucus lining covered with silt or sand grains as found in spionids, a heavy parchment-like structure in chaetopterids, or a calcium carbonate tube as in the serpulids and spirorbids. Oweniids are able to select and cement quartz grains and other minerals to their tubes, while pectinariids cement particles into a cone-shaped structure that they carry around with them while burrowing. Onuphids and eunicids are raptorial and extend from the tube to sieze passing prey. The majority of tube-dwelling polychaetes typically develop elaborate anterior feeding structures. Sabellids extend their elegant branchial plumes into the water to filter particles which they ingest or use to build their tubes. Spionids extend their two palps from the tube and either collect particles from the water or from the surface of the sediment.

Tubes of polychaetes have been reported to stabilize sediments (Fager, 1964). Polychaete tubes have also been found to alter particle flux in the benthic boundary layer by causing a vortex as the water flows around them. This results in resuspension of particles (Carey, 1983).

Some tube dwellers are modified to actually bore into calcareous structures such as coralline algae, coral, and shells of bivalves and gastropods. Spionids of the *Polydora*-complex are the best known examples of this group (Blake and Evans, 1972), although some terebellids, cirratulids, sabellids, and eunicids bore as well (Blake, 1969b; Chughtai and Knight-Jones, 1988). Borers break-up hard substrates and eventually contribute to the production of sands. Some species of *Polydora* are known as pests to the oyster industry because they form an excavation in the shell that becomes filled with mud. Mud-blisters form on the inside of the shell and are unsightly, thus reducing the market value of oysters. In some cases, when infestations of *Polydora* are high, the oysters are weakened to such an extent that other diseases may cause extensive mortalities. In California abalone farms, *Polydora* infestations of the shells of juvenile abalone have been shown to inhibit normal growth (Blake, unpublished).

Many polychaetes live in association with other invertebrates. *Spinther* is associated with sponges. Scale worms are known to live in burrows of maldanid polychaetes and echiurans or are associated with nudibranchs and echinoderms. The genus *Arctonoe* has several commensal species. *Podarke pugettensis* lives in the ambulacral grooves of starfish. All species of *Iphitime* are commensal in the branchial cavities of crabs (Pilger, 1971; Comely and Ansell, 1989). Blake (1990) recently described an unusual association between a polychaete and a deep-sea bivalve. True parasitic polychaetes are rare. Some arabellids may be encountered as endoparasites in other polychaetes such as syllids, onuphids, paraonids, cirratulids, and spionids (Pettibone, 1957; San Martin and Sarda, 1986; Blake, unpublished).

Surface dwelling polychaetes are frequently found beneath rocks and shell fragments, algal holdfasts, crevices, and among hydroids and bryozoans. These polychaetes tend to have elaborately developed anterior sensory structures and parapodia. Typical polychaetes occupying this habitat includes nereidids, syllids, phyllodocids, and scale worms. These polychaetes include predators, herbivores, and omnivores.

Six families of polychaetes live exclusively in the plankton. These pelagic polychaetes are remarkable in having highly transparent bodies, reduced setae, and unusual parapodia. Pelagic polychaetes are not treated in this Atlas, and the reader is referred to Dales (1957), Pettibone (1963), Day (1967), and Fauchald (1977) for information.

Feeding and Nutrition

The modes of feeding in polychaetes are closely tied to the various habitats just described. Free-living polychaetes tend to be raptorial, omnivores, or scavengers; burrowers tend to be deposit feeders; and tube dwellers tend to be filter feeders, although there are many exceptions. The best summary of feeding in polychaetes is by Fauchald and Jumars (1979).

Raptorial feeders are carnivores and include most of the surface dwellers, the pelagic families, some tubicolous eunicids and onuphids, the glycerids and goniadids, and the phyllodocids. Scaleworms encounter prey in their movement and attack with an eversion of their armed proboscis (Pleijel, 1983). tube dwelling carnivores such as glycerids typically lie in wait, and feed on small invertebrates by first capturing them with a rapid eversion of the proboscis (Ockelman and Vahl, 1970). This structure is typically armed with jaws or teeth. Prey items are seized and carried back to the mouth when the proboscis inverts. Syllid polychaetes of the genus *Autolytus* feed on hydroids by cutting off polyps with teeth at the end of the pharynx. Other syllids suck the contents from polyps.

There is considerable variability within some families and genera as to what type of feeding is present. For example, nereidids are usually thought of as carnivores, but some species of *Nereis*, such as *N. pelagica, N. virens*, and *N. diversicolor* are omnivorous and feed on algae, small invertebrates, and detritus (Goerke, 1971). *Nereis diversicolor* has been shown to filter feed by using a mucous net or bag (Goerke, 1966). *Nereis succinea* feeds primarily on detritus; *N. fucata* is an example for a "typical" nereidid and is carnivorous (Goerke, 1971). Occasionally, different investigators have attributed different modes to the same species. For example, Sanders (1956, 1960) reported that *Nephtys incisa* was a non-selective deposit feeder in New England, while Clark (1962) was convinced that the same species was a predator in Europe. The issue was revisited by Redmond and Scott (1989) who found that *N. incisa* in Narragansett Bay, Rhode Island sometimes changed its feeding mode and preyed on amphipods in laboratory experiments. These authors concluded that the species was an omnivore.

Although poorly understood, dorvilleids are thought to use their rows of maxillary denticles to rasp the surface of sand grains or other structures rather like molluscs use a radula. They may feed on small diatoms or other particles, although dorvilleids are often found with empty guts.

Some deposit feeding polychaetes are non-selective, and consume sand or mud directly when the mouth is applied against a substratum. A soft, unarmed proboscis that is ciliated facilitates this type of ingestion. Many burrowers and tube dwellers feed in this manner, including capitellids, opheliids, arenicolids, maldanids, scalibregmatids, and orbiniids. Kudenov (1977) provides a good general account of three non-selective feeding maldanids that are common on the California coast.

Selective deposit feeders lack a proboscis and have developed special types of feeding tentacles which they extend out over the sediment to collect particles. In the terebellids, *Amphitrite* and *Terebella*, large numbers of thin contractile tentacles stretch out over the substrate. Detrital particles on the surface adhere to the mucus secreted by the epithelium. The individual particles are then moved toward the mouth along the tentacles by cilia in grooves. Food accumulates at the base of the tentacles which is eventually moved into the mouth by other cilia. In ampharetids, the tentacles are retracted into the mouth where the food is removed. In spionids, particles are picked up from the sediment or captured in the overlying water and transported to the mouth along a ciliated ventral groove on the palps. *Pectinaria* is a deposit feeder that selects organic matter from sand grains and other types of organic aggregates below the surface (Whitlatch, 1974).

The biology of deposit feeding has been an active field of research because so many marine organisms derive their nutrition from the organic matter that is contained in marine sediments. This research is related to the larger issue of nutrient dynamics on the continental shelf and in coastal embayments and marsh systems. Polychaetes have been used to study particle selection, digestion, nutritional value of food resources, and other aspects of the relationships of organic carbon flux and benthic community dynamics. Capitellid polychaetes in particular, have proven to be excellent organisms for laboratory experimentation (Tenore, 1977a-b, 1983; Tenore *et al.*, 1982; Phillips and Tenore, 1984; Forbes and Lopez, 1987). Results have indicated that the actual feeding and tube building activities of deposit feeders can lower the abundance of fine particles that are available for ingestion (Rhoads, 1974). This is largely manifested through the production of fecal pellets, the packaging of which is believed to make them unavailable as a food resource which may lead to population crashes of opportunistic species such as *Capitella capitata* (Grassle and Grassle, 1974).

Filter feeding polychaetes are among the most modified. The head of sabellids, serpulids, and spirorbids is composed of a large fanlike structure called the tentacular crown. In sabellids, two half circles of bipinnate radioles form a funnel or one or two spirals when extended from the tube. Numerous rows of cilia beating on the individual pinnules on each radiole produce currents that bring particles in contact with the pinnules where they are trapped and carried to a groove that runs the length of each radiole. At the base of the radiole the particles are sorted in such a way that the large ones are rejected and fine material is carried to the mouth. Additional sorting defines which material is used for tube construction and for food. Detailed accounts of feeding and tube-building in sabellids are by Nicol (1930), Fitzsimmons (1965), and Bonar (1972).

Chaetopterus has highly modified, winglike (aliform) notopodia in a few anterior segments. Subsequent segments are fused and modified as fanlike structures that beat and set up a current that circulates through the U-shaped tube. The paired aliform notopodia stretch out, and a sheet of mucus is secreted that forms a bag between them. Water passing through the tube carries particles of detritus and plankton that are trapped in this bag. When this bag fills, it is rolled into a ball and passed along a ciliated groove to the mouth where it is swallowed (MacGinitie, 1939). New mucous bags are continuously being produced as old ones are rolled up into food balls. Other genera of chaetopterids also use a type of mucous bag feeding (Barnes, 1965). In *Spiochaetopterus* as many as 13 mucous bags are formed at one time.

Spionid polychaetes are able to switch between a water column filter feeding mode and that of a surface deposit feeder. This ability to change from deposit feeding to filter feeding is apparently induced by water flow. At moderate flows the worms cease their deposit feeding, lift their palps into the overlying water, and capture particles in suspension (Taghon *et al.*, 1980). Studies of filtering efficiency suggest that dense assemblages of spionids increase particle removal rates from the water column which at the same time results in a net increase in sedimentation (Frithsen and Doering, 1986).

Population Biology and Benthic Ecology

In benthic communities on the continental shelf and slope, polychaetes are the dominant components of the assemblages and typically comprise 45-50% of the total number of species present and as much as 80% of the total number of individuals. With the use of finer mesh screens (0.3- and 0.5-mm) a large variety of small species of polychaetes are found that were not considered to be important in earlier investigations. For example, as part of a 3-year monitoring program on Georges Bank off Massachusetts, syllid polychaetes of the genera *Exogone* and *Sphaerosyllis* were found to be numerically dominant when a 0.3-mm sieve was used, but were only moderately abundant when the 0.5-mm fraction was analyzed (Maciolek-Blake *et al.*, 1985).

Because of the importance of polychaetes in benthic communities, there have been many efforts to characterize the response of benthic communities to anthropogenic disturbance by observing the population dynamics of selected species. If a predictable relationship between disturbance and response of these species can be found, one or more indicator species could be determined for the degree of disturbance in a particular environment. For example, some burrowing or tubiculous species that occur in high numbers on the seafloor undergo rapid and dramatic changes in their densities. Such species are called opportunists[2] and usually include capitellids of the genera *Capitella* and *Mediomastus* and spionids of the genera *Polydora, Prionospio, Spio*, and *Streblospio.* Characteristic life history traits are associated with opportunistic species including small size, rapid colonization ability, short generation time, high reproductive rate (r), and high mortality rate (Grassle and Grassle, 1974). The recognition of different life history traits has led to the development of models of succession in benthic communities (Pearson and Rosenberg, 1978; Rhoads and Germano, 1986). When the seabed is disturbed by dredging, dredged material disposal, waste disposal, oil spills, severe storms, or other activities that might increase nutrients, the surface sediments will initially be colonized by these small opportunistic polychaetes that form dense assemblages on the surface. Typically, the RPD is relatively shallow at this stage of recolonization. During later stages of recolonization, populations of larger, deep-burrowing organisms such as maldanid polychaetes will successfully compete with the smaller species and become established. The larger organisms form feeding voids deep in sediment that permits oxygenated waters to penetrate and aerate the sediments. This results in a deeper RPD.

Recent investigations on *Capitella* and *Streblospio* have focused on the level of organic matter in the sediments and how it is related to the growth of the worms and their success in such an environment. This is an area of active research, and Levin (1986) suggested that the ability to translate elevated food supply directly into increased reproductive output may be fundamental to understanding the success of opportunists in benthic communities. It is probable that an understanding of increased reproductive output in areas of organic enrichment will ultimately be developed in a biochemistry laboratory.

There is little information on how long polychaetes live, but the life span of most species is probably not more than two years. However, Kirkegaard (1970; 1978) found evidence that some of the larger *Nephtys* species live for 4-5 years, and Nichols (1975) found that *Pectinaria californiensis* lived for five years. Life spans are tied closely with life history patterns. Monotelic species would obviously die after their single spawning (possibly in the second year of their life), while polytelic species would spawn several times in a year, and possibly in subsequent years, depending upon their life spans.

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[2] Opportunistic species that live in polluted, organically enriched sites are sometimes termed "pollution indicators."

Collection and Preservation

Polychaetes are delicate and fragile animals, and special care should be taken when handling them, especially when washing sediment samples through screens. If handled too roughly, the bodies will fragment, or critical parts will be lost, making identification difficult if not impossible. It is highly recommended that samples be sieved as soon as possible after collection, and before the samples are placed in fixative. By doing so, the animals are removed early from the sediments, which, particularly in the case of coarse sands, could damage the specimens by abrasion. When sieving samples, a gentle flow of water should be directed to the underside of the screen, rather than from above. This breaks the force of the water and helps prevent damaging specimens. Large samples should be handled in small portions, to avoid having too much material on the screen at one time. Contents of the screen should be gently washed into a jar, and kept separate from the sediment residue, which can be resieved at a later time to ensure removal of all specimens. Although these procedures may be more time-consuming than the usual method of dumping samples into formalin at the time of collection and sieving dead material, these techniques have been found to be extremely valuable in ensuring that the specimens are preserved in good condition. The extra time spent in carefully washing sediment samples is minimal compared to the extra time that may be necessary to identify poor material. Damaged specimens may be misidentified or completely lost to counts of total individuals recorded from quantitative samples.

Specimens may be relaxed prior to preservation, using a solution of 7.5% magnesium chloride or menthol. Fixation of free-living polychaetes is best in formalin of 5 to 20%, depending on the use of the material; preservation of quantitative benthic samples is usually done in 10% buffered formalin. Tubiculous worms generally have a softer cuticle than errant forms and should be fixed in Bouin's, Kahle's or a potassium dichromate fixative, all of which harden the cuticle, making study easier. After a suitable time in the fixative (normally no longer than 24 hours), the worms may be transferred to 70 or 80% ethyl or isopropyl alcohol.

Laboratory Methods

At a minimum, the optics required for the study of polychaetes includes a stereo microscope equipped with a good illuminator (fiber optics are preferred) and a compound microscope with an oil immersion objective. All material, particularly small-bodied forms, must be kept submerged in alcohol or mounted in glycerin at all times to avoid drying out the material. Since the ability to recognize the families is of great practical value, biologists should early learn to recognize the common family types. At that point, all that will be needed to a identify a specimen to family will be a quick scan under the stereo microscope, taking note of the anterior appendages, parapodial structure, and other large features such as branchiae.

In order to identify specimens to genus or species, more detailed examination will be necessary, and certain dissections may have be required. Individual parapodia should be removed and mounted in order to examine the parapodial structure and the setal types present. Parapodia can be excised using a scalpel or pair of iris scissors, or simply two pairs of forceps. The parapodium should be mounted as flat as possible on a slide, using glycerin or a glycerin/alcohol mixture as a temporary mounting medium. Basic characteristics of the parapodia may be observed at fairly low power under the compound microscope, but in order to see the fine details of the setal structure, oil immersion is often necessary. If the specimens are small enough, it may be possible to make a mount of the whole animal and then scan the body from the anterior to posterior for changes in setal types and distribution.

For taxonomic purposes, it is often necessary to dissect the proboscis to examine the jaws or other structures. Polychaetes are generally opened from the dorsal side for this purpose, although a total dissection is started from the ventrum to keep the nervous system undamaged. The jaws of euniciform polychaetes may be removed along with the entire pharyngeal apparatus, or may be left *in situ* to avoid the loss of small parts. Because important body structures are often located along the midline of the animal, medial incisions should be avoided. Rather, a longitudinal incision lateral to the midline should be made, and transverse cuts made at both ends of the longitudinal one. A flap of the body wall can then be lifted, and the pharynx removed using forceps, or observed while still in place. Euniciform jaws are always observed from the dorsal side and the jaw formulae are given from the posterior to the anterior end, the left jaw being the first mentioned in each formula. Therefore, it is important when dissecting the jaw apparatus to always treat material from different specimens in a similar fashion so that the orientation is identical.

The use of methyl green stain has recently become popular for elucidating differences between species. Staining patterns appear to be species-specific and can provide a quick recognition feature when sorting large amounts of material. It is particularly useful with sphaerodorids, capitellids, cirratulids, cossurids, maldanids, amphretids, and sabellids. A saturated solution of the stain is prepared using 70% ethyl alcohol. A few drops of this solution are added to a small watch glass or vial containing the specimen. The specimen is left in the stain for a few minutes, and then placed in clean alcohol for a few minutes to differentiate the pattern.

Additional techniques include clearing specimens with Amman's lactophenol as a temporary mounting medium. The mixture consists of 100 g phenol, 100 ml lactic acid, 200 ml glycerine, and 100 ml water. The specimen is mounted on a slide in this mixture and covered with a coverslip. The slide is heated carefully to avoid bubbling. This procedure clears the tissues, making internal sclerotized structures such as jaws and acicula more visible. Another technique for preparing specimens to see small jaw pieces is to clear them in Potassium hydroxide (KOH). A 10% solution of KOH is prepared in which the worms are placed for 2-3 hours. The worms should be checked periodically until they appear to be sufficiently clear for observation of the jaws. These specimens can be transferred back to alcohol for study, usually from a wet mount. Permanent mounts can be made using Euparal® or Permount®, which also clears the specimens. The normal procedure to prepare such mounts is to dehydrate the specimens in 100% alcohol, followed by a brief immersion in a clearing agent such a toluene or xylene prior to applying the mounting media. Specimens may be mounted directly in Euparal® from 100% alcohol, but each slide must be allowed to dry on a warming tray before storage. Permanent slides of parapodia, jaw pieces, setae, or whole specimens become valuable research tools and important voucher materials for a taxonomist.

Discussions of these and other techniques may be found in Blake (1975a), Fauchald (1977), and Hobson and Banse (1981).

Glossary

Abdomen. Posterior region of the body, behind the thorax.

Accessory branchiae. Small, single or palmately arranged finger-like lobes (gills) located behind the notopodial lamellae (on the genera *Dispio* and *Scolelepis*, family Spionidae).

Accessory tooth. A small subterminal tooth on the modified major spines of setiger 5 in some species of *Polydora* (**pointe laterale** of Fauvel, 1927:49; **Nebenzahn** of Söderström, 1920:262, 265).

Achaetous. Lacking setae; asetigerous.

Acicula(ae). A stout internal collagenous rod that supports each branch of a parapodium; one or several may be present.

Acicular seta. A very stout projecting seta homologous with other setae but similar in thickness and shape to an internal acicula.

Acuminate. Sharply pointed at the tip; abruptly tapered; mucronate.

Aileron. Accessory jaw plate in the Glyceridae, an imbedded winglike structure.

Alimbate. Without a wing; refers to capillary setae lacking sheath.

Anal cirrus(i). Elongated projection(s) from the pygidium.

Annulate. Ring-shaped; composed of ringlike segments.

Antenna(e). A sensory projection arising from the dorsal, lateral or anterior surface of the prostomium.

Apical tooth (teeth). The smaller denticles or teeth above the main fang of e.g., the hooks of lumbrinerids, spionids, and capitellids.

Apinnate. Lacking pinnules, smooth (e.g., the smooth, unadorned branchiae of spionids).

Apodous. Without parapodia.

Arborescent. Branched like a tree.

Areolate. Divided or marked by creases into small areas, e.g., in capitellids.

Aristate. A simple seta with a smooth shaft and one to several distal hairs, e.g., in paraonids.

Articulate. Jointed.

Asetigerous. Without setae; achaetous.

Atoke. An individual worm that is not modified for reproduction.

Auricle. Paired lateral appendages of antennal base (Family Sigalionidae, genus *Sthenelais*); also referred to as antennal ctenidia.

Auricular. Ear-shaped.

Avicular. Beaked; shaped like the head of a bird; used with reference to setae.

Awl. Needle-shaped seta (e.g., in the spionid genus *Polydora*)

Bacillary seta(e). Long, very thin, smooth or hirsute capillary seta(e) emerging from interramal thread glands in certain setigers in the spionid genus *Spiophanes*.

Basal ring. The base of the prostomium; the proximal prostomial ring of goniadids and glycerids.

Bearded. Setae having a tuft of fine hairlike structures below the main fang (e.g., the rostrate hooks of maldanids).

Biacicular. Having aciculae (one or more) in each of the two branches of a parapodium.

Biarticulate. Two-jointed, e.g., antennae, tentacles or palps.

Bidentate. With two teeth (setae and jaws).

Bifurcate. With two prongs, bifid.

Bilabiate. With two lips.

Bilimbate capillary. A simple hairlike seta enveloped by a sheath that in various views appears to form two wings or flattened margins.

Bilobate. With two lobes, as in the proboscis of *Paraprionospio pinnata*; bilobed.

Bipinnate. A structure formed like a feather with a main stem and two rows of side branches.

Biramous. With two rami or branches; used in reference to parapodia having both noto- and neuropodia present. Parapodia bearing setae in only one ramus are said to be **subbiramous**. Parapodia lacking a notopodium entirely are **uniramous**. In some families of errant polychaetes, these terms are restricted to describe the presence of embedded aciculae.

Blade. The distal portion of a compound seta.

Boathooks. Highly modified, stout, sickle shaped spines found in the posterior notopodia of certain species of Spionidae (e.g., *Boccardia, Polydora*), and Pilargidae (e.g., *Sigambra, Ancistrosyllis*).

Boss. A small projection or knob-like process on certain setae (e.g., in *Pectinaria*).

Branchia(e). An extension of the body wall containing a blood vessel loop, or well-supplied with capillary blood vessels; a gill.

Buccal. Pertaining to the mouth. The buccal segment is the peristomium, or segment in which the mouth is located. Buccal tentacles are used for feeding and sometimes can be retracted into the mouth.

Branchial crown. A circle of filaments or radioles used for filter feeding and/or respiration; found in sabellid, serpulid, and spirorbid polychaetes.

Calicinate. Shaped like the calyx of a flower.

Cameration. Divided into a large number of internal chambers (e.g., internal divisions in nereidid setae, Fig. 77G).

Campanulate, campanuliform. Bell-shaped (used regarding capitellid branchial lobes).

Canaliculate. With fine canals.

Capillary(ies). Long, slender, tapering, hairlike type of seta; may be limbate or without sheath (= **soie capillaire** of French authors, **Haarborste** of German authors).

Caruncle. Posterior sensory extension of the prostomium, sometimes extending over several anterior segments (e.g., amphinomids, spionids).

Caudal. Referring to the tail or posterior region.

Cephalic cage. Long, forwardly-directed setae which enclose and protect the head (e.g., in flabelligerids and uncispionids).

Cephalic rim. A flange encircling the head in maldanids.

Cephalic keel. A median ridge on the prostomium or head in maldanids.

Cephalic peak. Chitinized, anterolateral projection of the prostomium of certain polynoids (= prostomial peak, frontal peak).

Cephalic veil. A hood-like membrane between the opercular paleae and the buccal tentacles in pectinariids.

Cephalisation. The modification and fusion of anterior segments to form a head, i.e., a concentration of segmental nerve ganglia to form a brain, and segmental sensory cells to form sensory organs of greater complexity such as eyes, antennae, and nuchal organs.

Ceratophore. The basal joint of an antenna.

Ceratostyle. The distal joint of an antenna.

Chaetosyllis. The sexually reproducing form of certain syllid species in which the males and females are morphologically similar.

Chevron. V-shaped chitinized jaw piece at the base of the eversible pharynx in some goniadids.

Chromophile gland. A densely staining gland in the ventral pinnules of certain Tomopteridae.

Chromatophore. A special cell or group of cells carrying pigment.

Cirrigerous (segment). A segment bearing a cirrus.

Cirriform. Shaped like a cirrus; slender, cylindrical and tapering.

Cirrophore. Basal joint of a cirrus.

Cirrostyle. Distal joint of a cirrus.

Cirrus(i). A sensory projection, usually slender and cylindrical; refers to structures on various parts of the body, which may not be homologous with each other: e.g., the dorsal cirrus is derived from the superior part of the notopodium, the ventral cirrus is derived from the inferior part of the neuropodium; the occipital or nuchal cirrus is found on the posterior part of the prostomium in spionids.

Clavate. Club-shaped, with a slender base and inflated tip.

Coelom. A body cavity that arises as a cavity within embryonic mesoderm. The mesoderm provides the cellular lining of the cavity and is called peritoneum. The internal organs that bulge into the coelom are all bounded by peritoneum.

Collar. An anterior, encircling fold or flap, a rim of tissue, e.g., across the dorsum of setiger 2 in the spionid *Streblospio benedicti*, or the tissue encircling the first setiger and covering the base of the branchial crown of sabellids, serpulids, and spirorbids.

Collar seta(e). Modified notoseta(e) found in the collar of spirorbids, serpulids and sabellids; of great taxonomic importance.

Comb seta(e). A simple seta with a comblike arrangement of teeth on the distal end, found in species of onuphids and eunicids; pectinate setae.

Companion seta(e). Setae that alternate with modified setae in a fascicle, usually simple limbate capillary setae (e.g. in the modified fifth setiger of *Polydora*).

Compound seta(e). Jointed setae, composed of a proximal shaft and distal blade; blades may be falcigerous (wide and blunt-tipped) or spinigerous (slender, with hairlike tip). Sometimes called composite setae.

Compressed. Flattened in the lateral plane.

Copragogue. A groove along the posterior region of a tubicolous worm along which the fecal pellets pass before being voided from the tube (sabellids).

Cordate, cordiform. Heart-shaped.

Cortex. Histologically and ultrastructurally distinct outer layer of an annelid seta. Compare with **medulla**.

Crenulate (seta). With a series of small cusps, e.g., the capillary setae of orbiniids.

Crook seta, crooklike seta. A stout, highly modified, incurved, staff-shaped seta found in the neuropodia of setiger 1 in the spionid genus *Spiophanes*.

Crotchet. A long-shafted seta with a hooked or curved end, with one or more distal teeth at an angle to the main shaft; a hook; found in many families.

Ctenidium(a). A branchia or gill found in many sigalionids and orbiniids, situated on or between the parapodia; a heavily ciliated pad, shaped like a comb.

Cultriform. Shaped like a knife.

Deciduous. Liable to be easily lost (e.g., elytra of polynoids; antennae and tentacular cirri of hesionids; palps of spionids).

Dentate. With teeth.

Denticle. A small tooth.

Denticulate. With small teeth.

Depressed. Flattened in the dorso-ventral plane. (see also compressed)

Digitiform. Finger-shaped.

Dorsal sensory organs. Chemoreceptors found on the dorsum of the anterior body segments in all spionids; ciliated grooves or ridges; nuchal organs.

Dorsal tubercle. A dorsal swelling in segments with dorsal cirri, located in the same position as the elytrophore on segments with elytra in the Aphroditacea.

Echinulate. Spiny or prickly like a sea urchin.

Elytrigerous. Bearing an elytron or scale.

Elytron(a). Dorsal scales found in the scale worms; homologous with the dorsal cirrostyles.

Elytrophore. A cirrophore bearing an elytron (in scale worms).

Epigamy. The process of modification of an entire pre-existing atokous individual to a reproductive epitokous state.

Epitoke. Modified reproductive stage or specimen.

Equilateral. With sides of equal length.

Errantia. One of the artificial major groups into which the class Polychaeta has been divided historically. Generally characterized by a relatively undifferentiated body metamerism with fully developed intersegmental septa, a muscular proboscis generally armed with chitinous jaws or teeth, and frequently with well-developed parapodia bearing composite setae. Compare with **Sedentaria**.

Eversible. Capable of being extended by turning the inner part outwards like a glove; e.g., proboscis.

Falcate, falciform. Hook-shaped, distally blunt and curved; refers to stout, modified setae with hooked or bent tips. Also used to refer to posterior sickle-shaped notosetae (see **boathook**); refers to widely differing hooklike setae, both simple and compound, in different families.

Falciger. A stout, modified seta with a hooklike tip; may be simple (unarticulated or unjointed), as in the spionids, or compound (articulated or jointed), as in lumbrinerids and nereidids.

Facial tubercle. A projecting ridge or lobe on the upper lip below the prostomium; especially in scale worms.

Fascicle. A setal bundle; a group of similar or differing setae projecting from the tissue as a unit or group.

Felt. Matted setae produced by the notopodia in some species of aphroditids.

Fenestrated. Having one or more openings or transparent spots; refers to orbiniid setae (see also crenulate).

Fide. On the faith or authority of (someone); according to.

Filiform. Threadlike, slender.

Fimbriated. With a brushlike border.

Fimbricated. With flattened, leaflike processes.

Flail seta. The abruptly bent abdominal neuropodial seta present in some species of orbiniids.

Flanged (seta). An elongate seta with a flattened edge or margin.

Foliaceous. Leaflike.

Forceps. Maxilla 1; the main jaw fang in the Eunicea; the maxillae of the nereidids; also called pincers.

Furcate seta(e). Usually short, fork- or lyre-shaped seta(e); found in dorvilleids, scalibregmatids, orbiniids, nephtyids, paraonids and aberrantids.

Fusiform. Spindle-shaped or cigar-shaped.

Gametes. A collective term for sexual products (eggs and/or sperm).

Geniculate. Bent like a knee.

Genital hook or seta. Modified setae, found in capitellids, thought to be involved in copulation.

Genital papilla. Projection below the neuropodium on which a reproductive duct opens.

Gill(s). Common term for branchia(e).

Gizzard. A grinding organ in the anterior digestive system in several spionids and sabellariids.

Glabrous. Smooth and glistening.

Harpoon seta. A stout, pointed seta with recurved barbs near the tip; found in the aphroditid genus *Laetmonice*.

Hastate. Shaped like the blade of a spear.

Hemigomph. A compound seta with an asymmetrical joint between shaft and blade, articulation nearly at right angle to the long axis of the shaft. Compare with **homogomph** and **heterogomph**.

Heterogomph. A compound seta with a slanting or asymmetrical joint between shaft and blade, articulation clearly oblique to the long axis of the shaft.

Hirsute. With fine hairs or bristles.

Hispid. Minutely bristled, hirsute.

Homogomph. A compound seta with a transverse or symmetrical joint between shaft and blade; articulation distinctly at a right angle to the long axis of the shaft.

Hood. Hyaline envelope, or cowl entirely or partially covering the distal end of setae in many families (e.g., spionids, capitellids).

Hook. General term used to refer to a stout-shafted, blunt, often distally curved and dentate seta; smaller hooks arranged in single or double rows are often called uncini.

Imbricated. Overlapping like tiles.

Inferior. Ventralmost, lowermost.

Interparapodial. Located between or connecting successive parapodia.

Interramal. Located between the dorsal and ventral branches of a single parapodium.

Intrafascicular hook. A simple hooded hook in the middle of the setal fascicle in some onuphids. Compare with **subacicular hook**.

Involute. Curved inward, as in the interramal cirri of the nephtyid genus *Aglaophamus*.

Jaw. A set of opposable, chitinized structures (usually at least 2) present in some polychaete families (e.g., Dorvilleidae, Onuphidae, Lumbrineridae, Nereididae) used for grasping food; parts consist of **mandibles, maxillae, maxillary carriers, macrognaths, micrognaths** if present, **ailerons** (in glycerids) and **chevrons** (in goniadids). Small jaws are also found in syllids and nephtyids.

Lamella. A flattened, sheetlike or platelike fleshy structure; a flattened lobe (as pre- and postsetal lamellae)

Lanceolate. Pointed, shaped like a lance.

Lappet. A small, tongue-shaped flap or fleshy process; used in reference to the highly reduced pygidial lobes of polydorids, the ventral parts of sabellid collars, and the lateral extensions of anterior segments in some terebellids.

Ligule. A compressed conical lobe of a parapodium (in nereidids).

Limbate (seta). A simple seta appearing to have a flattened margin or wing; actually a seta covered with a transparent hyaline sheath that is visible on one or both sides of the seta depending on the orientation. See also **bilimbate**.

Lobe. A major parapodial process, e.g., presetal and postsetal lobes.

Long-handled. Refers to uncini with a long basal rod or manubrium as the supporting part of the uncinus (terebellids, maldanids, sabellids).

Lyrate. Furcate; shaped like a lyre; refers to certain setae (see also furcate).

Macrognath. A paired, large black jaw piece on the opening of the proboscis in the goniadids; compare with micrognaths.

Macrotubercle. 1) A large, chitinized projection of the elytron in some polynoids; 2). A large, spherical structure on the dorsal surface of most sphaerodorids. Compare with microtubercles.

Major spine. A heavy, stout seta, particularly the heavy modified setae in the fifth setiger of *Polydora* and related genera (Spionidae).

Mammiliform. Shaped like a breast.

Mandible. Ventral paired, flattened jaw piece found in euniciform families, more or less fused along the median line. See also **maxilla**.

Manubrium. A handle-like process or part; refers to the swelling and waistlike constriction seen in the neuropodial hooks of spionids or in the notopodial seta in the abdomen of sabellids.

Maxilla. Dorsally attached pharyngeal jaw pieces of the euniciform families.

Maxillary carrier. A paired jaw piece supporting the maxillae in the Eunicea, with or without a median, unpaired jaw piece.

Maxillary ring. The distal part of the everted proboscis in the Nereididae, numbered with Roman numerals I-IV, for paragnath distribution. Compare with oral ring.

Medial. Near or toward the mid-line of the body.

Median. In the mid-line.
Medulla. Histologically and ultrastructurally distinct inner core of an annelid seta. Compare with **cortex**.

Membranous. Thin, flattened, sheetlike.

Metamerism. Division of a body into similar, usually cylindrical segments with similar internal morphology.

Metanephridium. An excretory organ that originates in a ciliated coelomic funnel; anatomically most complex nephridium (see also **nephridium** and **protonephridium**).

Metastomium. The segmented portion of the polychaete body between the prostomium and pygidium, but including neither; "behind the mouth."

Micrognath. Small, black jaw pieces typically arranged on the opening of the proboscis in an arc above and below the macrognaths in the goniadids.

Microtubercle. 1) A small, chitinized projection of the elytron of some polynoids, 2) A small, soft, two-parted protuberance on the bodies of some sphaerodorids. Compare with **macrognath**.

Moniliform. Beaded, or like a string of beads; e.g., dorsal cirri of some syllids.

Mucro, mucronate. Abruptly tapered, having a sharply pointed tip. See also **acuminate**.

Multiarticulate. With many joints.

Multidigitate. With many fingerlike lobes or projections.

Natatory. Used for swimming, natatory setae are longer and sometimes broader than normal setae. They are best developed in some syllids and nereidids when they become reproductively mature and leave the benthic habit.

Neotenic. Retention of young, immature, or juvenile characters in a mature, sexually reproducing stage.

Nephridium. Excretory organ characteristic of various coelomic invertebrates, occurring paired in each body segment or as a single pair serving the whole body; consisting of a terminal cell or ciliated funnel and an often coiled tube opening into a pore in the body wall, sometimes in a conspicuous nephridial papilla.

Neuropodium. Ventral branch or ramus of the parapodium. Named after the ventrally situated nervous system.

Neuroseta(e). Setae associated with the neuropodium.

Notopodium. The dorsal branch or ramus of the parapodium.

Notosetae. Setae associated with the notopodium.

Nuchal organ. Refers to sensory organs found on the posterodorsal side of the head and variously developed as paired or single processes, pits, or grooves; sometimes paired epaulets extending posterolaterally from the prostomium.

Obcordate. Inversely heart-shaped.

Occipital. Referring to the posterodorsal part of the prostomium; literally, "back of the head."

Ocular. Referring to the eye.

Opercular palea. A seta-like structure formed in the thoracic segments of sabellariids, which migrates anteriorly and forms the operculum.

Operculum (a). A hard structure used as a stopper for a tube opening; a modified branchia in spirorbids.

Oral ring. The proximal part of the everted proboscis in the Nereididae; numbered with Roman numerals V -VIII for paragnath distribution. Compare with **maxillary ring**.

Palea(e). A broad, usually flattened seta, found in the chrysopetalids, sabellids, pectinariids, and ampharetids.

Palmate. With several digits diverging from a common base, multidigitate; resembling the fronds of a palm.

Palp. Paired tentacle-like feeding structure with a median ciliated groove arising from the peristomium in the spioniform and most sedentary families; anteroventral sensory structures in errant families. The two types are not homologous.

Paragnath. Chitinous denticle in the pharyngeal cavity of most Nereididae. The distribution and shape of paragnaths is of great taxonomic importance.

Parapodial stylode. The elongated papillae on the parapodia of species of *Sthenelais*.

Parapodium(a). Segmentally arranged, fleshy, foot-like projections bearing setae; may be reduced to a low glandular ridge, or well developed with associated lobes and ligules or lamellae.

Parapodial ramus. One of the major (dorsal or ventral) divisions or branches of the parapodium; usually distinguished by bearing either setae, aciculae, or both. Compare with **biramous, uniramous**.

Pectinate. With a series of projections arranged like the teeth of a comb, refers to setae and gills.

Penicillate. Brushlike, like a small paint brush.

Pennoned. Teardrop-shaped, refers to the shape of the tip of certain setae, such as thoracic notosetae in certain sabellids and the anterior or dorsal row of modified major spines of setiger 5 in certain spionids such as *Pseudopolydora paucibranchiata*.

Peristomium. The first distinct segment behind the prostomium, surrounding the mouth; also refers to the area including segments fused to this structure, as in the hesionids, phyllodocids, and nereidids.

Pharynx. Anterior part of the digestive tract, modified for feeding, sometimes eversible, sometimes also modified for burrowing.

Pick-axe seta. A distally flattened and curved seta found in the sabellids.

Pilose. Covered with very short hairs, refers to setae.

Pinnate. Feather-like, with a main stem and lateral side branches, the side branches may have either digitiform or flattened and platelike pinnules; refers to gills, e.g. in spionids and sabellids.

Polybostrichus. The male sexual stolon of certain species of syllids in which the males and females are dimorphic. Compare with **chaetosyllis and sacconereis**.

Postsetal. Posterior to the setae, refers to parapodial lobes or ligules.

Presetal. Anterior to the setae, refers to parapodial lobes or ligules.

Proboscis. Anteriormost part of the pharynx; epithelial and eversible and more or less branched to simple (as in Orbiniidae) or muscularized and armed (as in Nereididae).

Proboscideal organs. Minute structures, sometimes called papillae that cover the surface of the proboscis of glycerids. These structures are variously ornamented and may have both pores and canals.

Prostomial peaks. Chitinized anterolateral projections of the prostomium of certain polynoids. See also cephalic peaks.

Prostomium. Pre-segmental part of the body anterior to the mouth, often bearing eyes, antennae or palps; the head.

Proventricle. Muscularized anterior region of the digestive tract in syllids, behind to the pharynx.

Pygidium. Post-segmental terminal part of the body bearing the anus.

Radiole. One of the main tentacles or branches of the branchial (tentacular) crown of sabellids, spirorbids, and serpulids, normally bearing two rows of side branches or pinnules.

Ramose. Branched.

Reniform. Kidney-shaped.

Rhomboidal. Irregularly four-sided.

Ringet seta. A furcate or forked seta with a series of annular serrations on both prongs; typically used in reference to euphrosinid setae.

Rosette gland. Glands in the parapodia of certain tomopterids.

Rugose. Roughened, lumpy.

Sacconereis. The female sexual stolon stage of certain syllid species in which the male and female forms are dimorphic. Compare with **chaetosyllis and polybostrichus**.

Sabre seta. A seta with a broad, curved blade, typically found in the ventralmost position in the neuropodial fascicle of certain spionids.

Scaphe. The flattened caudal appendage of pectinariids.

Secondary tooth. The second of two teeth on a seta, the first being the apical, terminal or primary one.

Sedentaria. One of the two artificial major groups into which the class Polychaeta has been divided historically. Generally characterized by the reduction or loss of body metamerism, a tendency towards loss of the internal septa and corresponding differentiation of the body into thorax and abdomen, absence of horny or chitinous proboscideal teeth or jaws, and typically with reduced parapodia and simple setae. Compare with **Errantia**.

Segment. Any part of the body apart from the prostomium or pygidium, set off internally by septa; externally divided by intersegmental furrows (in some families there are additional rings) and bearing one pair of parapodia.

Sesquiramous. Apparently uniramous; a parapodium in which the notopodium is reduced to a dorsal cirrus, an acicula and sometimes one or two setae. Compare with **subbiramous**.

Sessile. Without a stalk; refers to tubercles in sphaerodorids.

Seta(e). Chitinous structures emerging from the parapodia; **bristles** or **chaetae** of some authors.

Setiger. A segment bearing setae.

Shaft. The proximal portion of a compound seta. Compare with blade.

Simple seta. Unjointed seta.

Spatulate. Blade-shaped, usually blunt-tipped, sometimes with a mucron. Refers to sabellid setae.

Spine. Stout, modified seta, found in the posterior notopodia of many spionids and orbiniids and also in the modified fifth setiger of certain spionid genera.

Spiniger. A seta or blade of a compound seta that tapers to a fine point. Compare with falciger.

Spinous pocket. An enlarged serration on the seta of some scaleworms in which the edge is divided into spinules which surround a pocket-like cavity.

Sternal shield. A ventral plate on the last segments of a sternaspid.

Stomach papillae. Small papillae or lamellae occurring ventral to the podial lamellae and crossing the ventrum as in some orbiniids. See also **ventral fringe**.

Stylet. A small, pointed, tooth-like structure.

Stylode. A small, digitiform projection associated with a parapodium.

Subacicular hook. A simple hooded hook in a position ventral to the acicula in onuphids and eunicids. Compare with **intrafascicular hook**.

Subbiramous. A parapodium that is neither completely uniramous nor biramous, with the neuropodium well developed and the notopodium reduced in size and bearing very few setae.

Subterminal. Almost at the end.

Subequal. Approximately equal.

Subulate. Awl-shaped; elongate, blunt and tapering.

Subuluncinus(i). Seta(e) with a stout shaft suddenly tapering to a slender tip, intermediate between a capillary seta and an uncinus. Found in some orbiniid genera.

Superior. The more dorsal of two or more structures; uppermost.

Tentacle. A slender outgrowth of sensory function emerging from the head (more appropriately called antenna), peristomial segment (e.g., tentacular cirrus of many errant families), and anterior body segments (e.g., multitentaculate cirratulid genera; cossurids).

Tentacular cirrus. A sensory projection arising either from the peristomium or from cephalized segments; in the latter case they are considered to be homologous with the dorsal and ventral cirri of normal, post-cephalic parapodia.

Tentacular formula. A series of letters and numbers used to indicate the arrangement of the tentacular cirri and setae in phyllodocids and alciopids.

Tentaculophore. The basal projection on which a tentacle is mounted.

Terete. Nearly cylindrical in cross section.

Tessellated. A surface with a network of grooves.

Thorax. The anterior region of the body; compare with abdomen. Division of the body into thorax and abdomen is found in sedentary worms.

Trepan. The chitinized, anteriorly toothed part of the eversible pharynx of some syllids.

Tridentate. With three teeth.

Truncate. With the end bluntly cut off, not tapering.

Uncinigerous. Bearing small hooks.

Uncinus(i). Sharply dentate, clawlike setae, often with a square or oval platelike base and several curved teeth, or S-shaped with a broad base and a single tooth.
Unciniger. A segment bearing uncini.

Unidentate. Distally entire.

Uniramous. A parapodium with one branch only, usually a condition in which the notopodium is absent and the neuropodium remains. Compare with sesquiramous, subbiramous, and biramous.

Ventrum. The ventral surface of the body, or the side where the mouth is located.

Ventral fringe. A row of small papillae or lamellae occurring below the parapodia and crossing the ventrum, as in some genera of Orbiniidae. See also **stomach papillae**.

List of Abbreviations on Figures

The explanation of letter symbols on figures follows. Roman numerals indicate body segments (in Phyllodocidae), areas of the proboscis (in Nereididae and Goniadidae), and maxillary jaw pieces (in Eunicea).

aC, anal cirrus
aK, achaetous knob
aLa, anterior lamella
aP, anal or pygidial plate
ac, acicula
acB, accessory branchia
acL, acicular lobe
acS, acicular seta
ai, aileron or wing on jaw
an, antenna
ap, accessory papilla
br, branchia
buS, buccal segment
cG, chromophile gland
cP, cephalic peak of prostomium
ca, capsule
car, caruncle
cer, ceratophore
ch, chevron
co, cortex
cph, cirrophore or base of dorsal cirrus
cr, crotchet
ct, ctenidium or ciliated cushion
D, dorsal
dC, dorsal cirrus or notocirrus
dLa, dorsal lamella
dT, dorsal tubercle of cirrigerous or non-elytra bearing segment
DtC, dorsal tentacular cirrus
el, elytron or scale
elph, elytrophore
ey, eye
fAn, frontal antenna
fTu, facial tubercle
g, gap
gl, gland
hG, hyaline gland
InfLatAn, inferior lateral antenna
intC, interramal cirrus or intercirrus
intSo, interramal sensory organ
lAn, lateral antenna
li, ligule

lo, lobe
m, mouth
mAn, median antenna
MC, maxillary carriers
mPa, median papilla
mR, maxillary ring
mt, macrotubercle
macG, macrognath
man, mandible
max, maxilla
me, medulla
microPap, micropapilla
mid Pc, middle piece
micG, micrognath
ne, neuropodium or ventral ramus of parapodium
neAc, neuroacicula
neLi, neuropodial ligule
neL, neuropodial lobe or lamella
no, notopodium or dorsal ramus of parapodium
noAc, notoacicula
noL, notopodial lobe or lamella
noLi, notopodial ligule
noRu, notopodial rudiment
noS, notoseta
nuE, nuchal epaulet
nuF, nuchal fold
nuH, nuchal hood
nuO, nuchal organ
nuP, nuchal papilla
nuT, nuchal tubercle
ocAn, occipital antenna
ocP, ocular peduncle
oR, oral ring
ov, ovary
pLa, posterior lamella
pa, palp
paPh, palpophore
paSty, palpostyle
pap, papilla
parag, paragnath
PC, peristomial cirrus
per, peristomium

pi, pinnule
poL, podial lobe
postL, postsetal (postacicular) lobe or lamella
postPap, postsetal papillae or podial fringe
pr, prostomium
preL, presetal (preacicular) lobe or lamella
prob, proboscis
probO, proboscideal organs
ro, rosette organ
sO, sense organ
sS, swimming seta
semR, seminal or sperm receptacle or pouch
set, setigerous segment or setiger
setLo, setigerous lobe
SupLatAn, superior lateral antenna
st, style
sty, stylodes of parapodia or parapodial fringe
subF, subpodial fringe or ventral pad
subPap, subpodial lateral papilla or ventral cirrus
supNeL, superior neuropodial lobe
tC, tentacular cirrus
tS, tentacular segment
tPa, tentacular palp
to, tooth
tOr, terminal organ
uNeL, upper neuropodial lobe
V, ventral
vC, ventral cirrus or neurocirrus
vPap, ventral or stomach papillae
VtC, ventral tentacular cirrus

Key to the Families of Polychaeta

This key is limited to those polychaete families that are known to occur off California. Pelagic families and the so-called archiannelid families are not included.

1A. Body a flattened disc with indistinct segmentation (Fig. 3.14A); ectoparasitic on sponges........................ Spintheridae

1B. Body not a flattened disc, segmentation usually distinct, body clearly longer than wide.................2

2A. Dorsal surface more or less covered with overlapping elytra (scales), paleae or felt......................3

2B. Dorsal surface not covered with elytra, paleae or felt..8

3A. Dorsal surface more or less concealed by felt (Fig. 3.14B); notosetae may be harpoon-shaped (Fig. 3.6B), held erect over dorsum .... Aphroditidae

3B. Dorsal surface more or less concealed by elytra or paleae; harpoon-shaped setae absent...............4

4A. Dorsal surface more or less concealed by paleae (Fig. 3.14C-D) .... Chrysopetalidae

4B. Dorsal surface more or less concealed by elytra (Figs. 3.14E, H)..5

5A. Setae all simple...6

5B. Compound neurosetae present...7

6A. Eyes sessile (Fig. 3.14F); elytra and dorsal cirri alternate regularly from setiger 4 to about 23; thereafter every second elytra is followed by a dorsal cirrus .... Polynoidae

6B. Eyes stalked (Fig. 3.14G); elytra regularly alternating with dorsal cirri from setiger 5 to posterior end...Acoetidae

7A. At least some compound setae with long, slender, articulate blade (Fig. 3.14J); 1-3 antennae present (Fig. 3.14H) .... Sigalionidae

7B. Compound neurosetae falcigerous, with short, unidentate blade (Fig 26K); a single median antenna present (Fig. 3.14I)...Pholoidae

8A. Pharynx well developed, muscular, often armed with jaws or teeth; parapodia well developed, commonly bearing compound setae; setal lobes supported by internal acicula; prostomium usually with sensory appendages (except in Lumbrineridae, Oenonidae, and *Exogonella* in the Syllidae)...9

8B. Pharynx without jaws or teeth, usually saclike, not muscular; parapodia reduced, simple setae predominant; prostomium seldom with sensory appendages and often fused with the peristomium which may bear grooved palps, buccal cirri, or a branchial crown..27

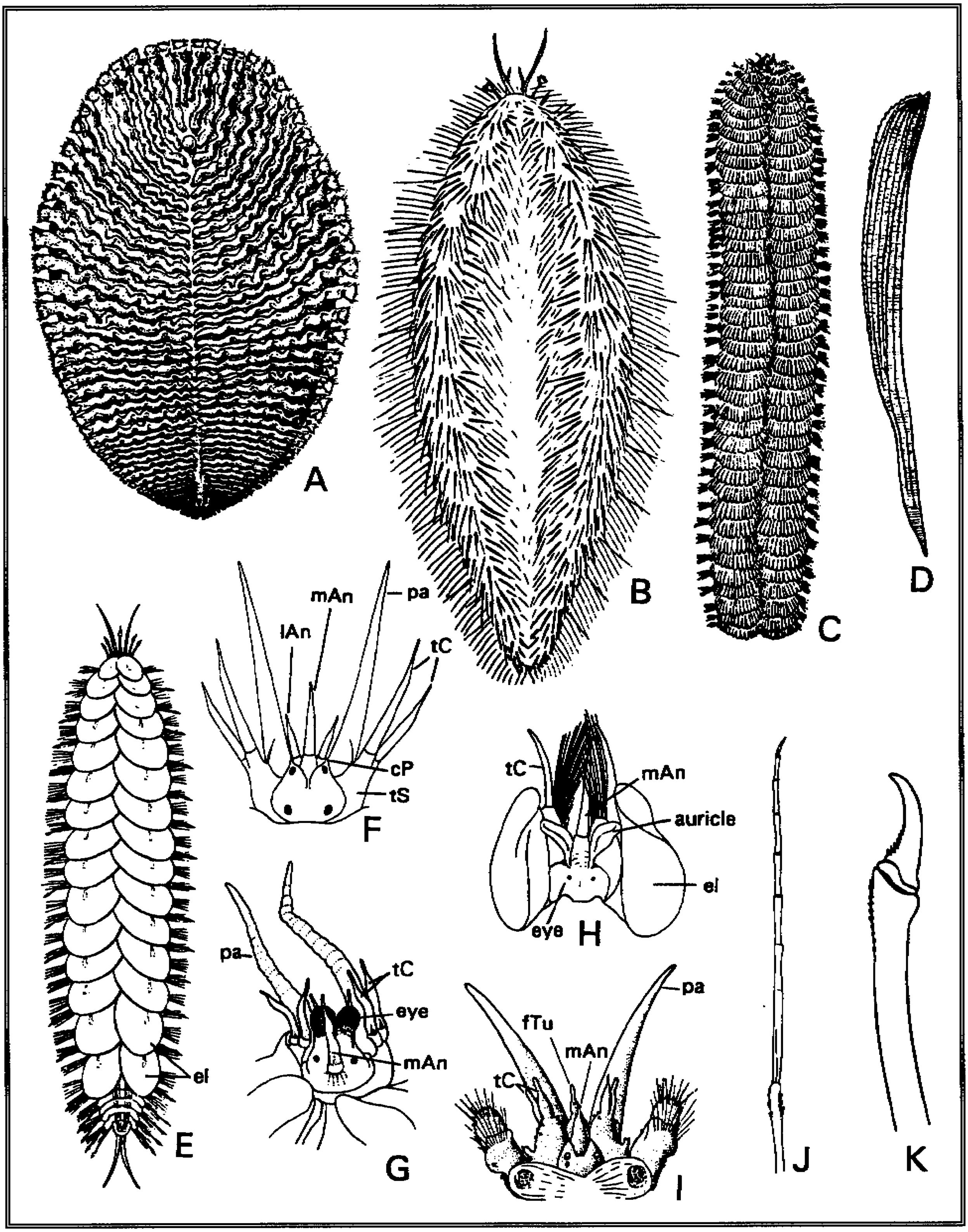

Figure 3.14. A, *Spinther*, dorsal view; B, *Aphrodite*, dorsal view; C, *Chrysopetalum*, entire animal, dorsal view; D, palea from same; E, Polynoidae, *Harmothoe imbricata*, entire animal, dorsal view; F, anterior end of same; G, Acoetidae, *Polyodontes*, anterior end; H, Sigalionidae, *Sthenelais*, anterior end; I, *Pholoe*, anterior end; J-K, compound setae; J, *Sthenelais*; K, *Pholoe*. (A, after Hartman, B, after McIntosh, C-D, after Imajima; E, after McIntosh; F, after Pettibone; G-H, after Hartman, I, after Blake).

9A. Prostomium completely retracted between first parapodia with three pairs of tentacular cirri partially supported by acicula (Fig. 3.15A) .... Pisionidae

9B. Prostomium not completely retracted between first parapodia 10

10A. Notosetae arranged in transverse rows across dorsum (Fig. 3.15D); heavy furcate ringet notosetae present .... Euphrosinidae

10B. Notosetae arising from defined fascicles or absent; furcate setae if present, thin delicate, not heavy 11

11A. Dorsal cirri digitiform or filiform, inserted posterior to spreading fascicles of notosetae and tufts of numerous branchiae; prostomium continuing posteriorly as conspicuous caruncle (Fig. 3.15E) (except genus *Hipponoe*) .... Amphinomidae

11B. Dorsal cirri absent, reduced to inconspicuous lobe, or enlarged as broad, leaflike or lamellate structure (Fig. 3.15B); branchiae if present either single, paired, simply branched, or spiraled, never as numerous tufts; caruncle absent 12

12A. Dorsal and ventral cirri flattened, leaflike, paddlelike, or globular; prostomium with 4 frontal antennae and sometimes a median one as well (Fig. 3.15C); tentacular cirri 2-4 pairs; parapodia uniramous (Fig. 3.15B) (parapodia subbiramous in *Notophyllum*); setae compound .... Phyllodocidae

12B. Dorsal cirri and ventral cirri if present not leaflike or globular 13

13A. Prostomium conical, annulated, terminating distally in 4 minute antennae; peristomium fused with prostomium, without tentacular cirri; proboscis large, powerful 14

13B. Prostomium otherwise; tentacular cirri present or absent 15

14A. Body with parapodia similar throughout, either all uniramous or all biramous; dorsal cirri small, globular; ventral cirri larger, conical; proboscis with 4 subequal jaws or macrognaths (Fig. 3.15F); chevrons never present .... Glyceridae

14B. Body with 2-3 regions: 1) anterior uniramous region; 2) transitional region where notopodia gradually develop (this region may be lacking); 3) posterior biramous region with noto- and neuropodia well separated; dorsal and ventral cirri conical to fingerlike; proboscis with a pair of dentate macrognaths and few to many micrognaths (Fig. 3.15G); chevrons often present .... Goniadidae

15A. Body with 2 or more rows of large spherical capsules or tubercles, arranged segmentally (Fig. 3.16A); prostomium and tentacular segment indistinct; segments indistinct, except for parapodia .... Sphaerodoridae

15B. Body without spherical capsules or tubercles; prostomium distinct; segmentation distinct 16

16A. Prostomium with 4 small frontal antennae 17

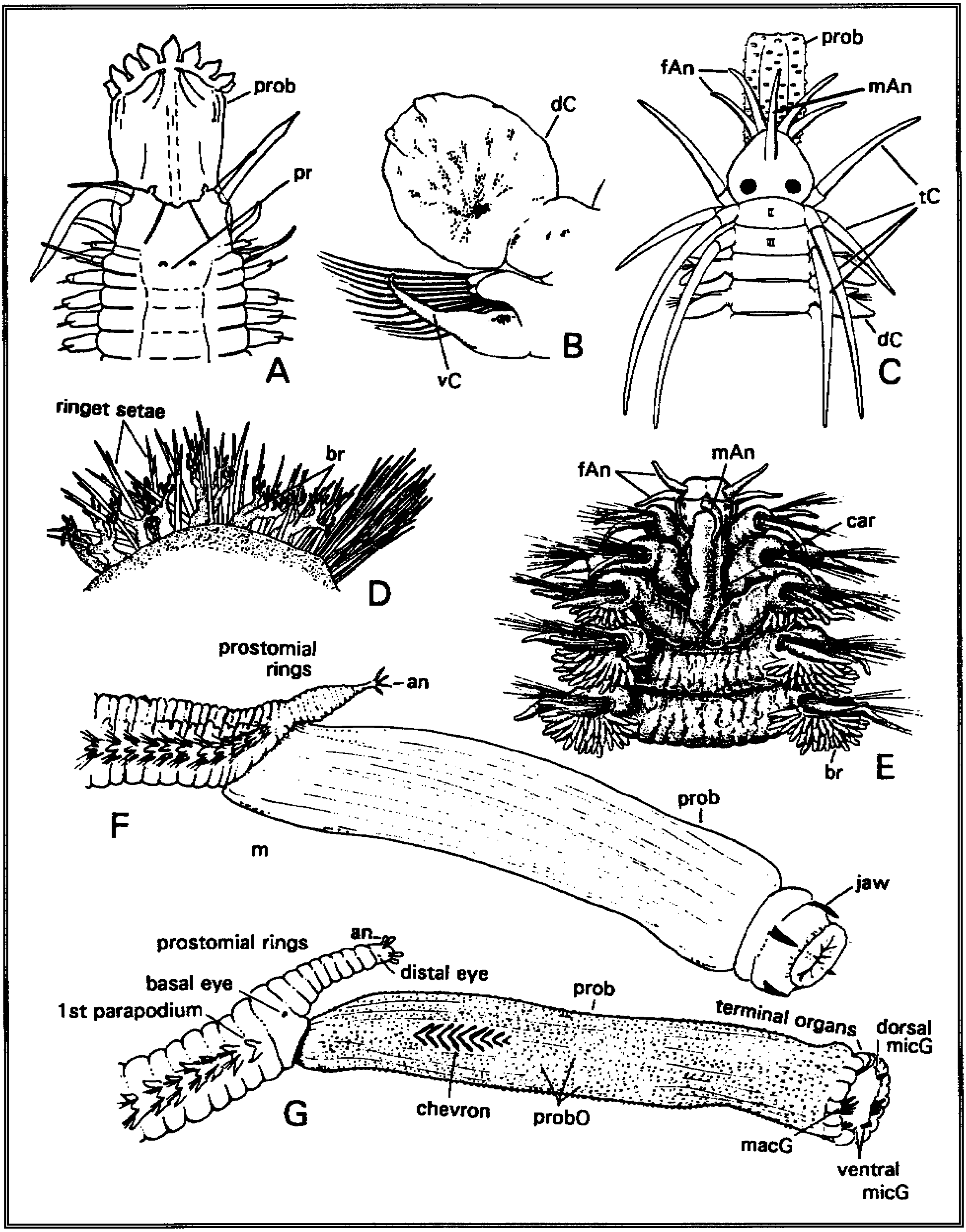

Figure 3.15. A, *Pisione*, anterior end; B-C, *Phyllodoce*, parapodium and anterior end; D, *Euphrosine*, parapodium; E, Amphinomidae, *Eurythoe*, anterior end; F, *Glycera*, anterior end; G, *Goniada*, anterior end. (A, E, and G after Hartman: B, F after Blake, C, after Pettibone; D, after Wesenberg-Lund).

16B. Prostomium with 0-3 or 5 or 7 antennae, but never 4 19

17A. Prostomium flattened, pentagonal, with 4 small antennae (Fig. 3.16B); body subrectangular in cross section; biramous parapodia with rami well separated (Fig. 3.16C) and with long cilia along interramal border, most species with interramal cirrus or branchia; notosetae and neurosetae all simple, arranged in fan-shaped fascicles, with more or less developed presetal and postsetal lamellae; muscular proboscis with a pair of internal jaws .... Nephtyidae

17B. Prostomium rounded or truncate, not pentagonal, with short or minute antennae; parapodia with rami separated and sometimes with interramal ciliation, but interramal cirri or branchiae lacking; notosetae simple, neurosetae compound; presetal and postsetal lamellae moderately developed; proboscis without internal jaws 18

18A. Peristomium with one pair of tentacular cirri; with following 3 segments uniramous, remaining segments biramous (Fig. 3.16D) .... Lacydoniidae

18B. Peristomium without tentacular cirri; followed by 1 uniramous segment, biramous segments thereafter (Fig. 3.16E) .... Paralacydoniidae

19A. With an elaborate jaw apparatus consisting of a pair of ventral mandibles and dorsal maxillae consisting of few to numerous paired pieces; with 1-2 achaetous and apodous tentacular or buccal segments, without tentacular cirri, or with only a single short, dorsolateral pair 20

19B. Jaws absent or otherwise; with 0-8 pairs of tentacular cirri 24

20A. Prostomium simple, conical or suboval, without antennae or distinct palps; parapodia without dorsal or ventral cirri; first 2 segments achaetous and apodous, without tentacular cirri; body smooth, elongate, cylindrical, resembling an earthworm 21

20B. Prostomium suboval, with 1-7 antennae, 2 palps; parapodia with dorsal and ventral cirri; body otherwise 22

21A. Neurosetae consisting of 1) limbate setae with fine tips (Fig. 3.16G-H) and 2) hooded hooks (Fig. 3.16I); jaw apparatus with 2 short, broad maxillary carriers, no median piece (Fig. 3.16J); eyes absent (Fig. 3.16F) .... Lumbrineridae

21B. Neurosetae consisting of limbate setae (Fig. 3.17B-C) with or without projecting acicular setae; without hooks or crotchets; jaw apparatus with 2 long, slender maxillary carriers plus a median piece (Fig. 3.17D); eyes present or absent (Fig. 3.17A) .... Oenonidae

22A. First segment apodus and achaetous; 7 prostomial antennae (5 long occipital, 2 short frontal); paired palps short, globular (Fig. 3.17E); tube dwelling .... Onuphidae

22B. First 2 segments apodous and achaetous 23

23A. Prostomium with a pair of antennae and a pair of palps (Fig. 3.17F); crawlers and burrowers .... Dorvilleidae

23B. Prostomium with 1-5 occipital antennae (Fig. 3.17G-H) and a pair of short, globular ventral palps more or less fused to prostomium; tube dwelling .... Eunicidae

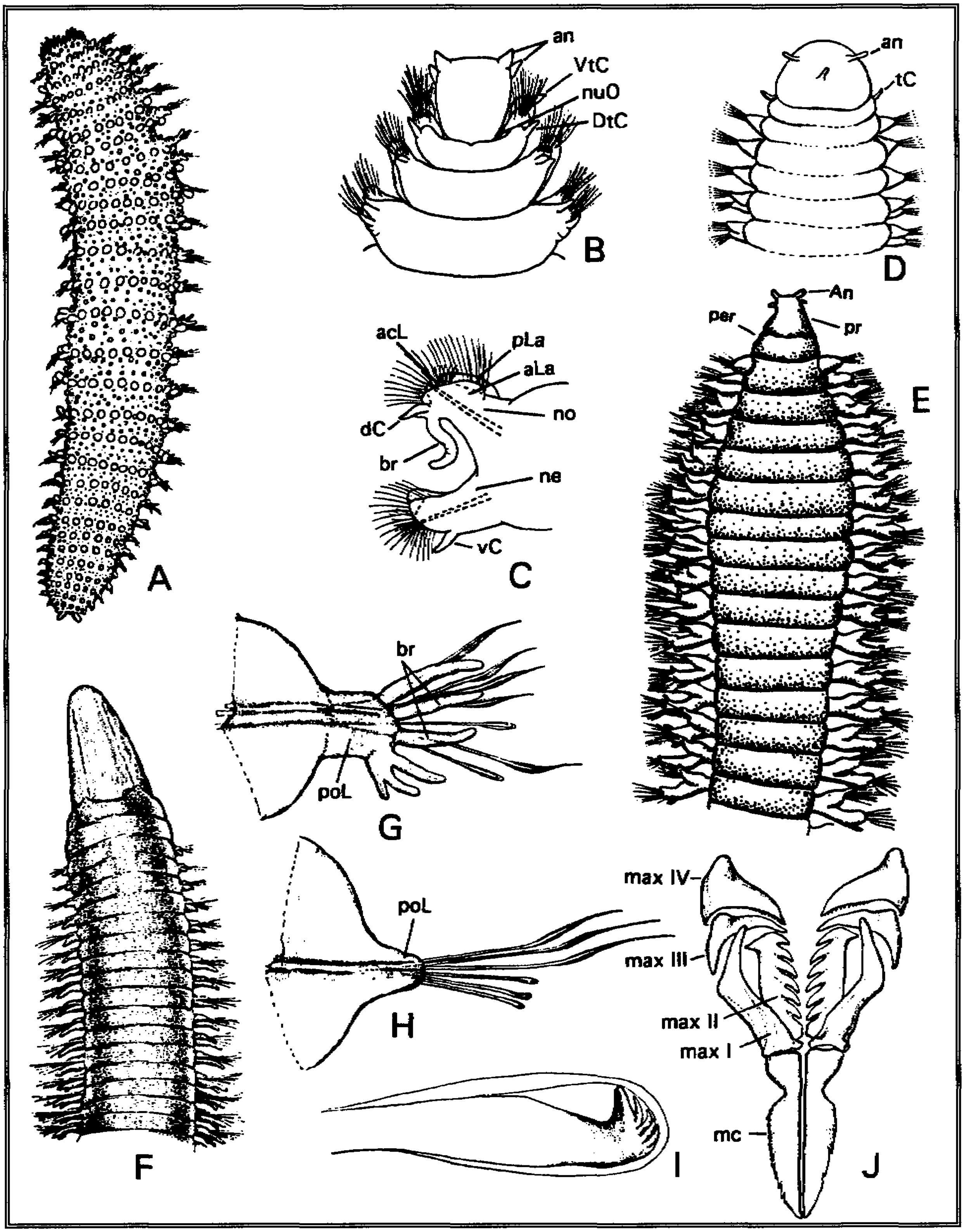

Figure 3.16. A, *Sphaerodoridium*, anterior end.—B-C, *Nepthys*: B, anterior end; C, parapodium; D, *Lacydonia*, anterior end; E, *Paralacydonia*, anterior end.—F-J, Lumbrineridae, *Ninoe*: F, anterior end; G, parapodium with branchiae; H, postbranchial parapodium; I, hooded hook; J, maxillary apparatus. (A, after Imajima; B-C, after Pettibone; D, after Uschakov; E-J, after Hartman).

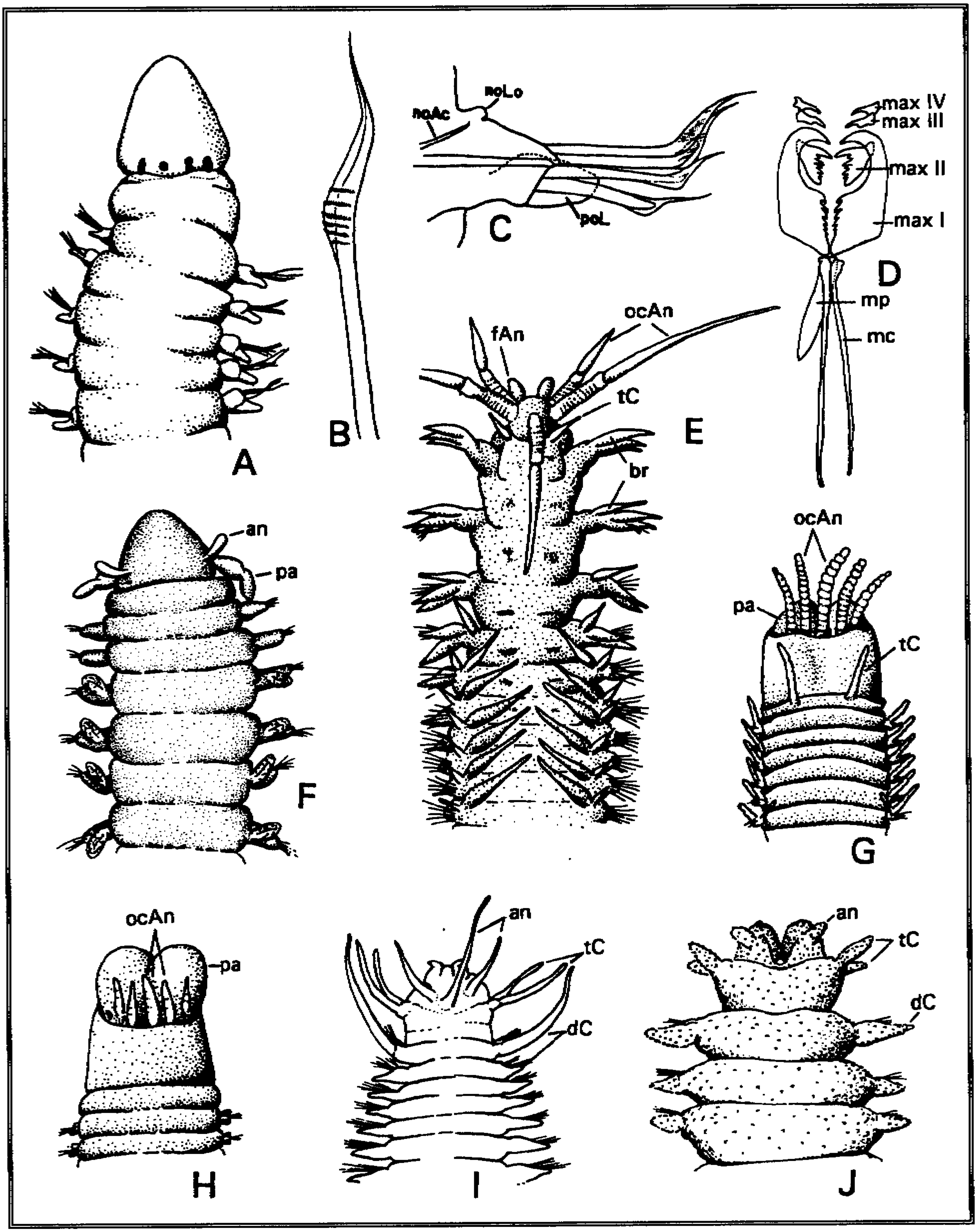

Figure 3.17. A-C, Oenonidae, *Arabella*: A, anterior end; B, limbate seta; C, parapodium; D, Oenonidae, *Drilonereis*, maxillary apparatus.—E, Onuphidae, *Onuphis*, anterior end.—F, Dorvilleidae, *Pettiboneia*, anterior end.—Eunicidae: G, *Eunice*; H, *Marphysa*.—I-J, Pilargidae: I, *Sigambra*; J, *Pilargis*. (A-C, after Uebelacker; D-H, after Blake; I-J after Hartman).

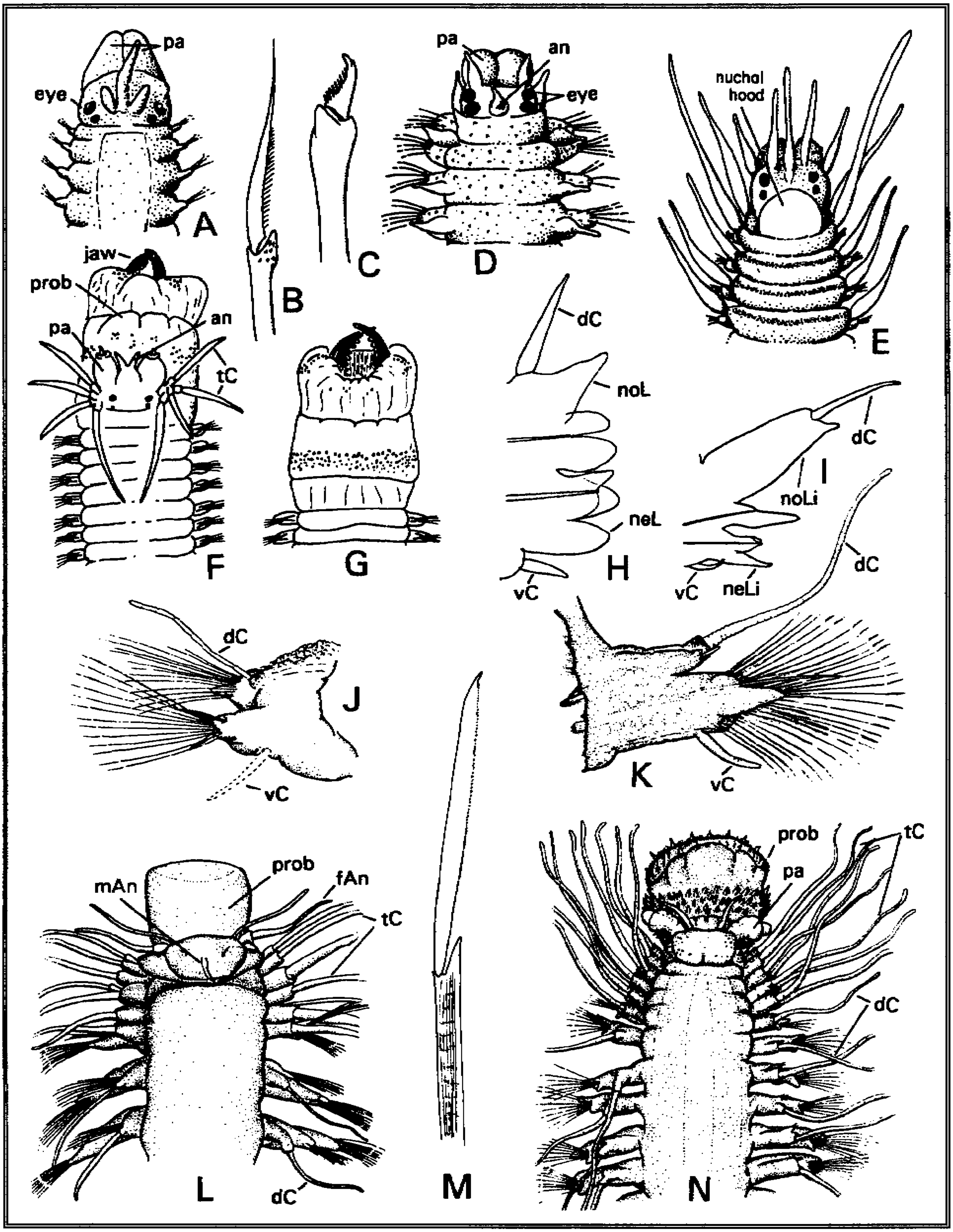

Figure 3.18. A-E, Syllidae: A, *Exogone*, anterior end; B, compound spiniger; C, compound falciger; D, *Sphaerosyllis*, anterior end; E, *Odontosyllis*, anterior end.—F-I, Nereididae, *Nereis*: F, anterior end, dorsal view, proboscis everted; G, same, ventral view; H-I, parapodia.—J-N, Hesionidae: J-K, biramous and subbiramous parapodia; L, *Amphiduros*, anterior end; M, compound seta; N, *Hesiospina*, anterior end. (A-G, J-N, after Blake).

24A. Neurosetae compound (Figs. 3.18B-C, M) (blades sometimes secondarily fused to shaft) 25

24B. Neurosetae and notosetae (if present) simple, not compound (notosetae may be stout or hooked); tentacular segment apodous and achaetous, more or less fused with prostomium, usually with 2 pairs of tentacular cirri (Fig. 3.17I-J) .... Pilargidae

25A. Parapodia biramous or subbiramous; notopodia represented at least by internal acicula 26

25B. Parapodia uniramous (may be biramous in sexual epitokes); tentacular segment apodous and achaetous, with 1-2 pairs of tentacular cirri; prostomium suboval with 3 antennae, 2 palps (Figs. 3.18A, D, E) (palps may be reduced or fused; prostomial appendages absent in *Exogonella*) .... Syllidae

26A. Parapodia with varying degrees of development of extra lobes or ligules (Fig. 3.18H-I); prostomium suboval to subpyriform, with 2 frontal antennae and 2 biarticulate palps (Fig. 3.18F); proboscis with a pair of distal, dentate, hooked jaws (Fig. 3.18G); with single apparent tentacular segment bearing 3-4 pairs of cirri; notosetae compound .... Nereididae

26B. Parapodia without ligules (Fig. 3.18J-K); prostomium suboval to subquadrangular, with 2-3 antennae (Figs. 3.18L, N); 2 palps (may be biarticulate); proboscis without jaws or with 2-4 simple teeth; with 1-4 achaetous tentacular segments and 2-8 pairs of tentacular cirri; notosetae simple or lacking .... Hesionidae

27A. Body short and stout; posterior end covered ventrally by a chitinized shield; anus surrounded by filamentous gills (Fig. 3.19A) .... Sternaspidae

27B. Body elongate; posterior end not covered by shield; without anal gills 28

28A. Anterior end modified by development of frilly membranes (Fig. 3.24A), buccal tentacles (Figs. 3.25A, D, E), or a branchial crown of feathery tentacles around mouth (Figs. 3.25J, L, M); prostomium often reduced and indistinguishable from buccal segments 52

28B. Anterior end not greatly modified; prostomium usually well developed and obvious; buccal segment sometimes with parapodia and may bear a pair of palps or a few grooved tentacles 29

29A. Buccal segment with tentacles retractile into mouth; tentacles either grooved or papillose (Fig. 3.19B) .... Ampharetidae

29B. Buccal segment otherwise 30

30A. Buccal segment with pair of palps, or several grooved tentacles located on anterior setigers 31

30B. Buccal segment without palps; anterior setigers without grooved tentacles 41

31A. Anterior end with a pair of papillose adhesive palps (Fig. 3.19C); head flattened and spadelike; branchiae absent; abdominal parapodia with well-developed parapodial lamellae; hooded hooks present .... Magelonidae

31B. Palps, if present, not papillose or adhesive; head not flattened; branchiae often present 32

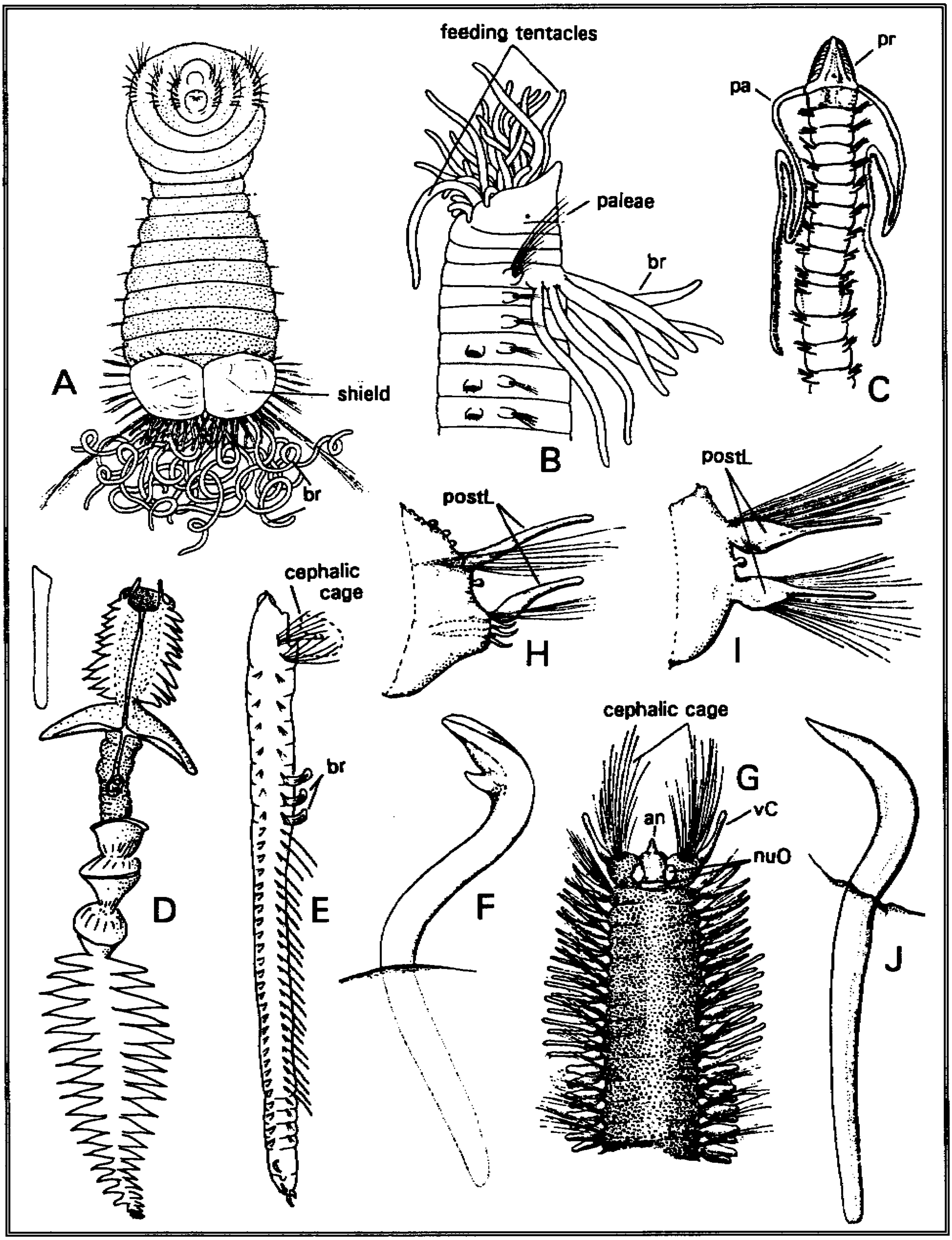

Figure 3.19. A, *Sternaspis*, entire animal; B, *Ampharete*, anterior end; C, *Magelona*, anterior end; D, *Chaetopterus*, anterior end with detail of modified hook from setiger 4; E, *Uncispio*, anterior end; F, giant hook of same.—*Poecilochaetus*: G, anterior end; H-I, parapodia; J, modified spine. (A-B, originals by M. Litterer; C, F-J after Hartman)

32A. Body divided into 2 or 3 distinct regions 33

32B. Body not divided into distinct regions 38

33A. Body divided into 3 distinct regions 34

33B. Body divided into 2 regions 35

34A. Prostomium reduced; peristomium with large lip (Fig. 3.19D); setiger 4 with large modified setae; inhabiting distinct parchmentlike or annulated tubes .... Chaetopteridae

34B. Prostomium small, rectangular or tapered; occipital tentacle present or absent, first setiger directed anteriorly with setae forming cage (Fig. 3.19F); branchiae may be present on anterior and median segments; setae include hooded hooks with the posterior setae modified into giant hooks (Fig. 3.19F) .... Uncispionidae

35A. With 1 or 2 anterior parapodia directed forward, bearing long setae and appearing to form a cage... 36

35B. Anterior parapodia not directed forward 37

36A. Prostomium small, subglobular, with an anteroventral median antenna and a trifid nuchal organ; first setiger enlarged, directed anteriorly with setae forming a cage, ventral cirrus prolonged (Fig. 3.19G); postsetal lobes of anterior setigers flask-shaped (Fig. 3.19I); branchiae absent; neuropodia of 2-4 anterior setigers with stout acicular setae (Figs. 3.19H, J) .... Poecilochaetidae

36B. Prostomium small, rectangular, usually with median occipital antenna; first two setigers directed anteriorly, with setae projecting anterior to prostomium (Fig. 3.20A); neuropodia of setigers 2-4 bearing stout acicular setae (Fig. 3.20B); following setigers with capillaries; far posterior notopodia with heavy spines, sometimes arranged as rosettes (Fig. 3.20C); branchiae absent .... Trochochaetidae

37A. Parapodia inconspicuous; abdominal segments elongated, with spines and capillaries forming complete cinctures around body (Fig. 3.20F) .... Heterospionidae

37B. Parapodia distinctive, appearing uniramous, but actually subbiramous with notopodia reduced to cirriform process penetrated by acicula (Fig. 3.20E); some anterior neuropodia with serrated postsetal lobes; interramal cirrus present on segments 1-7 (Fig. 3.20D) .... Apistobranchidae

38A. Neuropodia with compound falcigers (Fig. 3.20H); body frequently covered with minute papillae; prostomium with 2 small palps (Fig. 3.20G) .... Acrocirridae

38B. All setae simple, never compound 39

39A. Prostomium deeply bilobed and with pair of grooved palps attached to anterior margin (Fig. 3.20I); first 2 or 3 segments with notosetae only; neurosetae include hundreds of minute, bidentate, non-hooded hooks in dense fields .... Oweniidae (Genus *Myriowenia*)

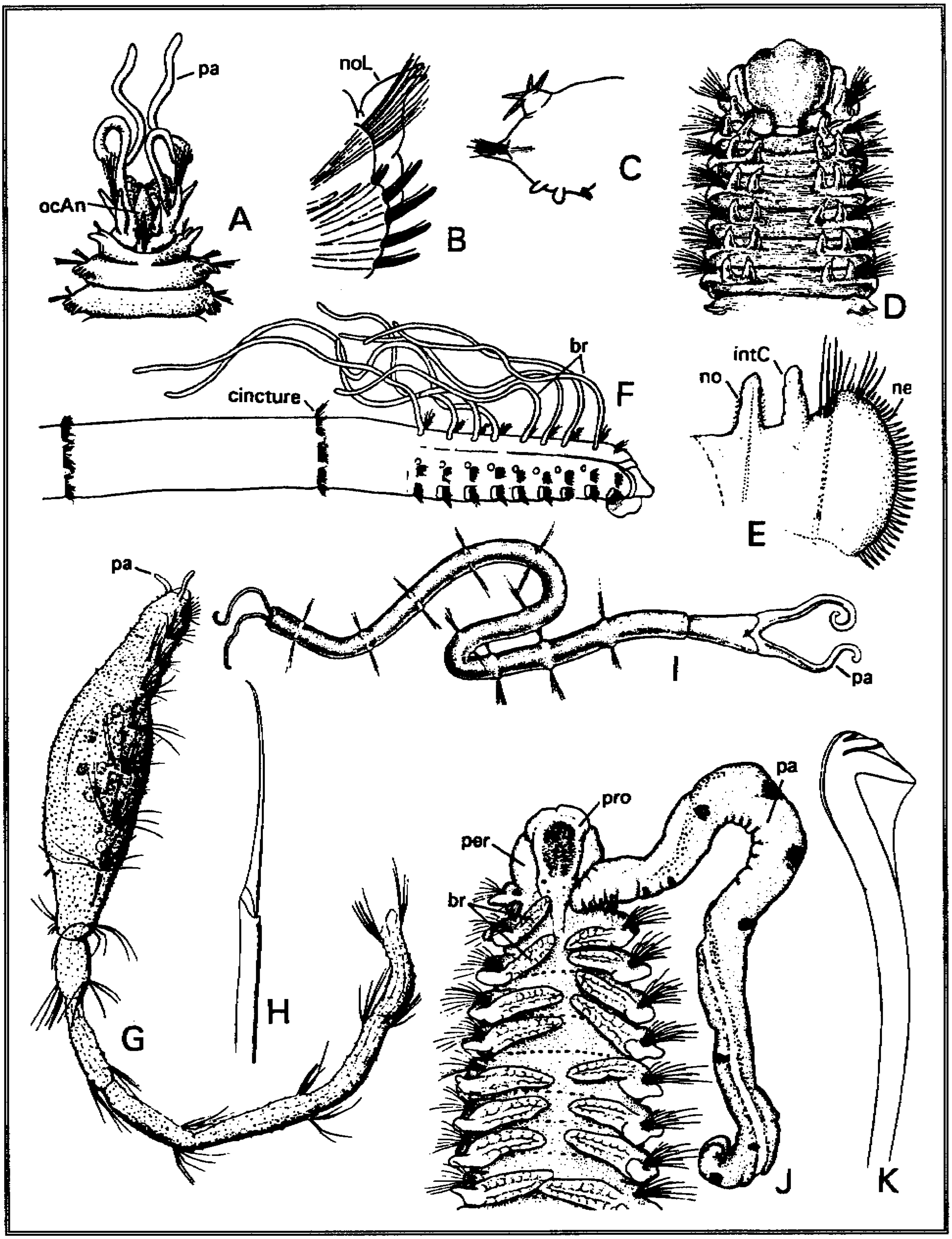

Figure 3.20. A-C, *Trochochaeta*: A, anterior end; B, anterior parapodium; C, posterior parapodium.—D-E, *Apistobranchus*: D, anterior end; E, anterior parapodium.—F, *Heterospio*, anterior end.—G-H, Acrocirridae, *Flabelligella*: G, entire animal; H, compound seta.—I, Oweniidae, *Myriowenia*, entire animal.—J-K, *Spio*: J, anterior end; K, hooded hook. (B-C, after Pettibone; D-I, after Hartman; J-K, after Blake).

39B. Prostomium entire to incised on anterior margin, but never having palps attached to anterior margin; neurosetae present on all anterior segments; neurosetae include hooks, capillaries or spines in defined rows or fascicles, never in dense fields 40

40A. Anterior end with pair of dorsolateral grooved palps, often long and coiling (Fig. 3.20J); anterior margin of prostomium rounded, incised, or with horns; neuropodia and/or notopodia of posterior setigers bear hooded hooks (Fig. 3.20K); none, some, or many segments with paired branchiae .... Spionidae

40B. Prostomium usually lacking appendages; anterior margin usually conical, narrowly rounded, first setigerous segment often bearing a pair of large grooved palps (Fig. 3.21A) or numerous grooved tentacular filaments (Fig. 3.21B); numerous long, filamentous gills present on several body setigers (0-few in *Dodecaceria*) .... Cirratulidae

41A. Multidentate hooks present at least in posterior setigers 42

41B. Setae not including multidentate hooks, but may include unique serrated setae (Ctenodrilidae) 45

42A. Multidentate hooks with hoods; body resembling an earthworm 43

42B. Multidentate hooks without hoods; body not resembling an earthworm 44

43A. Body divided into more or less distinct thoracic and abdominal regions (Fig. 3.21C-D), with thoracic setigers bearing limbate capillary setae and abdominal setigers bearing long-handled, multidentate hooded hooks (Fig. 3.21E); some genera with some thoracic or abdominal segments with both capillaries and hooks .... Capitellidae

43B. Body not divided into distinct regions (Fig. 3.21F); setae including serrated capillaries (Fig. 3.20G) and bidentate hooks with half hoods (Fig. 3.21H-I) .... Questidae

44A. Body segments elongated, with body appearing jointed, but never annulated, often pygidial plate or funnel (Fig. 3.22A-B); branchiae rare; constructing sand- or mud-covered tubes ("Bamboo worms") .... Maldanidae

44B. Body segments not elongated, always annulated (Fig. 3.22C); branchiae present (Fig. 3.22C-D); posterior setigers apodous and achaetous; constructing L- or U-shaped burrows in mud .... Arenicolidae

45A. Body minute, usually with 9-12 segments (Fig. 3.22F); setae include unique serrated (Fig. 3.22E) or furcate setae [reproduces asexually by fragmenting, commonly found in marine aquaria and seawater tables of marine labs; found in fine muds of fouling communities] .... Ctenodrilidae

45B. Body larger, with at least 15 setigers when mature; setae otherwise 46

46A. With a single filiform tentacle or branchia arising from dorsum of an anterior setiger (Fig. 3.22G) .... Cossuridae

46B. Branchiae if present, in pairs along body segments 47

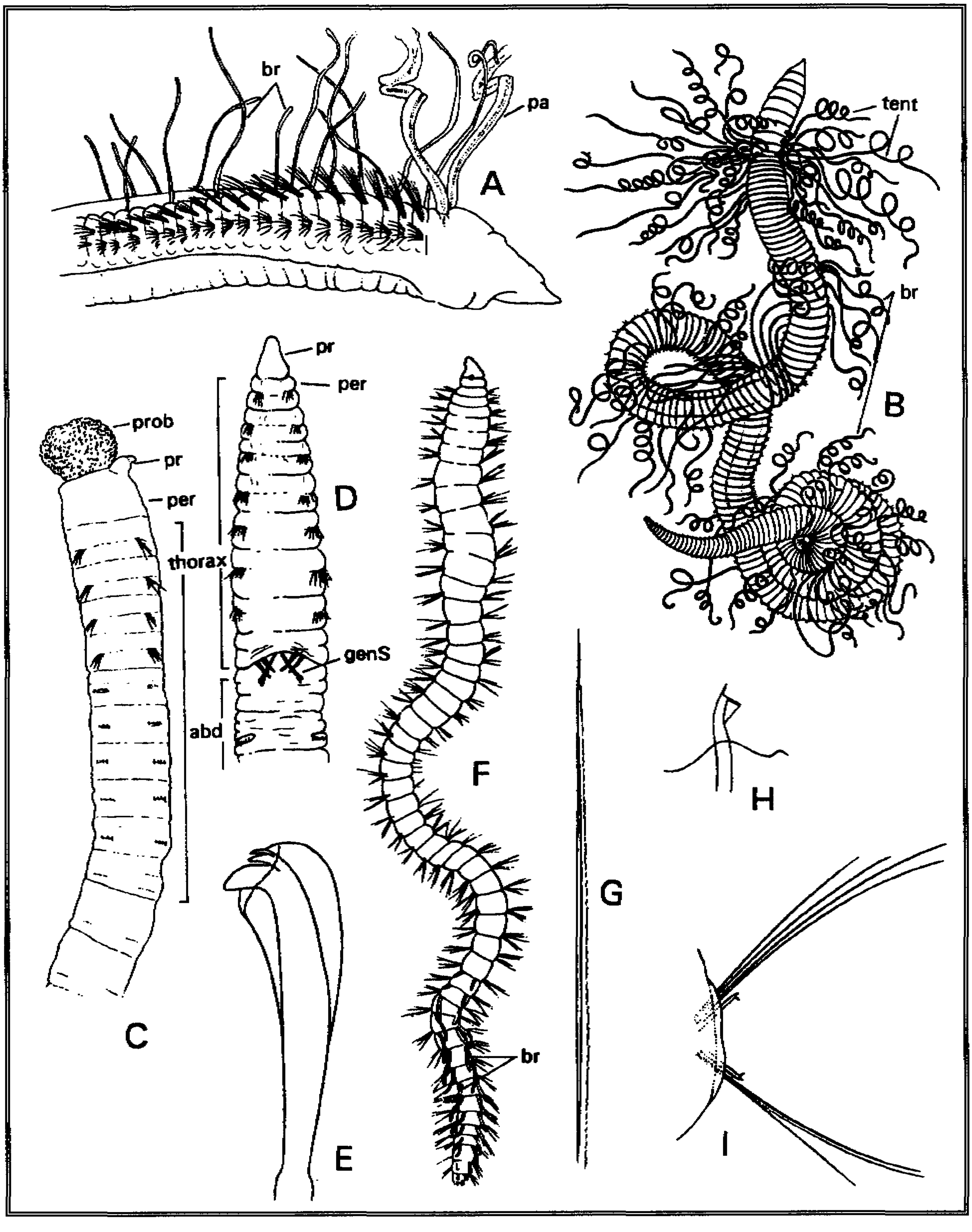

Figure 3.21. A-B, Cirratulidae: A, *Tharyx*, anterior end; B, *Cirriformia*, entire animal.—C-E, Capitellidae: C, *Mediomastus*, anterior end; D, *Capitella*, anterior end; E, hooded hook.—F-I, *Questa*: F, anterior end; G, serrated capillary seta; H, bidentate hook; I, parapodium. (B, after McIntosh; C, E-I, after Hartman; D, after Berkeley and Berkeley).

47A. Body sleek, ventral groove often present (Fig. 3.22H); segmental eyes sometimes present; prostomium a sharply tapering cone sometimes with terminal palpode; pair of retractile nuchal organs present .... Opheliidae

47B. Body otherwise; segmental eyes absent; prostomium conical, blunt or lobed, not sharply tapering; nuchal organs not retractile 48

48A. Prostomium reduced to simple lobe or retractable, providing simple unadorned appearance to anterior end 49

48B. Prostomium distinct, well-developed, extending anteriorly as notched, pointed or rounded lobe.... 50

49A. Body elongate, with long anterior segments (Fig. 3.22I-J) and short posterior ones; notosetae serrated capillaries, neurosetae very small bidentate hooks in dense fields (Fig. 3.22K) ... Oweniidae

49B. Body short to elongate, all segments same length, anterior and posterior ends appearing very similar (Fig. 3.23A); setae including heavy acicular spines, capillaries present or absent; with small papilla between reduced parapodial rami (Fig. 3.23B) .... Fauveliopsidae

50A. Prostomium T-shaped, notched or lobed on anterior margin; body swollen anteriorly, often with a rough, areolated appearance (Fig. 3.23C); branchiae if present branched and restricted to anterior segments .... Scalibregmatidae

50B. Prostomium conical or rounded; body not swollen anteriorly; not rough in appearance; branchiae if present dorsally directed and usually distributed over a long body region 51

51A. Parapodia with internal acicula, lobes well developed; often elongate; branchiae continuing to posterior end of body (Fig. 3.23G); setae including crenulated or camerated capillaries (Fig. 3.23E), with or without lyrate setae (Fig. 3.23F), flail setae (Fig. 3.23H), or modified neuropodial uncini, capillaries often arranged in palisades; prostomium without median antenna (Fig. 3.23D) .... Orbiniidae

51B. Parapodia without internal acicula, lobes reduced; branchiae absent from posterior end of body (Fig. 3.23I); setae all smooth or faintly striated, not crenulated; lyrate setae (Fig. 3.23K) and various forms of modified spines may be present (Fig. 3.23L-O) or absent; prostomium with median antenna present (Fig. 3.23J); or absent; .... Paraonidae

52A. Anterior end terminating in frilled membrane (Fig. 3.24A); body enclosed in tube of closely fitting sand grains; setae including serrated capillaries (Fig. 3.24B); and bidentate hooks (Fig. 3.6C) .... Oweniidae (Genus *Owenia*)

52B. Anterior end with tentacles, palps or branchial crown of feathery tentacles around mouth 53

53A. Multiarticulate compound setae present (Fig. 3.24E-F); capillary setae and uncini, when present appearing annulated; cephalic cage present (Fig. 3.24D) or absent; body regions indistinct.............. .... Flabelligeridae

53B. Multiarticulate compound setae absent; body regions well defined 54

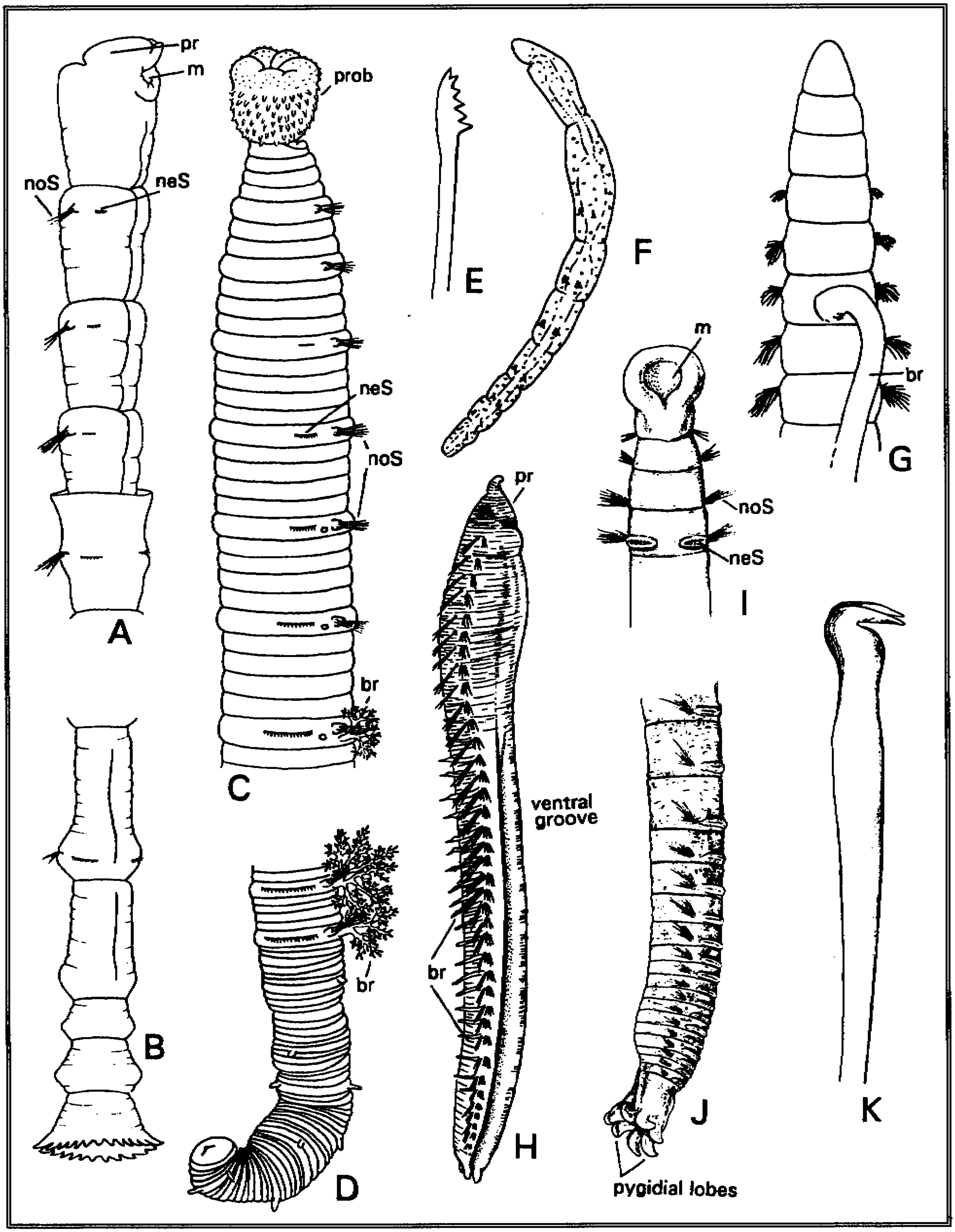

Figure 3.22. A-B, Maldanidae, *Clymenella*: A, anterior end; B, posterior end.—C-D, *Arenicola*: C, anterior end; D, posterior end.—E-F, *Ctenodrilus*: E, serrated seta; F, entire worm.—G, *Cossura*, anterior end.—H, *Ophelia*, entire animal.—I-K, Oweniidae, *Myriochele*: I, anterior end; J, posterior end; K, hook. (A-D, originals by M. Litterer; E-F, H, G after Blake; I-K, after Hartman).

54A. Anterior end with paleae present in 1 or 3 very distinct rows 55

54B. Anterior end without setae or paleae, or paleae present as fascicle of heavy spines 56

55A. Paleae in a single row; caudal region short and flattened (Fig. 3.24G); tube free, conical, formed of close fitting sand grains (Fig. 3.24H) .... Pectinariidae

55B. Paleae in 2-3 rows (Fig. 3.24I); caudal region long, cylindrical (Fig. 3.24I); rigid sand tubes attached to rocks or shells, often in dense colonies .... Sabellariidae

56A. Anterior end with soft tentacles for deposit feeding (Fig. 3.24J); branchiae often present on anterior segments (Fig. 3.24J-K); notosetae simple capillaries, neurosetae uncini in 1 or 2 rows; setal types not inverted in abdominal region 57

56B. Anterior end with a crown of bipinnate radioles (Figs. 3.25J, L); branchiae absent on body segments; notopodial setae and neuropodial uncini of thoracic region with positions reversed or inverted in abdominal region (Figs. 3.25H-I, J-K) 59

57A. Tentacles either grooved or papillose, retractile into mouth (Fig. 3.24J); with 1-4 pairs of gills, usually in 1 row across anterior segment, always simple .... Ampharetidae

57B. Tentacles not retractile into mouth, grooved but never papillose (Figs. 3.25A, D, E); gills when present on 1-3 segments, inserted dorsolaterally, simple to branched; or dorsomedially on one stalk. 58

58A. All thoracic uncini long-handled (Fig. 3.25B), abdominal ones short-handled (Fig. 3.25C); some genera with a single branchial trunk (Fig. 3.25A) .... Trichobranchidae

58B. Both thoracic and abdominal uncini short-handled (Fig. 3.25F); sometimes with a posterior prolongation on thoracic uncini (Fig. 3.25G); branchiae absent (Fig. 3.25D) or elaborated into numerous forms (e.g., Fig. 3.25E) .... Terebellidae

59A. Tubes leathery or of mucus, sand or mud; radioles of tentacular crown not modified into operculum (Fig. 3.25H, J) .... Sabellidae

59B. Tubes calcareous; one radiole usually modified into operculum (Fig. 3.25L) 60

60A. Tube irregularly twisted or straight, sometimes coiled near base; body symmetrical; with more than 4 thoracic setigers, joined by thoracic membrane (Fig. 3.25L) .... Serpulidae

60B. Tube coiled into dextral or sinistral spiral (Fig. 3.25N); body asymmetrical, with thoracic notosetae sometimes missing on convex side; with only 4 thoracic setigers (Fig. 3.25M) .... Spirobidae

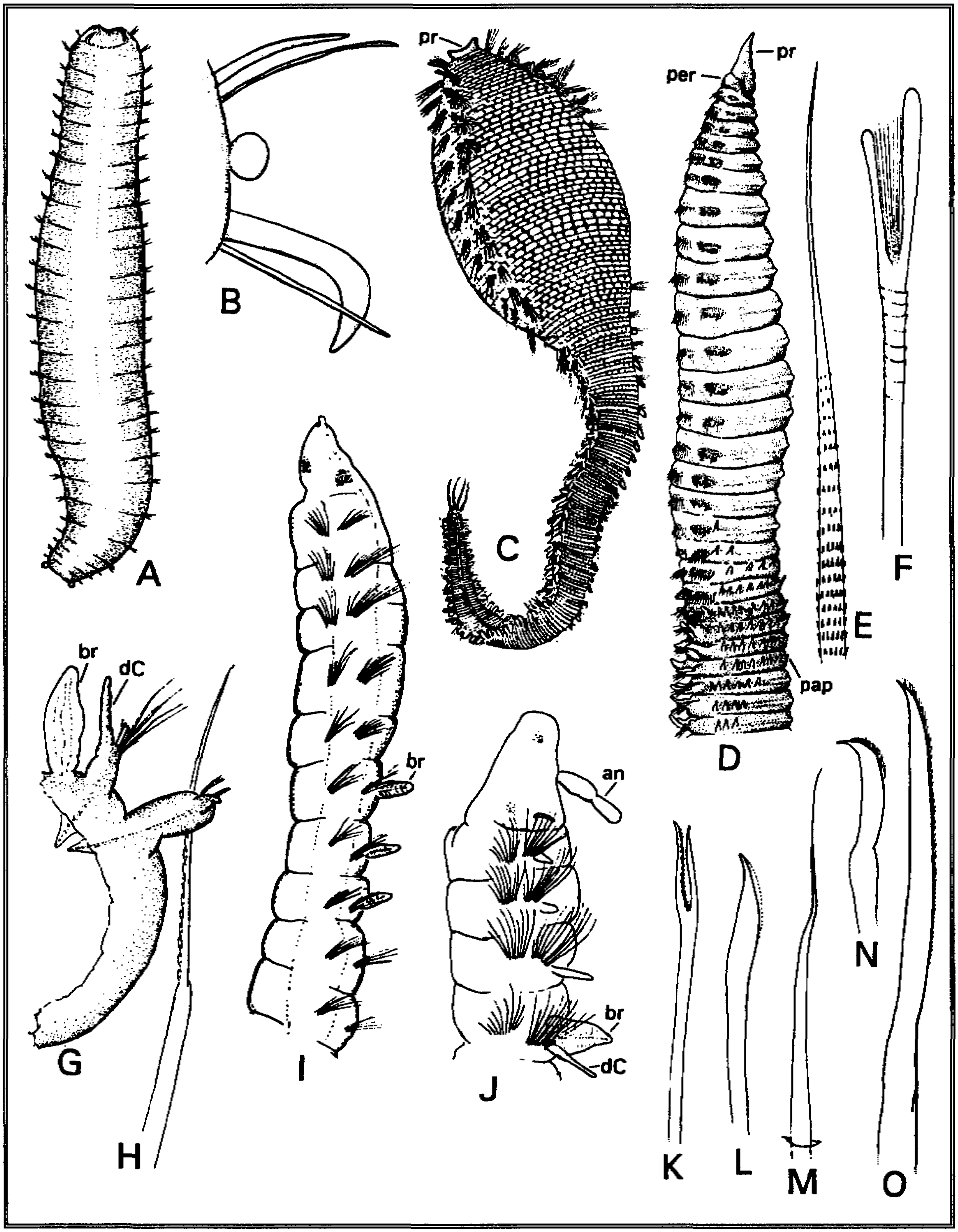

Figure 3.23. A-B, *Fauveliopsis*: A, entire animal; B, parapodium.—C, *Scalibregma*, entire animal.—D-H, *Orbinia*: D, anterior end; E, camerated capillary seta; F, lyrate seta; G, posterior parapodium; H, flail seta.—I-O, Paraonidae: I, *Paradoneis*, anterior end; J, *Aricidea*, anterior end; K, lyrate seta; L-O, modified neuropodial spines. (A-B, D after Hartman; C, after Uschakov; rest originals).

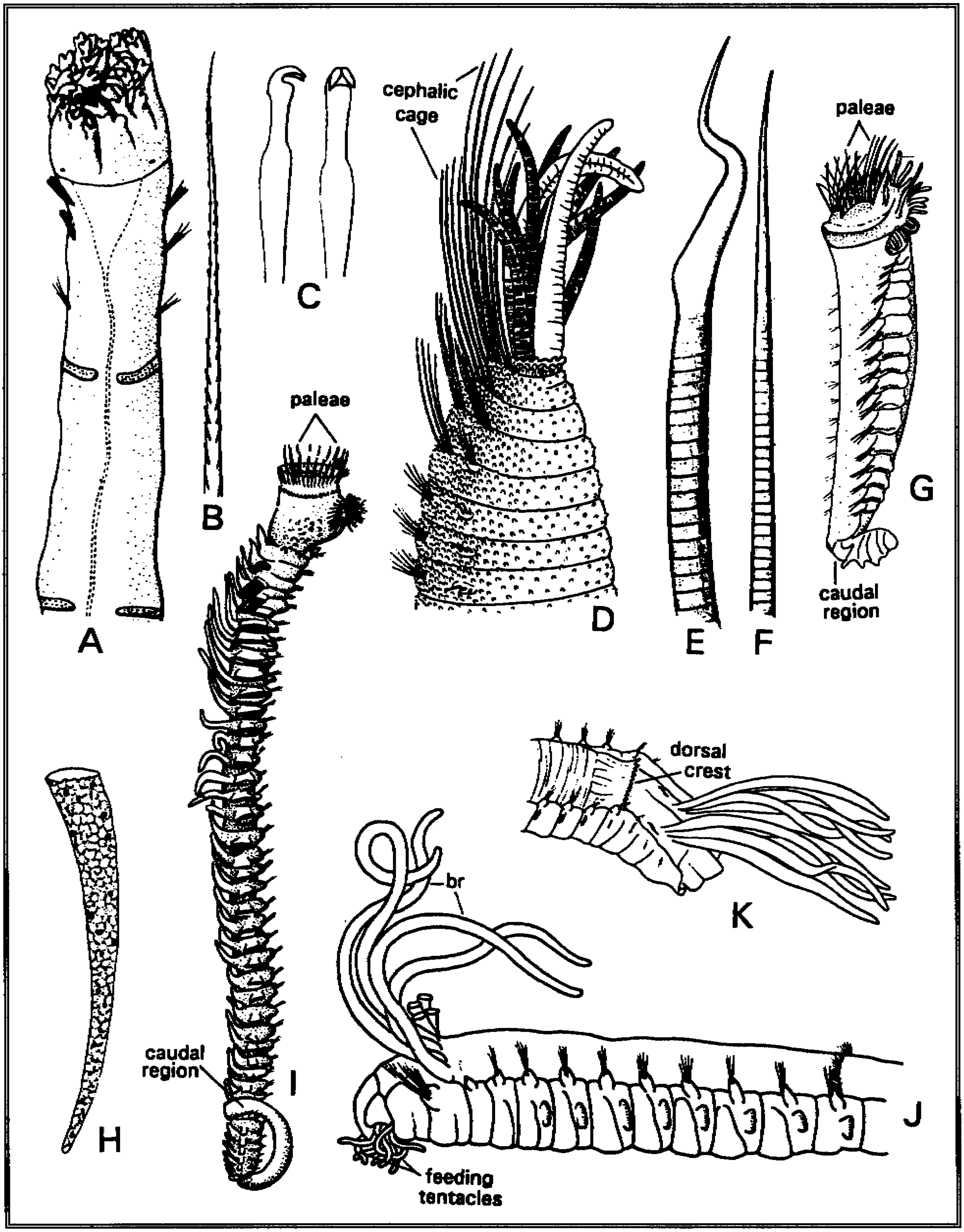

Figure 3.24. A-C, *Owenia*: A, anterior end; B, serrated capillary seta; C. uncini.—D-F, Flabelligeridae, *Pherusa*: D, anterior end; E-F, multiarticulate setae; G-H, *Pectinaria*: G, entire animal; H, tube.—Sabellaria, entire animal.—J-K, Ampharetidae, anterior ends. (A-C, after Hartmann-Schröder; D, J, K, originals by M. Litterer; E-F, after Hartman; G-H, after Blake; I, after Blake from Okuda).

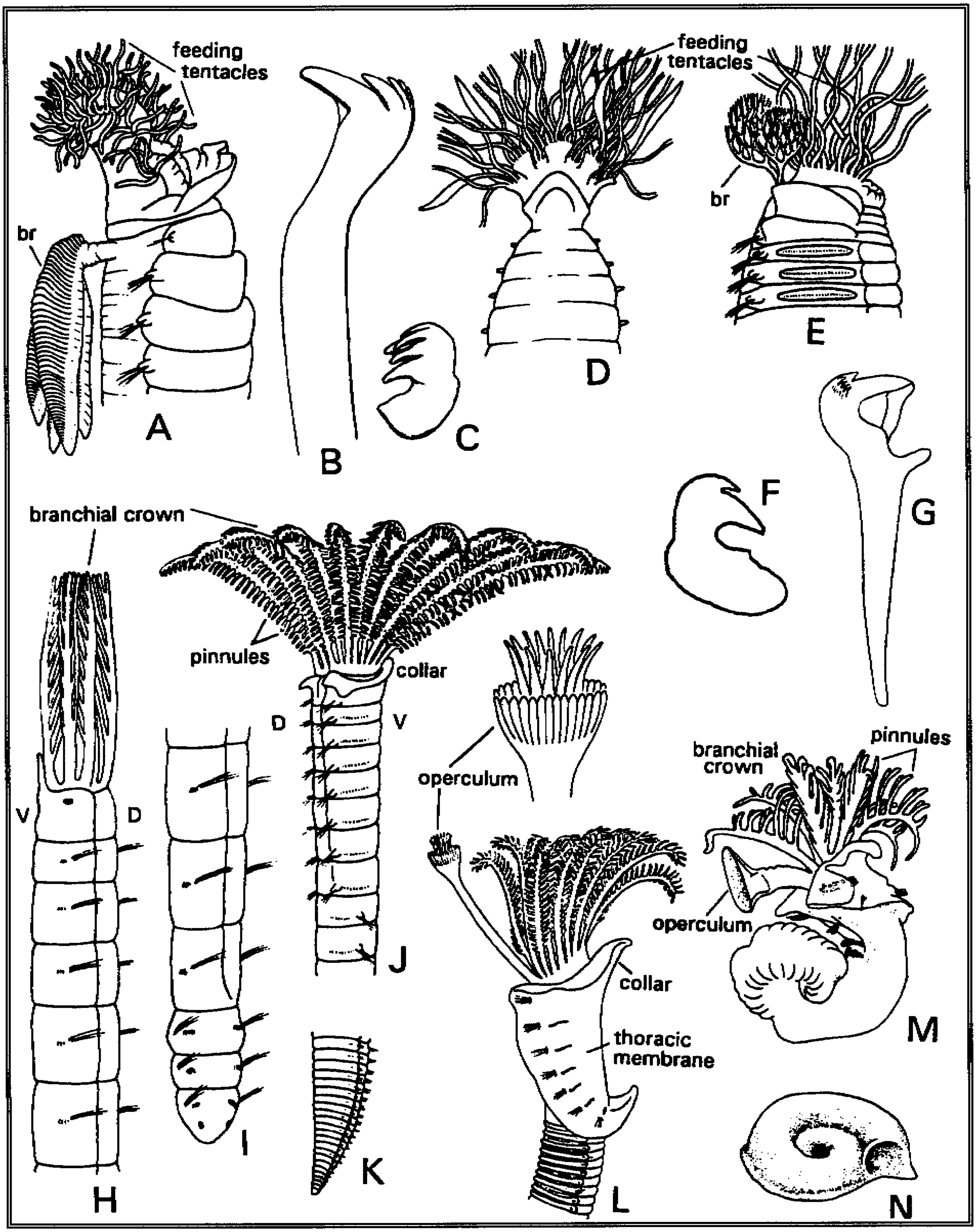

Figure 3.25. A-C, *Terebellides*: A, anterior end; B, thoracic unicinus; C, abdominal uncinus.—D-G, Terebellidae: D, *Lysilla*, anterior end, E, *Pista*, anterior end; F, short-handled uncinus; G, uncinus with posterior extension.—H-K, Sabellidae: H-I, *Fabricia*, anterior and posterior ends; J-K, *Sabella*, anterior and posterior ends.—L, Serpulidae, *Hydroides*: anterior end, with operculum detailed in inset.—M-N, Spirorbidae, entire animal and sinistral tube. (A, D-E, H-L, originals by M. Litterer; M-N, after Knight-Jones; F-G, originals).

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4. Family Phyllodocidae Savigny, 1818

by

James A. Blake[1]

Introduction

The phyllodocids are among the most active and common polychaetes found along the shore. They are most common and conspicuous in shallow-water habitats, especially associated with hard substrata, although some genera are typical of the soft sediments of mud flats and some are found in deep water. Phyllodocids are frequently brightly colored and may have diagnostic pigment patterns. Unfortunately, the pigments fade rapidly in preservatives. One of the most noticeable features of these worms is their production of copious amounts of mucus when disturbed.

Morphology

The bodies of phyllodocids are typically long and slender. The prostomium bears four frontal antennae and sometimes a fifth median antenna or nuchal papilla; eyes may be present or absent; a pair of nuchal organs are present. The proboscis is eversible and usually covered with soft papillae. Three species have hard denticles on the proboscis (e.g., *Phyllodoce armigera*, *P. rosea*, and *P. pettiboneae*), but such structures are not typical for the family.

Two, three, or four pairs of tentacular cirri may be present on the first one to three segments. The arrangement of these tentacular cirri, the fusion of tentaculate segments, and the presence or absence of setae on these same segments are of major importance at the generic level. A "tentacular formula" has been developed to summarize these characters in which 1 represents a tentacular cirrus; N represents a normal dorsal (D) or ventral (V) lamellar cirrus; and S or 0 indicate the presence or absence of setae. For example, the following formula is typical of the genus *Phyllodoce*: $(0^{1}/_{0} + 0^{1}/_{1}) + \mathrm{S}\ ^{1}/_{\mathrm{V}}$. This formula describes a worm having three tentacular segments, the first of which has only one elongate tentacular cirrus, the second has no setae but has elongate dorsal and ventral tentacular cirri; and the third segment has setae, a dorsal tentacular cirrus, and a normal ventral cirrus. Parentheses around the formula for the first two segments indicate that those segments are fused.

Parapodia are normally uniramous, although genera with subbiramous parapodia are known. Notopodia are represented by a short stalk to which a prominent foliose dorsal cirrus is attached; in genera with subbiramous parapodia, the notopodia have an internal acicula and sometimes a few emergent simple setae. Ventral cirri are smaller and less conspicuous. The shape and size of the dorsal cirrus is an important species level character. Neurosetae are always compound, with the sculpturing of the shaft sometimes being diagnostic (Eibye-Jacobsen, 1991a). However, very high magnification (1000×) is required to observe these details.

One pair of pygidial cirri present; a medial papilla may be present or absent.

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Taxonomic History

The most important recent monographs on the Phyllodocidae are by Uschakov (1972) and Pleijel (1991). Uschakov provides a complete review of the biology, anatomy, morphology, and systematic history of the family and its pelagic relatives. Although the scope of Uschakov's work is limited to the northwestern Pacific and Arctic Oceans, reviews of individual genera frequently contain references and keys to all of the then known species. Pleijel's review provides an update to generic diagnoses and lists all of the currently valid species.

Useful works that emphasize species from California or the eastern Pacific include Hartman (1936, 1968), Kravitz and Jones (1979), McCammon and Montagne (1979), and Blake (1992). Revisionary works and taxonomic reviews by Bergström (1914), Hartmann-Schröder (1963), Banse (1973), Gathof (1984), Pleijel (1987, 1988, 1990, 1991, 1993), Blake (1988), Wilson (1988), Pleijel and Dales (1991), and Eibye-Jacobsen (1991a-b) provide important information on several genera that occur in the eastern Pacific.

Most of the taxonomic problems with phyllodocids appear to be at the generic level. Pleijel (1991) reviewed and defined all of the phyllodocid genera and used cladistics to assess phylogenetic relationships. Among other things, he partitioned the family into three subfamilies. Despite this work and other recent generic revisions, several problems remain, especially with the deep-sea species currently assigned to the genera *Protomystides*, *Mystides*, and *Pseudomystides* (see below).

The nature of the proboscis, form of the ventral tentacular (or normal) cirrus on segment 2, placement of the median antenna, the presence or absence of a superior podial lobe, shape of the anal cirri, and the form of the setae are all morphological characters that have been used to define genera. Some characters are used at the generic level in one instance and at the specific level in another. For example, a superior podial lobe is an important character in defining the genus *Sige* according to Pleijel (1990), yet this same character is an important species level character for *Phyllodoce longipes*. In the present study, a new species having this character has been found and referred to the genus *Sige*, yet because the median antenna is placed anteriorly on the prostomium, the species might also be referred to the genus *Pterocirrus*.

Wilson (1988) has provided a thorough review of the species of the genus *Eteone* and divided the group into three genera: *Eteone, Hypereteone,* and *Mysta.* The latter two genera have sometimes been used at the subgeneric level. The characters that Wilson used to separate these three genera included the presence or absence of papillae on the proboscis and whether the anal cirri were short, thick and blunt tipped or long and tapering. In the present study *E. brigitteae* has been found to be most closely related to species that Wilson (1988) has referred to the genus *Hypereteone*. However, the new species has blunt-tipped anal cirri and should be referred to *Eteone.* These problems suggest that the characters used by Wilson to separate these genera are not consistent and like Pleijel (1991), I prefer to use only a single genus, *Eteone.*

In a study of polychaetes from hydrothermal vent ecosystems, Blake (1985) described a new genus and species, *Galapagomystides aristata*, that lacked a dorsal cirrus on segment 3 and was similar in this regard to species of *Mystides*. The vent species, however, had unusual setae with a thin, aristate-like blade, and a papillated instead of a smooth proboscis. Subsequently, both Miura (1988) and Blake and Hilbig (1990) described new species of *Protomystides* from deep-sea cold-seep communities and hydrothermal vents that had the same type of setae. There thus appears to be considerable confusion in the characters that are used to define genera related to *Mystides* and *Protomystides*. Species in this complex lacking a dorsal cirrus on segment 3 but having a prominent nuchal papilla or median antenna should be referred to the genus *Pseudomystides*.

The presence of a flattened or enlarged tentacular cirrus on the second segment has been used as a generic level character, but has been found to be highly variable (Pleijel, 1987). In the present study the genus *Genetyllis* has been combined with *Nereiphylla* on that basis. Pleijel (1987) has already synonymized *Steggoa* with *Eulalia* because of observed variability in the flattening of the ventral tentacular cirrus in several species.

Eibye-Jacobsen (1991b) has revised the genus *Eumida*. This work includes descriptions of 21 valid species. The relationships of *Eumida* and the closely related genus *Sige* are discussed.

The genus *Phyllodoce* has been subdivided into as many as three subgenera (or genera) on the basis of the papillation of the proximal portion of the proboscis. Pleijel (1988) elected not to use these taxa because additional characters that were originally used by Bergström (1914) to separate species of *Phyllodoce* were found to be incorrect. It is obvious that there is sufficient variability in the papillation of the proboscis to preclude a consistent subgeneric division. Indeed, one species found in the present study, *P. cuspidata*, appears to be a composite of two different types of proboscideal papillation.

Biology

Phyllodocids are typically active, predatory or possibly omnivorous polychaetes, often having bright colors or characteristic pigment patterns. In shallow waters, individual species are often cryptic, crawling among rocks or shell fragments, in mussel beds and between barnacle tests, in and around algae and their holdfasts; other species crawl over the surface of muds seeking prey items. The habits of species from deeper habitats are not known, but they presumably follow the same patterns.

The various color patterns exhibited by phyllodocids are probably protective. For example, a living specimen of *Clavadoce splendidia* collected by this author from among algae on the rock jetty at Bodega Harbor moved its variously patterned dorsal cirri in such a way that they resembled the blades of red algae moving in the water. A predator thus camouflaged, could easily lie in wait until a prey species came near. The green color of *Eulalia viridis* is another example of a species that would be rendered invisible against certain types of algal backgrounds. Generally, the species with the most variable color patterns are those that live associated with seaweed or the more brightly colored faunas associated with hard bottoms. Species living on the soft bottoms tend to be more uniformly colored brown, tan, or beige.

As part of a review of the feeding modes of phyllodocids, Fauchald and Jumars (1979) suggested that while many species are definitely predatory, others may be scavengers or carrion eaters. The long, eversible proboscis is used to strike at and capture prey. The proboscis is everted by coelomic pressure that moves from the posterior segments into the anterior segments; the reverse, invagination or inversion is results from contraction of longitudinal retractor muscles (Uschakov, 1972). The proboscis is often covered with numerous papillae that may contain gland cells producing a secretion that may possibly immobilize the prey species. Michel (1968) determined that the glands of *Eulalia viridis* contained enzymes that promoted digestion.

In a series of laboratory observations of recently metamorphosed specimens of *Phyllodoce williamsi*, I was able to watch active predation by these juveniles on larvae of spionids and nephtyids (Blake, 1975a). Prey capture and ingestion involved extrusion of the pharynx that attached to the body of the prey. The phyllodocid then exerted a powerful suction that literally caused the body fluids and parts of the prey item to be drawn down the pharynx. Prey items were seemingly located by chance, suggesting that once the prey was located, tactile sensations were all that was required to initiate the attack. Other studies have shown that species of *Eteone* follow mucous trails of prey items on mud flats and feed on them when they catch up (Simon, 1965; Fauchald and Jumars, 1979).

There is conflicting evidence concerning the specificity of prey items in the diet of individual species (Fauchald and Jumars, 1979). For example, these authors reviewed studies on feeding of *Eteone longa* that indicated specificity for spionids as prey items, but of different species in different areas, while another study indicated that the species fed on a variety of metazoans. I would suspect that the latter observation is closer to the truth. My own observations of the feeding of juvenile *Phyllodoce williamsi* suggest that random encounters with various types of prey items are the norm. There is some evidence that

Eteone species can also subsist on ingested sediment in the absence of prey items (Sanders *et al*., 1962; Simon, 1965).

Phyllodocids have been observed to deposit their eggs in gelatinous masses on eel grass, algae, rocks, or other structures both in the field or the laboratory (Thorson, 1946; Cazaux, 1969; Blake, 1975a; Lacalli, 1980). The structure of these egg masses is somewhat variable, from loose, saclike structures (e.g., *Phyllodoce groenlandica*) to firmly attached spiral egg masses (e.g., *Phyllodoce williamsi*). The reproductive behavior of *Phyllodoce mucosa* (Oersted) was observed by Sach (1975) on tidal flats in northern Germany. The species appeared in great numbers (≤148 individuals per m^2) at the surface of the sediment from February to April. Mucous bags were formed that contained about 10,000 green eggs ($\overline{x}$=113.4 ± 5.4 mm in diameter). To form the egg mass, 4 to 17 males and a single female interweave their bodies forming a ball. As the mucous is secreted, eggs and sperm are shed into the mucus.

For most species, the eggs undergo embryonic development within the egg masses, hatching as planktic trochophores. Several weeks are spent in the plankton as planktotrophic larvae passing through the metatrochophore and nectochaete stages until finally undergoing metamorphosis into benthic juveniles. The form of reproduction and larval development is unknown for most of the California species, with the best studied species being *Phyllodoce williamsi* and *Eteone dilatae*[2], both common in intertidal and shallow subtidal habitats on the central and northern coasts (Blake, 1975a). In Blake's paper, descriptions are provided of the planktic stages and the earliest benthic juveniles. Planktic larvae of an unidentified *Phyllodoce* sp. A in the same paper may refer to *P. hartmanae* (see below). Observations on the ultrastructure of trochophores of *P. mucosa* have been made by Lacalli (1981: apical organ), Lacalli and Marsden (1977: nervous system), and Bartolomaeus (1987: photoreceptors).

There is little information on the role of phyllodocids on the ecology of benthic populations. As is typical of predatory-like organisms, phyllodocids are rarely among the 10 or 20 most abundant species in benthic communities. These groups are usually dominated by deposit feeders in soft-bottom communities and filter feeders, omnivores, and herbivores in rocky habitats. In other words, the most abundant species are the ones that are potential prey items of phyllodocids.

In soft-bottom benthic communities, the species composition changes with depth and type of substrate. For example, species of the genera *Phyllodoce, Nereiphylla*, and *Eteone* are prevalent on the continental shelf, whereas species of *Mystides* and *Protomystides* are prevalent in continental slope depths. Other genera, such as *Paranaitis, Eumida,* and *Sige* and are less predictable in their depth distributions. Individual species tend to be associated with soft sediments or hard surfaces.

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[2] The larvae described by Blake (1975a) as *Eteone dilatae* apparently represent two species. The metatrochophore is *E. dilatae*, while the nectochaete appears to be a species of *Lugia*.

Key to the Genera and Species

1A. With 2 pairs of tentacular cirri on first segment (Fig. 4.1 A,C) .... Genus *Eteone*....2

1B. With 1 pair of tentacular cirri on first segment (Fig. 4.2 C,E); total number of tentacular cirri 2 to 4 pairs 9

2A. Prostomium wider than long 3

2B. Prostomium longer than wide or about as wide as long 5

3A. First segment dorsally reduced (Fig. 4.1A); dorsal cirri pointed, nearly triangular in shape (Fig. 4.1B); ventral cirri distinctly pointed, directed ventrally .... *Eteone lighti*[3]

3B. First segment dorsally entire, well developed; dorsal cirri rounded apically, oval in shape; ventral cirri rounded, not directed ventrally 4

4A. Eyes present; body and cirri heavily pigmented (Fig. 4.7A); ventral cirri large, with broad basal attachment (Fig. 4.7B) .... *Eteone pigmentata*

4B. Eyes absent; body and cirri lightly pigmented (Fig. 4.3A); ventral cirri small, with narrow basal attachment (Fig. 4.3B) .... *Eteone balboensis*

5A. Prostomium semicircular, as long as wide (Fig. 4.5A); dorsal cirri as wide as long, thickened (Fig. 4.5B); body and cirri darkly pigmented .... *Eteone californica*

5B. Prostomium longer than wide (Fig. 4.6A); dorsal cirri longer than wide or wider than long; body and cirri either pale, lightly pigmented, or pigment in distinct patterns 6

6A. Dorsal cirri asymmetrical, broadly curved dorsally (Fig. 4.4B); anal cirri more than 2-½ times longer than wide (Fig. 4.4G); dorsal tentacular cirri distinctly smaller and shorter than ventral ones (Fig. 4.4A) .... *Eteone brigitteae*

6B. Dorsal cirri symmetrical (Fig. 4.1F); anal cirri oval or only slightly longer than wide; tentacular cirri subequal 7

7A. Body thin, threadlike; with distinct pigment pattern (Fig. 4.6A) .... *Eteone leptotes*

7B. Body larger, more robust; pigment not in distinct pattern 8

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[3] *Eteone lighti* Hartman, 1936. Known only from bays and estuaries of northern California. See Hartman (1936, 1968); Blake (1975b).

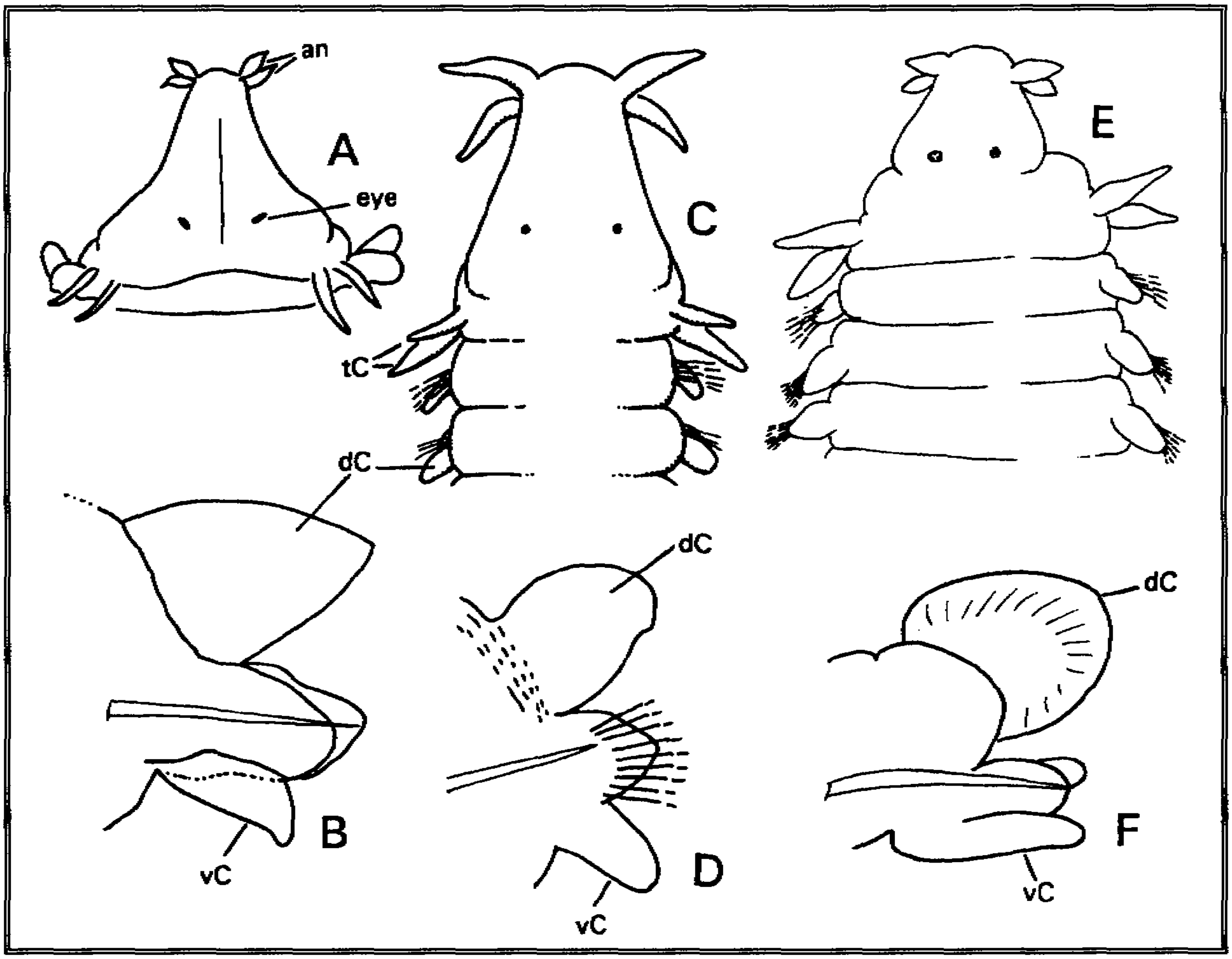

Figure 4.1. Examples of *Eteone* species: A, *Eteone lighti*, anterior end; B, parapodium; C, *Eteone dilatae*, anterior end; D, parapodium; E, *Eteone pacifica* (holotype), anterior end; F, parapodium. (A-D, F after Blake, 1975b).

8A. Dorsal cirri broadly rounded (Fig. 4.1F); pale with irregularly spaced black spots; a large species, to more than 100 mm .... *Eteone pacifica*[4]

8B. Dorsal cirri subrectangular, slightly longer than wide (Fig. 4.1D); body pale green with numerous small brown spots; a smaller species, not exceeding 50 mm in length .... *Eteone dilatae*[5]

9A. With 2 or 3 pairs of tentacular cirri on first 2 segments 10

9B. With 3 or 4 pairs of tentacular cirri on first 3 segments 13

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[4] *Eteone pacifica* Hartman, 1936. Intertidal to shallow subtidal, in mud. Washington to California. See Hartman (1936, 1968); Wilson (1988).

[5] *Eteone dilatae* Hartman, 1936. Common in sand and mixed sand and mud beaches in northern and central California. See Hartman (1936, 1968); Wilson (1988).

10A. Segment 3 with dorsal cirri (Fig. 4.8A); setae from segment 2; tentacular formula: $0^{1}/_{0} + S\,^{1}/_{1} + S\,^{D}/_{V}$ .... *Lugia uschakovi*

10B. Segment 3 without dorsal cirri; setae from segment 2 or 3 11

11A. Setae from segment 2; tentacular formula: $0^{1}/_{0} + S\,^{1}/_{V} + S\,^{0}/_{V}$ or $0^{1}/_{0} + S\,^{1}/_{1} + S\,^{0}/_{V}$ .... Genus Mystides 12

11B. Setae from segment 3; tentacular formula: $0^{1}/_{0} + 0\,^{1}/_{0} + S\,^{0}/_{V}$; prostomium longer than wide. .... *Hesionura coineaui difficilis*

12A. Large prostomial eyes present (Fig. 4.9A); dorsal cirri smaller than ventral cirri (Fig. 4.9B) .... *Mystides borealis*

12B. Eyes absent (Fig. 4.10A); dorsal and ventral cirri subequal (Fig. 4.10B) .... *Mystides caeca*

13A. Four frontal and 1 median antenna present 14

13B. Four frontal antennae present; nuchal papilla present or absent 24

14A. Paired nuchal epaulets present (Fig. 4.2A); parapodia subbiramous, with dorsal aciculae (Fig. 4.2B), with or without simple notosetae .... Genus *Notophyllum*

14B. Nuchal epaulets lacking; parapodia uniramous 15

15A. Ventral cirrus very large, reniform, oriented at right angles to acicula (Fig. 4.13B); antenna and tentacular cirri all large, flattened, club-shaped (Fig. 4.13A) .... Genus *Clavadoce* 16

15B. Ventral cirrus small, oval to elliptical, oriented in same direction as acicula; antennae and tentacular cirri cirriform, not flattened 17

16A. Antennae and tentacular cirri clavate (Fig. 4.13A); dorsal cirrus narrow, elongate (Fig. 4.13B) .... *Clavadoce splendida*

16B. Antennae and tentacular cirri lanceolate (Fig. 4.14A); dorsal cirrus broad, leaflike (Fig. 4.14B) .... *Clavadoce nigrimaculata*

17A. All 3 tentacular segments distinct dorsally; proboscis thickly papillated .... Genus Eulalia 18

17B. First tentacular segment reduced, with first pair tentacular cirri lateral to prostomium; proboscis smooth or only sparsely papillated 20

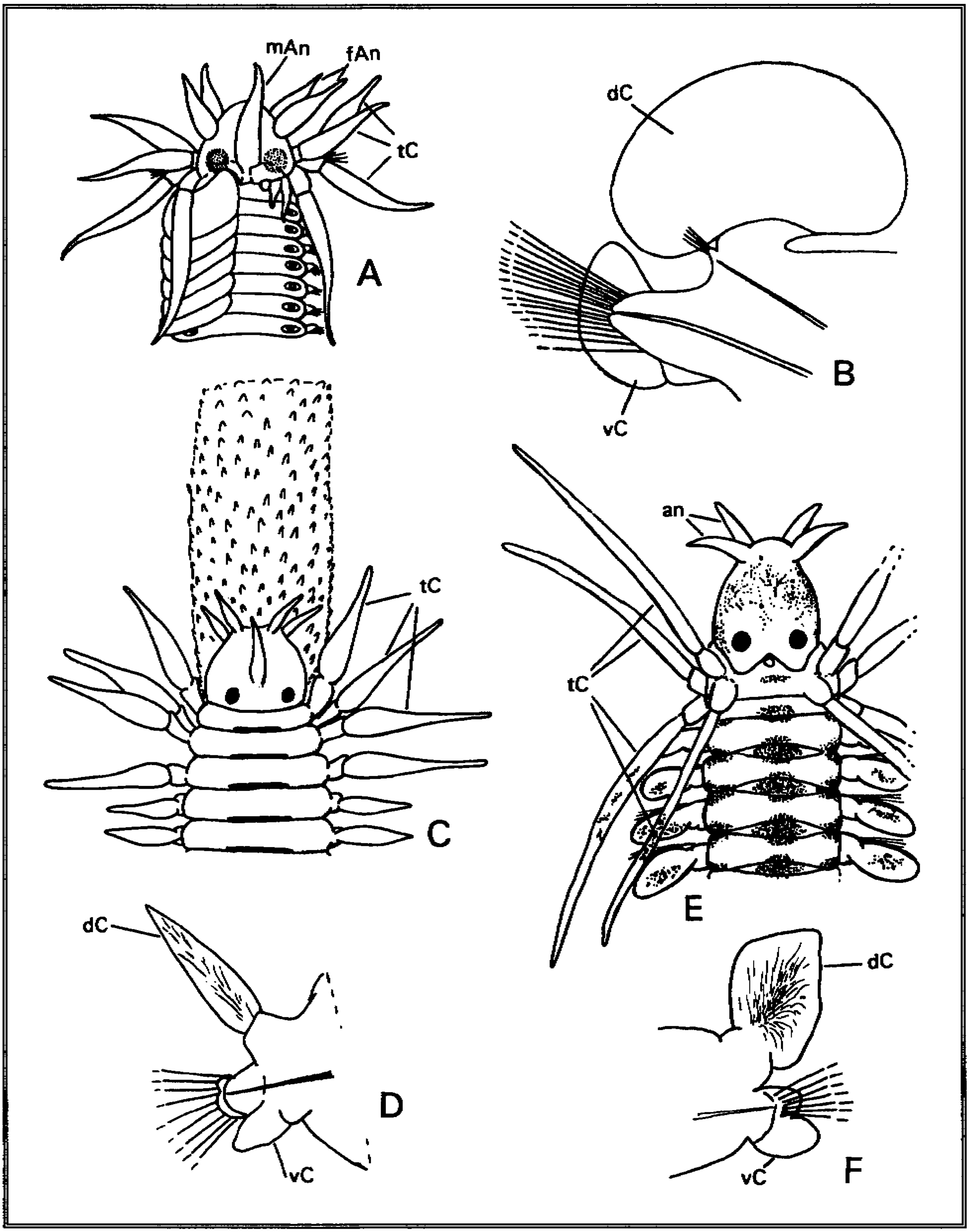

Figure 4.2. Representative phyllodocid species: A, *Notophyllum imbricatum*, anterior end; B, parapodium; C, *Eulalia quadrioculata*, anterior end; D, parapodium; E, *Phyllodoce williamsi*, anterior end; F, parapodium. (A-B, after Uschakov, 1972; C-F, after Blake, 1975b).

18A. Dorsal cirri of median parapodia elongate, lanceolate (Fig. 4.2D); body greenish, with black transverse stripes in intersegmental grooves (Fig. 4.2C) .... *Eulalia quadrioculata*[6]

18B. Dorsal cirri of median parapodia oval (Fig. 4.15B) or cordate (Fig. 4.16B) 19

19A. Antennae all short, none more than one-quarter length of prostomium (Fig. 4.16A); all tentacular cirri short, none extending more than 3 segments in length; dorsal cirri cordate, ventral cirri elongate with narrow base (Fig. 4.16B); body with 2 longitudinal rows of pigment derived from lateral segmental pigment .... *Eulalia bilineata*

19B. Antennae all long, each more than one-half length of prostomium (Fig. 4.15A); tentacular cirri all long, some extending 5 or more segments in length; dorsal cirri oval, darkly pigmented, ventral cirri large, oval, with broad base (Fig. 4.15D); body tan without rows of pigment, with reddish colored parapodia and additional random pigment elsewhere on body .... *Eulalia levicornuta*

20A. Neuropodia with superior dorsal lobe (Fig. 4.19B) .... Genus *Sige* 21

20B. Neuropodia without superior dorsal lobe (Fig. 4.17B) .... Genus Eumida 23

21A. Dorsal cirri cordate (Fig. 4.19B); prostomium with 2 large eyes (Fig. 4.19A) .... *Sige bifoliata*

21B. Dorsal cirri elongate (Fig. 4.19B, 4.21B); eyes absent (Fig. 4.20A) 22

22A. Median antenna located anteriorly on prostomium, near frontal antennae (Fig. 4.21A); tentacular cirri all short, with none extending more than 2 segments posteriorly .... *Sige pleijeli*

22B. Median antenna located in posterior half of prostomium (Fig. 4.20A); dorsal tentacular cirri of segment 2 extending posteriorly at least 8-9 segments .... *Sige brunnea*

23A. Neuropodia of posterior segments greatly elongated, more than 2-½ times as long as broad, distally divided into 2 prominent lobes (Fig. 4.18B); dorsal cirri cordate, slightly longer than wide .... *Eumida tubiformis*

23B. Neuropodia of posterior segments relatively short, thickened, not greatly elongated, distally divided into 2 broadly rounded lobes (Fig. 4.17B); dorsal cirri longer than wide or wider than long .... *Eumida longicornuta*

24A. Tentacular segments all free from one another, not reduced dorsally (Fig. 4.12A,B); with 3 to 4 pairs of tentacular cirri (ventral cirrus of segment 2 sometimes not differing from normal ventral cirrus) .... Genus *Protomystides*

24B. Tentacular segments 1 to 2 fused dorsally; with 4 pairs of tentacular cirri 25

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[6] *Eulalia quadrioculata* Moore, 1906 is one of the most common polychaetes of the northern and central California coast. The species occurs among mussels and barnacles, in algal holdfasts, and under rocks. The species is a synonym of *E. aviculiseta* Hartman, 1936. See Banse (1972). The holotype of *E. quadrioculata* (USNM 5516) has been compared with numerous specimens from central California that agree with Hartman's *E. aviculiseta* and there are no significant differences. The holotype lacks intersegmental pigmentation, but this is undoubtedly faded. The proboscis is smooth proximally and papillated distally, but may appear entirely papillated if only partially everted.

25A. Segments 1 to 2 well developed, forming distinct collar around tapering posterior half of prostomium (Fig. 4.22A); segments 1 to 2 bearing 3 pairs tentacular cirri; segment 3 distinct, bearing fourth pair tentacular cirri; tentacular formula: $(0^{1}/_{0} + 0\,^{1}/_{V}) + S\,^{1}/_{V}$ .... Genus *Paranaitis*

25B. Segment I reduced, not visible dorsally, bearing first pair tentacular cirri lateral to prostomium; segments 2 to 3 distinct, bearing 3 pairs tentacular cirri 26

26A. Peristomium oblong or rounded, without nuchal papilla (Fig. 4.23A); tentacular formula: $(0^{1}/_{0} + S\,^{1}/_{1}) + S\,^{1}/_{V}$ .... *Nereiphylla castanea*

26B. Peristomium heart-shaped, with or without nuchal papilla (Fig. 4.25A)...... Genus *Phyllodoce*..... 27

27A. Neuropodium with elongate superior lobe or protuberance (Fig. 4.28A); distal half of proboscis with large, elongate papillae scattered over surface (Fig. 4.28B) .... *Phyllodoce longipes*

27A. Neuropodium with smoothly rounded tip, without superior lobe (Fig. 4.24B); distal half of proboscis with low, rounded or rugose lobes (Fig. 4.24A), conical papillae limited to around oral opening 28

28A. Setae first present from segment 3 29

28B. Setae first present from segment 4 31

29A. Ventral cirri unusually long, narrow, extending for one-half its length beyond podial lobe (Fig. 4.29B); proximal half of proboscis with 4 to 5 large lateral, hardened cusps among rows of smaller papillae (Fig. 4.29A,C); prostomium without nuchal papilla .... *Phyllodoce pettiboneae*

29B. Ventral cirri shorter, as long as podial lobe, or extending only up to one-fourth its length (Fig. 4.25C); proximal half of proboscis with 6 rows of lateral papillae on each side; prostomium with distinct nuchal papilla (Fig. 4.25A) 30

30A. (*Note 3 Choices*) All anterior segments heavily pigmented; proximal papillae of proboscis all of one type, conical, arranged in 6 rows of 13 to 16 papillae on each side; ventral cirri pointed apically, at least half again as long as neuropodial lobe (Fig. 4.25C)........ *Phyllodoce groenlandica*

30B. First 4 anterior segments without pigment (Fig. 4.26A); proximal papillae on proboscis of 2 types: most proximal platelike, arranged in 6 rows of 10 to 12 on a side, then grading into smaller, more conical papillae in diffuse arrangement (Fig. 4.26B); ventral cirri blunt to somewhat pointed, shorter than or only slightly longer than neuropodial lobe (Fig. 4.26C)........... *Phyllodoce cuspidata*

30C. Each body segment with 3 pigmented intersegmental areas across dorsum, forming 3 longitudinal lines along body (Fig. 4.2E); proximal papillae of proboscis all of one type, arranged in 6 rows of 9 papillae on a side; ventral cirri thick, fleshy, blunt-tipped, slightly longer than neuropodial lobe (Fig. 4.2F) .... *Phyllodoce williamsi*[7]

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[7] *Phyllodoce williamsi* (Hartman, 1936) is one of the most common phyllodocids in estuaries and embayments in central and northern California. The species is found in sand and mud flats in the intertidal zone and in the shallow subtidal. In Tomales Bay, Blake (1975a) found the species to deposit green egg masses on the blades of *Zostera marina*.

31A. Body large, robust, with diffuse dark brown pigment dorsally on segments; prostomium wider than long, with lateral nuchal organs present when proboscis everted (Fig. 4.27A); proboscis with proximal papillae arranged in 6 lateral rows; ventral cirri rounded apically (Fig. 4.27B) .... *Phyllodoce medipapillata*

31B. Body slender, delicate, with distinct mid-dorsal intersegmental dark chromatophore; prostomium as wide as long, or slightly longer than wide, nuchal organs never present; ventral cirri apically pointed; proboscis with proximal papillae arranged in numerous spiral rows (Fig. 4.24A); ventral cirri elongated, pointed (Fig. 4.24B,C) .... *Phyllodoce hartmanae*

Descriptions of Species

In addition to species taken as part of the MMS Phase I and II surveys, this chapter includes information on most of the Phyllodocidae known from California. Descriptions and illustrations are prepared for 27 species in 12 genera, listed below. Notes are provided on additional species that are included in the keys.

Eteone balboensis Hartman, 1936
Eteone brigitteae Blake, 1992
Eteone californica Hartman, 1936
Eteone leptotes Blake, 1992
Eteone pigmentata Blake, 1992
Lugia uschakovi Blake, 1992
Mystides borealis Théel, 1879
Mystides caeca Langerhans, 1880
Hesionura coineaui difficilis (Banse, 1963)
Protomystides mariaensis Blake, 1992
Clavadoce splendida Hartman, 1936
Clavadoce nigrimaculata (Moore, 1909)
Eulalia levicornuta Moore, 1909
Eulalia bilineata (Johnston, 1840)
Eumida longicornuta (Moore, 1906)
Eumida tubiformis Moore, 1909
Sige bifoliata (Moore, 1909)
Sige brunnea (Fauchald, 1972)
Sige pleijeli Blake, 1992
Paranaitis polynoides (Moore, 1909)
Nereiphylla castanea (Marenzeller, 1879)
Phyllodoce hartmanae Blake and Walton, 1977
Phyllodoce groenlandica Oersted, 1843
Phyllodoce cuspidata McCammon and Montagne, 1979
Phyllodoce medipapillata Moore, 1909
Phyllodoce longipes Kinberg, 1866
Phyllodoce pettiboneae Blake, 1988

Genus *Eteone* Savigny, 1820

Type species: *Nereis flava* Fabricius, 1780, designated by Bergström, 1914.

Diagnosis. Prostomium with 4 antennae; nuchal papilla present or absent; 2 pairs of tentacular cirri on first segment; second segment lacking dorsal cirri. Proboscis smooth or rugose, lacking longitudinal rows of papillae. Anal cirri short, globular to digitiform with rounded tips, no more than 4 times longer than wide.

Remarks. *Eteone* was revised by Wilson (1988) to include three genera: *Eteone*, *Hypereteone* Bergström, and *Mysta* Malmgren. The genera were separated on the form of the anal cirri and the presence and location of papillae on the proboscis. *Hypereteone* was distinguished by having long tapering anal cirri and three or more rows of papillae or heavy ridges on the proboscis. Both *Eteone* and *Mysta* were said to have short anal cirri with rounded tips. *Mysta* was then distinguished from *Eteone* by having two lateral rows of papillae on the proboscis, whereas *Eteone* lacked such rows. While it is apparent that three distinct groups of species can be separated within the *Eteone*-complex of species, Pleijel (1991) did not recognize them at the generic level. He was concerned that *Eteone sensu stricto*, might represent a paraphyletic assemblage defined on plesiomorphic characters. This position was supported by Blake (1992), who noted that *Eteone brigitteae*, from the Santa Maria Basin, had asymmetrical dorsal cirri, and was most closely allied with species that were included with *Hypereteone* (Wilson 1988). However, the anal cirri of *E. brigitteae*, while elongate, were thick and blunt-tipped instead of tapering to a point.

Four species of *Eteone* have been identified from the Santa Maria Basin: *Eteone balboensis* Hartman, 1936, *Eteone brigitteae* Blake, 1992, *Eteone leptotes* Blake, 1992, and *Eteone pigmentata* Blake, 1992. Another specices, *E. californica*, is likely to be encountered.

Eteone balboensis Hartman, 1936

Figure 4.3

Eteone balboensis Hartman, 1936:131-132, figs. 49-51.—Wilson, 1988:390, figs. 1a, 14a.

Material examined. California: Santa Maria Basin, off Purisima Point, Sta. R-5 (1).

Description. A moderately sized specimen, posteriorly incomplete, measuring 19 mm long, 0.75 mm wide, for 103 segments. Color in alcohol: tan with heavy brown pigment on dorsal and ventral surfaces, and on dorsal and ventral cirri.

Prostomium wider than long, somewhat triangular in shape, tapering anteriorly, terminating in broad plate bearing four cirriform antennae (Fig. 4.3A); nuchal papilla present, eyes lacking. Proboscis unknown. Tentacular segment separated from prostomium; setae lacking; dorsal pair tentacular cirri, cirriform, smaller and shorter than thicker ventral pair (Fig. 4.3A). Segment 2 first with setae, lacking dorsal cirri. Dorsal cirri first present from segment 3, each cirrus oval, slightly longer than wide, glandular, with brown pigment spots (Fig. 4.3B). Ventral cirri considerably smaller than dorsal cirri, about twice as long as wide, also with glands and brown pigment (Fig. 4.3B).

Podial lobes elongate, with distinct pre- and postsetal lobes, between which setae emerge. Setae numbering 9 to 10 per fascicle; each seta with long denticulated blade and expanded shaft bearing 2 rostral teeth, one longer than the other, and each with several smaller subdistal barbs or spinelets (Fig. 4.3C-D). Pygidium of holotype reported bearing digitiform anal cirrus with rounded tip, about 3 times longer than wide (Wilson, 1988).

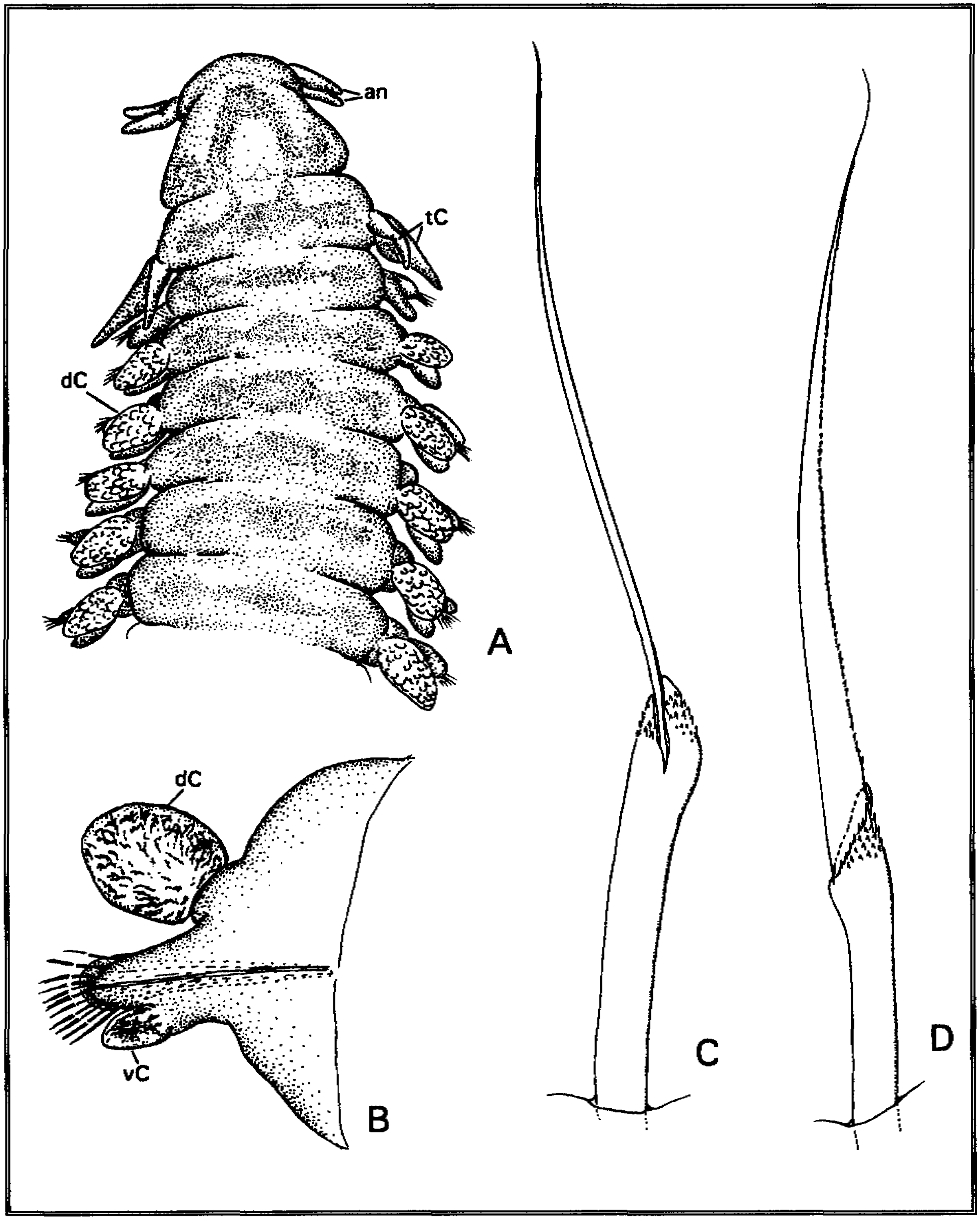

Figure 4.3. *Eteone balboensis*: A, anterior end, dorsal view; B, middle parapodium, anterior view; C-D, setae in different views.

Biology. This species was only taken at Station R-5. The sediments at this station were the coarsest in the program (percent sand: 50-79; silt: 18-41; and clay: 4-9).

Remarks. *Eteone balboensis* has not been reported since its original discovery on a sandy mud beach near Corona del Mar (Hartman, 1936). Except for one feature, the original description of the species agrees very well with the specimen from the Santa Maria Basin. Hartman's (1936) figure of the anterior end of her specimen indicates that the dorsal and ventral tentacular cirri are subequal, whereas in the Santa Maria Basin specimen, the dorsal cirri are slightly shorter and thinner than the ventral ones. However, other features such as the wide prostomium, lack of eyes, and very small dorsal cirri are only known in combination for *E. balboensis*, to which the Santa Maria Basin specimen is referred. Wilson (1988) examined the holotype of *E. balboensis*, but was unable to add to the description because the specimen was anteriorly incomplete.

Eteone balboensis was identified as *E.* nr. *longa* in the Phase II monitoring program. Specimens of *E. longa* from Boston Harbor were examined by the author. In *E. longa* the prostomium is longer than wide, a pair of eyes are present, and the dorsal and ventral pair of tentacular cirri are subequal. In contrast *E. balboensis* has a prostomium that is wider than long, lacks eyes, and the dorsal pair of tentacular cirri is slightly smaller and shorter than the ventral pair.

Type locality and Type specimens. Newport Bay, Corona del Mar, California. Holotype: USNM 20337.

Description. Central and southern California, intertidal to 154 m.

Eteone brigitteae Blake, 1992

Figure 4.4

Eteone brigitteae Blake, 1992:694-696, fig. 1.

Material examined. California: Santa Maria Basin, off Point Sal, Sta. R-8 (holotype and paratype, USNM 148680-148681).—Off San Francisco, Sta. 3-12, 37°25.03'N, 123°18.00'W, 1745 m, coll. Sept. 1991 (1).

Description. A moderate sized species, up to 20.5 mm long and 0.6 mm wide for about 140 segments. Color in alcohol: light tan, relatively unpigmented except for some brown spots along dorsal midline. Prostomium about as long as wide, tapering abruptly to about mid-way to anterior end, then expanding again, terminating in bluntly rounded tip bearing 4 short cirriform antennae (Fig. 4.4A); with one pair of dark eyes (lacking in San Francisco slope specimen); nuchal papilla absent.

Tentacular segment weakly separated from prostomium, demarcated by thin line (Fig. 4.4A). Dorsal pair tentacular cirri short, extending posteriorly only to anterior of segment 2; second pair longer, extending to segment 3 (Fig. 4.4A). Second segment with setae and ventral cirrus. Dorsal cirri first present from segment 3; each cirrus asymmetrical, especially in anterior segments, where dorsal edge curves and ventral edge is relatively straight (Fig. 4.4B); middle dorsal cirri longer, with less extreme asymmetry (Fig. 4.4C). Ventral cirri elongate, with broad basal attachment; ventral cirri of anterior segments nearly as long as podial lobes. Podial lobes with weakly developed anterior and posterior lobes, between which setae emerge. Setae number 9 to 10 per fascicle; each with finely denticulated blade and shaft with a single large rostral tooth and shorter double spike; larger tooth with several smaller teeth

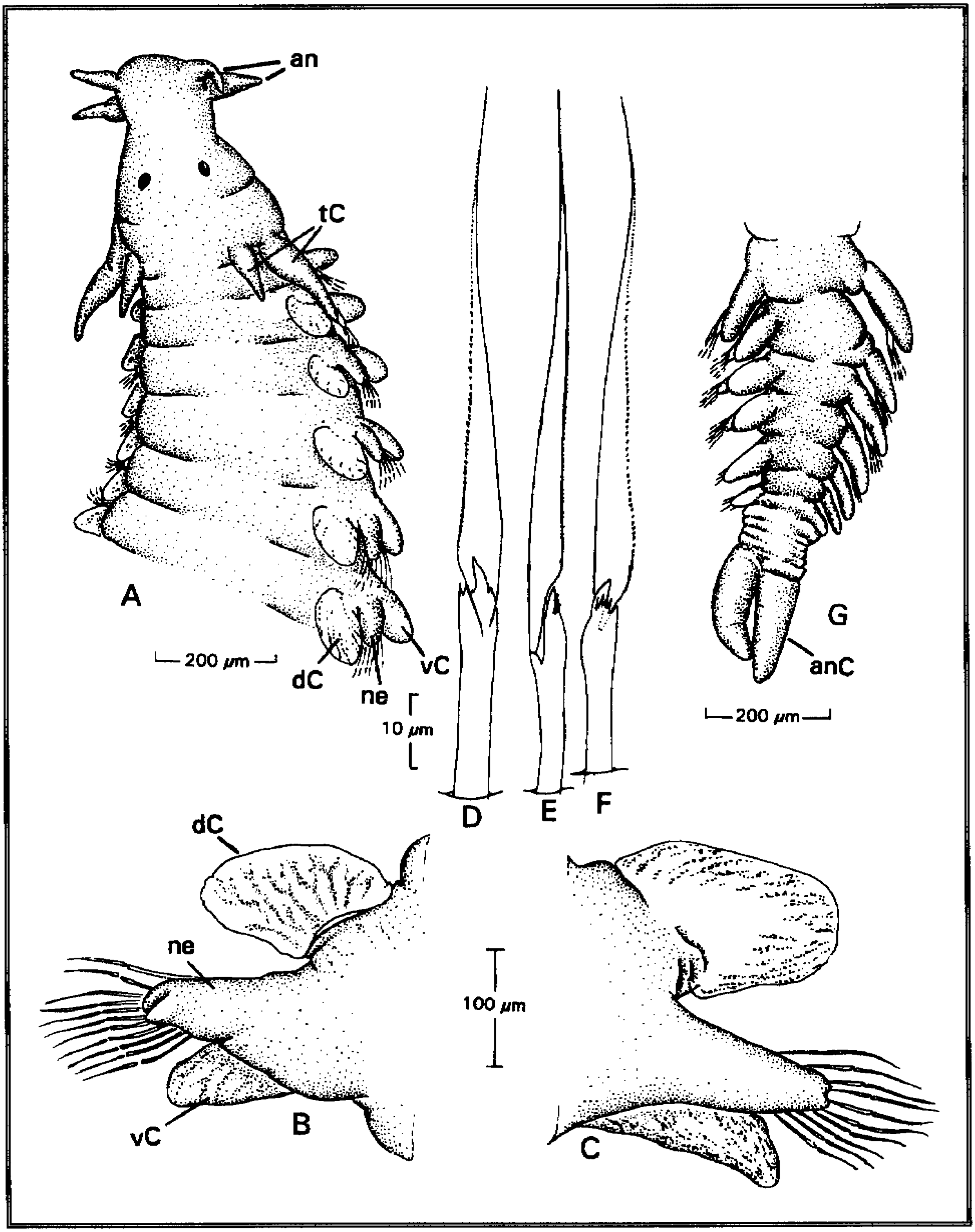

Figure 4.4. *Eteone brigitteae*: A, anterior end, dorsolateral view; B, anterior parapodium, anterior view; C, middle parapodium, anterior view; D-F, setae in various views; G, posterior end, dorsal view.

around base (Fig. 4.4D-F). Pygidium with 2 thick, elongated lobes with blunted tips, each about 2.25 times as long as wide (Fig. 4.4G).

Biology. This species was taken from sediments having high sand and silt content.

Remarks. *Eteone brigitteae* is closely related to *E. fauchaldi* Kravitz and Jones (1979) from off Oregon and Washington in shelf depths and *E. aestuarina* Hartmann-Schröder (1959) from El Salvador in shallow water estuarine habitats. All three species have elongate pygidial lobes, setae from segment 2, a prostomium that is longer than wide, and dorsal cirri that are more or less asymmetrical in shape. In *E. fauchaldi*, the ventral tentacular cirri are only slightly longer than the dorsal, while both *E. brigitteae* and *E. aestuarina* have ventral tentacular cirri that are at least twice as long as the dorsal. The dorsal cirri are only vaguely asymmetrical in *E. fauchaldi*, but are strongly asymmetrical in *E. brigitteae* and *E. aestuarina*. *E. brigitteae* differs from both *E. fauchaldi* and *E. aestuarina* in having thick, robust anal cirri that end in blunt tips instead of ones that are long, tapering, and end in pointed tips. Specimens of *E. brigitteae* from the continental shelf (Santa Maria Basin) are indistinguishable from the specimen from the continental slope off San Francisco, except the for presence of a single pair of small eyes in the former. This species was identified as *E. fauchaldi* in the Phase II database.

Distribution. Known only from the eastern Pacific, the Santa Maria Basin, 90 m; off San Francisco in slope depths, 1745 m.

***Eteone californica* Hartman, 1936**

Figure 4.5

Eteone californica Hartman, 1936:131, figs. 43-46; 1948: 20-21, figs. 4a-d; 1968:249, figs. 1-3.— Blake, 1975b:180, 182, figs. 97-98.—Kravitz and Jones, 1979:9.—Wilson, 1988:390-392, figs. 1b-e, 14b.

Material examined. California: Tomales Bay, numerous specimens collected from intertidal sand flats.

Description. A moderately sized species, up to 20 mm long, 1.0 mm wide, for 95 segments. Color in life: pale, with light brown pigment on body (Hartman, 1936); in alcohol, tan ground color obscured by heavy, dark brown pigment concentrated in numerous small glands scattered over dorsal and ventral surfaces and dorsal and ventral cirri (Fig. 4.5A-B).

Prostomium broadly truncate, longer than wide, bearing 4 subequal frontal antennae mounted on expanded anterior globular tip, somewhat set off from main part of prostomium (Fig. 4.5A); with 2 pairs of dark red eyes situated at posterior margin; nuchal papilla present. Proboscis smooth basally, distally with dorsal ridge and 6 to 8 diagonal lines on either side, appearing rugose; terminating in ring of small globular papillae.

Segment 1 with 2 pairs of subequal, tapering tentacular cirri, each about same length as antennae; parapodia well developed, with thickened glandular bases and thick, broadly rounded neuropodial lobes; dorsal cirri thick, inflated, broader than long in middle region, becoming as long as wide in posterior segments (Fig. 4.5B); ventral cirri smaller than dorsal, narrower, pointed. Setae with pair of large teeth and 4 to 5 smaller denticles on tip of shaft (Fig. 4.5C). Pygidium bearing 2 digitiform anal cirri, each about 3 times as long as wide.

Biology. This species is common in bays and estuaries in the eastern Pacific in sediments having high sand content.

Remarks. *Eteone californica* was redescribed by Wilson (1988). The species is closely related to the more widely distributed *E. longa* (Fabricius). In *E. californica*, the prostomium is slightly longer than wide instead of wider than long. Local specimens from central and northern California are covered with numerous small pigment granules.

Type locality and type specimens. San Francisco Bay. Syntypes: USNM 20339.

Distribution. West coast of North America, Alaska to central California, intertidal to 88 m.

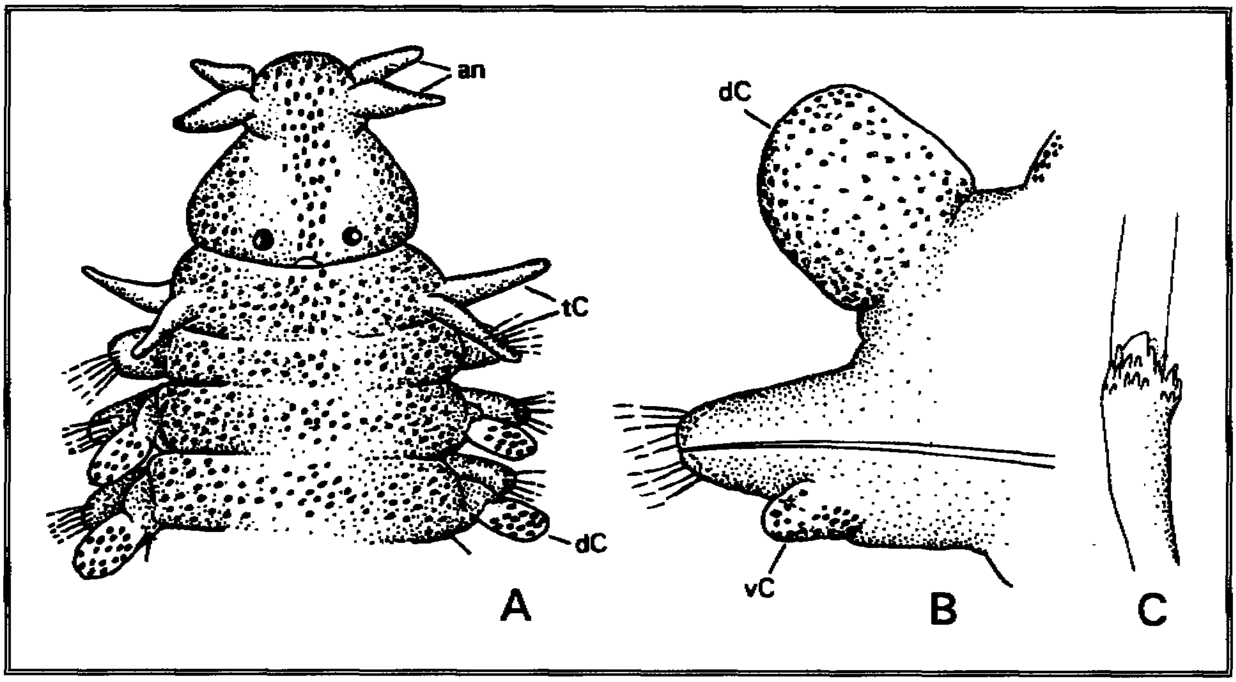

Figure 4.5. *Eteone californica*: A, anterior end, dorsal view; B, middle parapodium, posterior view; C, setae. (A, modified from Blake, 1975b; B, original; C, after Wilson, 1988).

Eteone leptotes Blake, 1992

Figure 4.6

Eteone sp. E. Hyland and Neff, 1988:A-3.
Eteone leptotes Blake, 1992:696, fig. 2.

Material examined. California: Santa Maria Basin, off Point San Luis, Sta. R-1 (11 paratypes SBMNH 35615); off Point Sal, Sta. PJ-2 (holotype and 2 paratypes, USNM 148682-148683), Sta. PJ-7 (3 paratypes USNM 148684), Sta. PJ-8 (2 paratypes USNM 148685), Sta. PJ-10 (1 paratype LACM-AHF Poly 1607), Sta. PJ-17 (13 paratypes LACM-AHF Poly 1608), Sta. R-7 (1 paratype, LACM-AHF Poly 1610), Sta. R-8 (100+ paratypes USNM 148686-148692); off Purisima Point, Sta. R-4 (2 paratypes LACM-AHF Poly 1609).

Description. A small, thin, threadlike species; holotype 2.8 mm long and 0.16 mm wide for 32 setigers; paratypes up to 6.3 mm long and 0.3 mm wide for 90 setigers. Color in alcohol: white to light brown with dark brown pigment organized in distinctive pattern; pigment concentrated in individual granules or spots concentrated on dorsum, ventrum, and dorsal cirri.

Prostomium and first segment fused, sometimes with notch at border of tentacular segment; prostomium narrowing abruptly anterior to eyes, then tapering to rounded tip, bearing 4 subequal antennae (Fig. 4.6A-B); 2 dark red eyes present at border of prostomium and peristomium; each eye with clear lens surrounded by dark red pigment; nuchal papilla located posterior to eyes. Proboscis entirely smooth. Tentacular cirri short, subequal (Fig. 4.6A-B). Second segment bearing prominent podial lobe with setae and ventral cirrus. Dorsal cirri first present from third segment (second setiger); each thickened, distally rounded, becoming longer, somewhat lanceolate in middle body segments (Fig. 4.6C); dorsal cirri of anterior and posterior segments as long as or shorter than podial lobe, in middle body segment slightly longer than podial lobe (Fig. 4.6C); all dorsal cirri covered with dark brown pigment granules. Ventral cirri short, non-pigmented, never longer than podial lobe (Fig. 4.6C).

Setae numbering 4 to 5 per fascicle; all compound spinigers with expanded tip of shaft bearing 2 prongs, covered with fine spinelets (Fig. 4.6E-F); blade with serrated cutting edge. Pygidium bearing 2 short, thick anal cirri (Fig. 4.6D), each bluntly rounded, darkly pigmented.

Biology. The minute, threadlike appearance of this species suggests that it may prey on small invertebrates, perhaps those that are of meiofaunal size. The species is most abundant at stations along the 90-m isobath having 50 to 60 percent sand. It is noteworthy that *E. leptotes* was not collected during the Phase I reconnaissance, but was taken regularly as part of the Phase II monitoring program. This may be a species that is normally lost when samples are live sieved through a 0.5-mm mesh sieve as was done during the Phase I program. In Phase II, the samples were live sieved through a 0.3-mm mesh sieve, and not sieved through a 0.5-mm mesh until later in the laboratory after preservation.

Remarks. *Eteone leptotes* is most closely related to *E. filiformis* Hartmann-Schröder, described from Western Australia in 1980. Both are minute, threadlike forms, and entirely different in this regard from other known species. *Eteone leptotes* differs from *E. filiformis* in having subequal dorsal cirri instead of dorsal ones that are longer. *Eteone filiformis* appears to be a larger species than *E. leptotes* because the three specimens described by Hartmann-Schröder (1980) are about twice as long and have more than twice as many setigers. Locally, this species has been previously identified as *E.* sp. E.

Distribution. Central California continental shelf, 90-150 m.

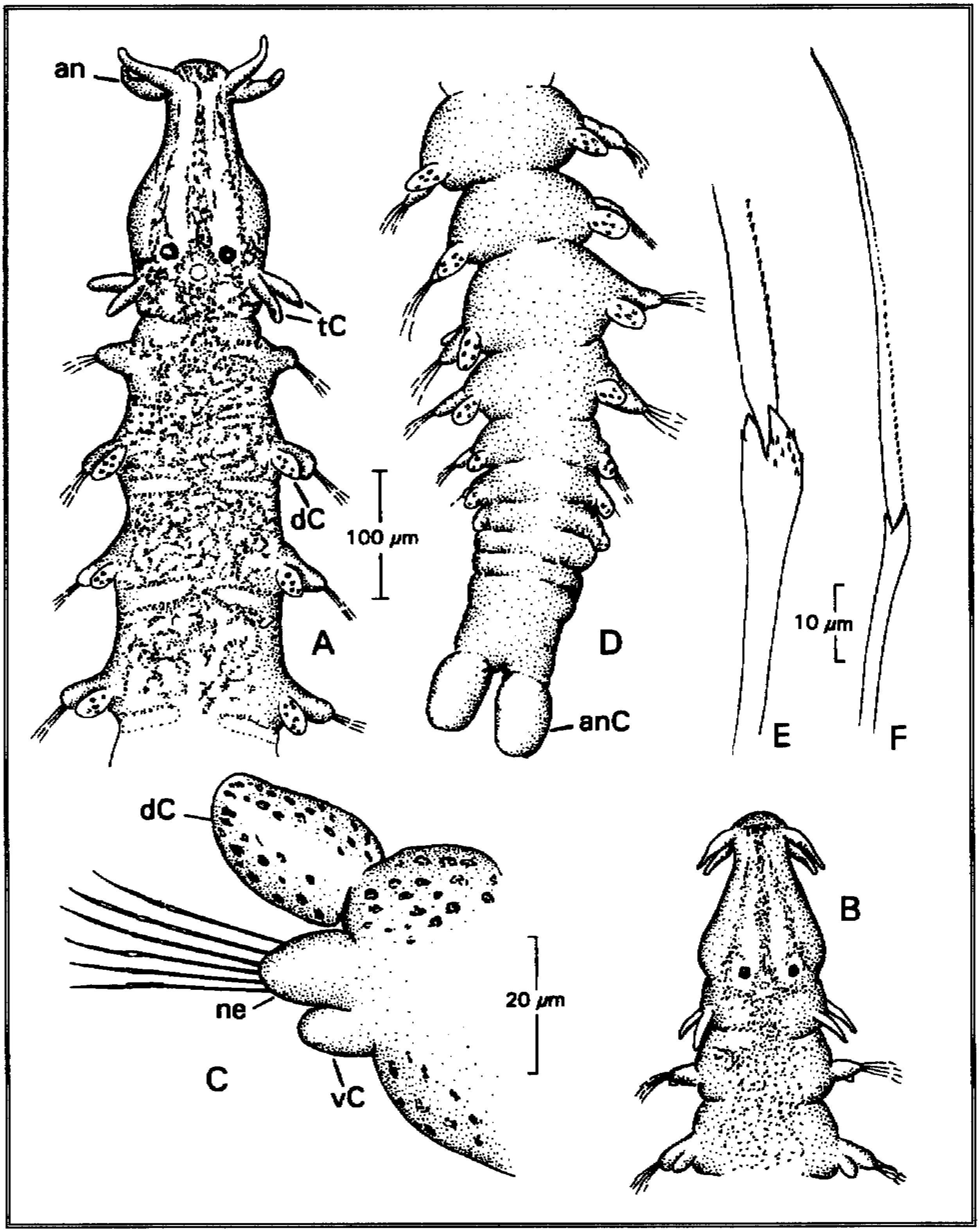

Figure 4.6. *Eteone leptotes*: A-B, anterior ends of different specimens, dorsal view; C, middle parapodium; D, posterior end, dorsal view; E-F, setae.

Eteone pigmentata Blake, 1992

Figure 4.7

Eteone sp. A. Lissner *et al.*, 1986:A-8.
Eteone sp. C. Hyland and Neff, 1988:A-3.
Eteone pigmentata Blake, 1992:696-698, fig. 3.

Material examined. California: Santa Maria Basin, off Point Sal, Sta. PJ-7 (holotype, USNM 148693); off Purisima Point, Sta. R-1, paratype (SBMNH 35616), R-8 (paratype, LACM-AHF Poly 1611), 12 (paratype, USNM 148694).

Description. A large robust species; holotype 28 mm long, 0.8 mm wide for 110 setigerous segments; paratype (USNM 000000) 18 mm long, 0.8 mm wide for 74 setigers and regenerating posterior portion. Color in alcohol: light brown with very dark brown to black pigment on segmental rings of anterior segments, dorsal and ventral cirri, podial lobes, and some lighter concentrations on prostomium; middle and posterior segments with less pigment; dark pigment concentrated in dense aggregations of small granules.

Prostomium and tentacular segment clearly separated by lateral furrow (Fig. 4.7A); prostomium about 1.5 times as wide as long, tapering abruptly from widest posterior portion to narrow anterior end; 4 antennae attached to expanded, rounded anterior tip; 2 subsurface eyes present, not conspicuous, each with lens and pigment cup. Small rounded nuchal papilla present posterior to eyes. Dorsal tentacular cirri slightly longer than ventral, extending posteriorly to border of setiger 3 (Fig. 4.7A). In dissection, proboscis appears smooth. Second segment bearing well-developed podial lobe with setae and ventral cirrus. Dorsal cirri first present from setiger 2; each dorsal cirrus thickened, inflated, oval, about as long as podial lobes (Fig. 4.7B); ventral cirri similar to dorsal, but with broader basal attachment. Both dorsal and ventral cirri with dark brown pigment granules, especially in anterior segments.

Setae numbering about 10 per fascicle; all compound spinigers with expanded tip bearing 4 to 5 long prongs (Fig. 4.7D-F); blade with very fine dentition along cutting edge. Pygidium bearing 2 short, thickened anal cirri, each darkly pigmented (Fig. 4.7C).

Biology. A relatively rare species, occurring in sediments having high sand and silt content.

Remarks. *Eteone pigmentata* appears to be closely related to *E. spilotus* Kravitz and Jones, 1979 described from shelf depths off the Columbia River, Oregon and Washington. Both species are darkly pigmented and have similarly shaped dorsal cirri. *E. pigmentata*, however, has a prostomium that is clearly wider than long, ventral cirri that are as long as the podial lobe, and dorsal tentacular cirri that are slightly longer than the ventral ones, whereas the prostomium of *E. spilotus* is longer than wide, the ventral cirri are always shorter than the podial lobe, and the tentacular cirri are subequal. The setae of *E. spilotus* were described by Wilson (1988) and were found to have four large teeth on the end of the shaft and several smaller ones. This arrangement was unique among the species of *Eteone* that he studied. Very similar setae are present in *E. pigmentata*, thus emphasizing the close similarity of these two species.

Distribution. Central California continental shelf, 90-150 m.

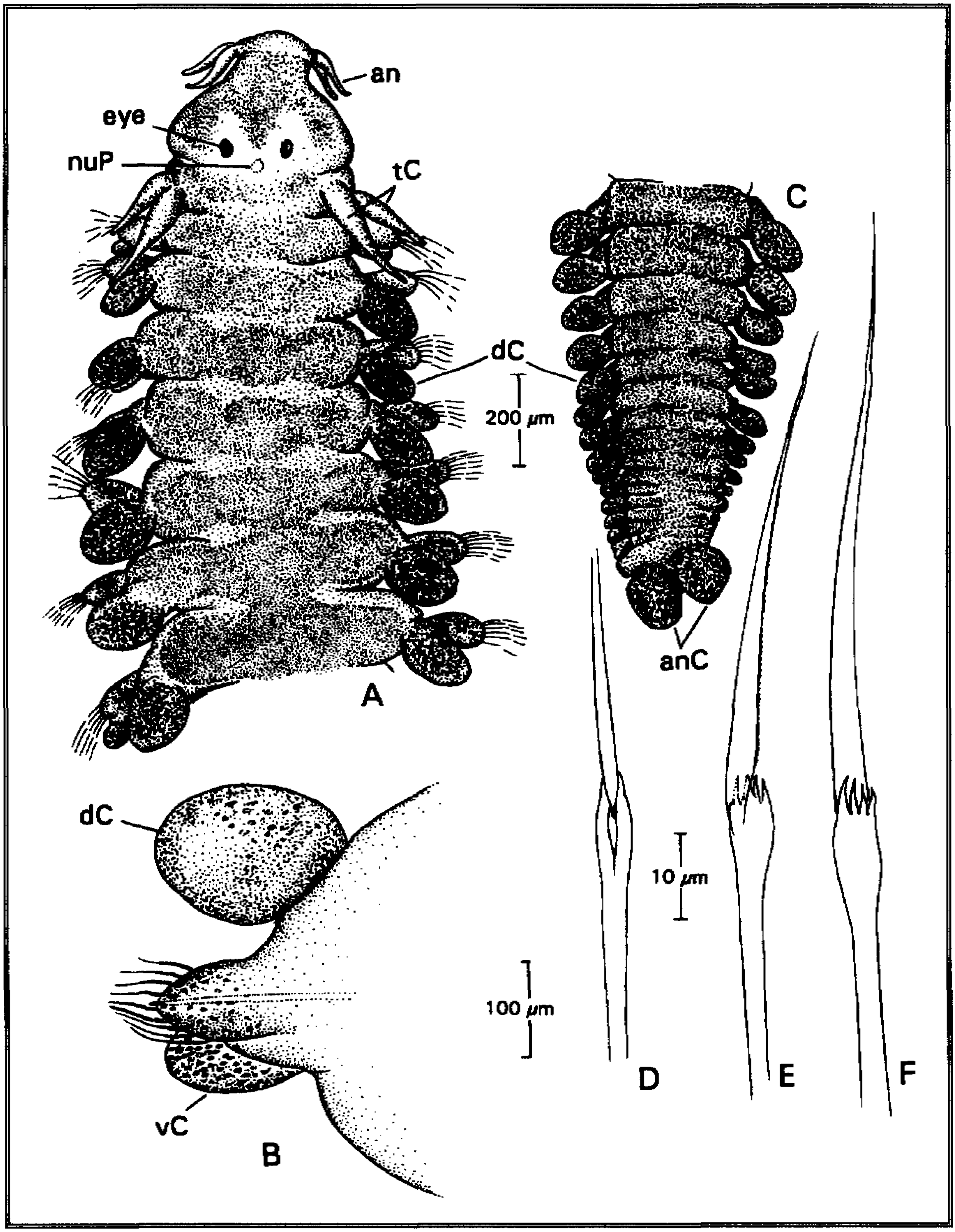

Figure 4.7. *Eteone pigmentata*: A, anterior end, dorsal view; B, middle parapodium, anterior view; C, posterior end, dorsal view; D-F, setae in different views.

Genus *Lugia* Quatrefages, 1865

Type species: *Eteone pterophora* Ehlers, 1864, by original designation.

Diagnosis. Prostomium with 4 antennae; median antenna and nuchal papilla lacking. One pair tentacular cirri on first segment, setae absent; second segment with 1 pair dorsal tentacular cirri, normal ventral cirrus or cirrus only slightly larger than normal, and setae present; third segment with normal dorsal and ventral cirri, and setae; tentacular formula: $0^1/_0 + S^1/_V + S^D/_V$ or $0^1/_0 + S^1/_1 + S^D/_V$. Proboscis with soft papillae. Tentacular segments more or less free from one another and from prostomium.

Remarks. Five species of the genus *Lugia* have been described: *L. pterophora* (Ehlers, 1864) from the Mediterranean, *L. abyssicola* Uschakov (1972) from deep water off Japan and California, *L. incognita* Campoy and Alquézar (1982) from off Spain, and *L. atlantica* Villalba and Viétez (1988), also from Spain; *Lugia rarica* Uschakov (1958) from off Kamchatka has been referred to *Mystides* by Uschakov (1972). Pleijel (1991), as part of review of benthic Phyllodocidae, reviewed the species assigned to *Lugia* and determined that the types of *L. incognita* and *L. atlantica* were both juveniles of Eulalia. He also considered that the type species, *L. pterophora*, was *nomina dubia* because no type material was available. Pleijel (1991) noted that *L. abyssicola* was the only known species of the genus that had the tentacular characters that agreed with the original generic diagnosis. Pleijel (1991) treated the genus *Lugia* as nomina dubia.

A new species, *L. uschakovi* Blake, that agrees fully with the generic diagnosis of *Lugia* has been discovered in the Santa Maria Basin and was described by Blake (1992). The preceding generic diagnosis was presented by Blake (1992) and follows that of Uschakov (1972). The genus is retained because both Uschakov's species, *L. abyssicola* and *L. uschakovi* agree with the definition. The status of the Type species, *L. pterophora*, is not known and it will be necessary to collect new specimens from the type-locality before the status of the genus *Lugia* can be fully assessed.

***Lugia uschakovi* Blake, 1992**

Figure 4.8

Lugia sp. A. Hyland and Neff, 1988:A-3.
Lugia uschakovi Blake, 1992: 700, fig. 4.

Material examined. California: Santa Maria Basin, off Point Sal, Sta. PJ-1 (paratype, USNM 148695), PJ-5 (paratype, USNM 148696), PJ-7 (3 paratypes, LACM-AHF Poly 1612), PJ-8 (holotype, USNM 148697; paratypes LACM-AHF Poly 1613), PJ-10 (paratype, LACM-AHF 1614), R-8 (2 paratypes, USNM 148698); off Purisima Point, R-4 (4 paratypes, SBMNH 35613 and 35614).

Description. A small species, up to 5 mm long, 0.2 mm wide, for about 65 setigers. Color in alcohol: light tan with brown specks on prostomium, body, and dorsal and ventral cirri.

Prostomium longer than wide, tapering anteriorly to slightly expanded apex bearing 4 short, cirriform antennae (Figs. 4.8A-B); eyes and nuchal papilla lacking; proboscis not observed. First segment only weakly distinguished from prostomium dorsally and ventrally, bearing a single pair of short, cirriform tentacular cirri; segment 2 first setigerous, with short podial lobe, short, cirriform dorsal tentacular cirrus and short lamellate ventral tentacular cirrus about 1-½ times length of normal ventral cirri on subsequent segments (Fig. 4.8B); segment 3 with normal dorsal and ventral cirri; tentacular formula: $0^1/_0 + S^1/_1 + S^D/_V$. Dorsal cirri short, conical, glandular, becoming larger in middle body segments (Fig. 4.8D); ventral cirri conical, about one-half size of dorsal cirri (Fig. 4.8D); both dorsal and ventral cirri with brown pigment

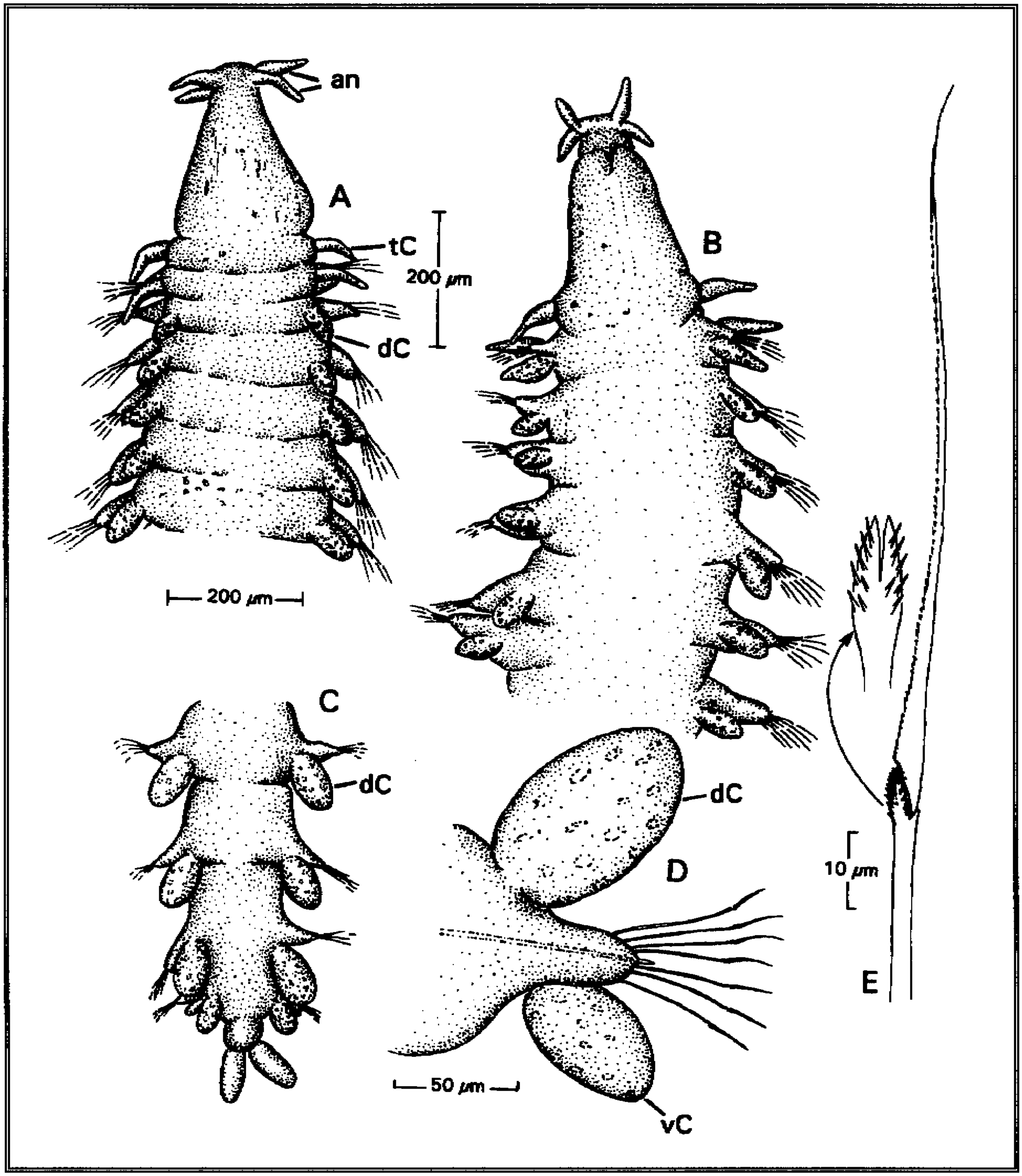

Figure 4.8. *Lugia uschakovi*: A, anterior end, dorsal view; B, same, ventral view; C, posterior end, dorsal view; D, middle parapodium, anterior view; E, seta [inset not to scale].

spots. Setae arranged in spreading fascicle of 5 to 7 compound spinigers; each spiniger with broad blade bearing conspicuous denticles on cutting edge; tip of shaft with 2 rostral teeth, each with numerous fine denticles (Fig. 4.8E). Pygidium with 2 narrow, blunt-tipped anal cirri (Fig. 4.8C).

Biology. The species occurred in sediments having high sand and silt content and little clay.

Remarks. *Lugia uschakovi* from the continental shelf off California, most closely resembles *L. abyssicola* Uschakov from deep water off Japan in having an elongated prostomium that lacks eyes. The two species are most readily distinguished from one another by the form and length of the tentacular cirri. In *L. uschakovi* the dorsal tentacular cirri of segments 1 and 2 are both short, cirriform and of the same length. In contrast, the dorsal tentacular cirri of segment 2 in *L. abyssicola* are about 1-½ times as long as that of the first segment. Further, the ventral tentacular cirrus of segment 2 in *L. uschakovi* is narrow and elongate instead of leaf-shaped.

Distribution. California continental shelf, 90-150 m.

Genus *Mystides* Théel, 1879

Type species: *Mystides borealis* Théel, 1879, by monotypy.

Diagnosis. Prostomium with 4 antennae; nuchal papilla absent; 1 pair of dorsal tentacular cirri on first segment, ventral cirri and setae absent; second segment with 1 or 2 pairs of tentacular cirri, setae present; dorsal cirri always lacking on segment 3; tentacular formula: $0^1/_0 + S^1/_N + S^0/_V$ or $0^1/_0 + S^1/_1 + S^0/_V$. Proboscis with soft papillae. All 3 anterior segments distinctly separated from one another and prostomium. Dorsal and ventral cirri usually broad, oval. Anal cirri short, oval or long, narrow.

Remarks. The genus *Mystides* as presently defined includes a diverse assemblage of species that are superficially quite different from one another. It is likely that a careful evaluation of species characters including fine structure of the setae, will provide criteria that will result in the genus being broken up. For example, the type species, *M. borealis* and its close relative *M. caeca* have short, nearly oval prostomia bearing long, thin antennae, and compound setae with prominent spiked teeth on the tip of the shaft (Blake, 1988), whereas other species have more elongated prostomia, short cirriform antennae, and setae with numerous teeth on the tip of the shaft (Hartmann-Schröder, 1963, 1979, 1983).

The majority of *Mystides* species are described from deep water. Two species, *M. borealis* and *M. caeca*, occur in continental shelf and upper slope depths along both the east and west coasts of North America. Both species have been found in the present collections from the Santa Maria Basin.

***Mystides borealis* Théel, 1879**

Figure 4.9

Mystides borealis Théel, 1879:35-37, pl. 2, figs. 29-32.—Fauvel, 1923:181, fig. 65a-d.—Pettibone, 1954:232, fig. 27b; 1963:74-75, Fig. 17c.—Uschakov, 1972:120, pl. 2, figs. 1-4.—Gathof, 1984:19-10, fig. 19-5, 19-6; Blake, 1988:251, fig. 3A-B.—Lissner *et al*., 1986:A-8.
Mystides notialis: Hartmann-Schröder, 1963:207-209, figs. 1-6.—Pleijel, 1993:127-128, fig. 89, map 43.
?*Mystides* nr. *borealis*: Eibye-Jacobsen, 1992:592-593.

Material examined. California: off Point Conception, Sta. BRA-2 (1).

Description. A small to moderate sized species, reported up to 16 mm long and 0.8 mm wide for 75 setigers; North American specimens smaller, usually no more than 5 to 6 mm long, 0.5 mm wide for 45 to 60 setigers; specimen from Sta. 2, 2.0 mm long, 0.4 mm wide for 21 setigers. Color in alcohol: opaque white to light tan, with scattered orange or brown pigment on dorsal and ventral cirri; specimen from Santa Maria Basin with non-pigmented dorsal cirri, and heavily pigmented ventral cirri.

Prostomium distinctly oval, with head appearing nearly rounded, set off from first segment (Fig. 4.9A); with 2 large dark red eyes, each with clear lens surrounded by pigmented cup; 4 long, thin antennae present (Fig. 4.9A). Three tentacular cirri present on first 2 segments; tentacular segments free from one another, visible dorsally; tentacular cirri expanded basally, tapering to narrow tips, arranged in the following formula: $0^{1}/_{0} + S^{1}/_{1} + S^{0}/_{V}$. Dorsal cirri smaller than ventral cirri throughout most of body, each oval, heavily glandular (Fig. 4.9B); ventral cirri with broad basal attachment, also glandular in appearance, usually with some orange or brown pigment. Setae all compound spinigers, with fine serrations on blade and several small teeth or denticles on 1 to 2 large rostral spines (Fig. 4.9C). Pygidium with 2 oval anal cirri.

Biology. *Mystides borealis* is a continental shelf species, but has also been recorded from middle and upper slope depths on the U.S. Atlantic. The species is usually found in coarse sediments of mixed sand and silt.

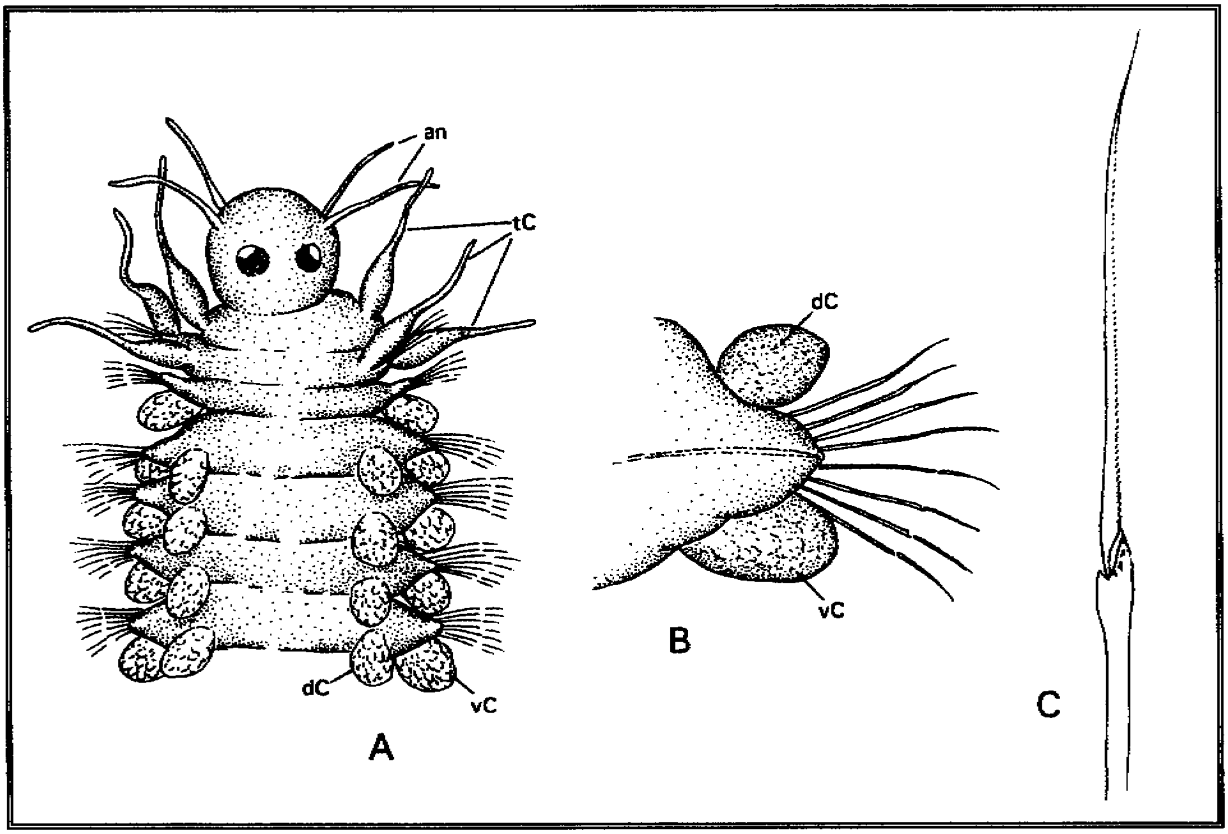

Figure 4.9. *Mystides borealis*: A, anterior end, dorsal view; B, middle parapodium, anterior view; C, seta.

Remarks. *Mystides borealis* is readily distinguished from *M. caeca* (see below) by the presence of conspicuous prostomial eyes. Eyes are entirely lacking in *M. caeca*. Furthermore, *M. borealis* has ventral cirri which are larger than the dorsal cirri throughout most of the body, a feature which is unusual among phyllodocids. The compound setae of *M. borealis* have several large spines and small denticles on the tips of the shaft of the compound setae instead of a single rostral spine with few denticles as in *M. caeca*.

Type locality. Arctic Ocean, Novaya Zemlya, 7-34 m.

Distribution. California, continental shelf, 225 m; U.S. Atlantic coast, Eastern Canada and New England to Delaware 100-1500 m; Gulf of Mexico, Ireland, Mediterranean, Madeira, intertidal to 391 m.

Mystides caeca Langerhans, 1880

Figure 4.10

Mystides caeca Langerhans, 1880:310-311, pl. 16, fig. 42 a-d.—Blake, 1988:251-252 figs. 3A-D.—Pleijel and Dales, 1991:64-65, fig. 11.—Pleijel, 1993:129-131, figs. 90-91, map 14.
Mystides borealis caeca: Hartman, 1959:156.—Uschakov, 1972:118-119.
Mystides (Mesomystides) borealis: Southern, 1914:72-73, pl. 8, fig. 19. *Not* Théel, 1879.
Mystides nr. *borealis*: Hyland and Neff, 1988:A-8.

Material examined. California: Santa Maria Basin, off Point Sal, Sta. PJ-1, (1), PJ-2, (2), PJ-5, (1); off Purisima Point Sta. R-4; off San Francisco, 37°23.94'N, 123°14.86'W, 1263 m (1).

Description. A small, thin species, up to 7 mm long, 0.25 mm wide for about 50 setigers. Color in alcohol: opaque white to light tan with distinct orange pigment on dorsal and ventral cirri.

Prostomium oval, bearing 4 long, thin antennae; eyes lacking (Fig. 4.10A). Three tentacular cirri present on first 2 segments; tentacular segments partially fused dorsally, free ventrally; setae first present on segment 2; each tentacular cirrus expanded basally, then tapering apically to thin tips (Fig. 4.10A). Tentacular formula: $0^{1}/_{0} + S^{1}/_{1} + S^{0}/_{V}$. Parapodia with thickened, conical dorsal cirri and narrower, blunt-tipped ventral cirri (Fig. 4.10B); each cirrus lumpy in appearance, with numerous orange colored glands. Each podial lobe with spreading fascicle of 7 to 8 compound spinigers, each spiniger with fine serrations along edge of blade and single narrow tooth or rostrum on tip of shaft; rostrum with 1 to 2 subapical denticles (Fig. 4.10C). Body terminating with 2 oval, orange cirri.

Biology. *Mystides caeca* occurs on the outer continental shelf to lower slope depths, thus occupying a considerably greater depth range than *M. borealis*. The species occurs in silty sediments with high sand and low clay inventories.

Remarks. Although originally described as a separate species, *M. caeca* was synonymized with *M. borealis* by Hartmann-Schröder (1963). Other authors preferred to treat *M. caeca* as a subspecies of *M. borealis* (Hartman, 1959; Uschakov, 1972), with the distinguishing character being the presence of eyes in the stem species. Blake (1988) demonstrated that *M. caeca* differed sufficiently from *M. borealis* to be considered a separate species. *M. caeca* differs consistently from *M. borealis* in lacking a large pair of prostomial eyes, and in having a less crowded appearance to the body segments. *M. caeca* bears characteristic orange pigment on the tentacular cirri, dorsal cirri, and anal cirri, whereas *M. borealis* has light brown pigment on the same structures. There are also differences between the two species in the dentition on tip of the setal shaft. In *M. caeca,* a single rostral spine is present, whereas several apical teeth are present in *M. borealis*.

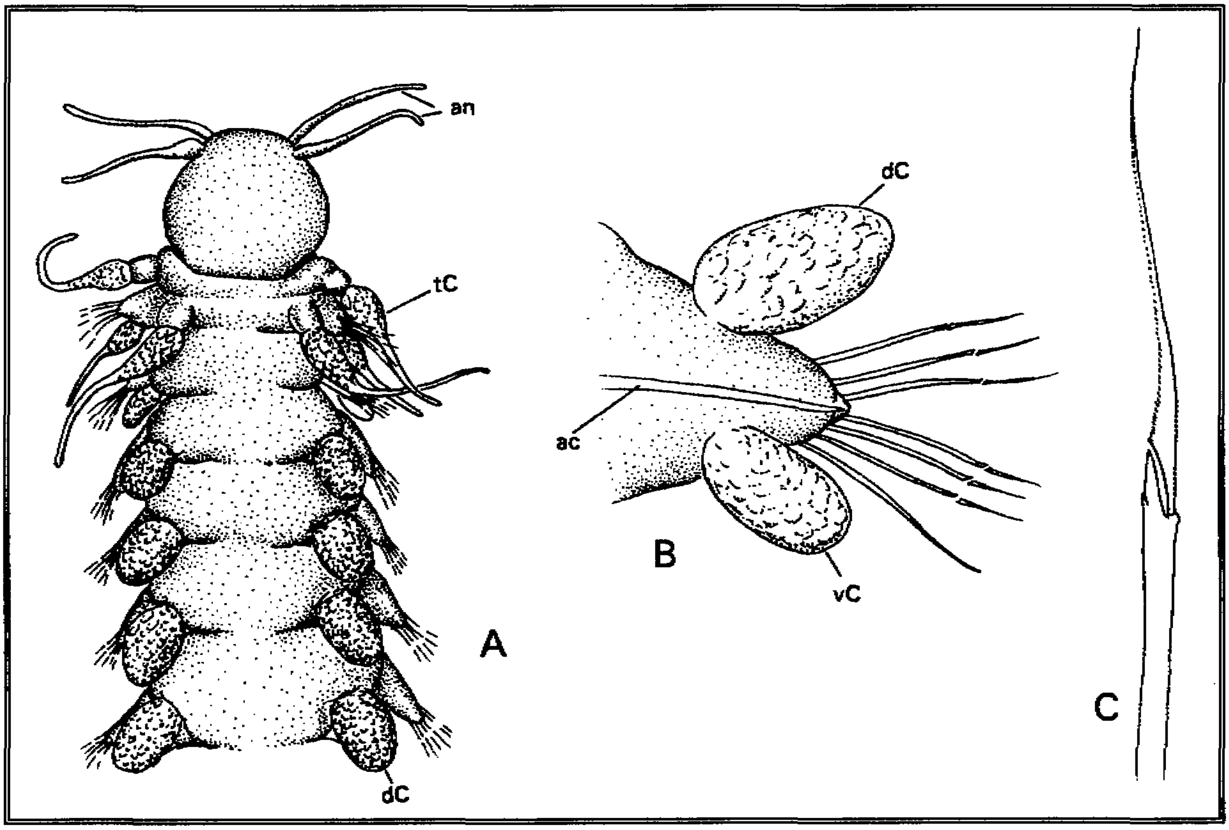

Figure 4.10. *Mystides caeca*: A, anterior end, dorsal view; B, middle parapodium, posterior view; C, seta.

Type locality. Madeira.

Distribution. Off California, Santa Maria Basin, 135-560 m; off the Farallones, 1263 m; western North Atlantic, 102-2180 m; eastern North Atlantic: Madeira; Ireland; Skagerrak; east coast of England, 10-400 m.

Genus *Hesionura* Hartmann-Schröder, 1958

Hesionura Hartmann-Schröder, 1958.
Eteonides Hartmann-Schröder, 1960.

Type species: *Hesionura fragilis* Hartmann-Schröder, 1958, by original designation.

Diagnosis. Prostomium longer than wide, with 4 antennae; nuchal papilla absent. With 2 tentacular segments free from one another and prostomium. Proboscis with numerous soft papillae. With pair of long, slender dorsal tentacular cirri on segments 1 and 2; segment 2 with normal ventral cirrus or sometimes with enlarged thickened cirrus; segment 2 always lacking setae; segment 3 always lacking dorsal cirrus. Tentacular formula: $0^1/_0 + 0^1/_V + S^0/_V$ or $0^1/_0 + 0^1/_1 + S^0/_V$. Dorsal and ventral cirri typically narrow, elongate. Anal cirri long, slender.

Remarks. The genus *Hesionura* is a senior synonym of *Eteonides* Hartmann-Schröder, 1960. The genus (as *Eteonides*) was reviewed by Hartmann-Schröder (1963) and a key and descriptions of all known species provided. Species of *Hesionura* are typically small, threadlike forms that are found in sediments having high sand content. The small interstitial faunal elements of sands have not been well studied in California and only a single species, *Hesionura coineaui difficilis*, has been recorded to date. This species was recorded in the Santa Maria Basin as part of the Phase I reconnaissance.

Hesionura coineaui difficilis (Banse, 1963)

Figure 4.11

Eteonides coineaui difficilis Banse, 1963:197.—Hartmann-Schröder, 1963:223-225, figs. 33-35.
Hesionura coineaui difficilis Hartman, 1968:285, figs. 1-3.—Lissner *et al.*, 1988:A-8.

Material examined. No specimens available, recorded from the Phase I reconnaissance.

Description. A small, slender species, 4.6 mm long for 65 segments. Prostomium longer than wide; with 2 small eyes at posterior margin; with 4 long frontal antennae (Fig. 4.11A). Proboscis covered with numerous papillae. Segments 1 and 2 free from one another; segment 1 bearing a single pair of long, slender tentacular cirri; segment 2 with long slender dorsal tentacular cirri and a short, foliaceous ventral tentacular cirrus (Fig. 4.11A), about twice size of normal ventral cirri; setae first present from segment 3. Parapodia with short, slender and pointed dorsal cirrus, long, cirriform ventral cirrus, and fascicle of 4 to 5 compound setae arising from short neuropodium (Fig. 4.11B). Setae with short ribbed blades and shaft with 2 or 3 distal teeth (Fig. 4.11C). Anal cirri long, slender.

Biology. From the Puget Sound the species has been reported from coarse sand, in 20-100 m, in water temperatures that range between 7-10°C.

Remarks. Although similar to the stem species, the subspecies *H. coineaui difficilis*, is a marine form rather than estuarine (however, Hartmann-Schröder (1963) found the species on the Mediterranean coast of France). The morphological differences between the stem form and subspecies are limited to pigment and setal details. In the stem form, pigment is distributed over the entire body, while in the subspecies it is limited to the ventral cirri. The setae of the stem form have blades that are all subequal in the fascicle, whereas in the subspecies, the two innermost setae have blades that are almost twice the length of the rest. It is likely that these differences, especially those involving the setae are actually sufficient to warrant a full species designation for Banse's subspecies.

Type locality and Type specimens. San Juan Islands, Washington. USNM.

Distribution. Eastern Pacific, Puget Sound, 20-100 m; Farnsworth Bank, west of Santa Catalina Island.

Genus *Protomystides* Czerniavsky, 1882

Type species: *Mystides bidentata* Langerhans, 1880, by monotypy.

Diagnosis. Prostomium with 4 antennae; elongate or rounded, nuchal papilla lacking; eyes present or absent; proboscis with soft papillae. All 3 tentacular segments distinctly separated from one another and prostomium; setae present from second segment. Tentacular cirri numbering 3 to 4 pairs of tentacular cirri on first 3 segments; tentacular formulae: $0^1/_0 + S^1/_V + S^1/_V$ or $0^1/_0 + S^1/_1 + S^1/_V$.

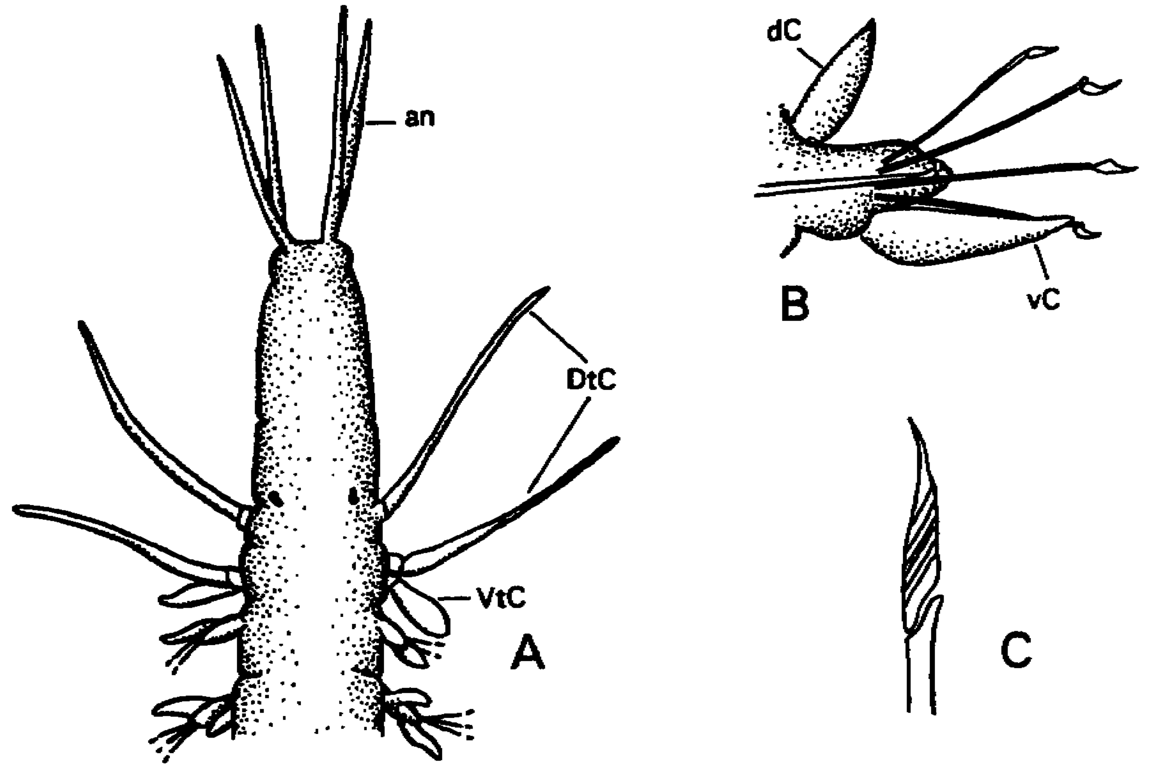

Figure 4.11. *Hesionura coineaui difficilis*: A, anterior end, dorsal view; B, parapodium; C, seta. (after Banse, 1963).

Remarks. Most of the known species of *Protomystides* are found in continental shelf or slope environments (Hartmann-Schröder, 1963) and several are known from the deep sea (Uschakov 1972; Blake & Hilbig, 1990; Blake, unpublished). Pleijel (1991) moved some species to *Eulalia* because a nuchal papilla was found that corresponded to a median antenna. Included in this revision was *P. papillosa* Blake from hydrothermal vents on the East Pacific Rise (Blake, 1985). The species has a small nuchal papilla and thus agrees with Pleijel's definition of *Eulalia*. There have been few reports of the genus *Protomystides* from North America. No species of *Protomystides* were recorded by Hartman (1968) in her Atlas of California polychaetes. Blake and Hilbig (1990) described *P. verenae* from hydrothermal vents on the Juan de Fuca Ridge. Additional undescribed species are known from deep-sea habitats, including three new species from the U.S. Atlantic slope, one new species from the deep-sea methane seep community on the Florida Escarpment, and at least two undescribed species from lower slope depths off northern California (Blake, unpublished). Another species has been discovered in the Santa Maria Basin and was recently described by Blake (1992) as *P. mariaensis*.

Protomystides mariaensis Blake, 1992

Figure 4.12

Protomystides sp. A. Lissner *et al.*, 1986:A-8.
Protomystides mariaensis Blake, 1992:702, fig. 5.

Material examined. California: Santa Maria Basin, off Point Buchon, Sta. 13 (holotype, USNM 148700).

Description. A small, slender species, 11.7 mm long, 0.32 mm wide for 96 segments. Color in alcohol: light tan with dark reddish, brown pigment on dorsal and ventral cirri and on anal cirri.

Prostomium slightly longer than wide, rounded anteriorly, bearing 4 frontal antennae on elevated cushion (Fig. 4.12A-B); with a pair of dark eyes; no nuchal papilla apparent (Fig. 4.12A). Segments 1 to 3 distinct, set off from one another and from prostomium; dorsal tentacular cirri of segments 1 to 2 elongate, cylindrical, tapering, with cirrus of segment 1 longest; ventral tentacular cirri of segment 2 broad, somewhat flattened, tapering, about 3 times larger than normal ventral cirrus (Fig. 4.12A-B); tentacular formula: $0^1/_0 + S^1/_1 + S^1/_V$. Neuropodia short, rounded on tip, with fascicle of 6 to 8 compound setae; dorsal cirri thickened, oval, on basal cirrophore (Fig. 4.12C); ventral cirri smaller, elongate, rounded on tip (Fig. 4.12C). Setae with a large spike and numerous minute spinelets on tip of shaft (Fig. 4.12E-F). Anal cirri thick, with blunt tips, about 2-½ times as long as broad (Fig. 4.12D).

Biology. The specimen occurred at a single station, at 220 m, having sediment with 85% silt content.

Remarks. Differential diagnoses were provided by Blake (1992). *Protomystides mariaensis* is most similar to *P. bilineata* LaGreca (1947) from the Mediterranean in having an enlarged ventral tentacular cirrus on segment 2, in having eyes, and in having a prostomium that is slightly longer than wide. *P. mariaensis* differs in having the body uniformly pigmented with small dark granules including very darkly pigmented dorsal, ventral, and anal cirri instead of two distinctive dark lines of pigment that extend from segment 3 down along the dorsal surface of the body. Additionally, the dorsal cirrus of *P. bilineata* is only as long as or slightly longer than the neuropodium, whereas in *P. mariaensis*, the dorsal cirrus is a large structure, extending for at least one-half of its total length beyond the neuropodium. Keys to the known species of *Protomystides* are provided by Hartmann-Schröder (1963) and Uschakov (1972).

Distribution. Known only from the Santa Maria Basin, 220 m.

Genus *Notophyllum* Oersted, 1843

Type species: *Phyllodoce foliosum* Sars, 1835, designated by Bergström (1914).

Diagnosis. Prostomium with 5 antennae; 1 pair of eyes present, usually large; posterior margin bearing distinctive nuchal organs, called epaulets; proboscis with lateral rows of leaf-shaped papillae. Segments 1 or 1 and 2 reduced dorsally; with 4 pairs of cylindrical tentacular cirri; tentacular formula: $(0^1/_0 + S^1/_1) + S^1/_V$. Parapodia subbiramous, with notoaciculae and 1 to few thin capillary setae in notopodium; neuropodium with aciculae and numerous compound setae. Dorsal cirri large, wider than long, nearly covering dorsal side of body.

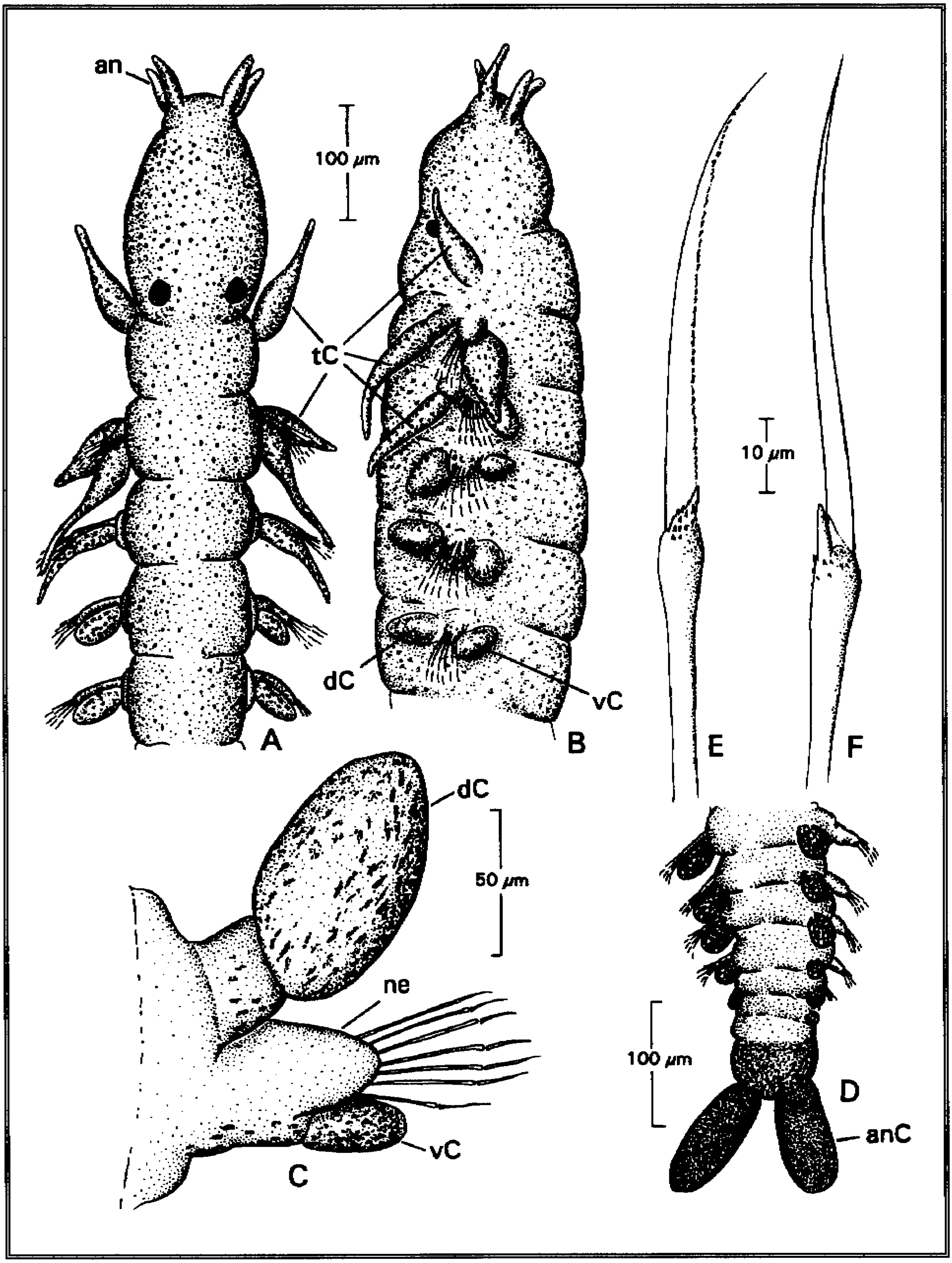

Figure 4.12. *Protomystides mariaense*: A, anterior end, dorsal view; B, same, lateral view; C, middle parapodium; D, posterior end, dorsal view; E-F, setae.

Remarks. *Notophyllum* was summarized by Uschakov (1972) and redefined by Pleijel (1991). *Notophyllum imbricatum* Moore (1906) has been recorded from off California by Treadwell (1914) and Hartman (1961; 1968). Another species, *N. tectum* (Chamberlin, 1919) is known from a single account from Southern California (see Banse, 1972 for redescription). No specimens of *Notophyllum* have been collected as part of the MMS Phase I and II programs.

Genus *Clavadoce* Hartman, 1936

Type species: *C. splendida* Hartman, 1936, by original designation.

Diagnosis. Prostomium with 5 antennae; 1 pair of large eyes present; proboscis with diffusely arranged papillae. All tentacular segments free from one another, segment 1 dorsally reduced; tentacular formula: $(0^{1}/_{0} + S^{1}/_{1}) + S^{1}/_{V}$; tentacular cirri flattened. Ventral cirri very large, oriented at oblique or right angle to acicula.

Remarks. Banse (1973) reviewed species related to *Eulalia* having a large, reniform-shaped ventral cirrus with a broad basal attachment. He determined that a distinct group of species could be identified that were distinct from *Eulalia*. Banse divided these species into two genera: (1) *Clavadoce* Hartman, 1936, which had a proboscis with diffusely arranged papillae along the entire length and flattened tentacular cirri; and (2) *Bergstroemia* which had a proboscis with diffusely arranged papillae proximally and rows of papillae distally, and cylindrical tentacular cirri. The flattened or cylindrical nature of the tentacular cirri is not a consistent feature (Blake, 1988), and in fact, the type species of *Clavadoce*, *C. splendida*, has cylindrical rather than flattened cirri (see below). In a revision of benthic phyllodocids, Pleijel (1991) has referred the type species of *Bergstroemia* to *Austrophyllum*, and referred the second species that Banse (1973) had referred to *Bergstroemia*, *Eulalia nigrimaculata* Moore, to *Clavadoce*. Pleijel (1991) examined the holotypes of both *Eulalia nigrimaculata* and *Clavadoce splendida* Hartman and concluded that the latter species was junior synonym of the former.

In general, the species of this genus would appear to be rare. In reviewing the phyllodocids of California for this project, several additional specimens of *C. splendida* have come into my possession from central and northern California. Two specimens labeled as *Genetyllis ?castanea* from the Phase I collections in the Santa Maria Basin have also been identified as *C. splendida*. After examining these specimens and the holotype of *Eulalia nigrimaculata*, I have concluded that both species are valid and quite distinct from one another both with regard to morphology and habitat. *C. splendida*, occurs in rocky habitats from the intertidal to shallow subtidal depths (Hartman, 1936, 1968; Blake, 1975b; this study), *C. nigrimaculata* (Moore), occurs in outer continental shelf depths, apparently in soft sediments (Banse, 1973).

***Clavadoce splendida* Hartman, 1936**

Figure 4.13

Clavadoce splendida Hartman, 1936:123-126, figs. 13-14; 1959:145; 1961:12, 59; 1968:241, figs. 1-2.—Blake, 1975b:182, fig. 104.
Clavadoce nigrimaculata: Pleijel, 1991:234, 253-254 (in part)

Material examined. California: Bodega Harbor, Doran Jetty, intertidal in algal holdfast, 12 June 1972, coll. J.A. Blake (1).—Cayucos, intertidal, rocky area with abundant algae, 28 June 1961, coll. K.H. Woodwick (4, 1).—Santa Maria Basin, off Point Arguello, Sta. BRA-6, 54-63 m (2, SBMNH).

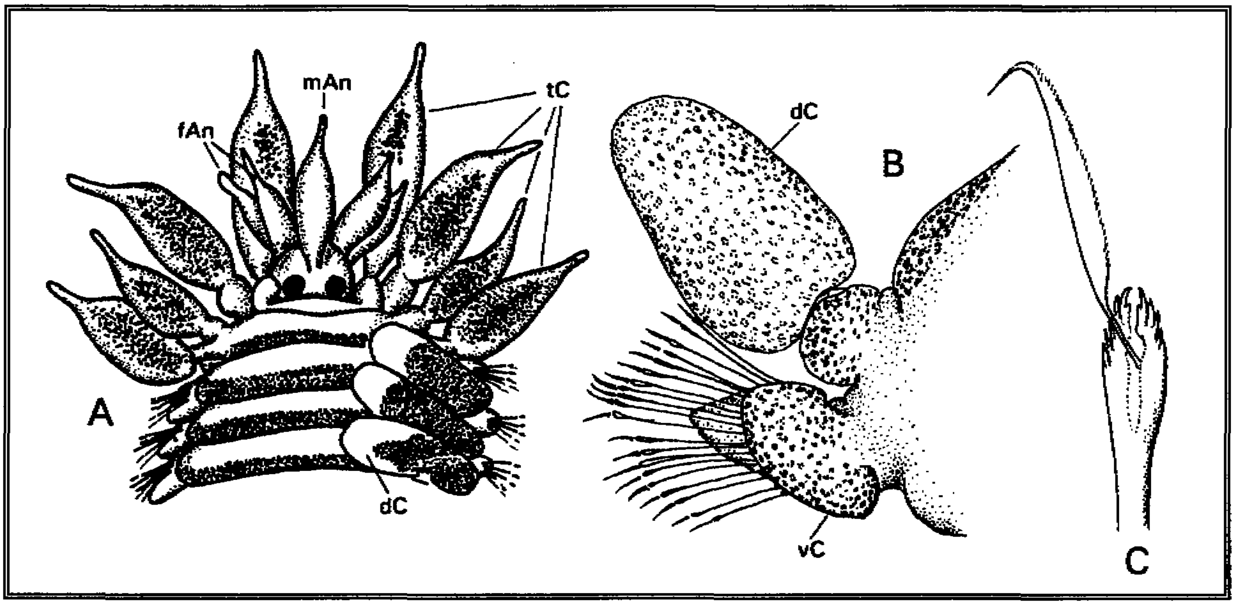

Figure 4.13. *Clavadoce splendida*: A, anterior end, dorsal view; B, middle parapodium, anterior view; C, seta.

Description. A small species, largest specimen 8 mm long, 0.8 mm wide for 60 segments. Color in alcohol: orange, with dark pigment spots concentrated on tentacular cirri, dorsal and ventral cirri, and across dorsal and ventral segmental ridges (Fig. 4.13A). Body dorsoventrally compressed, uniformly wide, narrowing in last 10 to 15 segments.

Prostomium oval, broadly rounded on anterior margin bearing 4 large, widely spaced frontal antennae and 1 median antenna (Fig. 4.13A); each antenna cylindrical, clavate, tapering distally to form narrow, papillate tip; with 2 large eyes, each with lens. Segment 1 reduced, not visible dorsally; segments 2 and 3 visible dorsally. Setae first present from segment 2. Tentacular cirri cylindrical, clavate, tapering to narrow tips, none flattened (Fig. 4.13A). Normal dorsal cirri present from segment 1; each dorsal cirrus elongate, about twice as long as wide, with smoothly rounded distal ends (Fig. 4.13B); each dorsal cirrus arising from rounded basal cirrophore. Ventral cirri first present from segment 3; each ventral cirrus oblique to axis of neuropodium, reniform, about twice as long as wide (Fig. 4.13B); ventral cirrus extending slightly dorsal to neuropodium; neuropodium distally pointed, bearing fascicle of 12 to 20 compound spinigers. Each seta with tip of shaft prominently expanded apically, bearing several short teeth on tip; blade narrow, with finely serrated edge (Fig. 4.13C). Pygidium lacking anal cirri.

Biology. *Clavadoce splendida* is found among algae in rocky intertidal habitats. In 1972, I was able to observe the specimen from Bodega Harbor alive in an aquarium. The specimen was highly mottled in its coloration, with various shades of orange, yellow, and brown. The dorsal cirri were held more or less erect over the dorsum. The specimen moved with an unusual mode of locomotion. The worm's body of 60 segments moved in units of about 20 each, so that the first 20 segments would, for example, move to the right rapidly, while the trailing middle and posterior blocks of segments would follow with similar movements. As each section of the body moved, the dorsal cirri would be thrown in the opposite direction. In this manner, the worm moved forward in jerky, sidestepping manner. The lateral movements of the dorsal cirri appeared to mimic the motion of the fronds of small seaweeds found in the tidepools where the species was collected. This behavior thus appeared to represent a type of camouflage, permitting the worm to remain virtually invisible against the background flora.

Remarks. *Clavadoce splendida* differs from *C. nigrimaculata* in having dorsal cirri that are narrow and elongate, instead of broad and leaflike, in having ventral cirri that project dorsally only slightly above the neuropodia instead of well above the neuropodia, nearly meeting the dorsal cirri. Furthermore, the antennae and tentacular cirri of *C. splendida* are distinctly clavate or flask-shaped instead of lanceolate or cirriform as in *C. nigrimaculata*.

Type locality and type specimens. Central California. Holotype: USNM 20343.

Distribution. Central California, among rocks and algae, intertidal to 63 m.

Clavadoce nigrimaculata (Moore, 1909)

Figure 4.14

Eulalia nigrimaculata Moore, 1909b:344-346, pl. 15, figs. 24-26.—Bergström, 1914:165.—E. Berkeley and C. Berkeley, 1948:49.—C. Berkeley, 1967:1053.—Banse and Hobson, 1974:41.
Genetyllis nigrimaculata: Hartman, 1936:117; 1959:153; 1961:13, 59; 1963:283; 1968:283, figs. 1-2.
Bergstroemia nigrimaculata: Banse, 1973:687-688, figs. b-f.
Clavadoce nigrimaculata: Pleijel, 1991:234, 253 (in part).

Material examined. California: Monterey Bay, *Albatross* Sta. 4454, 12 May 1904, green mud and sand, 130 m, holotype of *Eulalia nigrimaculata* (USNM 17105).

Description. A moderately sized species, holotype 28 mm long, 1.2 mm wide for about 86 segments; reported up to 36 mm long (Moore, 1909b). Color in alcohol: brown, with patterns of pigment visible on dorsal and ventral cirri, but only after clearing. Body slightly dorsoventrally compressed, uniformly wide throughout, tapering slightly in last 10 to 15 segments.

Prostomium oval, broadly rounded on anterior margin, bearing 4 large, widely spaced frontal antennae and median antenna located between 2 large eyes (Fig. 4.14A); each antenna cylindrical, lanceolate, tapering distally to narrow tip. Segment 1 reduced, not visible dorsally; segments 2 and 3 visible dorsally. Setae first present from segment 2. Tentacular cirri cylindrical, clavate, tapering to narrow tips, none flattened; dorsal tentacular cirri of segments 1 and 2 longest, extending posteriorly for 9 to 10 segments (Fig. 4.14A). Normal dorsal cirri present from segment 4; each dorsal cirrus broad, leaflike, slightly wider than long, tapering and narrowing distally, arising from rounded basal cirrophore (Fig. 4.14B). Ventral cirri first present from segment 3; each ventral cirrus oblique to axis of neuropodium, reniform, about 2-½ times as wide as long (Fig. 4.14B). Neuropodium distally pointed, bearing fascicle of 15 to 18 compound spinigers. Each seta with tip of shaft expanded along long region, bearing several short teeth on tip; blade narrow, with finely serrated edge (Fig. 4.14C). Pygidium of holotype lacking anal cirri.

Biology. The species is only known from subtidal depths to 130 m in mud and sand.

Remarks. See remarks under *C. splendida* (above).

Distribution. Western Canada to central California, subtidal to 130 m.

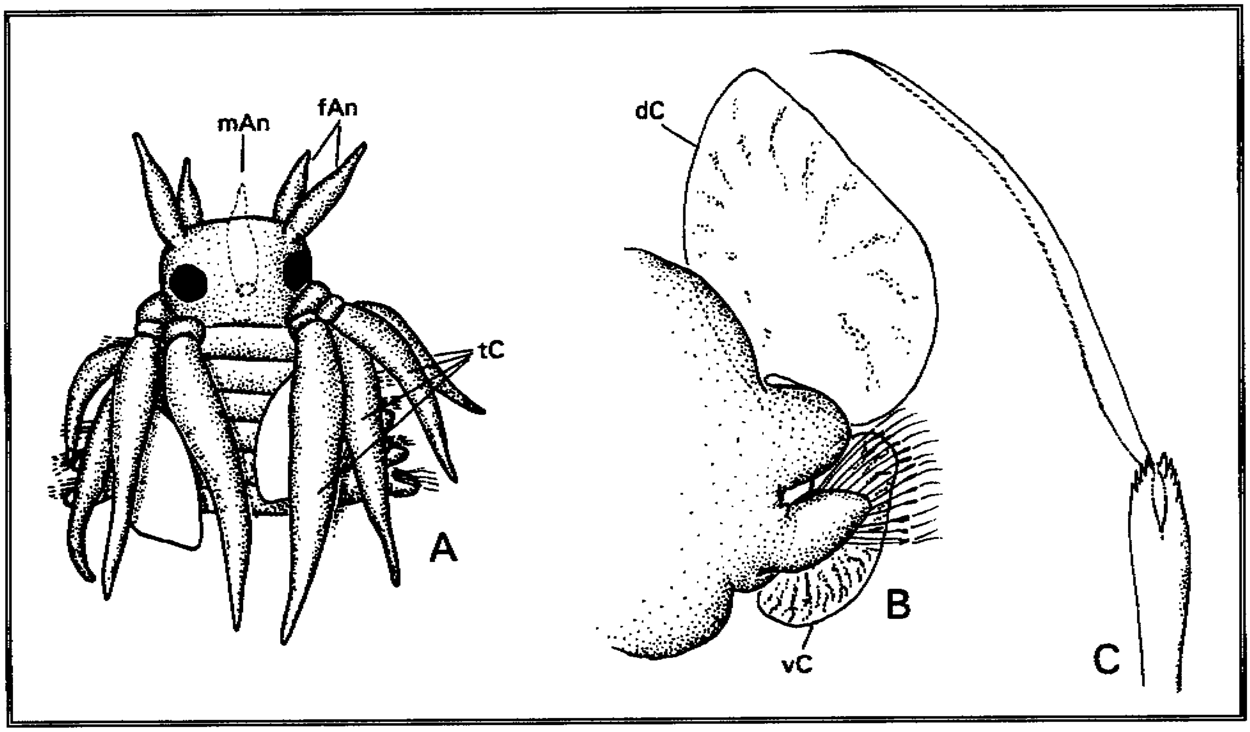

Figure 4.14 *Clavadoce nigrimaculata*: A, anterior end, dorsal view (median antenna indicated by broken line); B, middle parapodium, anterior view; C, seta. (A, modified from Banse, 1973; B-C, original).

Genus *Eulalia* Savigny, 1817

Type species: *Nereis viridis* Linnaeus, 1767, designated by Bergström (1914).

Diagnosis. Prostomium with 5 antennae; proboscis with papillae, diffusely arranged or forming rows. Segments 1 to 3 all complete, visible dorsally, free from one another and prostomium; with 4 pairs of tentacular cirri, all of the same form or with ventral tentacular cirrus of segment 2 flattened and broad; setae from segment 2 or 3; tentacular formula: $0^1/_0 + S^1/_1 + S^1/_V$ or $0^1/_0 + 0^1/_1 + S^1/_V$. Parapodia uniramous, with pointed dorsal and ventral cirri. Rostrum of setal shaft with large number of teeth, slightly decreasing in size proximally.

Remarks. This definition more or less follows that of Pleijel (1987, 1991) and includes the genus *Steggoa* as a synonym. The ventral tentacular cirrus of some species of *Eulalia* has been found to have differing degrees of flattening, precluding the need for the genus *Steggoa*.

Two species, *Eulalia levicornuta* and *E. bilineata*, have been found in the Santa Maria Basin. The first species appears to be rather rare and limited to continental shelf and slope depths in the eastern Pacific, while the second species is a widespread form that occurs in a variety of habitats and depths.

Eulalia levicornuta Moore, 1909

Figure 4.15

Eulalia levicornuta Moore, 1909b:346-348, pl. 16, figs. 27-30.—Hartman, 1936:118; 1968:263, figs. 1-3.—Banse and Hobson, 1968:7-9, figs. 2a-c.—Kravitz and Jones, 1979:16.

Material examined. California: western Santa Barbara Channel, off Point Conception, Sta. BRA-2, 110-126 m, from rocks (1, 1); Sta. BRC-2, 120-123 m (1); off Point Arguello, Sta. 71, 306 m (1).—off Gull Islet, south of Santa Cruz Island, *Albatross* Sta. 4430, 14 April 1904, 360 m, holotype (USNM 17288).

Description. A moderately sized species, specimen from station BRC-2 nearly complete, 23.2 mm long, 1 mm wide (including parapodia) for 107 segments. Color variable, with tan ground color and very dark, reddish colored parapodia; with scattered dark pigment granules on dorsum, ventrum, neuropodium, and tentacular cirri; some specimens with less extreme color contrast.

Prostomium longer than wide, with smooth curved sides; frontal antennae subequal, long, cirriform, tapering to narrow tips, mounted on frontal cushion (Fig. 4.15A); median antenna shorter than frontal antennae, arising from middle of main part of prostomium; with 2 pair of large, dark red eyes, each with distinct lens (Fig. 4.15A). Segment 1 distinct, fused dorsally with prostomium, or appearing separated in some specimens; segments 2 and 3 complete, free from one another. Dorsal tentacular cirri of segments 1 to 3 elongate, cylindrical, tapering to narrow tips; ventral tentacular cirrus of segment 2 shorter, broad, flattened (Fig. 4.15A); setae first present from segment 2. Neuropodia with entire, rounded tips, bearing fascicle of 10 to 15 compound setae; dorsal cirri thickened, broad, and slightly longer than wide (Fig. 4.15B); ventral cirri also thickened, round in shape, slightly longer than neuropodium (Fig. 4.15B). Setae with 2 long terminal spines on tip of shaft and numerous smaller denticles; blade with fine serrations (Fig. 4.15C-D). Pygidium with 2 short, bluntly rounded anal cirri.

Biology. *Eulalia levicornuta* has only rarely been encountered, probably because it occurs at about the shelf break and on the upper continental slope. One specimen came from a rock and suggests that the species might be found in more cryptic habitats. The specimen from Puget Sound reported by Banse and Hobson (1968) came from very fine silty sediments. The shallowest records are by Kravitz and Jones (1979) from off Oregon, where the species was recorded in mixed sand and silt in 86 to 88 m.

Remarks. Previous records, only refer to four specimens. Three additional specimens are available from the Phase I collections, and permit confirmation of published descriptions. The new California specimens agree very well with the specimen described from the Puget Sound by Banse and Hobson (1968), except that the first segment is partially fused dorsally to the prostomium instead of being entirely free. Banse and Hobson's observation that the ventral tentacular cirrus of segment 2 is broader and somewhat flattened is confirmed. Setal details more or less conform to the Puget Sound observations.

The holotype from off Santa Cruz Island has a short median antenna which appears to be broken or damaged. The first segment of this specimen is separated from the prostomium instead of being fused. Other characters agree well with the new specimens.

Distribution. Eastern Pacific, Puget Sound to southern California, 86-582 m.

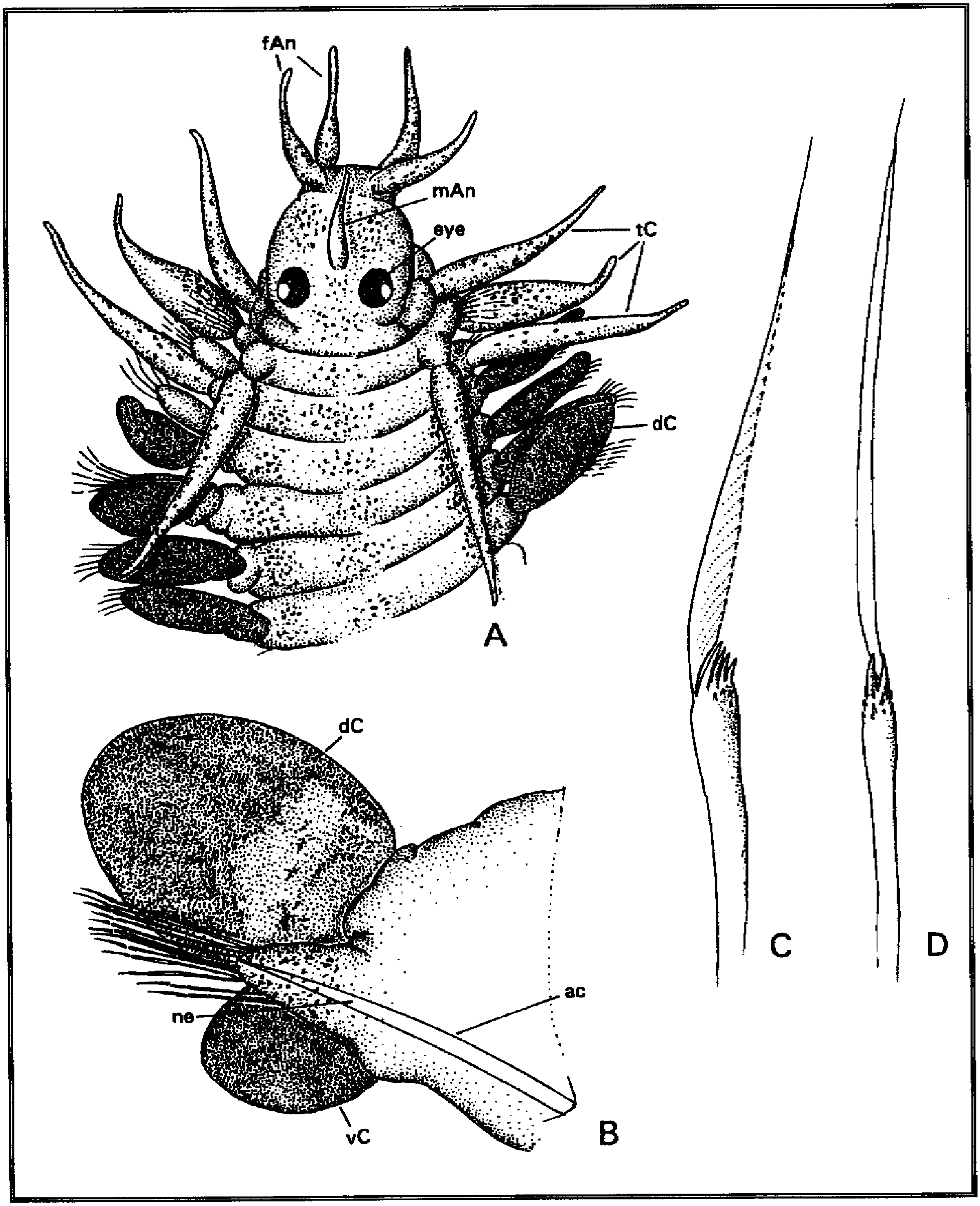

Figure 4.15. *Eulalia levicornuta*: A, anterior end, dorsal view; B, middle parapodium, anterior view; C-D, setae.

Eulalia bilineata (Johnston, 1840)

Figure 4.16

Eulalia (Hypoeulalia) bilineata: Bergström, 1914:165-166, fig. 57.
Eulalia bilineata: Fauvel, 1923:162-163, fig. 58a-e.—Berkeley and Berkeley, 1948:48, fig. 71.—Uschakov, 1955:98, fig. 5A-C; 1972:147-149, pl. 7, figs. 5-8.—Pettibone, 1963:86-88, fig. 20 (Synonymy).—Imajima and Hartman, 1964:61-62, pl. 13, figs. a-d.—Hartman, 1968:261, figs. 1-2.—Gathof, 1984:19-14, figs. 19-9, 19-10.—Pleijel and Dales, 1991:100-101, fig. 29.—Pleijel, 1993:89-91, figs. 62-63, map. 30.
Steggoa sp. A. Lissner *et al.*, 1986:A-8.
Eulalia levicornuta: Hyland and Neff, 1988:A-3. *Not* Moore, 1906.

Material examined. California: Santa Maria Basin, off Port San Luis, Sta. R-1 (2); off Point Sal, Sta. R-8 (3); off Purisima Point, Sta. R-4 (12); Sta. BRA-16 (1); off Point Arguello, Sta. BRA-4 (1).

Description. A long slender species, recorded up to 50 mm long and 2 to 3 mm wide with 150 segments; Santa Maria Basin specimens smaller: complete specimen (Sta. 16) 11 mm long, 0.25 mm wide for 105 segments; incomplete specimen from Station R-4 14 mm long, 0.5 mm wide for 98 segments. Color light to dark tan with dark dorsolateral pigmented areas along length of body, sometimes forming longitudinal lines; dorsomedial pigmented area at posterior margin of most segments also present of some specimens; small pigment granules present on antennae, tentacular cirri, and dorsal and ventral cirri.

Prostomium about as long as wide; frontal antennae emerging from small cushion developed on anterior margin; each frontal antenna short, tapering; median antenna short, arising from near posterior margin of prostomium (Fig. 4.16A); 2 medium-sized eyes present near posterior margin of prostomium. All 3 tentacular segments distinct dorsally; segment 1 vaguely separated from prostomium; segments 2 and 3 each distinct (Fig. 4.16A); all tentacular cirri relatively short, none more than twice length of normal dorsal cirri; tentacular cirri of segment 1 shortest, barely extending half length of prostomium; dorsal tentacular cirri of segments 1 to 3 all cylindrical, tapering; ventral tentacular cirrus segment of 2 wider, slightly flattened (Fig. 4.16A). Neuropodia with short, weakly bilobed lips, between which a fascicle of composite setae emerge; dorsal cirri thick, oblong, oval in shape, with rounded tip; ventral cirri similar, but smaller and more pointed (Fig. 4.16B). Setae with 2 elongate spines on tip of shaft and numerous smaller spinelets; blade relatively short, with denticulated edge (Fig. 4.16C). Pygidium with 2 long anal cirri with blunt tips.

Biology. *Eulalia bilineata* is found on a variety of bottom types including sand, shelly gravel, among crevices in rocky habitats, and in algal holdfasts.

Remarks. *Steggoa* sp. A. from Phase I and all species identified as *Eulalia levicornuta* in Phase II are actually *E. bilineata*. These specimens agree very well with the description of European specimens by Pleijel and Dales (1991). This is in contrast to comments by Banse and Hobson (1968) that suggested that Pacific specimens of the species differed in the degree of fusion of the first few segments and shape of the ventral tentacular cirri.

Type locality. Berwick Bay, Firth of Forth, Scotland.

Distribution. Widespread globally; California continental shelf and upper slope, 90-582 m.

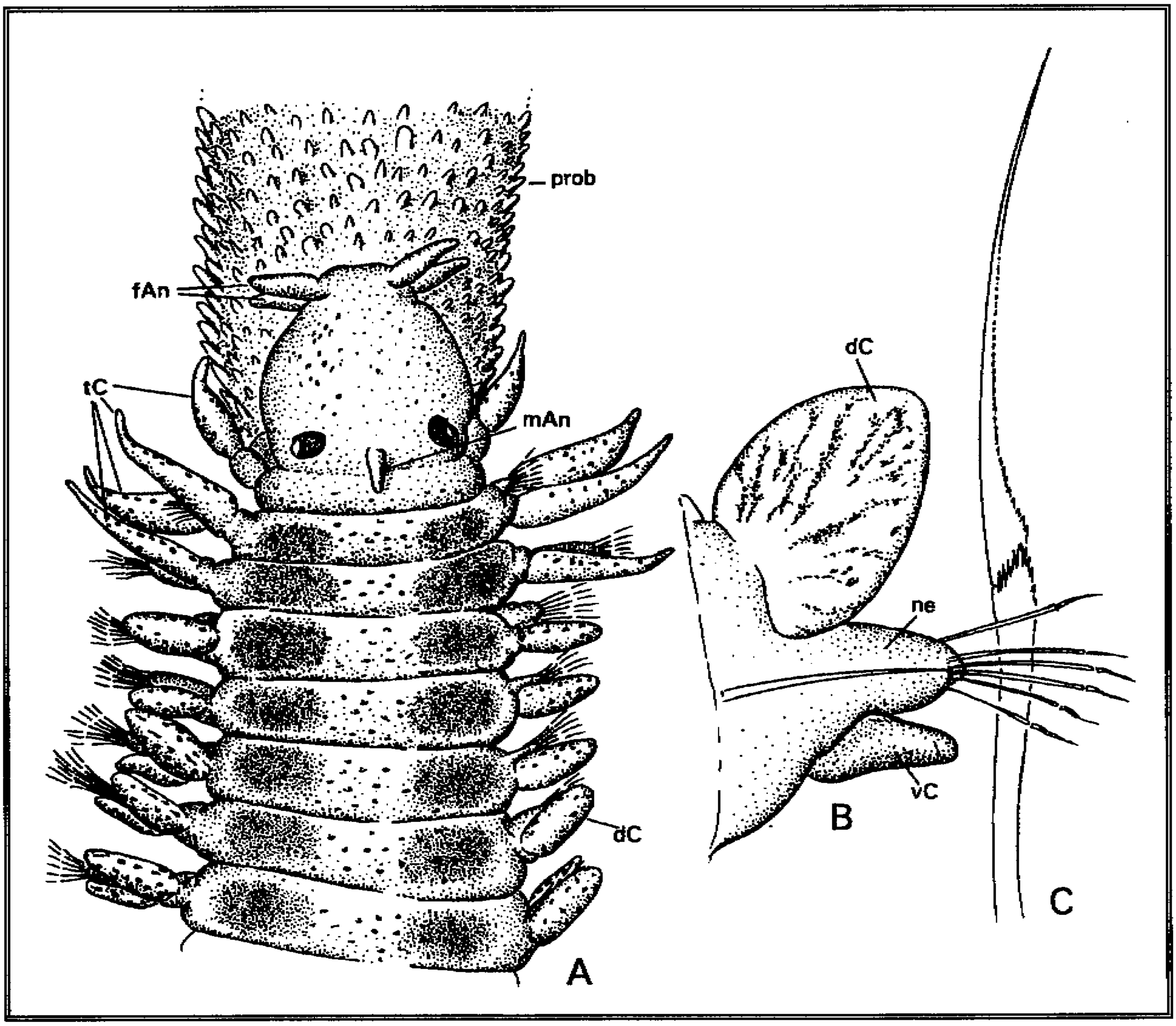

Figure 4.16. *Eulalia bilineata*: A, anterior end, dorsal view; B, middle parapodium; C, seta.

Genus *Eumida* Malmgren, 1865

Type species: *Eulalia sanguinea* Oersted, 1843, by monotypy.

Diagnosis. Prostomium with 5 antennae; surface of proboscis with minute papillae; with larger terminal papillae. Segment 1 dorsally reduced, fused to segment 2; with 4 pairs of tentacular cirri, all of the same form; setae from segment 2; tentacular formula: $(0^1/_0 + S^1/_1) + S^1/_V$. Parapodia uniramous, with dorsal and ventral cirri pointed. Rostrum of setal shaft with large number of teeth, slightly decreasing in size proximally.

Remarks. This genus is very closely related to *Sige* Malmgren and some species may be confused. The most important character that separates the two taxa is the presence of an elongate superior presetal lobe in *Sige* and its complete absence in *Eumida*. Further, in *Sige*, the dorsolateral margins of the prostomium are extended posteriorly as nuchal organs, leaving a distinct medial notch, whereas in *Eumida*, nuchal organs are less prominent and the posterior margin of the prostomium is relatively smooth, or only weakly indented. The genus has been revised by Eibye-Jacobsen (1991).

There is considerable confusion concerning the identify of California species of *Eumida*. Hartman (1936) separated three species: *E. longicornuta* (Moore, 1906), *E. tubiformis* Moore (1909b), and *E. sanguinea* (Oersted, 1843) in a key to California phyllodocids. In 1968, she again recognized these three species and included *Sige bifoliata* (Moore, 1909b) as a species of *Eumida*. However, the first three species are true *Eumida* species, while the latter species should be treated as *Sige* (see below). In considering the identification of species of *Eumida* from California, the ability to distinguish between *E. longicornuta* and *E. tubiformis* appears to be the most difficult based upon available descriptions. Neither species has been fully illustrated. Specimens of *E. longicornuta* have been collected in Tomales Bay and are compared with the holotype from Port Townsend, Washington. The holotype of *E. tubiformis* from southern California has been examined and is redescribed. From these observations it is apparent that the two species are very different from one another and easily distinguished. Both are redescribed. No specimens of *E. sanguinea* have been obtained, although the species might be expected in an estuary such as San Francisco Bay where numerous species have been introduced from the Atlantic and elsewhere.

Eumida longicornuta **(Moore, 1906)**

Figure 4.17

Eulalia longicornuta Moore, 1906:222-223, pl. 10, figs. 7-8.—Treadwell, 1914:187.
Eumida longicornuta: Hartman, 1936:117-118; 1961:13; 1968:273, figs. 1-2.—Eibye-Jacobsen, 1991b:108-110, fig. 6.

Material examined. California: Tomales Bay, shallow subtidal, collected at various times (15).—Washington: Port Townsend, intertidal among serpulid tubes, 27 June 1903, holotype (USNM 5515).

Description. A moderately sized species, up to about 50 mm long and 1 mm wide for 90 segments. Color variable, but ground color light to dark brown, with distinct dark transverse stripes developed across segments to varying degrees; dorsal cirri with concentrations of dark pigment; all pigment tending to fade in alcohol.

Prostomium about as wide as long, rounded anteriorly, tapering posteriorly, with slight indentation on posterior margin (Fig. 4.17A); 2 large black eyes present in posterior half; frontal antennae subequal, cirriform; median antenna slightly longer than frontal antennae, located in middle of prostomium (Fig. 4.17A). Proboscis smooth, but with some ridges and terminal papillae. Segment 1 reduced dorsally; segment 2 complete dorsally, free from segment 3. Tentacular cirri cirriform, dorsal tentacular cirri of second and third segments longest, extending posteriorly 4-7 segments (Fig. 4.17A). Neuropodia relatively short, with 2 postsetal lamellae; dorsal cirri heart-shaped, slightly asymmetrical, slightly longer than wide, widest in middle and posterior segments (Fig. 4.17B); ventral cirri small, distally pointed, shorter than neuropodial lobe (Fig. 4.17B). Setae with numerous small denticles on tip of shaft and fine teeth along edge of blade (Fig. 4.17C). Pygidium with 2 spindle-shaped anal cirri.

Biology. *Eumida longicornuta* is reported from shallow embayments and rocky intertidal habitats. Little is known concerning the biology of this species.

Remarks. *Eumida longicornuta* is a relatively common eastern Pacific species in intertidal and shallow subtidal habitats. The species superficially resembles *Sige bifoliata*, but differs in lacking instead of having a superior presetal lobe on the neuropodium. Further, *Sige bifoliata* has a very deep indentation on the posterior edge of the prostomium instead of a weak indentation. In *S. bifoliata*, the deep indentation is caused by prominent lateral nuchal extensions. Eibye-Jacobsen (1991b), in his redescription of the types of *E. longicornuta*, noted that the antennae were unusually long and that the dorsal cirri, especially in posterior segments were about 1-½ times as long as wide. My own examination of the holotype and the Tomales Bay specimens indicates that these characters are more variable, possibly due to the mode of preservation. I do not agree with the proporations of the dorsal cirri presented by Eibye-Jacobsen. Most of the dorsal cirri I examined were only slightly longer than wide, not 1-½ times; proportions of the length and width of Eibye-Jacobsen's published figures (1991b:Figs. 6 C-D) of the cirri do not support his statements.

The Tomales Bay specimens have been compared with specimens of *E. sanguinea* from the U.S. Atlantic coast. *Eumida longicornuta* differs from *E. sanguinea* in lacking instead of having papillae on the proboscis, in having broader and shorter dorsal cirri, and shorter, stubbier ventral cirri.

Eumida longicornuta is closely related to *E. tubiformis* Moore, a larger species. The most conspicuous difference between the two species is that the former has short neuropodial lobes with two bluntly rounded lobes, whereas, *E. tubiformis*, has an elongate neuropodium with two prominent, narrow lobes.

Distribution. Eastern Pacific, Washington to California, intertidal to shallow subtidal in rocky habitats.

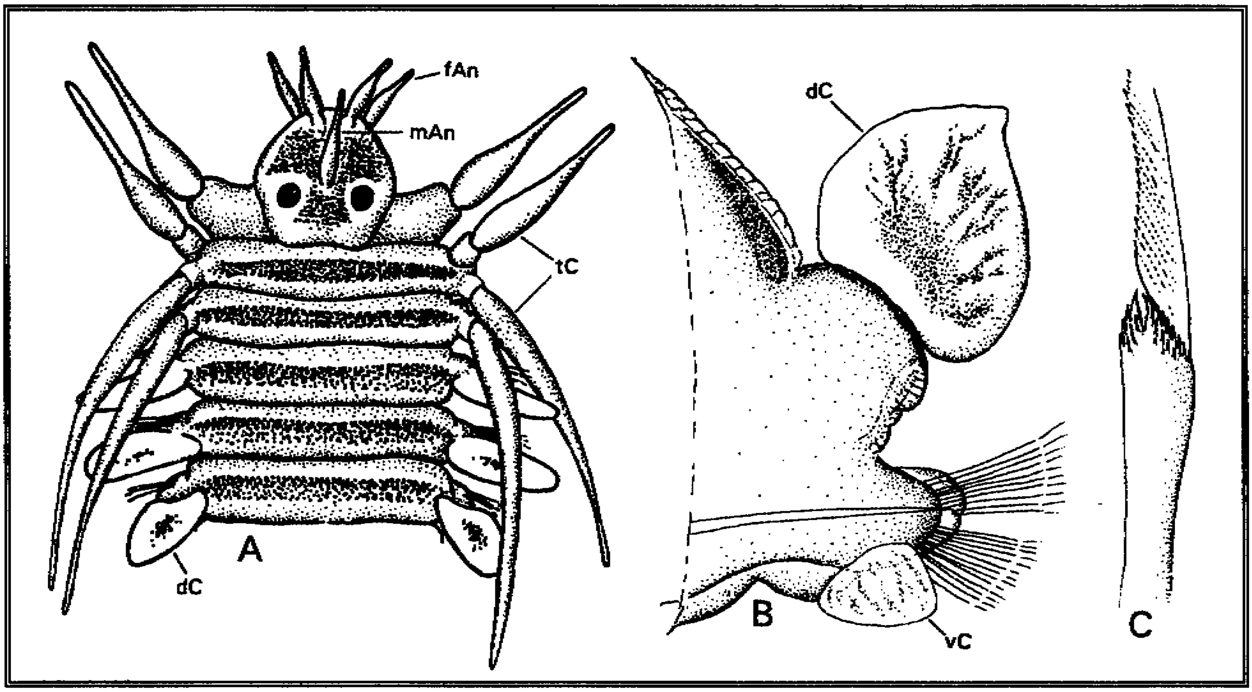

Figure 4.17. *Eumida longicornuta*: A, anterior end, dorsal view; B, middle parapodium, anterior view; C, seta.

Eumida tubiformis **Moore, 1909**

Figure 4.18

Eumida tubiformis Moore, 1909b:342-344, pl. 16, figs. 22-23.—Hartman, 1968:277, figs. 1-2.—Uschakov, 1972:155-156, pl. 10, figs. 1-3 (synonymy).

Material examined. California: off Santa Cruz Island, 14 April 1904, black sand and pebbles, 360 m, holotype (USNM 16879).

Description. A large species, holotype complete, in 2 pieces, 67 mm long, 7 mm wide for 137 segments. Color in alcohol: tan.

Prostomium twice as wide as long, subelliptical, slightly concave posteriorly; with a single pair of large circular eyes, each with central lens (Fig. 4.18A); frontal antennae inserted subapically; median antenna short, slender, inserted between eyes (Fig. 4.18A). Proboscis smooth throughout most of length, with transverse ridges developing in distal one-third; opening of proboscis surrounded with 18 to 20 rounded papillae; each papilla with numerous small micropapille on surface (Fig. 4.18A). Tentacular cirri with well-developed cirrophores and large, stout, subulate styles; tentacular cirri each relatively short; only dorsal tentacular cirrus of segment 2 extending for more than 6 segments (Fig. 4.18A). Neuropodia elongated throughout; each neuropodium with 2 prominent lobes, with dorsal one being slightly longer than the ventral (Fig. 4.18B). Dorsal cirri broadly foliaceous, heart-shaped; ventral cirri about one-fourth size of dorsal cirri, with broad basal attachment, somewhat foliaceous with pointed tip (Fig. 4.18B). Setae numbering 20 to 30 per fascicle, each with finely spinous tip and thin, elongate blade (Fig. 4.18C-D).

Biology. *Eumida tubiformis* is a rare species that appears to be limited to continental shelf and upper slope depths in coarse sediments.

Remarks. *Eumida tubiformis* has two well-developed lobes on the tip of the neuropodium, with the dorsal one slightly longer than the ventral, but not greatly elongated as in species of the genus *Sige*.

Distribution. Central and southern California, 359-617 m; western Pacific, Sea of Japan, Sea of Okhotsk, Kurile Islands, 2-80 m.

Genus *Sige* Malmgren, 1865 Emend Pleijel, 1990

Type species: *Sige fusigera* Malmgren, 1865, by monotypy.

Diagnosis. Prostomium pentagonal, with nuchal organs as posterior outgrowths; with 5 antennae; proboscis with numerous, mostly small papillae. Segment 1 fully developed, or reduced; with 4 pairs of tentacular cirri; ventral tentacular cirri of segment 2 cylindrical or slightly flattened; setae from segment 2; tentacular formula: $0^{1}/_{0} + S^{1}/_{1} + S^{1}/_{V}$. Parapodia uniramous, with dorsal and ventral cirri pointed; presetal dorsal lobe of parapodia distinctly prolonged, digitiform. Rostrum of setal shaft with large number of teeth, slightly decreasing in size proximally.

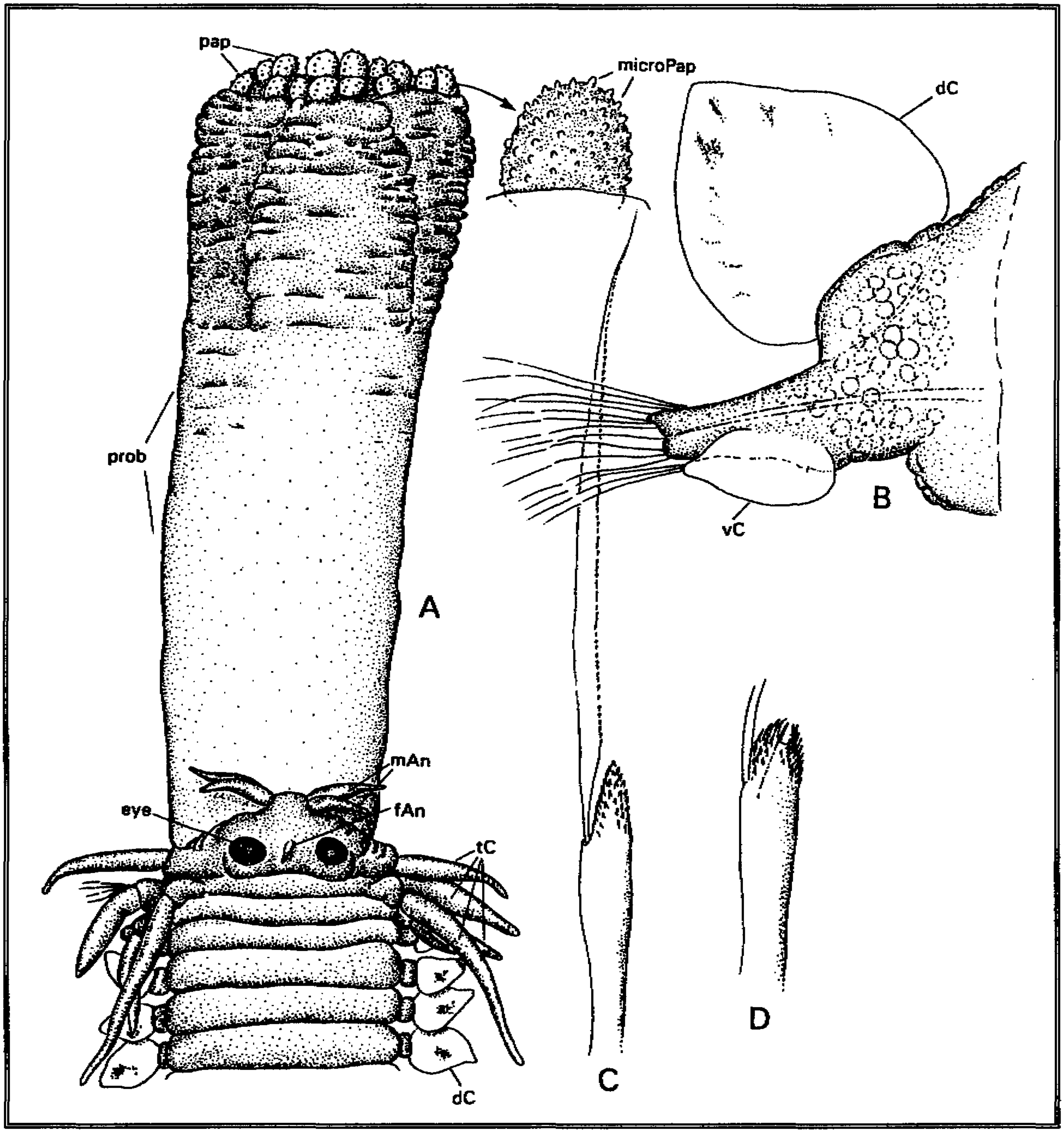

Figure 4.18. *Eumida tubiformis* (holotype, USNM 16879): A, anterior end, dorsal view, with inset of papilla from anterior margin of proboscis; B, posterior parapodium, posterior view; C-D, setae.

Remarks. The genus *Sige* was redefined and revised by Pleijel (1990). *Sige* differs from all other described phyllodocids having five antennae by the nature of the prolonged superior parapodial lobes. A similar character occurs independently in *Phyllodoce longipes* Kinberg, 1866. *Sige* differs from the closely related genus *Pterocirrus* Claparède, 1866 in having a centrally inserted median antenna instead of an anteriorly inserted one and in having a reduced proboscideal papillation instead of papillae that are long and filiform. *Sige* is separated from *Eumida* on the presence of the prolonged superior podial lobe.

Sige bifoliata (Moore, 1909)

Figure 4.19

Eulalia (Sige) bifoliata Moore, 1909b:349-350, pl. 16, figs. 31-34.
Eulalia bifoliata: Berkeley, 1924:288.
Eumida bifoliata: Hartman, 1961:61; 1968:271, figs. 1-3.
Sige bifoliata: Pleijel, 1990: 167-169. *Not* Hartman, 1936. *Fide* Pleijel, 1990.

Material examined. California: Gulf of the Farallones, off San Francisco Bay, numerous specimens, 10-15 m (JAB).—Monterey Bay, *Albatross* Sta. 4532, 28 Mar 1901, 55 m, holotype (USNM 17287).—Santa Maria Basin, off Point San Luis, Sta. 21 (1); off Point Sal, Sta. PJ-1 (1), Sta. PJ-5 (2), Sta. R-8 (1); off Purisima Point, Sta. R-6 (1);

Description. A large complete specimen from Santa Maria Basin 15 mm long, 1 mm wide (excluding parapodia) for 80 segments. Color in alcohol: light to dark brown body, with dorsal and ventral cirri lighter, each bearing faint venation and small dark pigment granules; specimens from Sta. R-8 with tan body and dark brown pigment in mid-dorsal and dorsolateral locations, appearing as 3 longitudinal rows along body.

Prostomium pentagonal, wider than long, with posterior dorsolateral nuchal extensions; frontal antennae subequal, slightly subapical; median antenna located in middle of prostomium, nearly twice length of frontal antennae; 2 large, dark eyes present, each with prominent lens (Fig. 4.19A). Proboscis smooth, with distal end surrounded by about 18 papillae. Segment 1 dorsally reduced; segment 2 partially reduced; segment 3 dorsally distinct (Fig. 4.19A). With 4 pairs of tentacular cirri, each long, extending over 4 to 6 segments; setae first present from segment 2. Parapodia with elongate neuropodia bearing pointed superior presetal lobe, internal acicula, and fascicle of more than 20 compound spinigers; dorsal cirri cordate, about as wide as long; ventral cirri long, pointed, somewhat asymmetrical (Fig. 4.19B). Setae with numerous small denticles on tip of shaft and widely spaced teeth on blade (Figs. 4.19C-D). Pygidium rounded, anal cirri not observed.

Biology. This species has been found in mixed sand/silt sediments.

Remarks. Pleijel (1990) has redescribed the holotype and it has been reexamined here. The most important differences between the new specimens from the Santa Maria Basin and the original specimen from off Monterey are with the length of the median antenna and the degree of reduction of segments 1 and 2. Moore (1909b) described and figured the median antenna as being shorter than the frontal antennae; Pleijel (1990) repeated this fact in his reexamination of the holotype, although he stated that the median antenna was in poor condition. In fact, the median antenna of the holotype is only a basal remnant of the original structure. The median antenna on the Santa Maria Basin specimens is longer than the frontal antennae. Berkeley (1924) reported on a specimen from British Columbia that had a median antenna that was equivalent to the frontal antennae in length. All observations indicate that the first segment is greatly reduced. The second segment of the holotype, however, is a complete segment. In the Santa Maria Basin specimens the second segment is either entirely free or reduced by about half of its width. The degree of reduction of segment 2 is apparently an artifact of contraction during preservation.

Sige bifoliata is readily separated from other species of the genus by the nature of the broad dorsal cirri. The species may be superficially confused with *Eumida longicornuta* in most characters, but is a true member of the genus *Sige* by having a prolonged superior presetal lobe on the neuropodia. The Phase II voucher specimen of *E. tubiformis* is actually *S. bifoliata*.

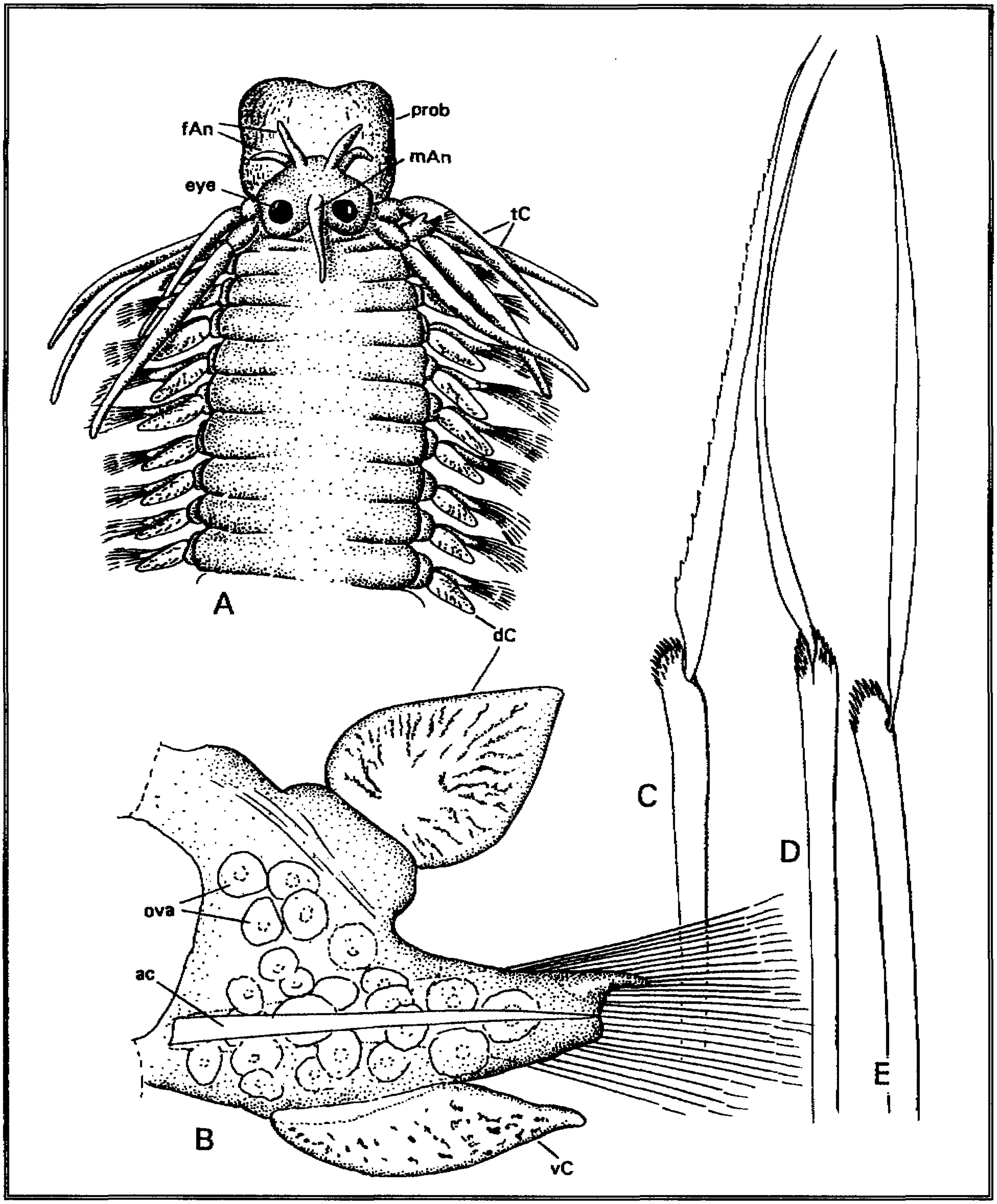

Figure 4.19. *Sige bifoliata*: A, anterior end, dorsal view; B, middle parapodium, posterior view; C-D, setae in various views.

Distribution. Eastern Pacific: British Columbia, shallow subtidal; central California, continental shelf, 15-160 m.

Sige brunnea (Fauchald, 1972)

Fig. 4.20

Pirakia brunnea Fauchald, 1972:53-54, pl. 4, figs. C-D.
Sige brunnea: Pleijel, 1990:169-170, fig. 4.—Blake, 1992:702, 704-705, fig. 6.

Material examined. California: the continental slope off San Francisco, Gulf of the Farallones, 100+ specimens from 20 stations in depths ranging from 1100-2955 m; Santa Catalina Basin, 1240 m in sediments associated with a whale skeleton, coll. Nov. 1988, C. Smith (2).

Description. A small species, most specimens juveniles, with 14-18 segments, up to 2.0 mm long and 0.5 mm wide; two large complete specimens available: (1) 5-mm long, 0.8-mm wide for 45 segments; (2) 8-mm long, 1-mm wide for 42 segments. Color in alcohol: tan with heavy concentrations of orange-brown pigment on prostomium, dorsal and ventral cirri, and on anterior and posterior margins of individual segments.

Prostomium wider than long, with prominent anterior projection arising between bases of frontal antennae; frontal antennae cirriform, subequal; median antenna shorter and more delicate than frontal antennae, arising from posterior one-third of prostomium (Fig. 4.20A). Proboscis smooth proximally, rugose distally with transverse ridges; terminal opening surrounded by 15-16 conical papillae (Fig. 4.20B), each with 3 projecting micropapillae; posterior margin of prostomium with broad, deep indentation.

All 3 tentacular segments complete and visible dorsally; first segment reduced, narrow dorsally; tentacular cirri all cylindrical, expanded basally, tapering apically; dorsal tentacular cirrus of segment 1 and ventral tentacular cirrus of segment 2 short, only extending posteriorly 2-3 segments; dorsal tentacular cirri of segments 2 and 3 longest, extending posteriorly 6-8 segments (Fig. 4.20A). Neuropodia with prominent, fingerlike superior lobe; dorsal cirri flattened, expanded basally, tapering apically to relatively sharp point; ventral cirrus more cirriform and elongate than dorsal cirri, extending for about one-third length beyond neuropodium (Fig. 4.20B). Setae numbering 12-20 per fascicle; each with thick, rounded rostrum on shaft bearing numerous small denticles; blade elongate, with serrated edge (Fig. 4.20C). Pygidium a rounded lobe.

Remarks. *Sige brunnea* was originally described from deep water off western Mexico (Fauchald, 1972) and has subsequently been reported from deep basins off southern California (Pleijel, 1990). The species is the most abundant phyllodocid in the lower slope benthos off northern California (Blake, 1992) and has been collected in association with a whale skeleton in the Santa Catalina Basin (Blake and Hilbig, unpublished). *S. brunnea* is most closely related to *S. pleijeli* in having elongate, tapering dorsal and ventral cirri. The two species differ most conspicuously in that the median antenna of *S. brunnea* is located in the posterior one-third of the prostomium, whereas, it is located anteriorly on the prostomium of *S. pleijeli*. In addition, the tentacular cirri of *S. pleijeli* are all short, never extending more than 2 segments posteriorly, while the dorsal tentacular cirri of segments 2 and 3 of *S. brunnea* are long, extending 6-8 segments in length.

Biology. A deep-sea species, occurring on the middle and lower continental slope in fine, silty sediments.

Type locality and type specimen. Mexico, Baja California, in deep water. Holotype: LACM-AHF Poly 1003.

Distribution. Northern California to Baja California, 1110-2955 m.

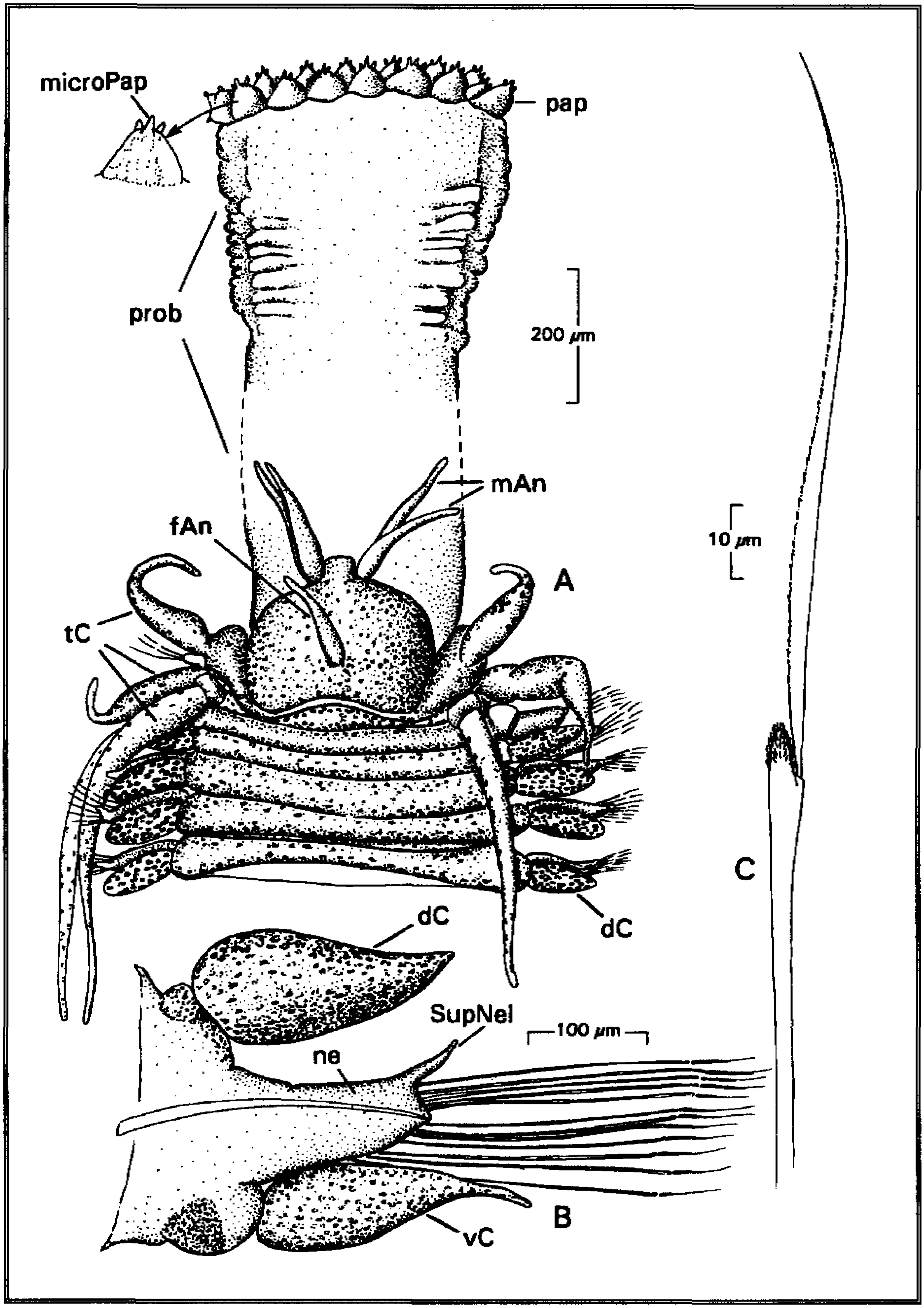

Figure 4.20. *Sige brunnea.* A, anterior end, dorsal view; B, middle parapodium, anterior view; C, seta.

Sige pleijeli Blake, 1992

Figure 4.21

Pirakia brunnea: Lissner *et al.*, 1986:A-8. *Not* Fauchald, 1972.
Sige pleijeli Blake, 1992:705-707, fig. 7.

Material examined. California: Santa Maria Basin, off Point Arguello, Sta. 56, 900 m (holotype, USNM 148699).

Description. A small species, holotype incomplete, broken into 4 parts, totalling 4 mm long and 1 mm wide for 43 segments. Body pale, with brown pigment on dorsum and prostomium, dorsal and ventral cirri, and tips of superior presetal lobes.

Prostomium slightly longer than wide, weakly notched on anterior margin, bearing 4 long frontal antennae and 1 shorter, thinner median antennae near anterior end (Fig. 4.21A); eyes absent. Proboscis appearing smooth in dissection. First segment dorsally reduced, bearing pair of thick tentacular cirri; second segment first with setae, bearing broad dorsal and ventral tentacular cirri; segment 3 with dorsal tentacular cirri and normal ventral cirri (Fig. 4.21A). Parapodia with podial lobes bearing elongate, fingerlike superior lobe (Fig. 4.21B); dorsal cirri variable in length along body, but usually shorter than ventral cirri, especially in middle and posterior body segments; ventral cirri protruding well beyond tip of inferior podial lobe, but only as long as superior podial lobe (Fig. 4.21B). Setae numbering 10 to 12 per fascicle, each seta with expanded tip of shaft bearing numerous short teeth on two larger rostral teeth (Fig. 4.21C); blade with fine denticles along one edge (Fig. 4.21D). Pygidium unknown.

Remarks. *Sige pleijeli* differs from all known species of the genus in having the median antenna emerging from the anterior part of the prostomium instead of the center. In this respect the species approaches species of *Pterocirrus*, but is allied to *Sige* in the nature of the elongated superior presetal lobe.

The species closely resembles *S. brunnea* (Fauchald, 1972), described from deep-water off Western Mexico and reported from the San Diego Trough (Pleijel, 1990). It differs in the position of the median antenna and in details of the shape of the dorsal and ventral cirri. The species was identified as *Pirakia brunnea* in the Phase I report (Lissner *et al.*, 1986).

Biology. The species appears to be limited to upper slope depths; the single specimen occurred at a station having a very mixed sediment type (sand, 33%; silt, 47%; clay 20%).

Distribution. Known only from the upper slope depths off Point Arguello, California, 900 m.

Genus *Paranaitis* Southern, 1914

Type species: *Anaitis wahlbergi* Malmgren, 1865, by monotypy.

Diagnosis: Prostomium with 4 antennae, broadly oval, with posterior margin rounded or conical; nuchal papilla present or absent; with 1 pair of eyes, or eyes absent; proboscis with lateral longitudinal rows of large papillae. Segments 1 and 2 distinctly larger than following segments and more or less fused, forming a "collar" which surrounds prostomium laterally. With 4 pairs of cylindrical or slightly flattened tentacular cirri; tentacular formula: $(0^{1}/_{0} + 0^{1}/_{1}) + S^{1}/_{V}$. Parapodia uniramous; dorsal cirri typically very large, broad, oval covering dorsum and superficially resembling elytra of scale worms. Rostrum of setal shaft with a few longer teeth.

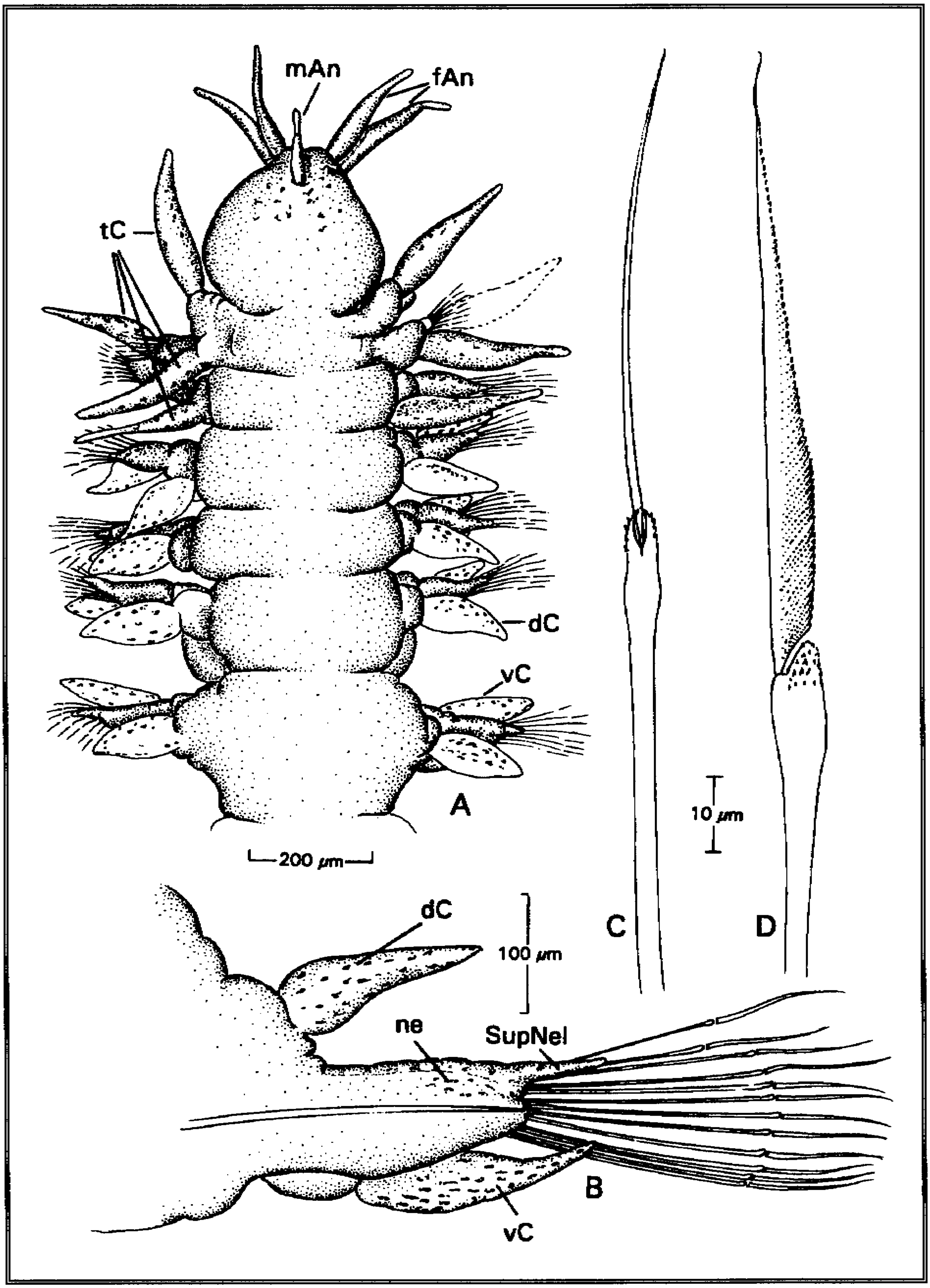

Figure 4.21. *Sige pleijeli.* A, anterior end, dorsal view; B, middle parapodium, posterior view; C-D, setae.

Remarks: *Paranaitis* is one of the more distinctive phyllodocid genera and contains about 12 species (Uschakov, 1972). *Paranaitis polynoides* Moore is the common continental shelf species from California waters and is well represented in the Santa Maria Basin. Two undescribed species have been discovered in deep water on the continental slope off San Francisco (Blake, unpublished).

Paranaitis polynoides (Moore, 1909)

Figure 4.22

Anaitis polynoides Moore, 1909b:339-342, pl. 16, figs. 19-21.
Phyllodoce (Paranaitis) polynoides: Berkeley and Berkeley, 1948:44, figs. 62-63.—Banse and Hobson, 1974:44, fig. 10j.
Paranaitis polynoides: Hartman, 1936:117, 119;1968, 291, figs. 1-3.—Hartman and Reish, 1950:12.—Uschakov, 1972:141-142, pl. 7, figs. 1-4.—Kravitz and Jones, 1979:16.—Gathof, 1984:19-21 to 19-23, figs. 19-17 to 19-18.—Hyland and Neff, 1986:A-3.

Material examined: California: off Tomales Point, dredged in 65 m (1); Santa Maria Basin, off Point Sal, Sta. R-8 (2), Sta. PJ-1 (1), Sta. PJ-2 (1), Sta. PJ-4 (1), Sta. PJ-5 (2), Sta. PJ-7 (2), Sta. PJ-8 (2), Sta. PJ-10 (1), Sta. PJ-11 (1).

Description: A moderate to large species recorded up to 44 mm long, 1.6 mm wide, for 88 segments; Tomales Bay specimen 27 mm long, 3 mm wide, for 80 segments; Santa Maria Basin specimens smaller, less than 15 mm long. Color in life: white with red pigment on dorsal midline, on dorsal cirri, and tentacular cirri (Blake, personal observations on Tomales Bay specimen); color in alcohol: light or dark tan with dark spots on dorsal cirri, tentacular cirri, and on each segment middorsally; ventral pigment lacking.

Prostomium pentagonal, as wide as long, broadly rounded anteriorly, bearing 4 short antennae; narrowing posteriorly, extending into first segment; with large knoblike nuchal papilla at posterior end; with 2 large reddish eyes, each with distinct lens (Fig. 4.22A). Proboscis with lateral rows of large papillae proximally, with numerous transverse folds; no papillae distally; with ring of papillae on terminal margin (Uschakov, 1972). Segments 1 and 2 fused dorsally, forming prominent, thickened, "collar", overlapping segment 3; tentacular cirri thick, tapering, with those of segments 1 and 2 shortest (Fig. 4.22A). Neuropodium with bifid tip, upper lip larger than lower; dorsal cirri rounded, very large, covering a large part of dorsum, each with prominent dark reddish pigment spot; ventral cirri oblong, oval, about as large as podial lobe; with distinct glandular pads dorsal and ventral to neuropodial lobes (Fig. 4.22B). Setae numerous, up to 50 reported in single fascicles (Uschakov, 1972); each seta with prominent rostrum and numerous small denticles on tip of shaft; blade with fine serrations along one edge (Fig. 4.22C). Anal cirri long, 3 times as long as wide.

Biology. *Paranaitis polynoides* has been recorded from sediments of silt and sand or sand in 60-66 m (Kravitz and Jones, 1979); from off Tomales Point in sand and rocks; and mixed sand and silt in the Santa Maria Basin. In the Santa Maria Basin the species is limited to continental shelf depths in stations of mixed sand and silt; not found deeper than about 165 m.

Remarks. Monro (1933) considered *Paranaitis polynoides* as perhaps identical with *Anaitis kosteriensis* (Malmgren). However the latter species is known from the western North Atlantic and differs from *P. polynoides* in that the posterior margin of the prostomium is rounded instead of elongate and the peristomial collar is larger and entire on its posterior margin instead of incised. Bergström (1914) suggested that *P. polynoides* might be the same as *P. wahlbergi* (Malmgren), a widespread circumboreal

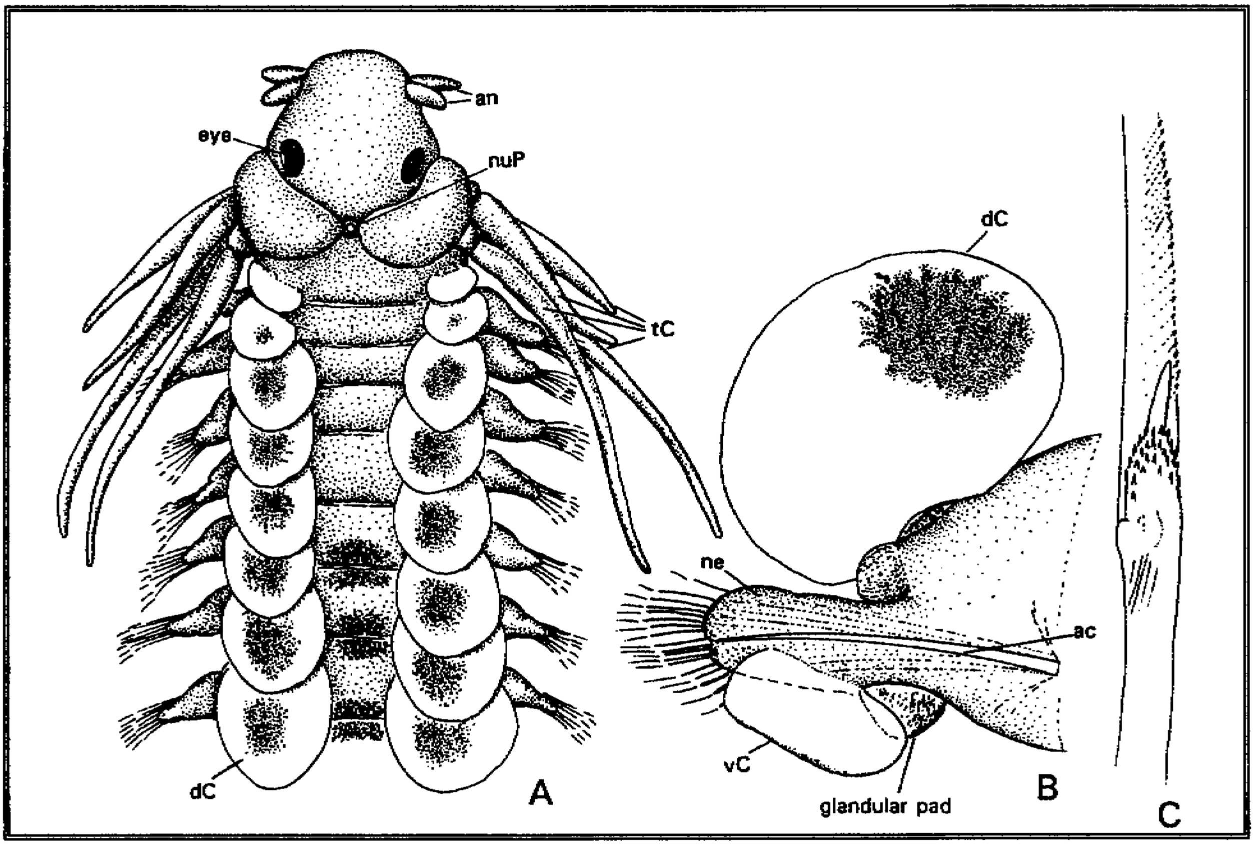

Figure 4.22. *Paranaitis polynoides.* A, anterior end, dorsal view; B, middle parapodium, posterior view; B, seta.

species. From this species, *P. polynoides* differs in having instead of lacking a nuchal papilla and in having an incised prostomial collar instead of one that is entire. According to Uschakov (1972) and Pleijel and Dales (1991), *P. polynoides* also differs from *P. wahlbergi* in the shape of the dorsal and ventral cirri and the type of papillation on the proboscis. Perkins (1984) referred the records of *P. polynoides* from North Carolina by Gardiner (1976) to a new species, *P. gardneri.*

Type locality and Type specimens. California, Monterey Bay, 92 m. Holotype: USNM 17267.

Distribution. Eastern Pacific, western Canada to central and southern California, intertidal to 165 m; Gulf of Mexico, 10-82 m; western Pacific, Sea of Japan, Kurile Islands, 8-286 m.

Genus *Nereiphylla* Blainville, 1828

Nereiphylla Blainville, 1828. **Type species**: *N. paretti* Blainville, 1828, designated by Bergström (1914).
Genetyllis Malmgren, 1865. **Type species**: *G. lutea* Malmgren, 1865, by monotypy.

Diagnosis. Prostomium rounded with 4 frontal antennae, without median antenna or nuchal papilla; 2 large eyes present; proboscis with soft papillae diffusely distributed. Segments 1 and 2 fused dorsally and reduced. Four pairs tentacular cirri present, either cylindrical or flattened: 1 pair on segment 1, 2 pairs on segment 2; 1 pair and normal ventral cirrus on segment 3; setae first present from segment 2.

Tentacular formula: $(0^{1}/_{0} + S^{1}/_{1}) + S^{1}/_{0} + S^{D}/_{V}$. Dorsal cirri cordiform, longer than broad. Pygidial cirri cylindrical, pointed.

Remarks. *Nereiphylla* and *Genetyllis* have traditionally been separated on the presence of flattened tentacular cirri in the first genus and cylindrical tentacular cirri in the second genus. In all other respects the two taxa are identical. The majority of workers have retained the two taxa as separate genera or as subgenera of *Phyllodoce*. Uschakov (1972), however, noted that the flattening of the tentacular cirri in *Nereiphylla* was insufficient to separate the two genera. He recognized *Genetyllis*, however, despite the seniority and priority of *Nereiphylla*. Because flattening of tentacular cirri has proven to be so variable among the phyllodocid genera (e.g., *Eulalia*, see Pleijel, 1987 and generic definitions in this paper), I have elected to combine *Genetyllis* with *Nereiphylla*. This synonymy is also followed by Pleijel (1991, 1993) and Pleijel and Dales (1991).

Nereiphylla is closely allied to *Phyllodoce*, but differs in the prostomial shape, in lacking instead of having a nuchal papilla, and by having the proboscideal papillae dispersed completely over the entire proboscis instead of having papillae limited to the distal area. A single species, *N. castanea*, has been found in the Santa Maria Basin.

Nereiphylla castanea **(Marenzeller, 1879)**

Figure 4.23

Carobia castanea Marenzeller, 1879:19-20, pl. 3, fig. 2.
Genetyllis castanea: Bergström, 1914:158-160, fig. 53.—Hartman, 1968:281, figs. 1-2.—Uschakov, 1972:127-128, pl. 4, figs. 1-3; 1974:122.—Blake, 1975b:183, fig. 99; 1988: 247-248.—Gathof, 1984:19-29 to 19-31, figs. 19-25 to 19-26.
Phyllodoce (Genetyllis) castanea: Berkeley and Berkeley, 1948:44.—Day, 1967: 149, fig. 5.3.e-f.—Gardiner, 1976:113, fig. h-k.—Hartmann-Schröder, 1979:82, figs. 23-26.
Phyllodoce ferruginea Moore, 1909b:337-339, pl. 15, figs. 15-18. New synonymy.

Material examined. California: Dillon Beach, rocky intertidal area, Sta. R-3, 19 June 1962, coll. K.H. Woodwick (1).—Tomales Point, rocky intertidal (1).—Monterey Bay, *Albatross* Sta. 4550, 7 June 1904, 91 m, green mud with rocks, holotype of *Phyllodoce ferruginea* (USNM 17361).—Cayucos, rocky intertidal, Sta. J-2, 19 Dec. 1961, coll. K.H. Woodwick (1).—Avila, among rocks in sand near cliff, Sta. L-8, 3 March 1962, coll. K.H. Woodwick (2).—Santa Maria Basin, off Point Arguello, Sta. BRA-6, in rocks, 54-63 m, (2).

Description. A large species, reported up to 40 mm long, 3 mm wide (including parapodia), for 150 to 200 segments; largest Santa Maria Basin specimen smaller, 8.5 mm long, 0.5 mm wide for about 95 setigers. Color in alcohol: dark red or orange, with dark orange-brown stripes across dorsum of each segment and same color on dorsal cirri, podial lobes, and ventral cirri.

Prostomium elongated, rounded anteriorly; antennae large, thickened, tapering; 2 large, black eyes present (Fig. 4.23A). Tentacular cirri round in cross section, with dorsal cirri of segments 2 and 3 weakly compressed, but not greatly flattened; dorsal cirri of segment 2 longest, extending posteriorly for about 6 segments (Fig. 4.23A). Dorsal cirri heart-shaped, as long as or longer than wide; paired cirri sometimes large enough to nearly conceal dorsum (Fig. 4.23A-B). Neuropodium relatively short, with 2 small rounded distal lobes; ventral cirri broadly oval, larger than podial lobe (Fig. 4.23B). Setae with expanded tip of shaft bearing numerous small teeth; blade unusually short, with fine denticles along one edge (Fig. 4.23C). Anal cirri thick, 3 to 4 times longer than wide.

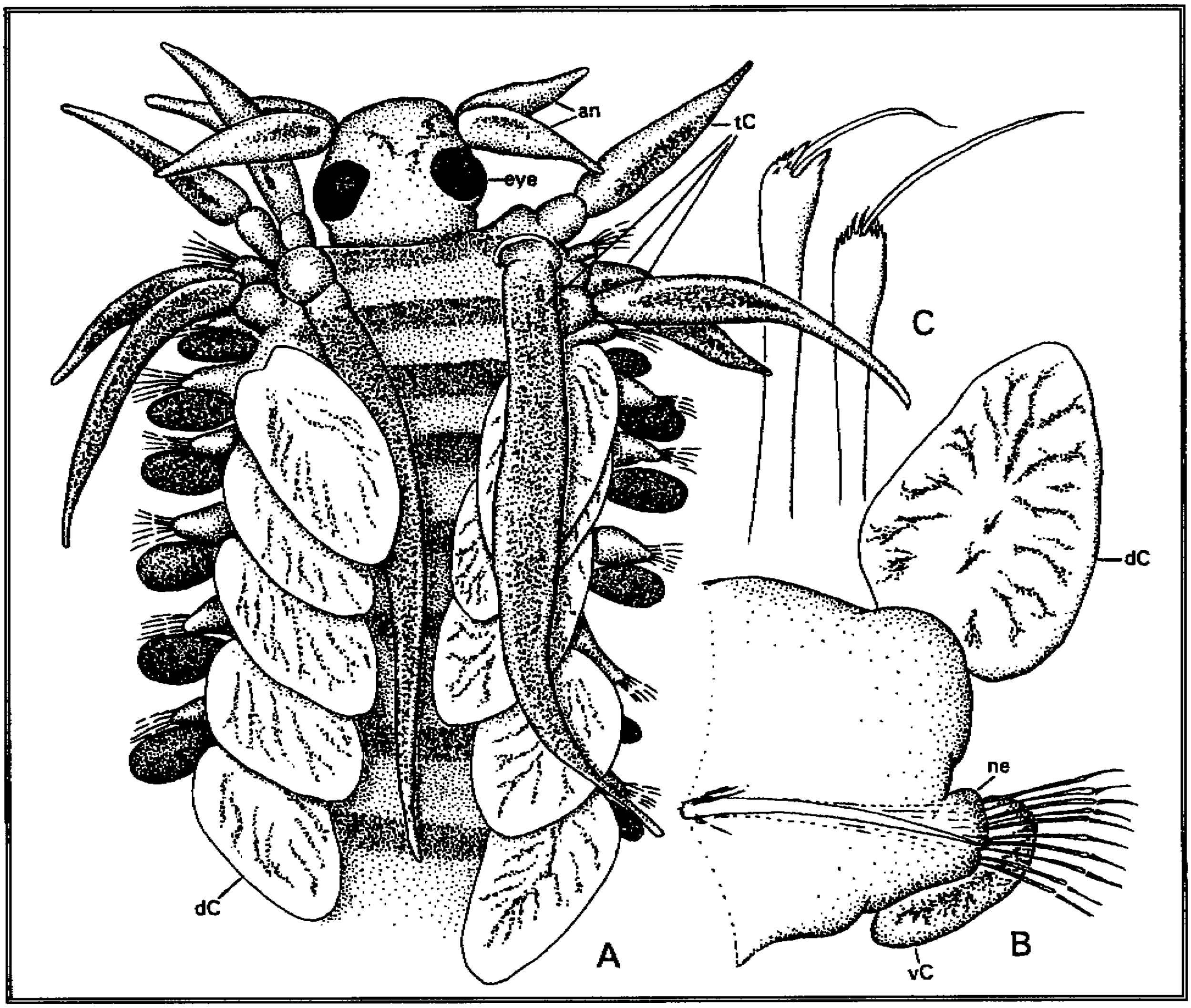

Figure 4.23. *Nereiphylla castanea.* A, anterior end, dorsal view; B, middle parapodium, anterior view; C, setae.

Biology. A commonly occurring species, found associated in rocky crevices, in algal holdfasts, and in coarse sediments and debris.

Remarks. These specimens agree well with previous descriptions. The species is not likely to be mistaken for other phyllodocids found in California because of the very large and thick frontal antennae and distinctive orange coloration that is highly diagnostic in casual examination. The holotype of *Phyllodoce ferruginea* is clearly a species of *Nereiphylla* and agrees well with the other specimens in the collections.

According to Eibye-Jacobsen (1992), the type-specimen of *N. castanea* from Japan has flattened dorsal tentacular cirri on segments 2 and 3. The California specimens do not exhibit such a flattening of tentacular cirri although they may be weakly compressed.

Type locality. Japan.

Distribution. Widely distributed, mainly in tropical, subtropical and temperate waters. U.S. Atlantic coast: Massachusetts to North Carolina; Gulf of Mexico; California; western Pacific: Sea of Okhotsk to Japan and off China; Indian Ocean; Australia and New Zealand; South Africa; intertidal to 500 m.

Genus *Phyllodoce* Lamarck, 1818

Type species: *Phyllodoce laminosa* Lamarck, 1818, by monotypy.

Diagnosis: Prostomium with 4 antennae, heart-shaped with posterior lobes variously developed, nuchal papillae present; proboscis with proximal and distal parts, proximal section with soft papillae in discrete rows or diffuse, hard cusps sometimes present; distal part with 6 divisions, sometimes with papillae. Segment 1 dorsally reduced, fused to second segment. Four pairs tentacular cirri: 1 pair on segment 1, 2 pairs on segment 2; 1 pair and normal ventral cirrus on segment 3; setae first present from segment 2, 3 or 4.

Remarks: The genus *Phyllodoce* has traditionally been divided into two genera or subgenera: *Phyllodoce* (*sensu stricto*) with a diffuse arrangement to the proximal proboscideal papillae and *Anaitides* with the papillae organized into distinct rows. However, there are several different patterns in the distribution of the proximal papillae that obscure these definitions. For example, there are species such as *P. hartmanae*, where the longitudinal rows of papillae form angled or spiral rows; at least two species that are now known to have hardened cusps among soft papillae (Blake 1988; Pleijel, 1988); and one species where the proximal papillae are organized both into rows and diffuse patterns (*P. cuspidata*). Pleijel (1988) pointed out that there is no correlation between the distribution of the proboscideal papillae and setal distribution and elected to refer *Anaitides* to synonymy with *Phyllodoce*.

The genus *Phyllodoce* is well-represented in California. Endemic species were described by Moore (1909a-b), Hartman (1936), Blake and Walton (1977), and McCammon and Montagne (1979). The latter authors reviewed and described six species from southern california. The most important recent revision of the genus is by Pleijel (1988), who redefined the genus and carefully redescribed eight species from northern Europe.

Phyllodoce hartmanae Blake and Walton, 1977

Figure 4.24

Phyllodoce hartmanae Blake and Walton, 1977:308-310, fig. 1.—Lissner *et al.*, 1986:A-8.—Hyland and Neff, 1988:A-3.
Anaitides hartmanae: Kravitz and Jones, 1979:15.
Phyllodoce (Aponaitides) hartmanae: McCammon and Montagne, 1979:353-368, fig. 6.

Material examined. California: Gulf of the Farallones, Jul 1973, 24 m (JAB); Santa Maria Basin, off Point Estero, Sta. 4 (2); off Point Sal, Sta. PJ-7 (1), Sta. PJ-11 (1), R-1 (3), R-8 (9); off Purisima Point, Sta. R-4 (2), R-5 (2).

Description. A moderate sized species, up to 28 mm long and 1.0 mm wide, with about 100 segments. Color in alcohol: pale to opaque white, with intersegmental mid-dorsal black pigment, and similar, less conspicuous ventral markings; additional dark pigment on anterior end of prostomium, around bases of tentacular cirri, and near insertion of dorsal cirri; dark branching melanophores also present in

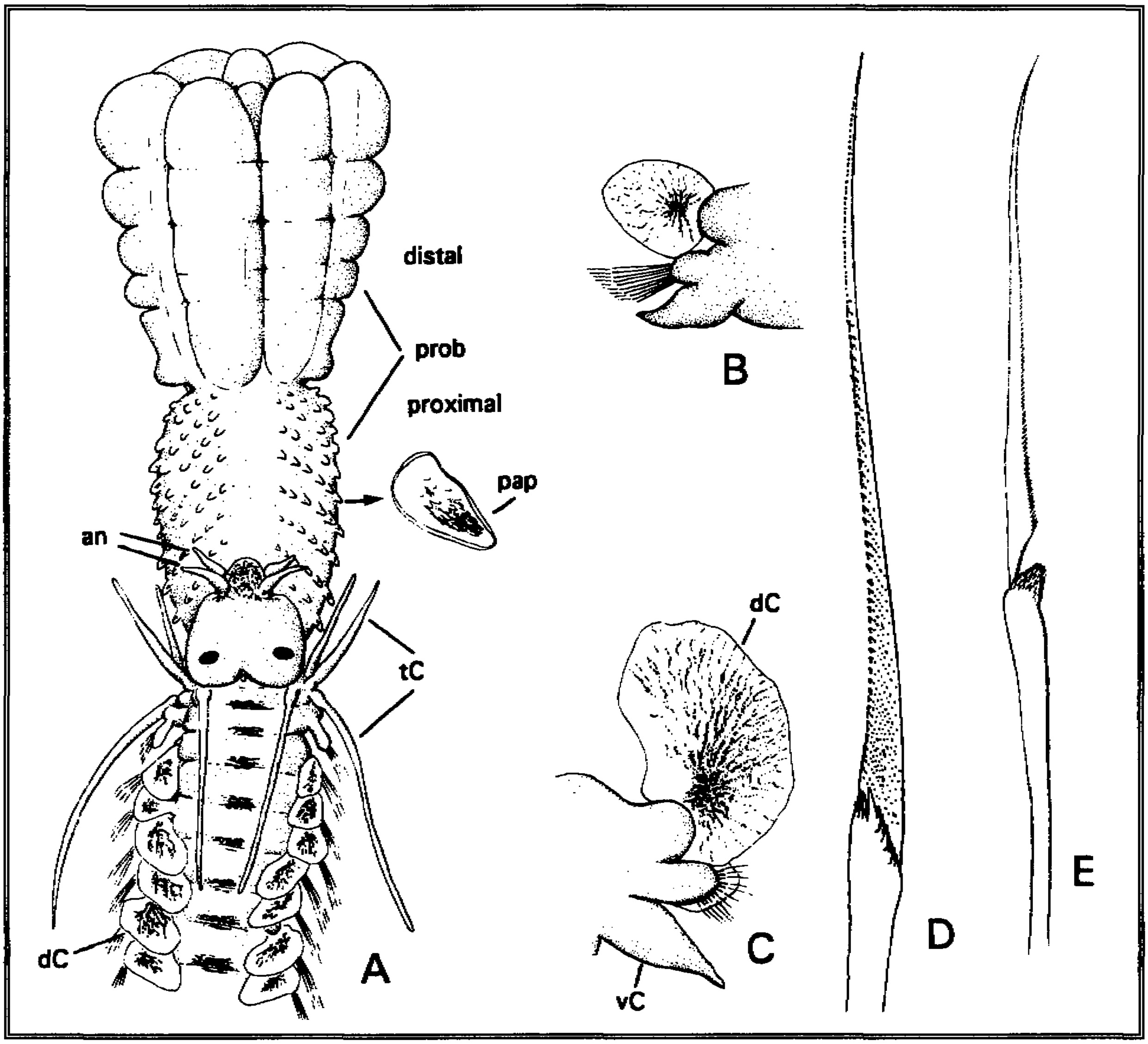

Figure 4.24. *Phyllodoce hartmanae.* A, anterior end, dorsal view, with inset of individual papillae from proximal region of proboscis; B, anterior parapodium, anterior view; C, middle parapodium, anterior view; D-C, setae. (A-C, E, after Blake and Walton, 1977; D, original).

middle of dorsal cirrus; some specimens with scattered reddish spots over various parts of body.

Prostomium cordate, about as wide as long, with narrow anterior end bearing 4 cirriform antennae; with notch bearing small nuchal papilla (Fig. 4.24A). Proboscis with proximal part bearing numerous rows of small papillae arranged in oblique rows; with smooth dorsal break in papillae; distal part of proboscis with 6 thickened ridged sections, each with indistinct lobes (Fig. 4.24A). Segment 1 reduced dorsally, fused with segment 2. Tentacular formula: $(0^1/_0 + 0^1/_1) + 0^1/_V + S^D/_V$; individual tentacular cirri long, tapering, with those of segment 2 longest, reaching posteriorly to segment 10 to 12 (Fig. 4.24A). Setae first present on segment 4.

Parapodia uniramous, narrow, bearing enlarged, thin dorsal cirri; cirri of anterior setigers shorter, more regularly cordate (Fig. 4.24B) than irregularly shaped, thin and leaflike dorsal cirri of middle segments (Fig. 4.24C). Ventral cirri triangular, pointed, extending well beyond setigerous lobe. Setae all compound spinigers; each with fine denticles on shaft and inflated end of shaft bearing single prominent rostral tooth, and numerous smaller spinelets (Figs. 4.24D-E).

Biology. A commonly occurring species continental shelf species in sediments having mixed sand an silt fractions.

Remarks. The spiral or oblique nature of the proximal papillae of this species readily separates *Phyllodoce hartmanae* from other co-occurring species. The arrangement of these papillae have caused some investigators to establish a separate subgenus (e.g., McCammon and Montagne, 1979: subgenus, *Aponaitides*). The rationale being that the form of the proboscis of *P. hartmanae* fell somewhere between the forms having the papillae in distinct rows and those having a completely diffuse pattern. Pleijel (1988), however, has demonstrated that these subgenera are not necessary because other characters such as the occurrence of acicular setae do not correspond to proboscideal morphology.

According to B. Hilbig (personal communication), this species is easily recognized among other polychaetes in a sample because the dorsal cirri retain the red color imparted by rose bengal stain during the sorting process.

Type locality and type specimens. California, Gulf of the Farallones. Holotype: LACM-AHF.

Distribution. Eastern Pacific, Oregon and California, 10-150 m.

Phyllodoce groenlandica Oersted, 1843

Figure 4.25

Phyllodoce groenlandica: Fauvel, 1923: 153-154, figs. 54 f-i.—Pleijel, 1988:144-145, fig. 3.—Pleijel, 1993:37-40, figs. 22-23, map. 12.

Phyllodoce (Anaitides) groenlandica: Uschakov, 1972:133-135, plate 5, figs. 1-4.—Pettibone, 1963:80-81, fig. 18e.—McCammon and Montagne, 1979:359-361, fig. 4.

Anaitides groenlandica: Bergström, 1914: 141-143, fig. 42.—Hartman, 1968:225, 2 figs.—Kravitz and Jones, 1979:14-15.—Gathof, 1984:19-35, figs. 19-29, 19-30.

Material examined. California: Santa Maria Basin, off Point Sal, Sta. PJ-6 (2); Tomales Bay, intertidal, coll. Jul 1964 (1).

Description. A large species, local specimens up to 55 mm long, 3 mm wide, for about 225 segments; reported up to 300 mm long, 6 mm wide, for 700 segments (Uschakov, 1972). Color variable, some specimens only faintly pigmented, but generally with elegant dark markings: body light tan to brown, with dark pigment on anterior half of prostomium; dorsum of body pigmented brownish green, with dark transverse bands in intersegmental areas; dorsal cirri with dark spots.

Prostomium cordate, wider than long, with 4 short subapical antennae; 2 small eyes present, widely spaced; posterior margin with slight medial notch, enclosing nuchal papilla (Fig. 4.25A). Proboscis with 6 longitudinal rows of 13 to 16 papillae on each side of proximal half, leaving dorsum and ventrum smooth, without papillae; distal half with 6 longitudinal rows of tubercles or large folds and ring of 16 to 18 papillae surrounding oral opening (Fig. 4.25B). Tentacular formula: $(0^1/_0 + 0^1/_1) + S^1/_V$; dorsal tentacular cirri of segments 2 and 3 longest, extending posteriorly for 10 or more segments; dorsal tentacular cirri of segments 1 and 2 shortest, only 4 to 5 segments long; setae first present from segment 3 (Figs. 4.25A-C). Neuropodium elongate, thickened, with 2 prominent lips; dorsal cirri large, foliaceous, rectangular in shape, longer than wide, becoming wider posteriorly; ventral cirri longer than neuropodial lobe, with distinct ventrally directed tip (Fig. 4.25C). Setae numbering 20 to 25 or more per fascicle, each seta with numerous 2 large and numerous small teeth on tip of shaft and fine denticles along edge of blade (Fig. 4.25D). Pygidium with 2 long tapering anal cirri.

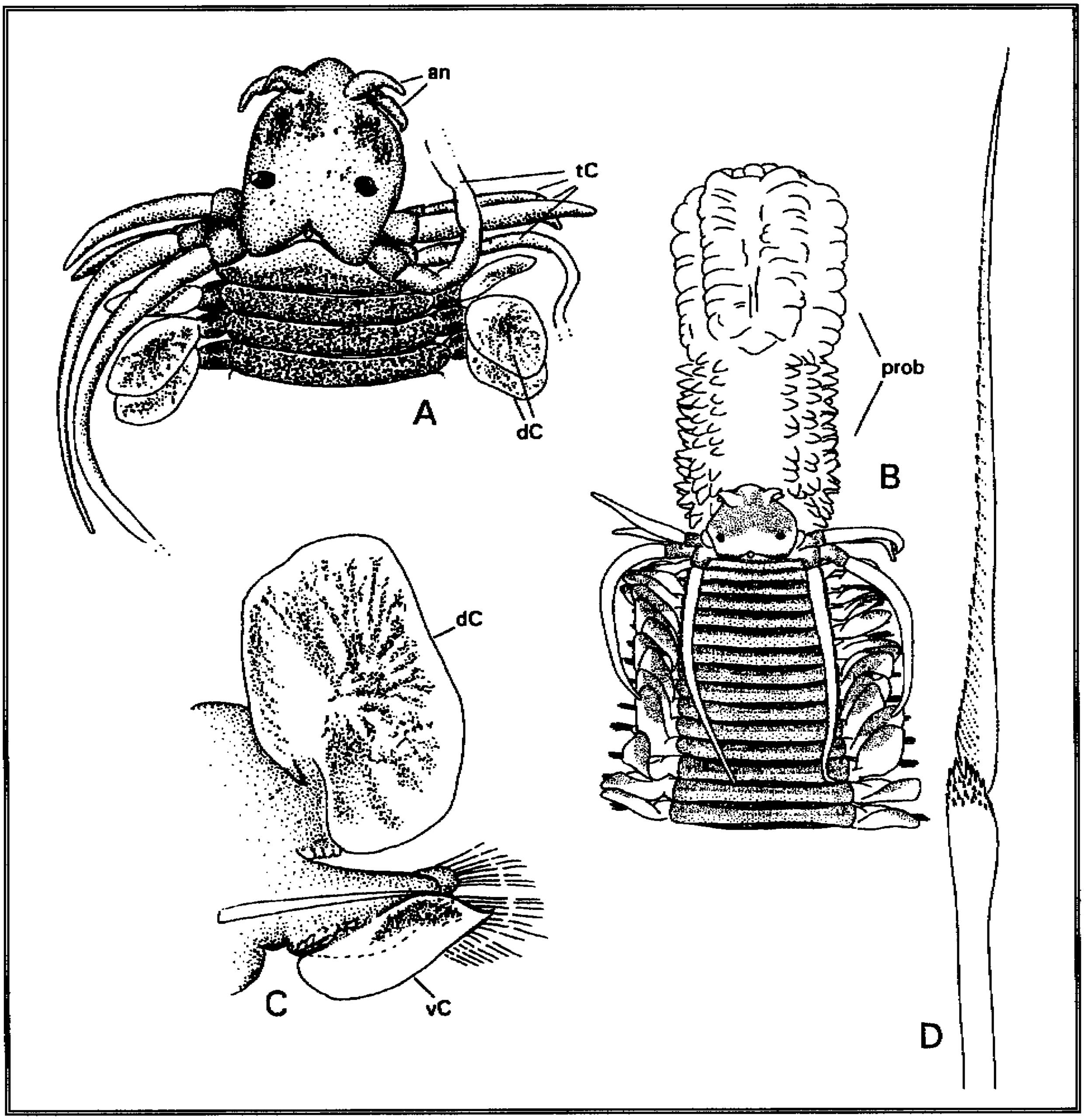

Figure 4.25. *Phyllodoce groenlandica*. A, Anterior end, dorsal view; B, same, with proboscis everted; C, middle parapodium, posterior view; D, seta. (B, after Pleijel, 1988).

Biology. The species occurs in coarse sediments with high sand inventories.

Remarks. *Phyllodoce groenlandica* is a well-known and widespread arctic-boreal species. Locally, it may be confused with *P. cuspidata* McCammon and Montagne. Both species have setae first present from segment 3 and superficial similarities in body form, prostomial shape, and pigmentation. However, *P. groenlandica* is readily distinguished from *P. cuspidata* by having ventral cirri that are longer than the neuropodium and ventrally pointed instead of shorter and blunt, and in having heavy pigment on the tentacular cirri instead of lacking such pigment. Furthermore, the proximal proboscideal papillae of *P.*

cuspidata grade from larger papillae arranged in 6 rows per side to smaller, irregularly spaced papillae that extend to the border of the distal region. In contrast, the papillae of *P. groenlandica* are all of the same size throughout the proximal region.

Type locality. Greenland. No type material (Pleijel, 1988).

Distribution. Widespread in arctic-boreal seas; continental shelf depths to about 200 m, some records to 1000 m.

Phyllodoce cuspidata **McCammon and Montagne, 1979**

Figure 4.26

Phyllodoce (Anaitides) cuspidata McCammon and Montagne, 1979:354-357, figs. 1-2.

Material examined. California: Santa Maria Basin, off Point Estero, Sta. 4 (1), off Point San Luis, Sta. 21 (1); western Santa Barbara Channel, Sta. 81 (1); off San Diego, coll. R. Velarde (1).

Description. A moderate to large species, reported up to 155 mm long, 5.5 mm wide across parapodia for 230 segments. Color in alcohol: body light tan, with brown pigment concentrated on anterior half of prostomium, and dorsum of individual segments from segment 5 (setiger 2), dorsum of posterior half of prostomium and segments 1 to 4 not pigmented; with some light brown pigment on dorsal cirri.

Prostomium cordate, wider than long with distinct triangular shaped notch at posterior border enclosing small nuchal papilla; anterior end with 4 short frontal antennae, each thick, tapering; with 2 darkly pigmented eyes, each with distinct lens (Fig. 4.26A). Proboscis with proximal region bearing 6 rows of flattened, platelike papillae on either side, no papillae dorsally and ventrally; these papillae becoming smaller, conical, irregularly arranged, and more numerous distally, forming boundary between proximal and distal regions; and closing gaps on dorsal and ventral sides; distal region with 6 rows of large, rugose papillae; oral opening surrounded by 17 papillae (Fig. 4.26A).

Tentacular formula: $(0^1/_0 + 0^1/_1) + S^1/_V$; dorsal tentacular cirri of segments 2 and 3 longest, extending posteriorly for 8 to 9 segments; dorsal tentacular cirri of segments 1 and 2 shortest, only 2 to 4 segments long; setae first present from segment 3. Neuropodium elongate, thickened, with 2 prominent lips; dorsal cirri large, foliaceous, elongate anteriorly (Fig. 4.26B), becoming rectangular in middle body segments (Fig. 4.26C); ventral cirri as long as or slightly shorter than neuropodial lobe; each ventral cirrus recurved, with tip pointed, sometimes directed ventrally (Fig. 4.26C). Setae numbering 16 to 18 or more per fascicle, each seta with 2 large and numerous small teeth on tip of shaft and fine denticles along edge of blade (Fig. 4.26D). Pygidium with 2 tapering anal cirri.

Biology. Found in silty sediments.

Remarks. *Phyllodoce cuspidata* is superficially similar to *P. groenlandica* and the specimens from Stations 4 and 81 had, in fact, been erroneously identified as *P. groenlandica* in the Phase I reconnaissance. In *P. cuspidata*, the ventral cirri are only as long as or shorter than the neuropodium instead of extending half again their length beyond the neuropodium; the first 4 segments are unpigmented instead of being heavily pigmented, and the papillae of the proximal half of the proboscis include 6 lateral rows of platelike papillae on either side and smaller, more diffuse conical papillae between the proximal and distal regions, instead of having only 6 rows.

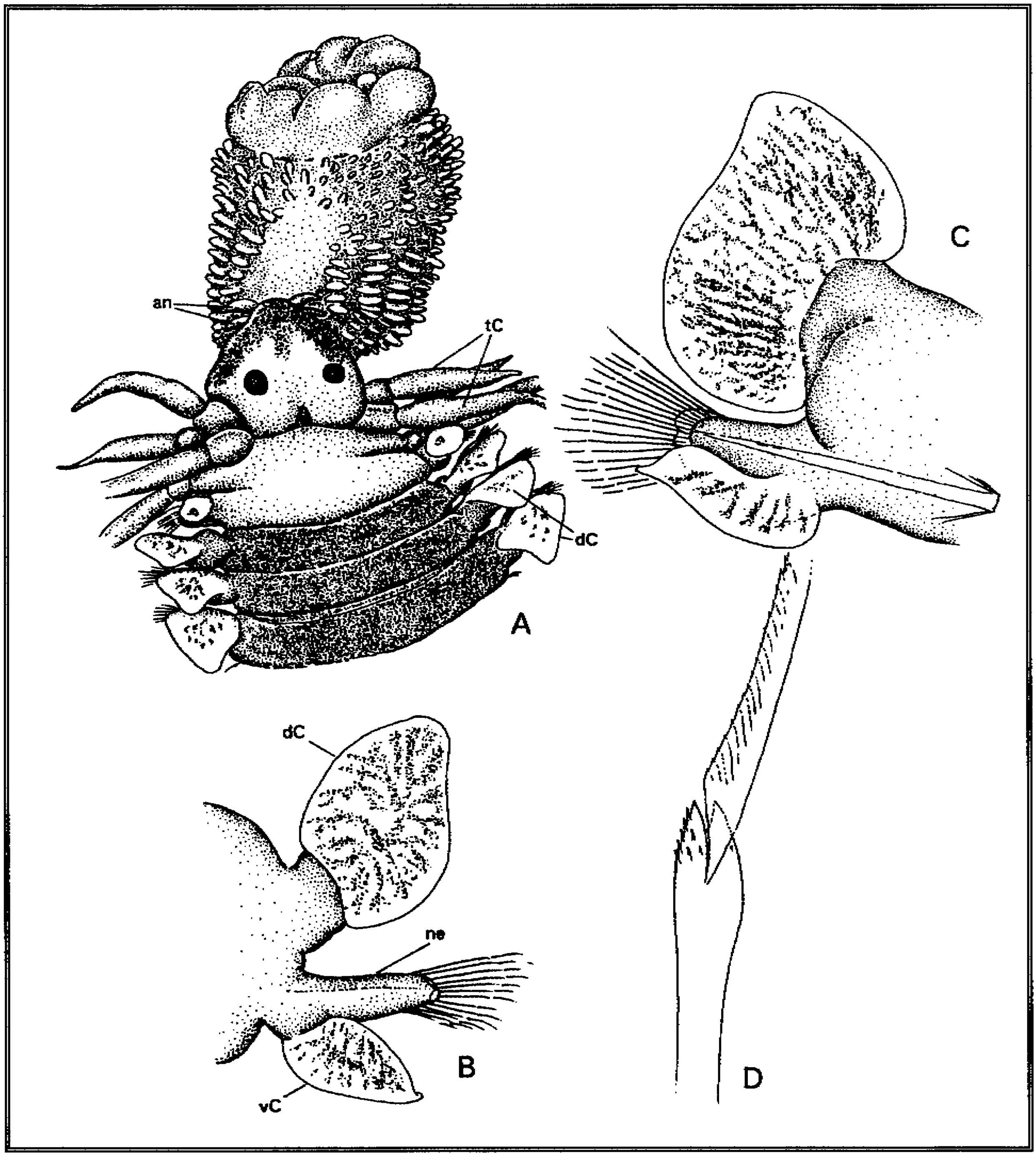

Figure 4.26. *Phyllodoce cuspidata*. A, anterior end, dorsal view; B, anterior parapodium, dorsal view; C, middle parapodium, anterior view; D, seta.

Type locality and type specimens. Southern California continental shelf. Holotype: LACM-AHF Poly 1217; Paratypes: LACM-AHF Poly 1219.

Distribution. Southern and central California continental shelf, 49-393 m.

Phyllodoce medipapillata Moore, 1909

Figure 4.27

Phyllodoce medipapillata Moore, 1909a:237, pl. 7, figs. 3-4.—Lissner *et al.*, 1986:A-8.
Anaitides medipapillata: Hartman, 1968:233, figs. 1-3.
Phyllodoce (Anaitides) medipapillata: McCammon and Montagne, 1979:362-363, fig. 5.

Material examined. California: Cayucos, rocky intertidal, 3 July 1962 (1); Santa Maria Basin, off Purisima Point, Sta. BRA-14, from rock (1); Off Point Arguello, Sta. BRA-4 (1, 1), Sta. 14, rock (1); Western Santa Barbara Channel, BRC-1, rock (1).

Description. A large species, up to 170 mm long, 3.5 mm wide across parapodia, and about 250 segments. Color in life: purplish brown and iridescent; in alcohol: tan with darker brown pigment on dorsum of most segments; some brown pigment granules scattered randomly over body. Prostomium cordate, wider than long, widest at level of 2 large eyes; with 2 pairs of short, cirriform subapical frontal antennae; posterior margin with medial notch, enclosing small nuchal papilla (Fig. 4.27A). Proboscis divided into proximal and distal sections; with 6 lateral rows of about 12 small papillae in proximal half; distal half with heavy rugose transverse ridges resembling papillae; oral opening with about 20 oval papillae (Fig. 4.27A). A prominent eversible nuchal organ present on each side lateral to prostomium and near bases of tentacular cirri of segment 1.

Tentacular formula: $(0^1/_0 + 0^1/_1) + 0^1/_V + S^D/_V$; dorsal tentacular cirri of segment 3 longest, extending posteriorly for 8 to 9 segments; dorsal tentacular cirri of segments 1 and 2 shortest, only 4 to 5 segments long; setae first present from segment 4. Neuropodium short, thickened, with 2 lips; dorsal cirri large, foliaceous, longer than wide in anterior and middle segments, becoming wider posteriorly; ventral cirri also foliaceous, with bluntly pointed ends extending slightly beyond tip of neuropodial lobe (Fig. 4.27B). Setae numbering 25 or more per fascicle, each seta with numerous small teeth on tip of shaft and fine denticles along edge of blade (Fig. 4.27C). Pygidium with 2 clavate anal cirri.

Biology. Most of the specimens examined in this study come from rocky habitats and it is likely that this species occupies cryptic habitats associated with hard substrates.

Remarks. The eversible nuchal organs are apparent when the proboscis is everted. Similar organs were mistaken by Hartman (1966) as bases of tentacular cirri. On this basis, she named a new genus, *Prophyllodoce*, for a Hawaiian species. Subsequent authors (Uschakov, 1972; Fauchald, 1977; McCammon and Montagne, 1979) have not accepted *Prophyllodoce* as a valid genus. *Phyllodoce medipapillata* is very similar to *P. madeirensis*, which according to McCammon and Montagne (1979) differs only in the absence of the eversible nuchal organs.

Type locality and type specimens. California, Monterey Bay. Holotype: CASIZ 53; Paratype: ANSP 2535.

Distribution. Central and southern California, intertidal to 300 m.

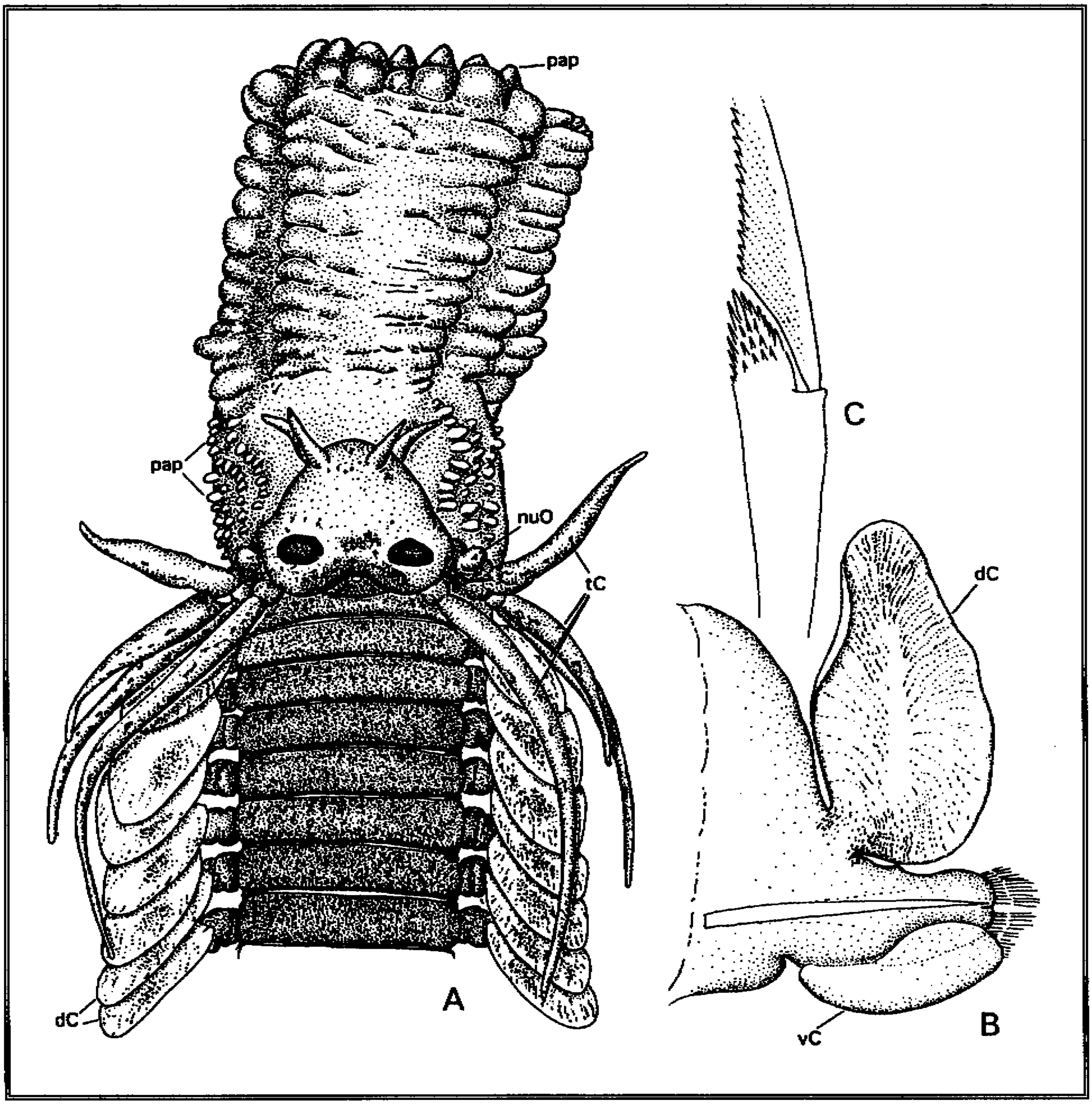

Figure 4.27. *Phyllodoce medipapillata.* A, anterior end, dorsal view; B, middle parapodium, posterior view; C, seta.

Phyllodoce longipes Kinberg, 1866

Figure 4.28

Phyllodoce longipes Kinberg, 1866:241.—Ehlers, 1901:72, pl. 7, figs. 1-4.—Bergström, 1914:149, fig. 47.—Day 1963:394, figs. 3d-f; 1967:144, fig. 5.2.a-c.—Pleijel, 1990:146-147, fig. 5 (synonymy).
Anaitides longipes: Hartman, 1968:229, figs. 1-3.—Kravitz and Jones, 1979:15-16.—Gathof, 1984:19-37, figs. 19-31, 19-32.—Parker, 1987:193-194.
Phyllodoce (Anaitides) papillosa: McCammon and Montagne, 1979:357-359, fig. 3. *Not* Uschakov and Wu, 1959.
Phyllodoce papillosa: Hyland and Neff, 1988:A-3.

Material examined. California: Santa Maria Basin, off Point Sal, Sta. R-1 (7), Sta. R-8 (5), Sta. PJ-1 (1), Sta. PJ-6 (1), Sta. PJ-10 (1); off Purisima Point, Sta. R-4 (8); Tomales Bay, subtidal in sand (1).

Description. A small to moderately sized species, local specimens 8 to 10 mm long, 1.0 mm wide across parapodia, for 45 to 60 segments; larger specimens reported by Pleijel (1990), up to 16 to 17 mm for 75 segments. Color in alcohol: light tan with brown pigment lightly scattered on prostomium, borders of body segments, dorsal and ventral cirri, and concentrated across dorsum of setigers 1 to 2; some specimens with heavier mid-dorsal pigment on body segments, corresponding to observations by Pleijel (1990).

Prostomium longer than wide, expanded medially, narrowing anteriorly to bluntly rounded tip bearing 4 subapical antennae and narrowing posteriorly forming 2 well-developed nuchal lobes encompassing nuchal papilla; both pairs of frontal antennae positioned slightly ventral; 2 large eyes present on peculiar elevated crest that forms a transverse anterior edge in middle of prostomium, merging posteriorly with nuchal lobes (Fig. 4.28A). Proboscis with proximal and distal parts, each bearing 9 papillae; papillae of proximal part small, arranged into 6 rows of 10 to 14 papillae on each side, leaving dorsum and ventrum smooth and free of papillae; distal part with larger conical papillae of different sizes, diffusely arranged (Fig. 4.28B); terminal or oral papillae not observed, but 18 "buccal papillae" observed by McCammon and Montagne (1979).

Tentacular formula: $(0^{1}/_{0} + 0^{1}/_{1}) + 0^{1}/_{V} + S^{D}/_{V}$; dorsal tentacular cirri of segments 2 and 3 longest, extending posteriorly for 6 to 7 segments (Fig. 4.28A); ventral tentacular cirrus of segment 2 shortest, only extending for about 2 segments; setae first present from segment 4. Neuropodium elongate, with short superior protuberance; dorsal cirri broad, leaflike, about as wide as long; ventral cirri elongated, pointed, as long as podial lobe (Fig. 4.28C). Setae numbering 9 to 12 per fascicle, each with numerous small teeth on tip of shaft and fine denticles along edge of blade (Fig. 4.28E). Pygidium with 2 long tapering anal cirri (Fig. 4.28D).

Biology. *Phyllodoce longipes* has been recorded from bottoms with shell, gravel, mud, and sand; the type specimen of Kinberg was taken from a kelp holdfast (Parker, 1987). The species has been widely recorded, but never abundantly. According to Parker (1987), no more than 50 specimens had ever been identified. Twenty-five specimens from California were examined in the present study.

Remarks. *Phyllodoce longipes* was recently redescribed by Pleijel (1990) based upon the holotype from Chile and other specimens from the North Atlantic. It is apparent from Pleijel's description, that specimens identified as *P. papillosa* in the Phase II monitoring program are actually *P. longipes*. The most diagnostic feature of this species is the superior extension on the podial lobe. This structure is a generic level character in the genus *Sige*. The large distal papillae on the proboscis of this species are also highly diagnostic, and have led to the confusion with *P. papillosa* described from China by Uschakov and Wu (1959; see also 1965). The latter species was not described with a superior lobe on the neuropodium,

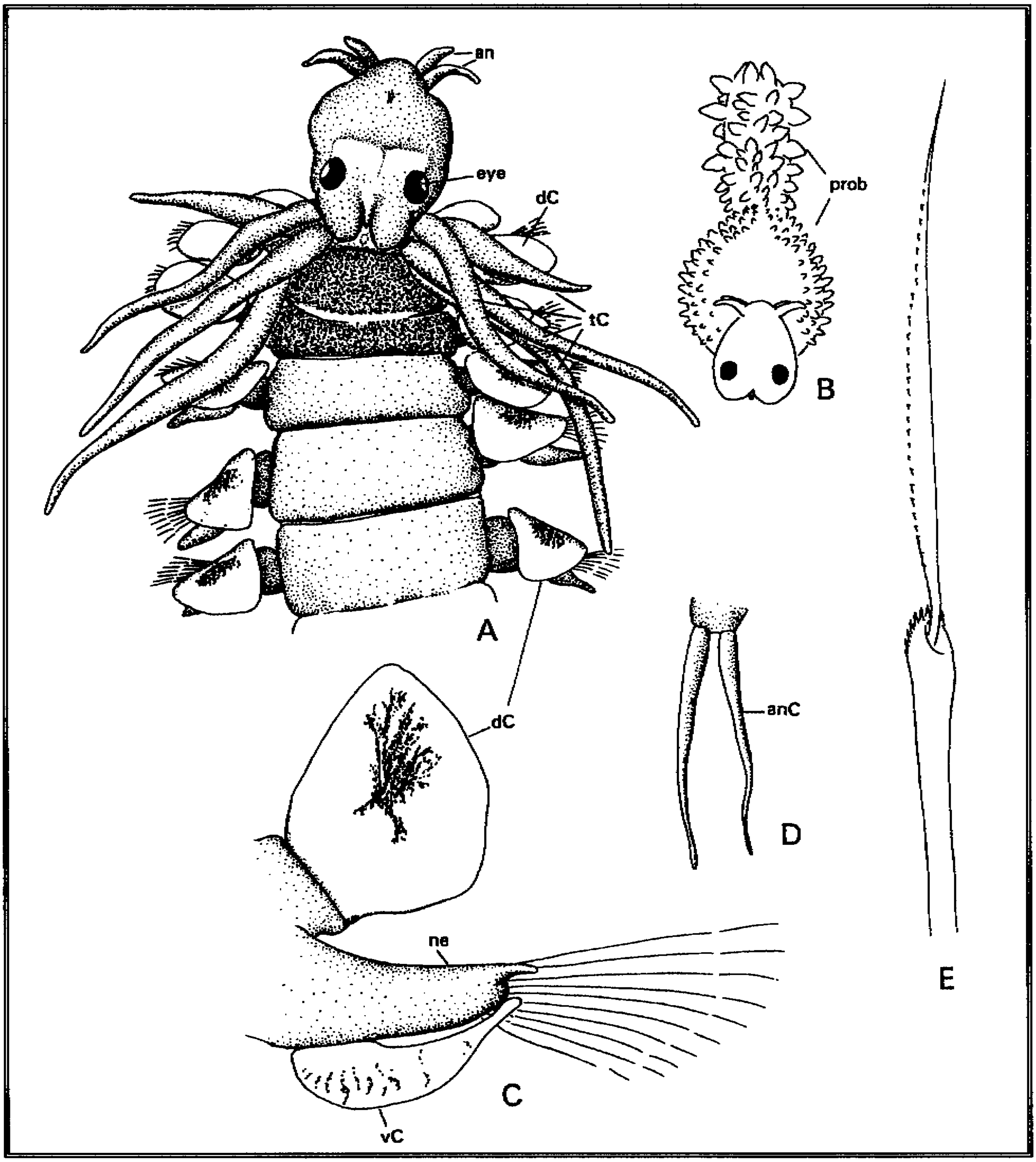

Figure 4.28. *Phyllodoce longipes.* A, anterior end, dorsal view; B, same, with proboscis everted; C, middle parapodium, posterior view; D, pygidium with anal cirri; E, seta. (B, after Pleijel, 1988).

although specimens should be reexamined in light of Pleijel's description of *P. longipes*. *Phyllodoce papillosa* was reported from California by McCammon and Montagne (1979), and these records are here referred to *P. longipes*. Although these authors did not describe a superior neuropodial lobe, it was probably present on their specimens because the characteristic anterior dorsal pigment markings of *P. longipes* were reported by McCammon and Montagne (1979).

The dorsum of the prostomium bears an unusual elevated crest that encompasses the eyes and posterior nuchal extensions. This crest does not appear to have been described previously.

Type locality and type specimens. Chile, Valparaiso. Holotype: SMNH 632.

Distribution. Chile; Gulf of Mexico; southeastern United States, South Africa; northern Europe; California, 20-150 m.

Phyllodoce pettiboneae Blake, 1988

Figure 4.29

Phyllodoce pettiboneae Blake 1988:252-254, fig. 4.
Phyllodoce sp. A: Lissner *et al*., 1986:A-8.—Hyland and Neff, 1988:A-3.

Material examined. California: Santa Maria Basin, off Point Sal, Sta. PJ-11 (1); off Purisima Point, Sta. R-4 (1); off Point Arguello, Sta. 65 (1); off San Diego, WUD Sta. A-8, 32°39.84'N, 117°16.84'W, 62.5 m, (2), Sta. A-3, 32°39.10'N, 117°17.83'W, 81.5 m, (1), Sta. A-4, 32°41.07'N, 117°18.42'W, 80.5 m, (1), all provided by Ron Velarde.

Description. A moderate sized species, up to 12 mm long and 0.5 mm wide for 75 setigers. Color in alcohol: light tan with brown pigment granules scattered over prostomium, and concentrated dorsolaterally on each segment and on dorsal and ventral cirri; medial pigment found in east coast specimens not present in California population.

Prostomium longer than wide, medially inflated, with antennae located subapically, leaving tip of prostomium free; with 2 dark reddish eyes, each with clear lens; antennae thin, cirriform, dorsal pair thinner than ventral pair; without nuchal papilla (Fig. 4.29A). Proboscis with proximal half bearing lateral clusters of numerous papillae and 4 to 5 hard cusps (Fig. 4.29A), dorsum and ventrum without papillae; papillae organized into irregular crowded rows, sometimes oriented anterior to posterior; individual papillae glandular, some with thickened walls, intermediate in form to larger thickened cusps; individual cusps appearing trapezoidal in some views, each with thickened, shiny walls, joined ventrally to large glandular sac (Fig. 4.29C); distal part of proboscis lacking papillae.

Segments 1 and 2 fused, not visible dorsally; segment 3 with first setae, visible dorsally, free from prostomium and setiger 2. Tentacular formula: $(0^1/_0 + 0^1/_1) + S^1/_V$. All tentacular cirri long, tapering, cirriform, extending posteriorly over 5 to 6 segments (Fig. 4.29A). Normal dorsal cirri longer than broad, especially in anterior setigers; ventral cirri long, thin, tapering to narrow tip (Fig. 4.29B). Neuropodium bilobed, bearing internal aciculae and spreading fascicle of 9 to 12 long composite spinigers; each spiniger with 5 to 6 sharp spines on tip of shaft and fine serrations on blade (Fig. 4.29D). Anal cirri absent.

Biology. In silty sediments with moderate amounts of sand.

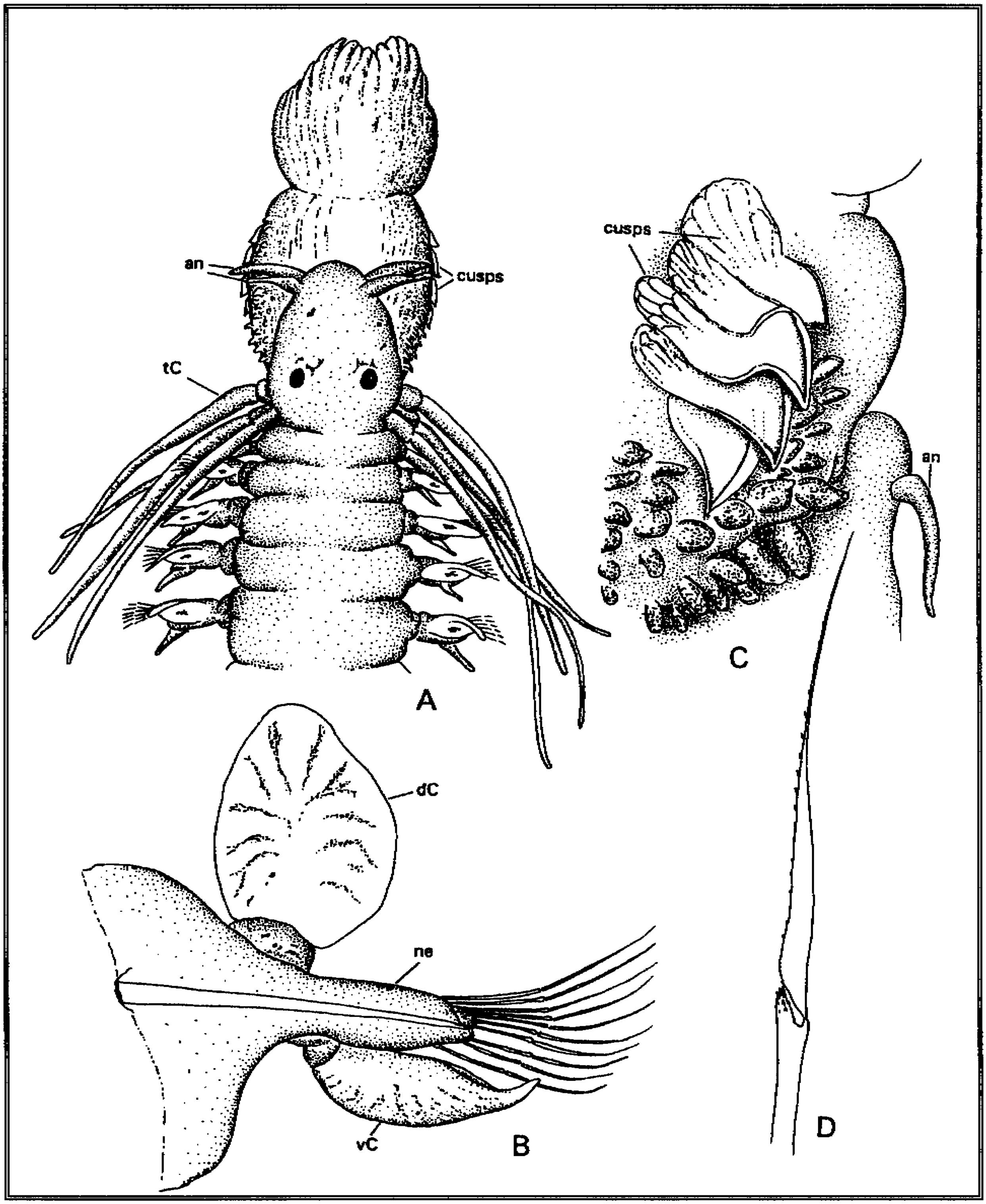

Figure 4.29. *Phyllodoce pettiboneae.* A, anterior end, dorsal view; B, middle parapodium, dorsal view; C, details of papillae and cusps on proboscis, lateral view; D, seta.

Remarks. This species has been called *Phyllodoce* sp. A in ecological surveys and monitoring programs in California. The California specimens have been carefully compared with specimens from the type locality off New England and, except for pigmentation, there are no morphological differences. The nature of the proboscideal papillae and hardened cusps is virtually identical. The differences in pigmentation should be expected in widely separated populations of the species.

Phyllodoce pettiboneae is most closely related to *P. rosea* (McIntosh) which has been redescribed by Pleijel (1988). Both species have hardened cusps on the proboscis. In *P. pettiboneae*, these cusps are arranged in a single series, whereas in *P. rosea*, they are grouped into two rows.

Type locality and type specimens. Massachusetts, continental shelf depths. Holotype: USNM 904920; Paratypes (14): USNM 90412-17, 90418-24.

Distribution. California, San Diego to Santa Maria Basin, 50-160 m; off Massachusetts, 55-167 m.

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5. FAMILY LACYDONIIDAE BERGSTRÖM, 1914

by

James A. Blake[1]

Introduction

The lacydoniids represent an obscure and poorly-known family of polychaetes having 7-8 species in a single genus *Lacydonia*. Another genus, *Paralacydonia* was referred to a separate family by Pettibone (1963). Lacydoniids are known through a few scattered accounts from Europe, the Mediterranean, the North Atlantic, the northwestern Pacific and the Antarctic. They are known from the intertidal to abyssal depths. No species of *Lacydonia* were encountered in the material collected from the Santa Maria Basin. However, specimens of an unknown species were collected from the continental slope off San Francisco as part of surveys conducted by the U.S. Navy and EPA in 1990 and 1991 (SAIC, 1991, 1992; Blake *et al.* 1992), and appear to be the first records from California. Specimens of what may be the same species were also collected from sediments near active hydrothermal vents in the Guaymas Basin in the Gulf of California and the Juan de Fuca Ridge off western Canada. Because of this overlapping distribution, it is likely that lacydoniids are widespread on the continental slope in the eastern Pacific. For this reason, the species is treated in this volume of the Atlas.

Morphology

The body of lacydoniids is small, linear, and has relatively few segments. The prostomium is rounded anteriorly and is usually wider than long. Two pairs of short frontal antennae and a pair of nuchal organs are present. A median antenna has been reported from most specimens, and it is likely that this fragile structure is present on all species. Eyes may be present or absent. There is a pair of very short tentacular cirri on the peristomial segment. A muscular pharynx is present but jaws are lacking. The first 2-3 segments are uniramous, lacking notopodia and notosetae; following parapodia are distinctly biramous. Setae include supporting acicula, simple notosetae, and compound, spinigerous neurosetae (Fig. 1C). Dorsal cirri are small, oval, flattened and attached subdistally on the dorsal ramus. Presetal and postsetal lobes are lacking. Pettibone (1963) considered lacydoniids to be closely related to the phyllodocids. In my opinion, they also exhibit similarities to the Hesionidae in parapodial form, structure of the setae, and nature of the pharynx.

Taxonomic History

Initially, *Lacydonia* was included in the Phyllodocidae. The family Lacydoniidae was formally established by Bergström (1914) as part of his revisionary work on the phyllodociform polychaetes. Fauvel (1913) described *Paralacydonia paradoxa* and later included this genus along with *Lacydonia miranda* in a subfamily (Lacydoniinae) of the Phyllodocidae (Fauvel, 1914, 1923). The two genera have been included together either as a separate family, the Lacydoniidae, or as a subfamily of the Phyllodocidae in most subsequent accounts (Hartman, 1959, 1968; Day, 1967; Uschakov, 1972; Fauchald, 1977; Gathof, 1984). Pettibone (1963), however, determined that *Paralacydonia* had stronger affiliations with the Nephtyidae and established a separate family, the Paralacydoniidae for that genus. After examining numerous specimens of *Paralacydonia paradoxa*, I agree with Pettibone's conclusion and retain Paralacydoniidae as

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a separate family. The similarities of *P. paradoxa* to nephtyids are readily seen in the form of the parapodia that bear long, flattened pre- and postsetal lamellae and the space between the noto- and neuropodia form a lateral ciliated channel that runs along the entire length of the body, a very nephtyid-like characteristic. *Lacydonia*, in contrast, has rather shortened and stubby parapodia that lack pre- and postsetal lamellae. In my opinion, species of *Lacydonia* share more affinities with phyllodocids and hesionids than with *Paralacydonia*.

One additional genus that has been referred to the Lacydoniidae deserves a brief comment. Rullier (1964) established the genus and species *Pseudolacydonia caeca* from the Cape Verde Islands. Examination of the description and illustrations of this species, however, indicate that it should be referred to the Family Goniadidae.

The taxonomic status of the various species that have been referred to the genus *Lacydonia* are confused. At least nine species have been described. The first species was *L. miranda* Marion and Bobretsky, 1875, the type-species of the genus, originally described from the Mediterranean, the Gulf of Marseille in shallow water. The species has subsequently been reported from other European locations including the Atlantic coast of France (Saint-Joseph, 1887), Ireland (Southern, 1914), Denmark and Sweden (Eliason, 1962), Sicily (Cantone, 1973), and Spain (Sarda, 1982). Fauvel (1923) and Hartmann-Schröder (1971) provide summary descriptions and illustrations. The only non-European record for *L. miranda* appears to be that of Gathof (1984), who reported the species from shallow waters off western Florida. Eliason (1962) appears to be the first investigator to notice the median antenna; it was reported in some detail by Cantone (1973). This structure is very fragile and easily lost. It is likely, however, that *L. miranda* and all subsequently described species of the genus actually have a median antenna even if it was not reported (see also Hartmann-Schröder and Rosenfeldt, 1992 for further discussion). Considerable review of the various records of *L. miranda* needs to be undertaken because it appears that several species may actually be involved. For example, Eliason's specimens from northern Europe lack eyes and have a different parapodial structure from that reported by Cantone (1973) from Sicily. The parapodia illustrated by Gathof (1984) from American waters appear different as well. Eliason's specimens may be more closely related to deep-water species such as *L. cirrata* (see below).

The second species to be described was *L. mikrops* Ehlers, 1913, from Antarctic waters in depths of around 380 m. Hartman (1964) summarized the main features of this species in her review of Antarctic polychaetes; small eyes were present, but a median antenna was not reported. Two syntypes of *L. mikrops* were subsequently examined by Hartmann-Schröder and Rosenfeldt (1992), who determined that notosetae began from setiger 4 instead of 3 and that a median antenna was indeed present. These authors also noted that the specimen that was described by Ehlers was apparently different from the types because it reportedly had fewer segments.

The third species to be described was *L. papillosa* Uschakov, 1958, from the Kuril-Kamchatka Trench in depths greater than 5000 m. This deep-sea species was also found off Japan in abyssal depths (Uschakov, 1972). Rullier (1965) described *L. incognita* from West Africa. This shallow-water species is *nomen dubium*, however, because it was described from an anteriorly incomplete specimen and the parapodia do not resemble those of other lacydoniids.

The fifth and sixth species of *Lacydonia* to be described were actually included in the Scalibregmatidae: genus *Scalispinigera* (Hartman, 1967; Hartman and Fauchald, 1971). *S. oculata* Hartman, 1967, came from the Antarctic Peninsula, had two large eyes, compound setae, lacydoniid-like parapodia, and was most certainly not a scalibregmatid. Blake (1981) noted that the species appeared to resemble a hesionid rather than a scalibregmatid. A subsequent examination of the holotype (USNM 47326) confirmed it to be a lacydoniid. Pleijel and Fauchald (1993) formally transferred the species to *Lacydonia* and provided a new description. The second species, *S. cirrata* Hartman and Fauchald, 1971, was described from deep-water off Delaware and New Jersey by Hartman and Fauchald (1971). Examination of the holotype and paratype of this species (LACM-AHF Poly 0894 and 0895) has also confirmed that it belongs to the genus *Lacydonia*. This latter species has been extensively collected as part of MMS supported surveys and monitoring programs of the U.S. Atlantic continental shelf and slope

(Maciolek-Blake *et al.*, 1985; Maciolek *et al.*, 1987a-b; Blake *et al.*, 1987; Blake *et al.*, 1993). The species ranges in depth from about 140 m on the shelf to more than 2000 m on the slope and has been found from Massachusetts to North Carolina. Neither *L. oculata* nor *L. cirrata* were originally described with a median antenna. Most of the *L. cirrata* specimens collected as part of the MMS studies have a small median antenna.

Laubier (1975) described *L. laureci*, an anoculate species from the Mediterranean in abyssal depths of 4700 m. This species was the first to be fully described with five antennae. The median antenna of *L. laureci* is long, about half the length of prostomium and longer than the frontal antennae.

As part of studies on various German expeditions to Antarctica on the R/V *"Polarstern,"* Hartmann-Schröder and Rosenfeldt (1988, 1992) and Hartmann-Schröder (1993) have described three additional species of *Lacydonia*. *L. antarctica* comes from a depth of 265 m off King George Island in the South Shetland Islands. This species was described with five very small antennae, two large eyes, and short, inflated parapodia. It is probable that this species is the same as *L. oculata* (Hartman), described from the nearby Antarctic Peninsula (Pleijel and Fauchald, 1993). *L. elongata* Hartmann-Schröder and Rosenfeldt, 1992 was described from the Antarctic Peninsula at a depth of 634 m. This species had a short, cirriform median antenna, no eyes, and very elongate parapodia. This species is similar to *L. mikrops*, according to Hartmann-Schröder and Rosenfeldt (1992), but differs in lacking eyes, by having frontal antennae that are filiform instead of papilliform, and by having parapodia that are long and narrow instead of short and broad. *L. elongata* is also similar to *L. laureci*, but differs by having long parapodia and in having the median antenna inserted in the anterior instead of the posterior half of the prostomium. *Lacydonia gordia* Hartmann-Schröder, 1993, has a short, broad prostomium with short, ovoid antennae and no eyes. The parapodia have short blunted postetal lobes. The species somewhat resembles *L. cirrata* from the western North Atlantic.

In summary, the previously described species of *Lacydonia* can be arranged in the following groups:

1. Species with large eyes

    L. miranda Marion and Bobretsky, 1875. All subsequent records except Eliason (1962). North Atlantic

    L. oculata (Hartman, 1967) = *L. antarctica* Hartmann-Schröder and Rosenfeldt, 1988. Antarctic Peninsula, subantarctic island groups

2. Species with small eyes.

    L. mikrops Ehlers, 1913. Antarctica, 384 m.

3. Species with no eyes.

    L. papillosa Uschakov, 1958. Western Pacific, abyssal depths.
    L. cirrata (Hartman and Fauchald, 1971). Western North Atlantic shelf and slope depths
    L. laureci Laubier, 1975. Mediterranean, abyssal depths.
    L. elongata Hartmann-Schröder and Rosenfeldt, 1992. Antarctica, deep water.
    L. miranda sensu Eliason, 1962. Skagerak between Sweden and Denmark, 271-487 m.
    L. gordia Hartmann-Schröder, 1993. Antarctic Peninsula, 165-177m.

Another species has been discovered in continental slope sediments off northern California. This species appears to be most closely related to *L. elongata* because the parapodia are long and narrow.

Descriptions of Species

Lacydonia Marion and Bobretsky, 1875

Type species. *Lacydonia miranda* Marion and Bobretsky, 1875.

Diagnosis. Prostomium usually rounded, bearing 4 anterior antennae and 1 median antenna; eyes present or absent; nuchal organs sometimes present. Tentacular segment reduced, bearing a single pair of short cirri. First 3 segments uniramous, all subsequent segments biramous. Parapodia well developed, bearing dorsal and ventral cirri and sometimes with well developed supracicular lobes. Notosetae all simple capillaries; neurosetae all compound spinigers.

Lacydonia hampsoni, Blake, new species

Figure 5.1

Material examined. California, off San Francisco, R/V *Point Sur*, Sta. 3-1, 37°23.82'N, 123°15.55'W, 1338 m, 12 Sep. 1991, **paratype** (CASIZ 089753); Sta. 3-6, 37°27.54'N, 123°16.99'W, 1505 m, 14 Sep. 1991 (1); Sta. 3-10, 37°26.00'N, 123°10.83'W, 985 m, 16 Sep. 1991, **paratype** (LACM-AHF Poly 1652); Sta. 3-11, 37°25.50'N, 123°15.02'W, 1225 m, 15 Sep. 1991, **paratype** (LACM-AHF Poly 1653); Sta. 3-13, 37°24.30'N, 123°20.02'W, 1780 m, **paratype** (CASIZ 092845); Sta. 3-18, 37°22.31'N, 123°19.24'W, 1990 m, 15 Sep. 1991, **paratype** (USNM 168089); Sta. 3-19, 37°26.05'N, 123°19.99'W, 1760 m, 16 Sep. 1991, **paratype** (LACM-AHF Poly 1654); Sta. 4-7, 37°13.47'N, 123°07.48'W, 1020 m, 18 Sep. 1991, **holotype** (CASIZ 089752); Sta. C-5, 37°17.01'N, 123°13.50'W, 1560 m, 19 Sep. 1991 (1).

Description. A small species, up to 4 mm long and 1 mm wide (across parapodia) for 30-35 setigers. Color in alcohol: tan with dark brown pigment spots concentrated on prostomium and first 3 setigers, less pigment on following segments; pigment spots concentrated on borders of parapodia and on dorsal and ventral cirri. Two heavy, thickened and darkly pigmented internal structures visible median to tentacular segment and setiger 1, best seen ventrally (Fig. 5.1B). Pharynx visible through body, with heavy transverse musculature.

Prostomium oval-shaped, broadly rounded on anterior margin, approximately 1.5 times wider than long (Fig. 5.1A, B); bearing 4 short digitiform antennae on anterior margin and a single short median antenna in anterior one-third of prostomium; eyes absent. Distinct nuchal cilia apparent in ventrolateral groove located between prostomium and tentacular segment (Fig. 5.1B). Tentacular segment well developed dorsally, forming complete ring, incomplete ventrally; bearing a single pair of short, digitiform cirri. Setigers 1-3 uniramous, with notopodia reduced to bulbous lobe bearing digitiform dorsal cirrus (Fig. 5.1A). Notopodia fully developed by setiger 4; each cirrus thickened, but elongate, with distinct supracicular lobe (Fig. 5.1C); dorsal cirrus short, thickened, very glandular; notosetae all simple capillaries, numbering approximately 12 per fascicle. Neuropodia long, narrow, with pointed supracicular lobe (Fig. 5.1C); ventral cirrus narrow pointed; neurosetae all compound spingers, numbering up to 25 per fascicle, each with long pointed tooth, blade with very fine dentitions along cutting edge (Fig. 5.1D).

Pygidium with 2 long lateral cirri and 1 short medial cirrus.

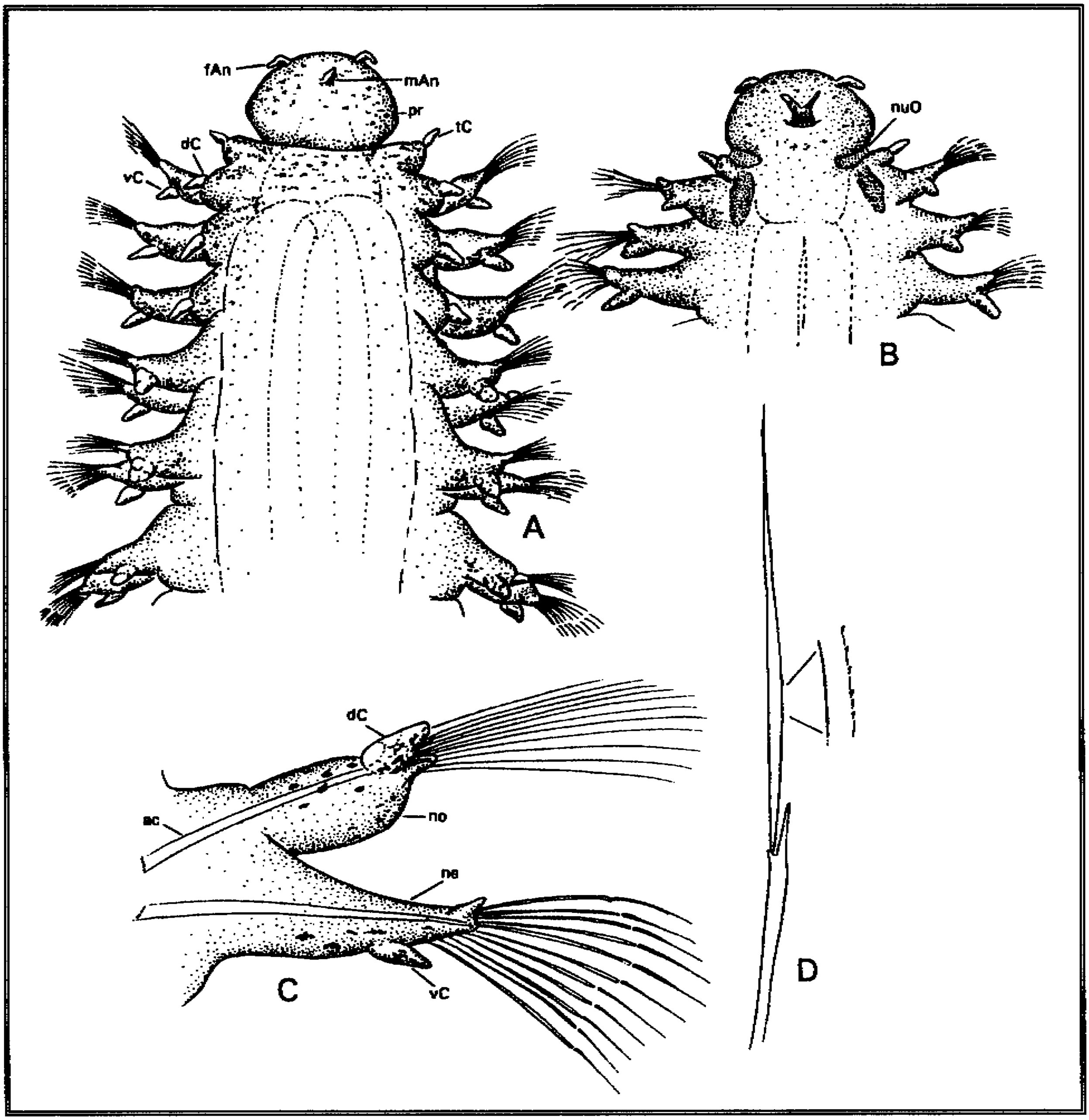

Figure 5.1. ***Lacydonia hampsoni* Blake, new species**: A, anterior end, dorsal view (75×); B, same, ventral view; C, middle parapodium, posterior view (225×); D, neuroseta, with inset showing detail of shaft (1000×).

Remarks. *Lacydonia hampsoni* belongs to the anoculate group of species (see above) and is most closely related to *L. elongata* Hartmann-Schöder and Rosenfeldt (1992) from the Antarctic Peninsula in 634 m. Both species have elongate parapodia, short antennae, and a median antenna that is located in the anterior half of the prostomium. The two species differ according to the form of the parapodia and associated cirri. The notopodium of *L. hampsoni* is thicker than the neuropodium instead of both the noto- and neuropodia being equally narrow. Furthermore, the dorsal cirri of *L. hampsoni* are thick, very glandular, especially in the anterior setigers, and are located near the tip of the notopodium. In contrast, the dorsal cirri of *L. elongata* are digitiform throughout and located more medially on the notopodium. There appear to be more setae in the fascicles of *L. hampsoni* (ca. 12 notosetae and 25 neurosetae) than in *L. elongata* (ca. 5 notosetae and 14 neurosetae) although the specimens of *L. hampsoni* were slightly larger.

A comparison of *L. hampsoni* with specimens of *L. cirrata* from the U.S. Atlantic continental slope reveals a considerable difference between the two species in the form of the parapodia. *L. cirrata* has a very distinctive short, globular notopodium and a relatively short, tapering neuropodium. It is unlikely that the two species would ever be confused.

Etymology. This species is named for Mr. George Hampson, marine biologist and research specialist, of the Woods Hole Oceanographic Institution, in appreciation of his expertise in deep-sea field sampling techniques that made the collection of this species and others from the continental slope possible. George has given freely of his time and experience to make our field programs a success and has willingly trained students and other novices in the use of box cores and other field samplers.

Distribution. California continental slope, 985-1990 m.

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6. FAMILY GLYCERIDAE GRUBE, 1850

by

Brigitte Hilbig[1]

Introduction

The glycerids, commonly called bloodworms, are cylindrical to somewhat depressed, terete polychaetes that can reach considerable size (up to 800 mm long). They are strongly muscular and usually remain in good condition when preserved. Glyceridae are easily recognized by their pointed, annulated prostomium and the usually numerous and very crowded segments. To separate the glycerids from the closely related goniadids, the parapodia and proboscis must be examined (see below), although goniadids are typically more cylindrical and slender than glycerids.

Morphology

The prostomium is conical, longer than wide, more or less distinctly annulated, and usually tapers to a very fine tip. The terminal ring bears two pairs of small, typically biarticulate antennae and sometimes a pair of minute eyes. The basal ring is fused with the peristomium and is often distinctly wider and longer than the other rings. A pair of more conspicuous eyes may be present, and the posterior margin bears a pair of nuchal organs. The very long and muscular proboscis is densely covered with small, transparent papillae called proboscideal organs, that occur in various shapes ranging from spherical to cylindrical and slender. When the proboscis is fully everted, four dark, chitinous terminal jaws are visible that each consist of a hook-shaped fang and a rodlike or V-shaped support, the aileron.

The peristomium and the first few setigers are fused ventrally and surround the mouth. The parapodia on these setigers are often reduced and bear only a few setae. From about setiger 5, the segments are essentially uniform. The parapodia are either all uniramous or all biramous, except for the first two setigers, with one or two pre- and postsetal lobes; the rami are indistinctly separated from each other, but clearly indicated by two diverging aciculae. The dorsal cirri are small, papilliform and often inserted well above the parapodium on the body wall. Ventral cirri are usually elongate and conical. Branchiae may be present as protrusions of the parapodia. They may be simple and digitiform or blister- or saclike in appearance, or they may be branched. Some species have retractile branchiae that may only be discernible, when retracted, as an area of somewhat loose, very thin epidermis on the parapodial wall.

The notosetae are simple capillaries usually covered with fine surficial spines. The neurosetae are compound spinigers or falcigers with smooth shafts and blades covered with surficial spines. The pygidium is small and usually bears a pair of slender anal cirri.

Only three genera are recognized in the family Glyceridae. They are easily distinguishable by the morphology of the parapodia (uniramous or biramous) and the shape of the neurosetal blades (spinigerous or falcigerous). The most commonly used species-level characters include morphological details of the parapodia, such as the number and shape of pre- and postsetal lobes and the presence, shape and insertion of branchiae, as well as the number of rings on the prostomium and segments, and the shape of the proboscideal organs and ailerons.

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Branchiae may not be present in juvenile specimens, but the shape of the pre- and postsetal lobes is quite consistent even in very small individuals. If the branchiae are retractile, they may be difficult to locate especially in small specimens, and it may be helpful to apply gentle pressure to the parapodial base to extrude them.

The segments are usually distinctly bi- or triannulated. This character is reliable for species discrimination in combination with other characters, however, the annulation of the segments may change along the body, and only median setigers should be examined (O'Connor, 1986).

The proboscideal organs occur in numerous very species-specific shapes and are an excellent diagnostic character. They are best examined on a piece of epidermis detached from the underlying muscular tissue; the piece should be dissected from the anterior part of the proboscis if possible, and it should be reasonably large because some species possess several types of proboscideal organs that may not be evenly distributed. The ailerons have proven to be useful to distinguish species that are otherwise very similar (O'Connor, 1986). Morphometric details, such as the length of the inner and outer ramus and the angle between the rami, should be examined on a dissected aileron because they are readily visible only if the aileron lies flat on a slide.

Taxonomic History

Due to the small number of genera in the family Glyceridae, the systematics are fairly straightforward and the generic definitions well established. By far the largest genus is *Glycera*, containing more than 50 valid species and an equal number of synonyms. Several attempts have been made by Verrill (1881) and Arwidsson (1899), among others, to divide the genus into subgenera of a more manageable size, but none have been successful. Hartman (1950) divided the genus into four groups based on the morphology of the proboscideal organs, but did not establish these groups as subgenera. *Hemipodus* was established by Quatrefages (1866); the genus contains only a few species. *Glycerella* Arwidsson, 1899, contains only one species, characterized by falcigerous rather than spinigerous neurosetae. The most important reviews of the family are by Hartman (1950), Day (1967), and O'Connor (1986).

Distribution and Biological Notes

Glycerids are widely distributed in the world's oceans from the intertidal to abyssal depths. They occur in soft sediments ranging from muds to sands, and are epibenthic on rocks or among algae. Many species burrow actively into soft substrates by performing fast, rotating motions after coiling their bodies and shooting out their proboscis into the sediment with considerable force (Fauchald and Jumars, 1979; Pettibone, 1963). Ockelmann and Vahl (1970) observed that *Glycera alba* initially burrows by thrusting the proboscis forward, anchoring it, and then pulling the body into the burrow. Once in the sediment, the animal moves slowly through the substrate by crawling and peristaltic/antiperistaltic movements. Swimming is atypical for glycerids. If pulled from their burrows, they perform vigorous, but undirected figure-eight swimming movements.

There are some publications on feeding behavior of a few *Glycera* species, including a very comprehensive and careful account of the biology of the bloodworm *G. dibranchiata*, a commercially harvested bait worm, by Klawe and Dickie (1957). Glycerids are generally considered carnivorous because of the eversible proboscis and heavy jaws connected with glands that produce a proteolytic and lipolytic toxin (Michel, 1966). Klawe and Dickie (1957) reported bites followed by swelling and itching, although they proved that *G. dibranchiata* is a deposit feeder and does not use the jaws and glands to seize prey. According to observations made by Ockelmann and Vahl (1970), burrowing species construct a system of semipermanent tubes with several exits to the surface for capturing prey. It was found that *Glycera alba* will not feed outside its tube; the species preferred motile prey organisms over sessile ones and was stimulated by a combination of chemical and mechanical signals. Some species, especially those living in deep water, seem to be detrivores and subsurface deposit feeders. Digestion starts in the pharynx, where the food is covered by a layer of mucus secreted by the proboscideal organs (Ockelmann and Vahl, 1970). Glycerids do not have a functional anus, even though a central pore can be seen in the pygidium, but regurgitate indigestible material through the mouth (Klawe and Dickie, 1957).

Sexes are separate, with sexually mature individuals becoming epitokous to varying degrees. The parapodia lengthen, the setae increase in length and number, and simple setae appear in the neuropodia. The proboscis is cast off, parts of the intestine and the muscles of the body wall may degenerate, and the entire body fills up with gametes that are extruded through the mouth or ruptures of the body wall. Spawning in temperate waters takes place between May and July (Støp-Bowitz, 1941), either close to the bottom or in surface waters, and the individuals die shortly thereafter. The larval development of glycerids is poorly known because larvae are seldomly found in the plankton and are thought to live close to the bottom. Blake (1975a) described the larva of *Glycera tenuis*, a species found in the intertidal and shallow subtidal in California and Oregon. The nectochaeta (Chapter 3, this volume, Fig. 3.9K) was collected in June. The only publication describing the complete larval development from fertilized eggs to benthic juveniles has been provided by Cazaux (1967) for *Glycera convoluta*.

Key to the Glyceridae

1A. Parapodia uniramous; all setae compound (Fig. 6.6F); postsetal lobe rounded, short; presetal lobe much longer and slender; proboscis with two types of proboscideal organs: tall, slender and short, spherical .... *Hemipodus borealis*

1B. Parapodia biramous; notosetae simple, neurosetae compound (Fig. 6.3G, H): genus *Glycera* 2

2A. Parapodia with 2 presetal and 1 postsetal lobe (Fig. 6.3E, F) 3

2B. Parapodia with 2 presetal and 2 postsetal lobes (Fig. 6.1F) 4

3A. Presetal lobes and ventral cirri long and foliaceous; proboscideal organs of three kinds (Fig. 6.2C-E) .... *G. branchiopoda*

3B. Presetal lobes and ventral cirri moderately long, not foliaceous; proboscideal organs of two kinds (Fig. 6.3B, C) .... *G. nana*

4A. Presetal lobes long, slender and conical; postsetal lobes short and pointed; proboscideal organs smooth and very tall, readily visible *in situ*; small and gracile species .... *G. tesselata*

4B. Pre-and postsetal lobes short, stout, pointed or rounded; proboscideal organs oval or spherical, with or without transverse ridges (Fig. 6.4B); large, robust species 5

5A. Postsetal lobes blunt, rounded, distinctly shorter than presetal lobes; parapodia obliquely wrinkled (Fig. 6.4F); proboscideal organs of one kind, with about 6 transverse ridges; nonretractile gills blisterlike, on posterior parapodial wall .... *G. robusta*

5B. Postsetal lobes conical, slightly shorter than presetal lobes; proboscideal organs of two kinds: smooth and with 3 ridges (Fig. 6.1B, C); retractile gills emerging from pore on posterior parapodial wall, dendritically branched when fully everted (Fig. 6.1E) .... *G. americana*

Description of Species

In the Atlas of Polychaetous Annelids from California, Hartman (1968) listed 13 glycerid species. The number of glycerids described in this chapter is much smaller because many of the species listed in Hartman's Atlas are typically inhabitants of shallow water. The following species are treated below:

Glycera americana Leidy, 1855
Glycera branchiopoda Moore, 1911
Glycera nana Johnson, 1901
Glycera robusta Ehlers, 1868
Glycera tesselata Grube, 1863
Hemipodus borealis Johnson, 1901

Genus *Glycera* Savigny, 1818

Type species: *Glycera unicornis* Savigny, 1818

Diagnosis. Prostomium pointed, annulated, with four small antennae and occasionally a pair of eyes in the basal and terminal annuli. Peristomium fused to basal prostomial annulus. Proboscis long, cylindrical, covered with numerous proboscideal organs of one or more kinds and armed with four fanglike terminal jaws supported by ailerons. Parapodia biramous except for first two setigers; with two presetal and one or two postsetal lobes; dorsal cirri short, spherical, arising from body wall well above parapodia; ventral cirri elongate, cirriform, inserted on ventral parapodial wall. Gills often present, developed as blisterlike areas of thinned epidermis on parapodial bases or as simple or branched structures attached to parapodium, sometimes retractable. Notosetae simple, neurosetae compound.

Glycera americana Leidy, 1855

Figure 6.1

Glycera americana Leidy, 1855:147; pl. 11, figs. 49, 50.—Augener, 1922:29; 1927:351.—Hartman, 1940:246; 1950:73 (synonymy); 1968:613.—Hartman and Reish, 1950:20 (synonymy).—Pettibone, 1963:213, figs. 54 a-e (synonymy).—Gilbert, 1984:32-15, figs. 32-11, 12 a-g.—Lissner *et al.*, 1986:D-11.—Hyland and Neff, 1988:A-2.—Hyland *et al.*, 1990: F-1. *Not* Rioja, 1944:128. *Not* Andrew and Andrew, 1953:9.
?Glycera cirrata Grube, 1856:176.
Glycera corrugata Baird, 1863:109.
Glycera peruviana Quatrefages, 1866:177.
Glycera jucunda Hansen, 1882:17.
Glycera laevis Kinberg, 1866:245.
?Glycera edentata Hansen, 1882:17.
?Glycera longissima Arwidsson, 1899:23.
Glycera rugosa Johnson, 1901:409.—Augener, 1934:143.—Hartman, 1940:246.—Berkeley and Berkeley, 1948:38.
Rhynchobolus americanus Verrill and Smith, 1874:38.—Webster, 1879:245.—Verrill, 1881:291. —Andrews, 1891:289.—Sumner, Osborn and Cole, 1913:623.

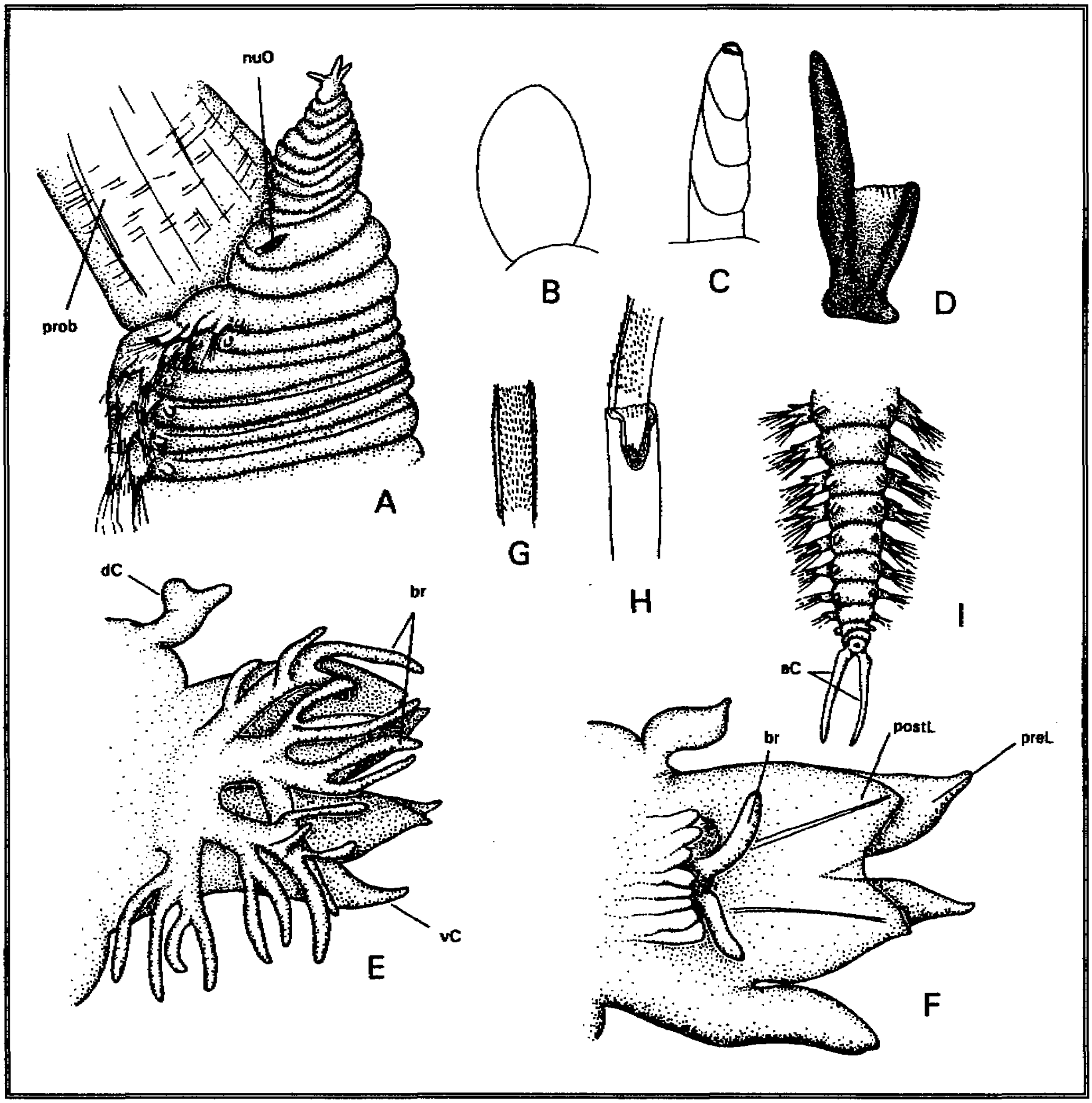

Figure 6.1. *Glycera americana*: A, anterior end, dorsolateral view, proboscis everted; B-C, proboscideal organs; D, aileron; E, median parapodium, posterior view, branchia fully everted; F, same, branchia retracted; G, detail of notoseta; H, detail of neuroseta; I, posterior end, dorsal view.

Material examined. California: Santa Maria Basin, off Point Arguello, Sta. 70 (1); off Point San Luis, Sta. R-1 (1); western Santa Barbara Channel, Sta. 80 (1); Tomales Bay, White Gulch (1); Bodega Harbor (1); central California, Cayucos (2).

Description. Length to 350 mm, width to 15 mm, setigers to 300. Body wide, robust, dorsoventrally flattened, widest in pharyngeal region, gradually tapering toward pygidium; segments biannulate, very short and crowded (Fig. 6.1A). Color in alcohol pale brown with dark pigment on tips of parapodial lobes and cirri.

Prostomium almost as wide as long, with 8 to 13 indistinct rings, bearing two pairs of well-developed antennae. Proboscideal organs in dispersed arrangement, of two types: ovate, smooth and elongate with 2 to 3 indistinct, widely spaced transverse ridges (Fig. 6.1B, C). Aileron with long outer ramus and short inner ramus completely fused to interramal plate; rami almost parallel (Fig. 6.1D). Peristomium and subsequent setigers much wider than basal prostomial annulus; peristomium with two lateral nuchal slits (Fig. 6.1A).

Parapodia inconspicuous, about 1/10 as long as body width in mature specimens, with 2 presetal and 2 postsetal lobes of subequal size and sharply conical shape. Dorsal cirri small, globular; ventral cirri long, conical (Fig. 6.1E). Retractable branchiae present from about setiger 9 to 16 to near end of body, emerging from pore in posterior parapodial wall; dendritically branched when fully everted, filiform when partially retracted (Fig. 6.1E, F). Notosetae capillary, neurosetae compound spinigers; notosetae and blades of neurosetae covered with minute surficial spines and finely serrated (Fig. 6.1G, H).

Posterior end slender, tapering to a ring-shaped pygidium with terminal anus and two slender anal cirri inserted ventrally (Fig. 6.1I).

Remarks. *G. americana* is easily recognizable when the branchiae are everted, but most specimens tend to retract them during fixation. However, other characters such as the proportions of the parapodia and the shape of the proboscideal organs are sufficient for species discrimination.

Biology. The species is common in sheltered areas and occurs in sand mixed with mud, gravel and shell fragments; sexually mature forms are found swimming in surface waters, most frequently in July and August; larvae occur in the plankton in September (Pettibone, 1963). Epitokous specimens are characterized by fan-like fascicles of very long and numerous setae.

Distribution. Atlantic and Pacific coasts of North and South America; Gulf of Mexico; Straits of Magellan; New Zealand, Southern Australia; intertidal to 530 m.

Glycera branchiopoda Moore, 1911

Figure 6.2

Glycera branchiopoda Moore, 1911:302, pl. 20, figs. 155-156, pl. 21, figs. 157-159.—Hartman, 1968:615.—Lissner *et al.*, 1986:D-11.—Hyland and Neff, 1988:A-2.—Hyland *et al.*, 1990: F-1.

Glycera capitata branchiopoda: Hartman, 1960:97.

Material examined. California: Santa Maria Basin, off Purisima Point, Sta. 50 (1), Sta. 55 (1).

Description. Length to 90 mm, width to 3 mm, segments to 137. Body slender, nearly cylindrical, widest in anterior third, then gradually tapering to small pygidium. Segments triannulate, relatively long, with middle ring bearing parapodia. Color in alcohol uniformly tan.

Prostomium very slender, with 7 to 9 rings, bearing four minute antennae (Fig. 6.2A). Proboscideal organs of 3 types: most numerous ones elongate, smooth; other 2 types scattered: (1) elongate with about 4 to 5 inconspicuous transverse ridges, (2) short, spherical, and smooth (Fig. 6.2C, D, E). Aileron with wide, long outer ramus and thin, short inner ramus completely fused to interramal plate; rami forming an angle of 45° (Fig. 6.2F). Peristomium and subsequent setigers only slightly wider than basal prostomial annulus (Fig. 6.2A, B).

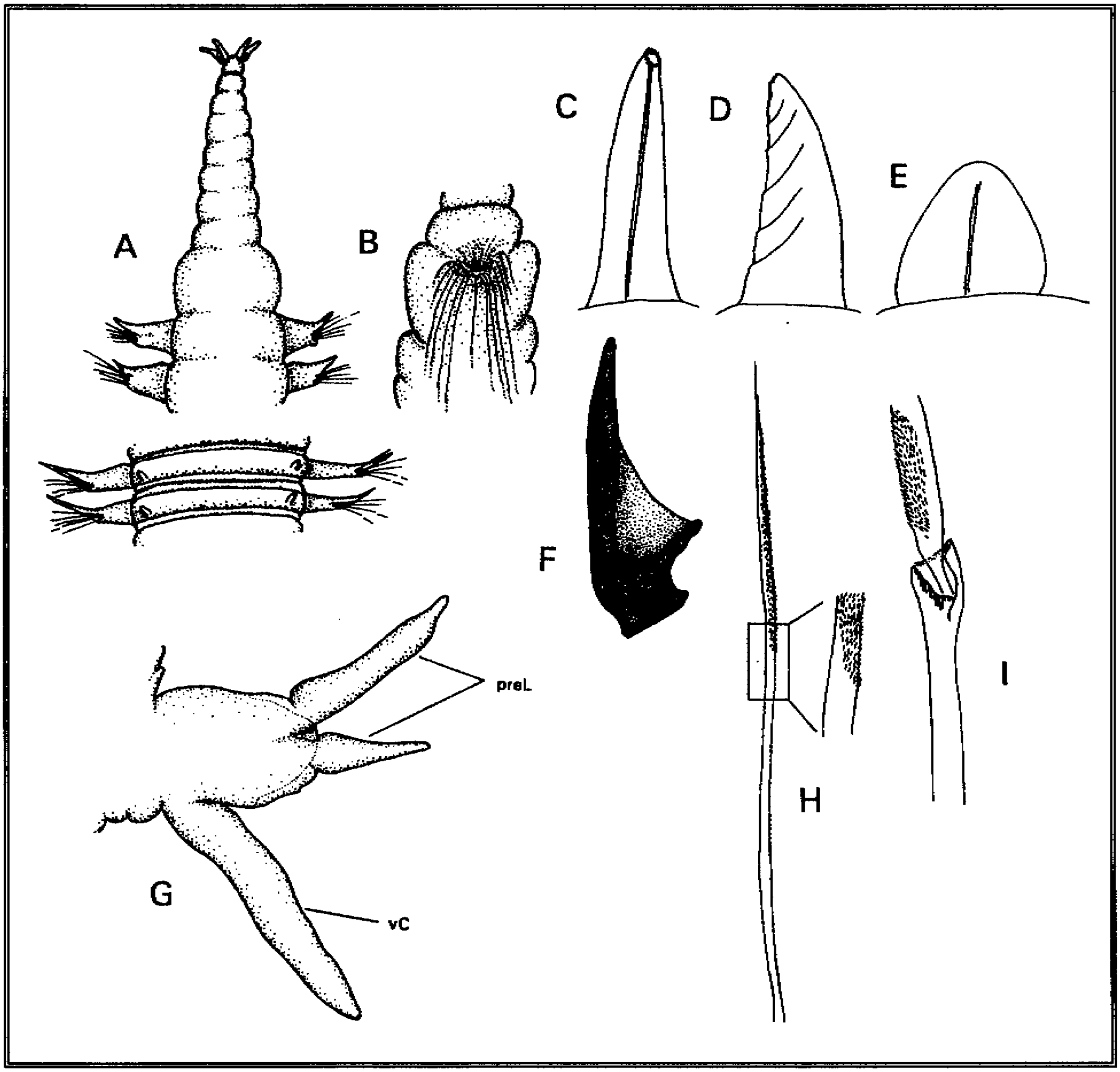

Figure 6.2. *Glycera branchiopoda*: A, anterior end and two median setigers, dorsal view; B, anterior end, ventral view; C-E, proboscideal organs; F, aileron; G, parapodium, anterior view; H, notoseta with detail; I, detail of neuroseta.

Parapodia conspicuous, one-third to half as long as body width; presetal lobes and ventral cirri long and foliaceous except for first 2 to 3 reduced parapodia (Fig. 6.2G). Notosetae thin capillaries with fine surficial spines and finely serrated edge; neurosetae compound spinigers with finely serrated blades covered with minute spines (Fig. 6.2H, I).

Pygidium small, probably bearing two anal cirri (scars visible in one complete specimen).

Remarks. *G. branchiopoda* is easily distinguished from the somewhat similar *G. nana* (see below) by the proportions of the parapodia, the presetal lobes being much longer in relation to the parapodial stem in *G. branchiopoda*. In addition, the proboscideal organs include three kinds in *G.*

branchiopoda, but only two kinds in *G. nana*, and the ailerons are shaped differently. *Glycera capitata* differs from both species in having biannulate rather than triannulate segments.

Type locality and type specimens. Southern California, off Cape Colnett, 2560 m: holotype (USNM 16847); off Monterey Bay, 1371-1401 m: paratype (ANSP 3077)

Habitat. The species occurs in sand and sand mixed with silt.

Distribution. Southern and central California, 440 to 2800 m.

Glycera nana Johnson, 1901

Figure 6.3

Glycera nana Johnson, 1901:411, pl. 10, figs. 103, 103 a.—Hilbig, 1992:716-719, fig.4.
Glycera capitata: Hartman, 1950:76, pl. 11, figs. 1-4 (in part); 1968:617 (in part).—Lissner *et al.*, 1986:D-11.—Hyland and Neff, 1988:A-2.—Hyland *et al.*, 1990:F-1. *Not* Oersted, 1843.

Material examined. Holotype: Puget Sound (MCZ 1878). —California: Santa Maria Basin, off Point Sal, Sta. PJ-1 (3), Sta. PJ-2 (9), Sta. PJ-3 (1), Sta. PJ-4 (2), Sta. PJ-5 (7), Sta. PJ-6 (4), Sta. PJ-7 (6); Sta. PJ-8 (9), Sta. PJ-10 (5); off the Farallon Islands, south of Pioneer Canyon (7). —Alaska: Hawk Inlet (5).

Description. Length to 64 mm, width excluding parapodia to 4 mm, segments at least 140. Holotype 30 mm long, 3 mm wide excluding parapodia, 69 setigers; largest Californian specimen 25 mm long, 2 mm wide, 107 setigers. Body of holotype robust, of California specimens slender, tapering at both ends, widest in pharyngeal region. Segments distinctly triannulate throughout, short and crowded in anterior half of body, somewhat longer in posterior half; with long, slender parapodia (Fig. 6.3A, K). Color in alcohol tan, sometimes with dark pigmentation on tips of parapodial lobes in posterior segments; dorsal body wall sometimes rugose and somewhat darkened in anterior segments of mature specimens.

Prostomium pointed, much longer than wide, with 8 to 10 rings; basal annulus only slightly narrower than peristomium (Fig. 6.3A). Proboscis densely covered with proboscideal organs of two kinds: (1) most numerous ones tall, slender, at least three times as long as basal width, with terminal pore and smooth surface; (2) second type oval, less than twice as tall as basal width, flat in side view, smooth, scattered among tall ones (Fig. 6.3B, C). Ailerons with moderately long outer ramus and short inner ramus completely fused to interramal plate (Fig. 6.3D). Peristomium with two dorsolateral nuchal slits.

Parapodia conspicuous, reaching about half body width in pharyngeal region and surpassing body width in posterior segments; with 2 slender, pointed, subequal presetal lobes and single, rounded, much shorter postsetal lobe; dorsal cirri small, papilliform, ventral cirri slender, conical (Fig. 6.3E, F). Setae long, flowing; notosetae simple capillaries, finely serrated in upper third (Fig. 6.3G, H); neurosetae compound spinigers, twice as wide as notosetae, with finely serrated blades (Fig. 6.3I, J).

Posterior end slender, tapering to small, ring-shaped pygidium bearing two slender anal cirri (Fig. 6.3K).

Remarks. *Glycera nana* belongs into a small group of glycerids characterized by a single, short, rounded postsetal lobe. Traditionally, glycerids with this character have been identified as *G. capitata* on both coasts of North America. However, O'Connor's (1986) revision of glycerids from the northeastern Atlantic and Mediterranean Sea led to a more precise definition of this species, with the consequence that

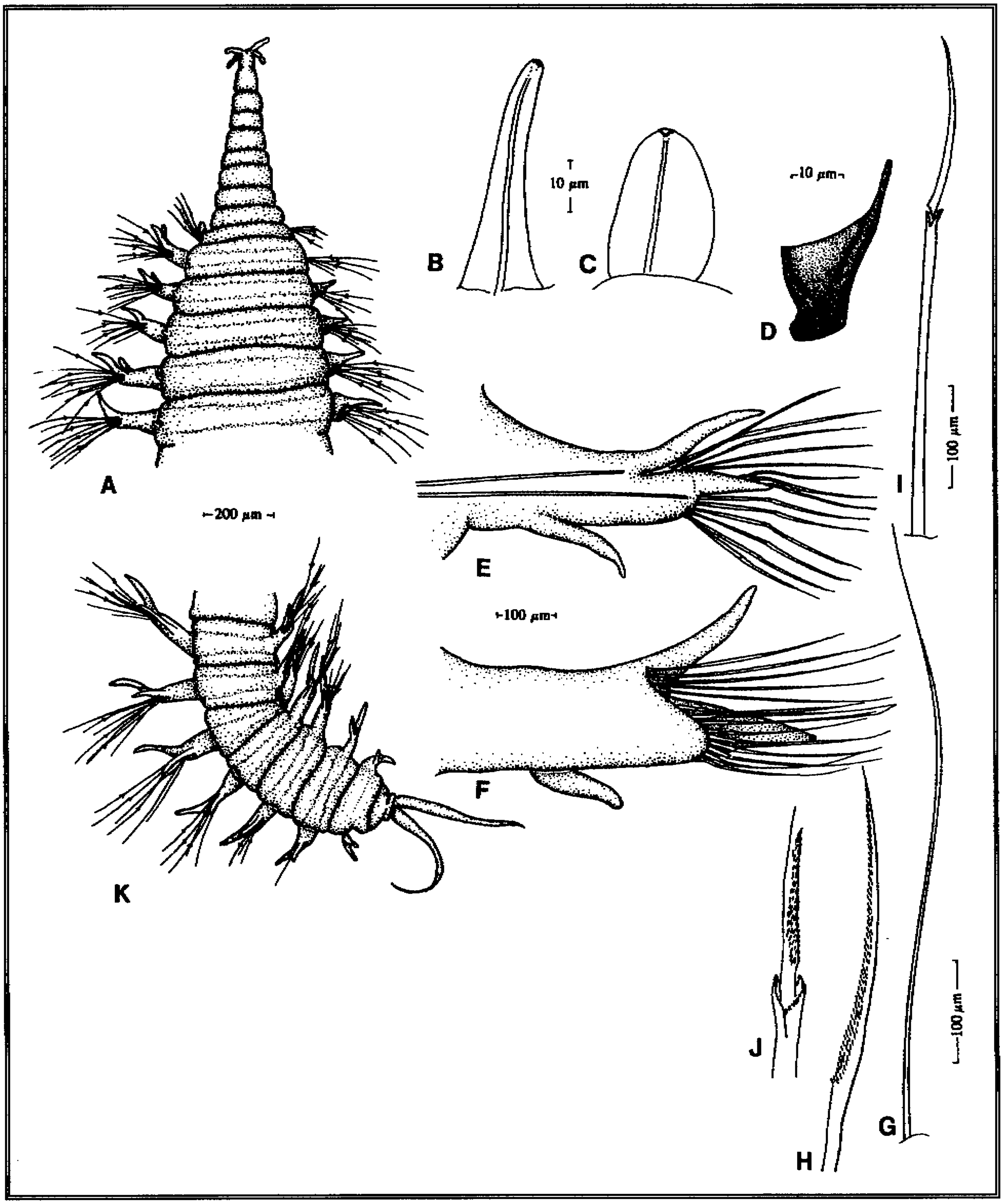

Figure 6.3. *Glycera nana*: A, anterior end, dorsal view; B-C, proboscideal organs; D, aileron; E, middle parapodium, anterior view; F, same, posterior view; G, notoseta; H, detail of notoseta: tip; I, neuroseta; J, detail: insertion of blade; K, posterior end, ventral view. (from Hilbig, 1992)

several of the North American specimens assigned to *G. capitata* no longer agree with the species definition. The most conspicuous difference between *G. nana* and *G. capitata* is with the number of rings per segment: two for *G. capitata* and three for *G. nana*. In addition, the former species has very short, papilliform presetal lobes and ventral cirri, whereas the latter has long, conical presetal lobes and ventral cirri. *G. nana* may be distinguished from the related species *G. branchiopoda* by the proboscideal organs, the aileron, and the length of the presetal lobes and ventral cirri.

Type locality and type specimens. Puget Sound, Washington; holotype: MCZ 1878.

Distribution. Alaska to central California, 123 to 1020 m.

Glycera robusta Ehlers, 1868

Figure 6.4

Glycera robusta Ehlers, 1868:656, pl. 23, figs. 43-46.—Hartman, 1940:246; 1950:69, pl. 10, figs. 7, 8 (synonymy); 1968:627.—Berkeley and Berkeley, 1942:193.—Pettibone, 1963:218, fig.54 f,g.—Blake, 1975b:197, fig. 159.—Hyland *et al.*, 1990:F-1
Glycera longissima Hartman, 1940:245.—*Not* Arwidsson, 1899.
Glycera sp. A: Lissner *et al.*, 1986:D-11.

Material examined. California: Santa Maria Basin, off Point Sal, Sta. 104 (1); Tomales Bay, N of Stemple Creek (1).

Description. Length to 800 mm, width to 22 mm, segments several hundred. Body very stout, inflexible, dorsoventrally flattened; widest in anterior third, then tapering towards pygidium. Segments very crowded, biannulate, with posterior annulus bearing parapodia. Color in alcohol brown with scattered dark pigment spots on dorsum and parapodia of anterior body.

Prostomium very small, conical, slightly longer than wide, with about ten rings, bearing 4 relatively large antennae (Fig. 6.4A). Proboscideal organs densely covering proboscis; of one kind: oval to flask shaped, with 6 to 8 ridges (Fig. 6.4B). Jaws and ailerons large and heavily sclerotized (Fig. 6.4C, D); aileron with long, thick outer ramus and much thinner and shorter inner ramus completely fused to interramal plate; rami forming an angle of about 30°, *in situ* appearing almost parallel (Fig. 6.4D). Peristomium and following setigers considerably wider than basal prostomial annulus.

Parapodia inconspicuous, about one-tenth of body width in middle setigers, wrinkled at base and along dorsal margin; with two conical presetal lobes and one rounded postsetal lobe in anteriormost setigers; from about setiger 10 on postsetal lobe gradually splitting into two rounded subequal lobes (Fig. 6.4E, F). Branchiae first apparent around setiger 23 as blisterlike structures on dorsal parapodial walls, from setiger 35 also along the ventral parapodial wall (large specimens only) (Fig. 6.4G). Notosetae slender, finely serrated capilllaries; neurosetae compound spinigers slightly wider than notosetae, with finely serrated blades (Fig. 6.4H, I).

Remarks. The specimens collected by Lissner *et al.* (1986) were originally thought to differ from *Glycera robusta* because ventral branchiae were present. However, Berkeley and Berkeley (1942) found among their material from Vancouver Island one very large specimen of *G. robusta* that showed these same ventral gills in addition to the dorsal ones. Among the California material examined here, the specimen from Tomales Bay was slightly smaller than the one from the Santa Maria Basin, and it possessed only very inconspicuous ventral branchiae in a few setigers. It seems therefore that the development of the branchiae varies with body size and is not a specific character.

Habitat. *G. robusta* is found in gravelly sand.

Distribution. Japan; Canada, Alaska to southern California; Gulf of St. Lawrence to Virginia, ?Florida; intertidal to 400 m.

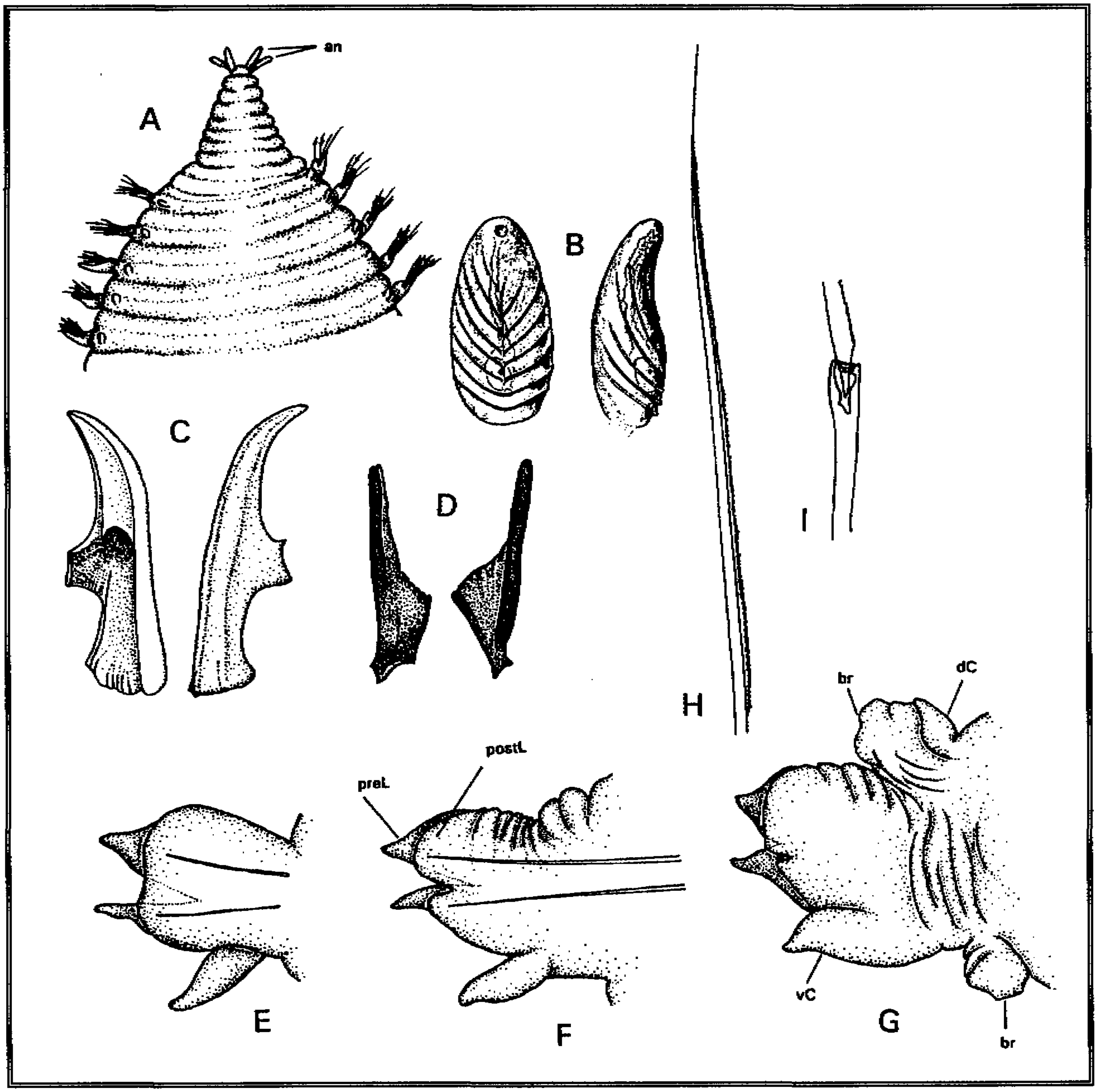

Figure 6.4. *Glycera robusta*: A, anterior end, dorsal view; B, proboscideal organ, frontal and lateral view (after Hartman, 1950); C-D, jaw and aileron, inside and outside view; E-G, parapodia of setiger 5, 15, and midbody, posterior view; H, notoseta; I, detail of neuroseta.

Glycera tesselata Grube, 1863

Figure 6.5

Glycera tesselata Grube, 1863:41.—Hartman, 1940:247 (synonymy); 1950:77, pl. 10, fig. 11 (synonymy); 1968:633.—Lissner *et al.*, 1986:D-11.
Glycera nana Treadwell, 1914:197. *Not* Johnson, 1901:411.
Glycera sagittariae Treadwell, 1906:1174. *Not* McIntosh, 1885:347.
Glycera spadix Treadwell, 1943:3

Material examined. California: Santa Maria Basin, off Point Estero, Sta. 1 (5), Sta. 2 (5).

Description. Length to 27 mm, width to 1.5 mm, segments to 100. Body slender and flexible, gradually tapering on both ends; segments biannulate, relatively long, rugose in anterior segments, smooth in median and posterior segments. Pigmentation very distinct, consisting of dark bands on each segmental annulus and dark coloring on parapodia.

Prostomium slender, much longer than wide, with 9 to 14 rings; eyes present in basal prostomial annulus, may be inconspicuous; terminal annulus bearing 2 pairs of slender antennae. Peristomium only slightly wider than basal prostomial annulus (Fig. 6.5A). Proboscideal organs of one kind: very tall, slender, smooth, visible *in situ* under low magnification as velvetlike cover of proboscis (Fig. 6.5B). Ailerons with long outer and inner rami incompletely fused to interramal plate, forming an angle of about 45° (Fig. 6.5C).

Parapodia conspicuous, stout, reaching about half body width in length, with 2 slender, conical presetal lobes and 2 much shorter, triangular postsetal lobes; dorsal cirri spherical, inserted close to parapodium; ventral cirri conical, projecting slightly beyond postsetal lobes (Fig. 6.5D). Notosetae slender capillaries with fine serrations and surficial spines along most of length (Fig. 6.5E); neurosetae compound spinigers, twice as wide as notosetae, with relatively short blades of almost falcigerous appearance; shafts smooth, blades covered with surficial spines and finely serrated (Fig. 6.5F).

Pygidium small, short, possibly bearing two deciduous anal cirri (Fig. 6.5G).

Remarks. The form of the proboscideal organs readily distinguishes this species from its congeners.

Type locality. Mediterranean Sea.

Habitat. The species lives in mixed sediments; in the Santa Maria Basin, it seems to prefer sandy bottoms.

Distribution. British Columbia to Panama; tropical Pacific; Japan; Indo-Pacific; West Indies, Caribbean Sea; Atlantic Ocean; Mediterranean Sea; sublittoral to 600 m.

Genus *Hemipodus* Quatrefages, 1865

Type species: *Glycera rosea* Blainville in Quatrefages, 1865

Diagnosis. Prostomium pointed, annulated, with two pairs of small antennae. Proboscis long, cylindrical, covered with proboscideal organs of one or more kinds and armed with four large, fang-shaped terminal jaws supported by ailerons. Peristomium fused with basal prostomial annulus. Parapodia uniramous throughout, with one presetal and one postsetal lobe. Dorsal cirri small, spherical, arising from dorsal body wall well above parapodium; ventral cirri, elongate, cirriform, inserted on ventral parapodial wall. All setae compound.

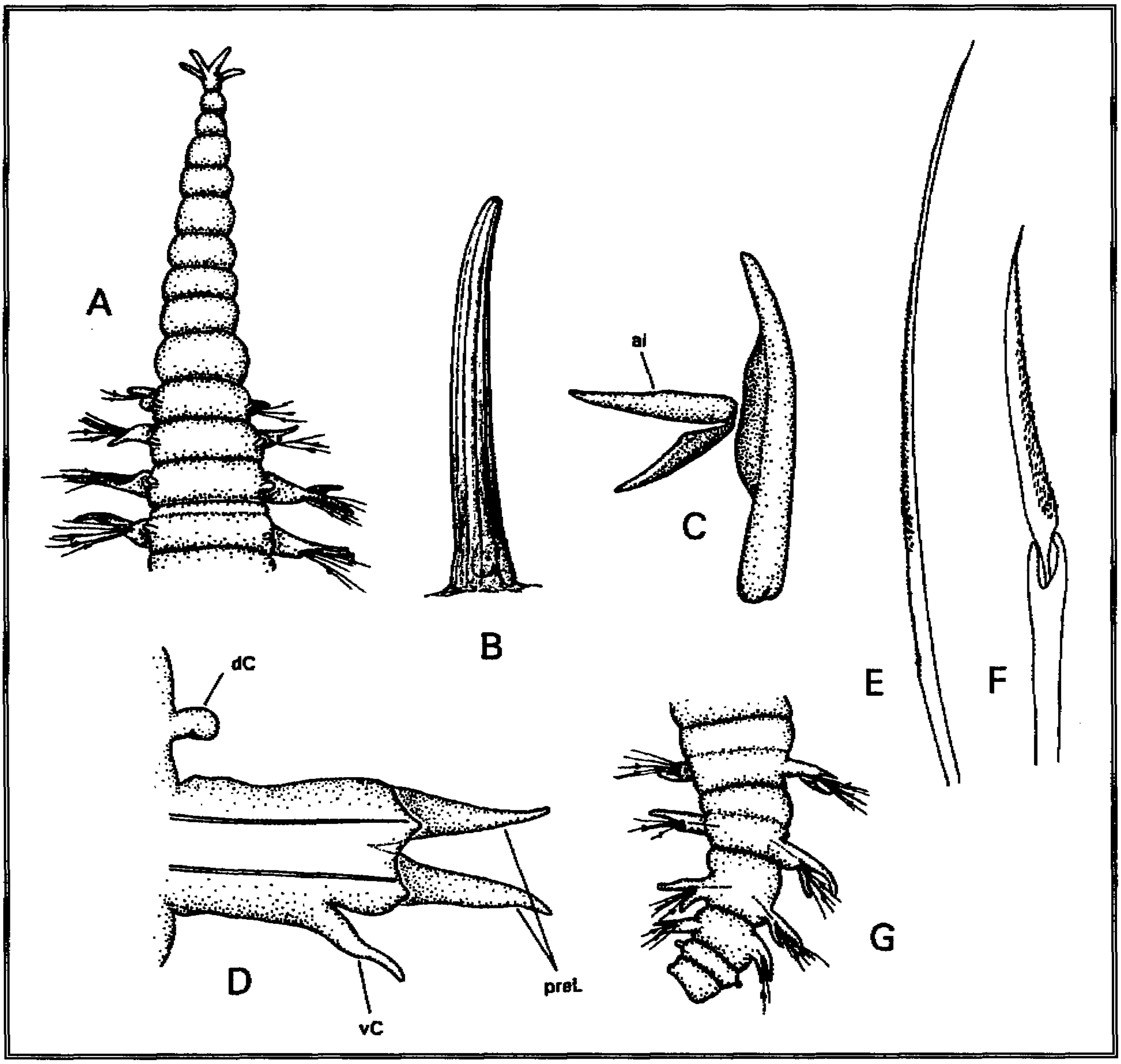

Figure 6.5. *Glycera tesselata*: A, anterior end, dorsal view; B, proboscideal organ (after Hartman, 1950); C, jaw and aileron *in situ* (after Hartman, 1968); D, midbody parapodium, posterior view; E, notoseta; F, neuroseta; G, posterior end, dorsal view.

Remarks. The genus was first described by Johnson as *Hemipodia*.

Hemipodus borealis Johnson, 1901

Figure 6.6

Hemipodia borealis Johnson, 1901:411, pl. 10, figs. 104, 104a.
Hemipodus borealis: Hartman, 1940:244, pl. 43, fig. 121; 1950:81 (table); 1961:21; 1968:637.—Hartman and Reish, 1950:20.—Blake, 1975b:196-197, fig. 163.—Lissner *et al.*, 1986:D-11.

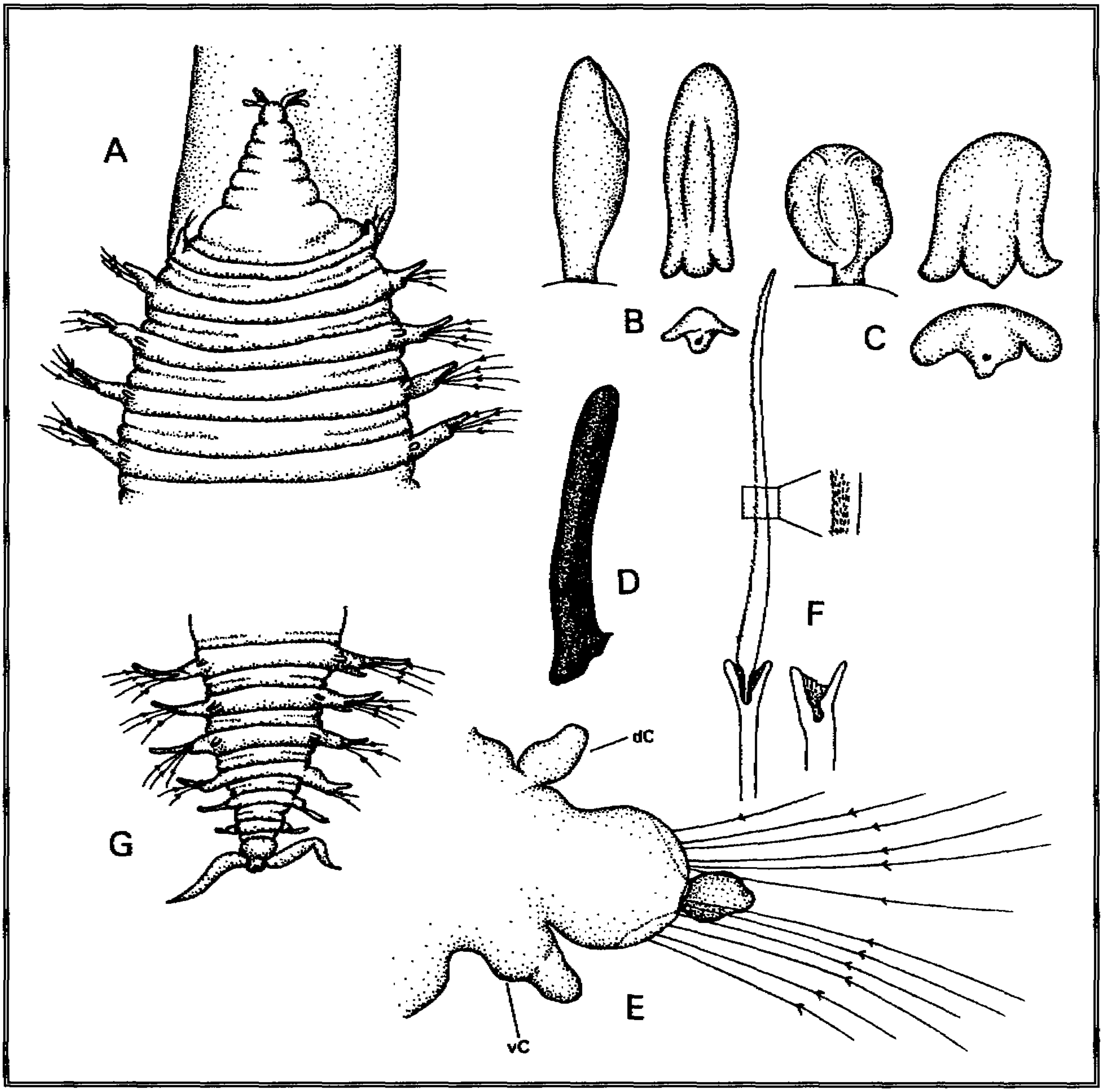

Figure 6.6. *Hemipodus borealis*: A, anterior end, dorsal view, proboscis everted; B-C, proboscideal organs in side, frontal, and apical view; D, aileron (after Hartman, 1968); E, parapodium, posterior view; F, seta with details of hinge and blade; G, posterior end, dorsal view.

Material examined. California: Tomales Bay (2).

Description. Length to 100 mm, width to 3 mm, segments at least 126. Body long, slender, terete, of equal width along most of body except for about 5 anterior and 25 posterior setigers. Segments long, triannulate; middle ring bearing parapodium, more distinct than others, not divided by middorsal groove. Color in alcohol tan.

Prostomium about 1.5 times longer than wide, with about 4 to 5 indistinct rings; terminal ring bearing four small antennae; eyes absent. Peristomium distinctly wider than basal prostomial annulus (Fig. 6.6A). Proboscideal organs of two kinds: elongate, oval and short, spherical (side view) (Fig. 6.6B, C), the former ones being more numerous than the latter. Ailerons simple, rodlike (Fig. 6.6D).

Parapodia uniramous, small, about one-fourth as long as body width, with slender, conical presetal lobe and much shorter, rounded postsetal lobe; dorsal cirri ovate, very small, first present on setiger 3, inserted close to parapodium; ventral cirri slightly longer, conical (Fig. 6.6E). Anterior 2 parapodia reduced, fully developed from setiger 6 or 7. All setae compound spinigers; shafts slender, with characteristically wide hinge; blades of varying length, longest in middle of fascicle, with fine serrations and surficial spines (Fig. 6.6F).

Pygidium small, ring-shaped, with terminal anus and two slender, fusiform anal cirri about as long as last 3 segments (Fig. 6.6G).

Remarks. *Hemipodus borealis* is easily distinguished from co-occurring species of *Glycera* by the uniramous parapodia; however, it may be confused with goniadids that have a large number of uniramous parapodia in the anterior body region (see below). To avoid misidentifications, several parapodia from different body regions should be dissected. Examination of the ailerons may also be useful.

Type locality. Washington, Puget Sound.

Habitat. *H. borealis* is found in sand and sandy mud.

Distribution. British Columbia, Alaska to southern California, western Mexico; Chile, Peru; New Zealand; intertidal to shallow shelf depths

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7. FAMILY GONIADIDAE KINBERG, 1866

by

Brigitte Hilbig[1]

Introduction

The goniadids are slender, cylindrical polychaetes that reach lengths up to 140 mm. They are easily recognizable by the elongate, conical, annulated prostomium and the slender, long body divided into an anterior region with uniramous parapodia and a usually wider posterior region carrying biramous parapodia. However, to distinguish the Goniadidae from the related Glyceridae, an examination of the parapodia and proboscis under a compound microscope may be necessary, although goniadids are typically more cylindrical and more heavily pigmented than glycerids.

Morphology

The prostomium is conical, longer than wide, annulated, and typically tapering to a fine tip. The terminal annulus bears two pairs of very small, usually biarticulate antennae and often a pair of small subdermal eyes. A second pair of eyes may be present in the basal annulus. The eversible proboscis is very long, cylindrical, equipped with a variety of terminal jaws (macro- and micrognaths) arranged in a more or less complete circlet, and covered with proboscideal organs of very different and sometimes striking appearances. The proboscideal armature may also include chevrons, which are dark, V-shaped jaw pieces arranged in two lateral rows close to the base of the proboscis.

The peristomium and the first few setigers are often fused and ventrally surround the mouth. The parapodia in these setigers are usually somewhat reduced. An often species-specific number of following segments bears uniramous parapodia; this anterior region may be followed directly by a posterior region with biramous parapodia (except for the genus *Progoniada* with uniramous parapodia occurring throughout), or a transitional middle region where gradually changing parapodia may be present. The notopodia are smaller than the neuropodia and possess one or two often irregular pre- and postsetal lobes, or they are represented only by two to four slender notoaciculae. Neuropodia are well developed, supported by one or two thick aciculae, and distally divided into one or two pre- and postsetal lobes. Dorsal and ventral cirri are large, conical, and inserted very close to the parapodial lobes. Branchiae are absent.

The notosetae are simple, either forming dense fascicles of capillaries or only few in number and acicular. Neurosetae are compound with falcigerous or spinigerous blades; either one or both types may be present in a fascicle. The pygidium is small and bears two slender anal cirri that can reach considerable length, but are often deciduous.

The family Goniadidae contains nine valid genera with 73 species. Generic characters include the shape of noto- and neurosetae; presence or absence of notopodia; and, most importantly, the composition of the proboscideal armature.

Unlike glycerids, goniadids rarely evert their proboscis when dying in the fixative; proboscideal organs and macro- and micrognaths are therefore only visible after dissection. Only the chevrons can sometimes be seen through the body wall unless the specimen is too large or heavily pigmented. The proboscis of goniadids can be extremely long, so that a longitudinal cut to open the pharynx should reach back about 50 segments to reveal the terminal jaws. For the observation of the proboscideal organs, it may

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be necessary to examine an entire cross section of the proboscis because shapes may vary greatly from dorsal to ventral. Parapodia should be dissected in the anterior, middle, and posterior body region to ensure that all types—uniramous, transitional, and biramous—are identified if present.

Important species specific characters within the genera present in California include the shapes of proboscideal organs and the setae for *Glycinde*; and the number of uniramous and transitional setigers, the shape of proboscideal organs, and the arrangement of the macro- and micrognaths for *Goniada*.

Taxonomic History

The family Goniadidae was established by Kinberg (1866) as Goniadea. Ehlers (1868) combined them with the Glyceridae to the superfamily Glycerea Grube. He renamed the Goniadidae "Glycerea Polygnatha" and the Glyceridae "Glycerea Tetragnatha". Fauvel (1923) moved the Glyceridae back to family level and consequently changed Ehlers' families to the subfamilies Glycerinae and Goniadinae. However, Hartman (1950) emphasized the clear distinctions between glycerids and goniadids and reestablished the two families. The first species described in the family are European species of the genus *Goniada*; *Glycinde* was erected in 1858 by Müller for a species from Brazil. These two genera are by far the largest in the family with 34 and 20 species, respectively. Several smaller genera are also known. The genus *Ophioglycera* Verrill, 1885, was long believed to have a smooth prostomium lacking antennae. Hartman (1950) demonstrated that these characters were false, but because of other characters, such as the absence of chevrons and proportions of the parapodia, the genus remained valid nonetheless. Other small genera include *Goniadopsis* Fauvel, 1928 (falcigerous neurosetae anteriorly, spinigerous neurosetae posteriorly); *Goniadella* Hartman, 1950 (both falcigers and spinigers in all neuropodial fascicles); *Goniadides* Hartmann-Schröder, 1960 (all neurosetae falcigerous, chevrons absent) *Progoniada* Hartman, 1965 (all parapodia uniramous), *Bathyglycinde* Fauchald, 1972 (similar to *Glycinde* except for capillary rather than acicular notosetae), and *Bookhoutia* Mohammed, 1973 (neurosetae falcigerous anteriorly, falcigerous and spinigerous posteriorly).

Distribution and Biological Notes

Goniadids are widely distributed from intertidal to abyssal depths, although they are rarely found in high densities. Fauchald and Jumars (1979) state that goniadids, in contrast to the closely related glycerids, are more frequently found in deep waters. Very little is known about the biology of the Goniadidae; they are thought to be mostly carnivorous because of their eversible, jawed proboscis and their ability to move quickly, but only one behavioral study has been published. Matson (1981) observed the burrowing and feeding of *Goniada maculata*; he found that the worms construct nonpermanent burrows from which they attack neighboring prey species. He identified gut contents from 24 specimens of *Goniada maculata* and found the remains of several spionids, orbiniids, cirratulids, and other sedentary polychaetes. Southward and Southward (1972) reported that goniadids may also feed through uptake of dissolved organic matter.

Sexes are separate; reproduction is mainly sexual, but asexual reproduction through schizogamy has been observed in the genus *Ophioglycera* (Schröder and Hermans, 1975). Sexually mature individuals become epitokous, characterized by a degenerated posterior intestine, long simple setae among the original compounds, and enlarged neuropodial lobes. They die shortly after spawning in surface waters, and larvae are found in the plankton in spring and summer (Blake, 1975). *Glycinde armigera* was found to be epitokous from October to February, and juveniles with about ten setigers were found from February to July (Hilbig, pers. obs.). Kirkegaard (1978) reported that in Danish waters *Goniada maculata* spawns during fall and winter (November to February), and larval settlement occurs during winter and spring (December to April). The adults mature in the summer of the second year. There have been the very few accounts of the larval development of goniadids. Cazaux (1972) described the larvae of *Goniada emerita* and Blake (1975a) provided a description of the larvae of *Glycinde armigera*.

Key to the Goniadidae

1A. Notosetae very few, short, stout, with hoodlike tip (Fig. 7.1Q); proboscis with elaborate, hard, translucent, prominent proboscideal organs (Fig. 7.1C-K), chevrons absent .... *Glycinde armigera*

1B. Notosetae capillary, long, about 5 to 15 per fascicle; proboscis with soft, digitiform to spherical proboscideal organs of one to three kinds; chevrons present (Fig. 7.2I) .... genus *Goniada* 2

2A. Prostomium with 4 to 5 irregular, indistinct rings; proboscis with 2 kinds of beaked proboscideal organs (Fig. 7.2B, E), about 20 chevrons on each side, and micrognaths grouped into 7 to 8 in the ventral arc and 14 to 21 in the dorsal arc.. *Goniada annulata*

2B. Prostomium distinctly annulated, with more than 5 rings; armature of proboscis otherwise............ 3

3A. Prostomium sharply conical, with 8 to 9 rings; proboscideal organs of 1 kind, spherical, beaked (Fig. 7.4B); 15 to 18 chevrons; 3 ventral and 10 to 12 dorsal micrognaths .... *Goniada littorea*

3B. Prostomium blunt (Fig. 7.3A); none or few dorsal micrognaths; proboscideal organs flat discs or scales (Fig. 7.3B) 4

4A. Proboscideal organs scale-shaped, round from above, conspicuous; notopodia with triangular postsetal lobe (Fig. 7.3F); adult specimens with 0 dorsal and up to 12 ventral micrognaths; large species with stout body... *Goniada brunnea*

4B. Proboscideal organs disc-shaped, cordate from above, often inconspicuous; notopodia without postsetal lobe (Fig. 7.5G); adult specimens with 2 minute dorsal and 1-4 large ventral micrognaths; gracile species with slender body... *Goniada maculata*

Description of Species

Four species of *Goniada* and one species of *Glycinde* were encountered in the Santa Maria Basin and Western Santa Barbara Channel; they are listed below:

Glycinde armigera Moore, 1911
Goniada annulata Moore, 1905
Goniada brunnea Treadwell, 1906
Goniada littorea Hartman, 1950
Goniada maculata Oersted, 1843

Genus *Glycinde* Müller, 1858

Type species: *Glycinde multidens* Müller, 1858

Diagnosis. Prostomium pointed, annulated, with four small antennae and a pair of eyes in the terminal and basal annuli. Proboscis very long, cylindrical, covered with conspicuous, sclerotized proboscideal organs of many different kinds and armed with a cicrlet of terminal jaws, consisting of two macrognaths and several micrognaths in dorsal and ventral arcs. Parapodia uniramous in anterior part of body, biramous in posterior part, sometimes intermediate over a number of setigers; dorsal cirri large, cirriform to foliaceous, attached to dorsal parapodial wall; ventral cirri similar. Notosetae few, simple spines with terminal pointed hood; ventral setae compound.

***Glycinde armigera* Moore, 1911**

Figure 7.1

Glycinde armigera Moore, 1911:307, pl. 21, figs. 160-171.—Hartman, 1950:49, pl. 6, figs. 1-12 (synonymy); 1968:643.—Lissner *et al.*, 1986:D-11.—Hyland and Neff, 1988:A-2.—Hyland *et al.*, 1990:F-1.

Glycinde multidens Hartman, 1940:249. *Not* Müller, 1858.

Material examined. California: Santa Maria Basin, off Point Sal, Sta. PJ-3 (4); western Santa Barbara Channel, Sta. 88 (1), Sta. 96 (1).

Description. Length to 118 mm, width to 3 mm, setigers to 191. Body slender, terete, divided into two distinctly separated regions (Fig. 7.1A). Anterior region comprising about 70 segments, devoid of gametes when mature; posterior region, filled with gametes when mature, separated from anterior region by slight constriction and characterized by larger notopodia and neural eyespots. Color in alcohol pale yellow to light brown, often mottled or with transverse pigment band in each segment.

Prostomium pointed, dorsoventrally depressed, distinctly longer than wide, with 8 to 9 rings; apical ring bearing four small biarticulate antennae and a pair of minute eyes; basal ring fused with peristomium, much longer than preceding annuli, with a pair of eyes (Fig. 7.1B). Proboscis very long, reaching back to about setiger 50 when fully retracted; cylindrical when everted, with radula-like surface formed by dense rows of very conspicuous proboscideal organs; dorsalmost ones spherical with small lateral beak (Fig. 7.1C); dorsolateral and ventrolateral ones elongate, erect, fang-shaped, entire or bifid (Fig. 7.1D-I); ventralmost ones spherical with small conical bosses or large lateral beak (Fig. 7.1J, K). Apical end of proboscis with 18 to 20 soft papillae and circle of paragnaths, consisting of two macrognaths with 3 to 4 large teeth and a dorsal arc of about 30 X-shaped micrognaths; dorsolateral ones much larger than dorsomedian ones; ventral micrognaths absent (Fig. 7.1L).

Parapodia conspicuous, as long as or longer than body width; uniramous in anterior setigers, biramous from setiger 30; neuropodial lobe in anteriormost segments much smaller than dorsal and ventral cirri (Fig. 7.1M); surpassing the cirri from about segment 20; neuropodial presetal lobes blunt, obcordate, with median slender process; neuropodial postsetal lobes longer and conical (Fig. 7.1N); presetal lobes in more posterior parapodia less blunt with broadly conical process (Fig. 7.1O). Notopodial pre- and postsetal lobes much smaller than neuropodial ones and conical. Neurosetae slender compound spinigers with smooth shafts and serrated blades, longest in middle of fascicle (Fig. 7.1P); notosetae present from first notopodium, small and delicate, with slightly bent, knoblike tip and long, pointed, finely serrated distal hood (Fig. 7.1Q); in posterior segments concealed between pre- and postsetal lobes.

Pygidium small, with terminal anus and two very long, filiform anal cirri (Fig. 7.1R).

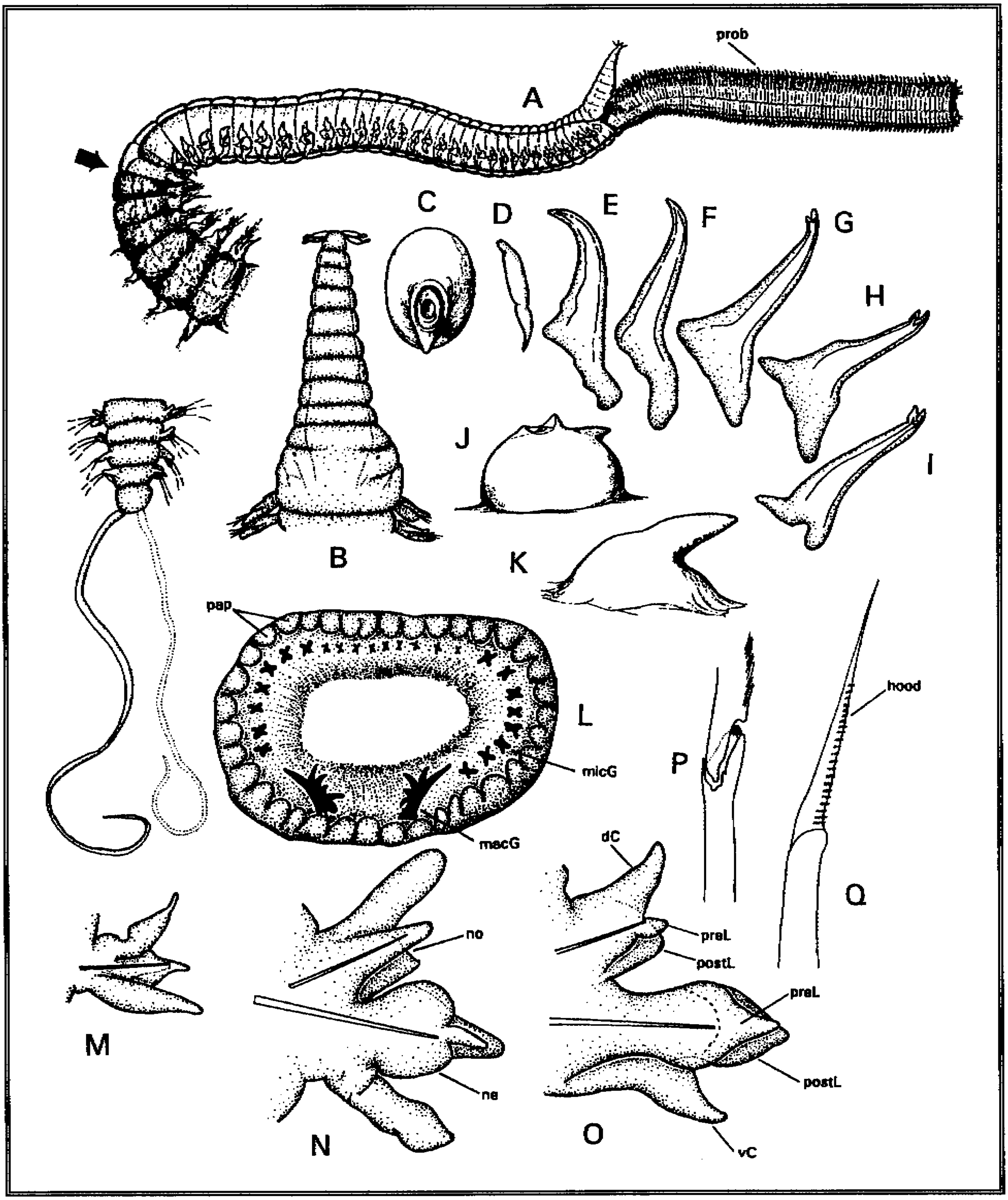

Figure 7.1. *Glycinde armigera*: A, anterior end, lateral view; arrow: start of posterior body region; B, anterior end, dorsal view; C-K, proboscideal organs from dorsal to ventral; L, micro-and macrognaths *in situ*, anterior view; M-O, anterior, middle, and posterior parapodium, anterior view; P, detail of neuroseta; Q, tip of notoseta; R, posterior end, dorsal view. (A, C-K after Hartman, 1950; B, M, O after Moore, 1911).

Remarks. Within its northern range, *G. armigera* may co-occur with the very similar species *G. picta*. The two species differ mainly in the distribution of micrognaths, a ventral arc being present in *G. picta*, but lacking in *G. armigera*. Usually, the integument is translucent enough to allow for examination of micrognaths without dissection; if necessary, gentle pressure may be applied to the ventral body wall.

Type locality and type specimens. Southern California: holotype (USNM 16884); paratypes: Monterey Bay, 84-99 m (USNM 17311); same, 66-99 m (ANSP 3088); off Santa Cruz lighthouse, 97-139 m (ANSP 3090).

Habitat. The species occurs in a wide variety of sediments ranging from mud to gravel and rocks.

Distribution. Eastern Pacific from British Columbia to Central America and Galapagos; low intertidal to 1100 m.

Genus *Goniada* Audouin and Milne Edwards, 1833

Type species: *Goniada emerita* Audouin and Milne Edwards, 1833

Diagnosis. Prostomium pointed, annulated, with four small antennae and often a pair of eyes in the terminal and basal annuli. Proboscis long, cylindrical, covered with proboscideal organs of one or more kinds; armed with two lateral series of V-shaped chevrons subdistally and a circlet of terminal jaws consisting of two macrognaths and several micrognaths in dorsal and ventral arcs. Peristomium fused to basal prostomial annulus. Parapodia uniramous in anterior part of body, biramous in posterior part, sometimes transitional over a number of setigers; dorsal cirri large, digitiform to foliaceous, attached to dorsal parapodial wall; ventral cirri large, conical. Notosetae numerous, simple capillaries; neurosetae compound, usually spinigerous.

Goniada annulata **Moore, 1905**

Figure 7.2

Goniada annulata Moore, 1905:549, pl. 36, figs. 45-48; 1911:305.—Hartman, 1950:20, pl. 2, figs. 1-9; 1968:651.—Lissner *et al.*, 1986:D-11.—Hyland and Neff, 1988:A-2.—Hyland *et al.*, 1990:F-1.

Material examined. California: Santa Maria Basin, off Point Estero, Sta. 11 (1); off Point Buchon, Sta. 15 (1); off Point Sal, Sta. R-9 (1).

Description. Length to 90 mm, width to 3 mm, setigers to 160. Body wide, tapering toward both ends, with well-defined cylindrical segments in anterior region, somewhat depressed in middle and posterior regions; softer and inflated when sexually mature. Color in alcohol: variable; yellowish brown with patches of dark brown pigment to solid bluish brown segments with pale intersegmental furrows; prostomium lightest in color. Regions bearing gametes with midventral pigment spots.

Prostomium triangular, about twice as long as wide, irregularly annulated with 4 dorsal and 5 ventral rings (Fig. 7.2A); terminal annulus blunt, bearing four minute biarticulate antennae; dorsal ones inserted slightly more proximal than ventral ones; eyes absent. Peristomium fused to prostomium, about as wide as prostomial base. Proboscis long and cylindrical, reaching back to about setiger 40 when fully retracted. Proboscideal organs irregularly but densely arranged, translucent, of two kinds: conical, tall (Fig. 7.2B-D) and short, spherical (Fig. 7.2E-G); both types with terminal beak and subterminal pore and

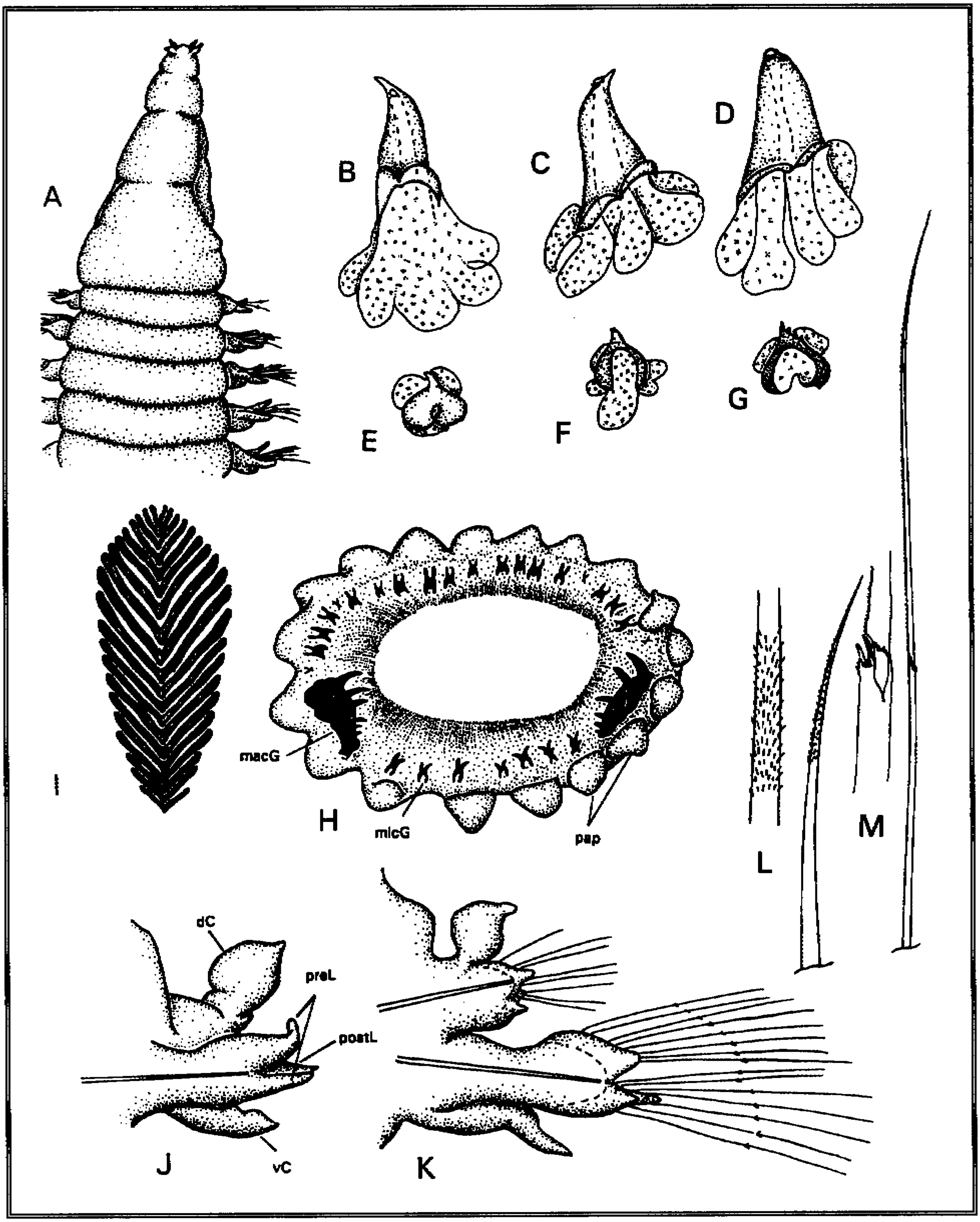

Figure 7.2. *Goniada annulata*: A, anterior end, dorsal view; B-G, tall and short proboscideal organs in frontal, lateral, and posterior view; H, micro- and macrognaths *in situ*, anterior view; I, chevrons; J-K, anterior and posterior parapodium, anterior view; L, notoseta with detail: beginning of surficial spines; M, neuroseta with detail: articulation. (A, I, K after Hartman, 1950; J after Moore, 1905).

basally attached multilobed cell with granular contents. Apical jaws black, very hard, consisting of two macrognaths with 4 to 6 fangs and H-shaped micrognaths of varying size, arranged in a ventral arc of about 7 to 8 and a dorsal arc of 14 to 21 micrognaths (Fig. 7.2H). Chevrons broadly V-shaped, close together, 18 to 20 on either side of the proboscideal base; largest ones in middle of each group (Fig. 7.2I).

Parapodia uniramous in first 33 to 35 segments; presetal lobe deeply cleft, postsetal lobe conical, as long as presetal lobes; doral cirri broadly foliaceous, basally constricted; ventral cirri conical, much slenderer than dorsal cirri, shorter than parapodial lobes (Fig. 7.2J). Notopodia occurring abruptly on setiger 34 to 36, with 2 broadly triangular, pointed presetal lobes and somewhat shorter, conical postsetal lobe; much smaller than neuropodium (Fig. 7.2K). Notosetae short, stiff capillaries with surficial spines on upper third, about 8-12 per fascicle; neurosetae compound spinigers, only half as wide as notosetae, silky and flowing; with finely serrated blades, much more numerous than notosetae (Fig. 7.2L, M).

Pygidium small, with one long, slender anal cirrus that is often missing in preserved specimens.

Remarks. The irregularly annulated prostomium of this species is unique for the genus and prevents any misidentification.

Type locality and type specimens. Alaska: vicinity of Yes Bay, Behm Canal, 238-353 m: holotype (USNM 5520) and 6 paratypes (ANSP 2089); other paratypes: off Freshwater Bay, Chatham Street, 516-536 m (ANSP 2091, USNM 5620).

Habitat. The species occurs in mud and fine sand.

Distribution. Alaska to western Mexico, 180 to 2800 m.

Goniada brunnea Treadwell, 1906

Figure 7.3

Goniada brunnea Treadwell, 1906:1174, figs. 67-70.—Moore, 1911:306.—Berkeley and Berkeley, 1942:194.—Hartman, 1950:17, pl. 1, figs. 1-6, pl. 4, fig. 1 (synonymy); 1968:653. —Pettibone, 1963:228, figs. 57a, b.—Lissner *et al.*, 1986:D-11.—Hyland and Neff, 1988: A-2.—Hyland *et al.*, 1990:F-1.
Goniada annulata Treadwell, 1914:198 (in part).
Goniada maculata: Hartman, 1940:251.—Berkeley, 1941:34. *Not* Oersted, 1843.

Material examined. California: Santa Maria Basin, off Point Sal, Sta. 42 (1), Sta. PJ-3 (1), Sta. PJ-8 (1); off Purisima Point, Sta. R-5 (1); western Santa Barbara Channel, Sta. 85 (1); Gulf of the Farallones: Sta. L-17, 37°38.94'N, 123°26.85'W, 2855 m (1); Tomales Bay (1).

Description. Length to 160 mm (one specimen reported by Hartman over 7 inches long), width to 2.6 mm, segments to about 200. Body large, robust, tapering on both ends. Color in alcohol mottled to dark brown with pale intersegmental furrows; large specimens darkest.

Prostomium broadly triangular, depressed, with 7 to 10 rings, number of rings diminishing with age; distal annulus with spatulate anterior margin, bearing two pairs of biarticulate antennae and occasionally a pair of subdermal eyes. Eyes also present in proximal ring, or entirely absent (Fig. 7.3A). Peristomium fused to basal prostomial annulus, much wider than preceding ring. Proboscis relatively short, cylindrical, reaching back to setiger 23 if fully retracted; surface covered with small, scale-shaped proboscideal organs (Fig. 7.3B); terminal jaws consisting of 2 macrognaths with 3 to 5 fangs, 0 to 4 Y-shaped micrognaths in the dorsal arc, and 3 to 12 micrognaths in the ventral arc (Fig. 7.3C); number of

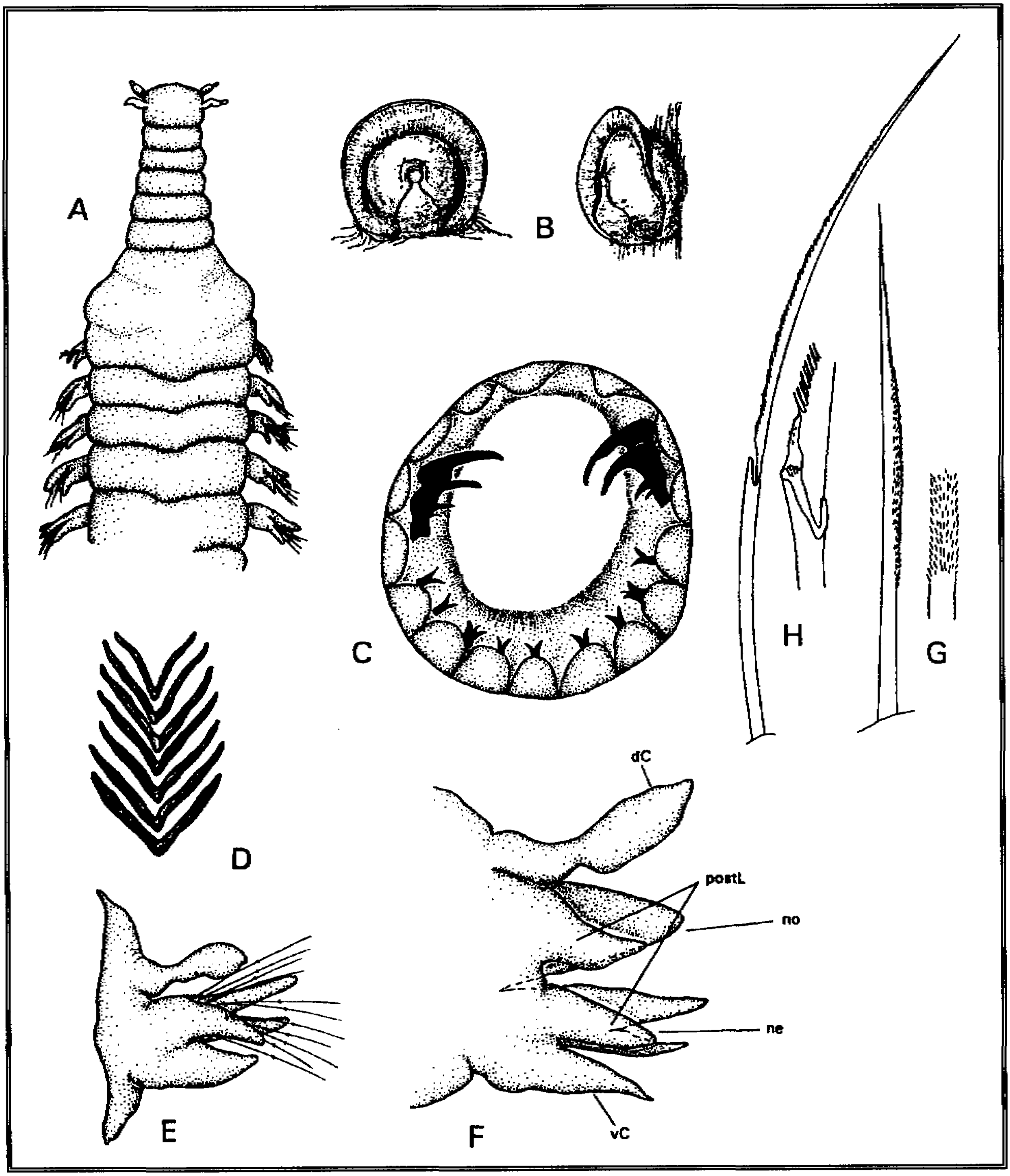

Figure 7.3. *Goniada brunnea*: A, anterior end, dorsal view; B, proboscideal organs from above and in lateral view; C, micro- and macrognaths *in situ*, anterior view; D, chevrons; E-F, anterior and posterior parapodium, anterior view; G, notoseta with detail: surficial spines; H, neuroseta with detail: articulation. (A, B, D-F after Hartman, 1950).

dorsal micrognaths diminishing with age, number of ventral micrognaths increasing. Chevrons broadly V-shaped, about 7 to 25 on each side of the proboscideal base, largest ones in proximal position (Fig. 7.3D).

Parapodia uniramous in first 41 to 44 segments; presetal lobes deeply incised, postsetal lobe conical; dorsal cirri foliaceous, ventral cirri long and conical (Fig. 7.3E). Notopodia first present on setiger 44 or 45 (32 or 33 in deep-sea specimens), with conical presetal lobe and much shorter triangular postsetal lobe (Fig. 7.3F). Notosetae simple capillaries covered with surficial spines, about 10 to 12 per fascicle (Fig. 7.3G); neurosetae compound spinigers with long, delicate dentition along cutting edge of blade, about 22 per fascicle (Fig. 7.3H).

Pygidium with two long, slender anal cirri.

Remarks. Many of the commonly used characters for species discrimination seem to vary somewhat in *G. brunnea*, depending on the age of a specimen and the water depth where it was collected. The shape of the proboscideal organs may be the only reliable character to distinguish this species from its closely related congeners, although the blunt prostomium and the abruptly widening peristomium give a very characteristic habitus to the animal.

Type locality and type specimens. Hawaii, 364-396 m: holotype (USNM 5218).

Habitat. The species occurs in mud, sand, and among shells and shell fragments.

Distribution. Eastern Pacific: Alaska to southern California, Hawaii; northwest Atlantic: Massachusetts to North Carolina; low intertidal to 2855 m.

Goniada littorea Hartman, 1950

Figure 7.4

Goniada littorea Hartman, 1950:23, pl. 3, figs. 1-10.—Gardiner, 1976:169, fig. 19i-l.—Gilbert, 1984:33-9, fig. 33-6.—Lissner *et al.*, 1986:D-11.
Goniada brunnea Treadwell, 1914:198 (in part).
Goniada uncinigera: Hartman, 1940:252. *Not* Ehlers, 1901.

Material examined. California: Santa Maria Basin, off Point Arguello, Sta. 64 (1).

Description. Length to 70 mm, width to 1.5 mm, segments to about 175. Body slender, tapering at both ends; cylindrical in anterior region, abruptly widening in transitional region and depressed in posterior region. Color in alcohol uniformly brownish orange, mottled brown or with striking, regular segmental pigment patches.

Prostomium pointed, much longer than wide, with 8 or 9 rings. Terminal ring bearing four small, biarticulate antennae; basal ring with a pair of faint eyes (Fig. 7.4A). Proboscis long, cylindrical, covered with spherical, beaked proboscideal organs (Fig. 7.4B, C). Terminal jaws surrounded by 18 soft papillae, consisting of two macrognaths with 4 to 6 fangs, 3 ventral H-shaped micrognaths, and 10 to 12 H- or Y-shaped micrognaths in dorsal arc (Fig. 7.4D). Proboscideal base armed with 15 to 18 broadly V-shaped chevrons on each side; largest ones in middle of each group; all chevrons with irregular edges (Fig. 7.4E).

Parapodia uniramous through setiger 35 to 43; first 9 to 14 parapodia with single presetal lobe and single postsetal lobe (Fig. 7.4F); subsequent parapodia with two digitiform presetal lobes (Fig. 7.4G). Notopodia fully developed after about 5 transitional setigers, with subequal, triangular pre- and postsetal lobes; neuropodia in posterior setigers with two conical presetal lobes of equal length and shorter, triangular postsetal lobe (Fig. 7.4H). Dorsal and ventral cirri wide, digitiform, shorter than parapodial

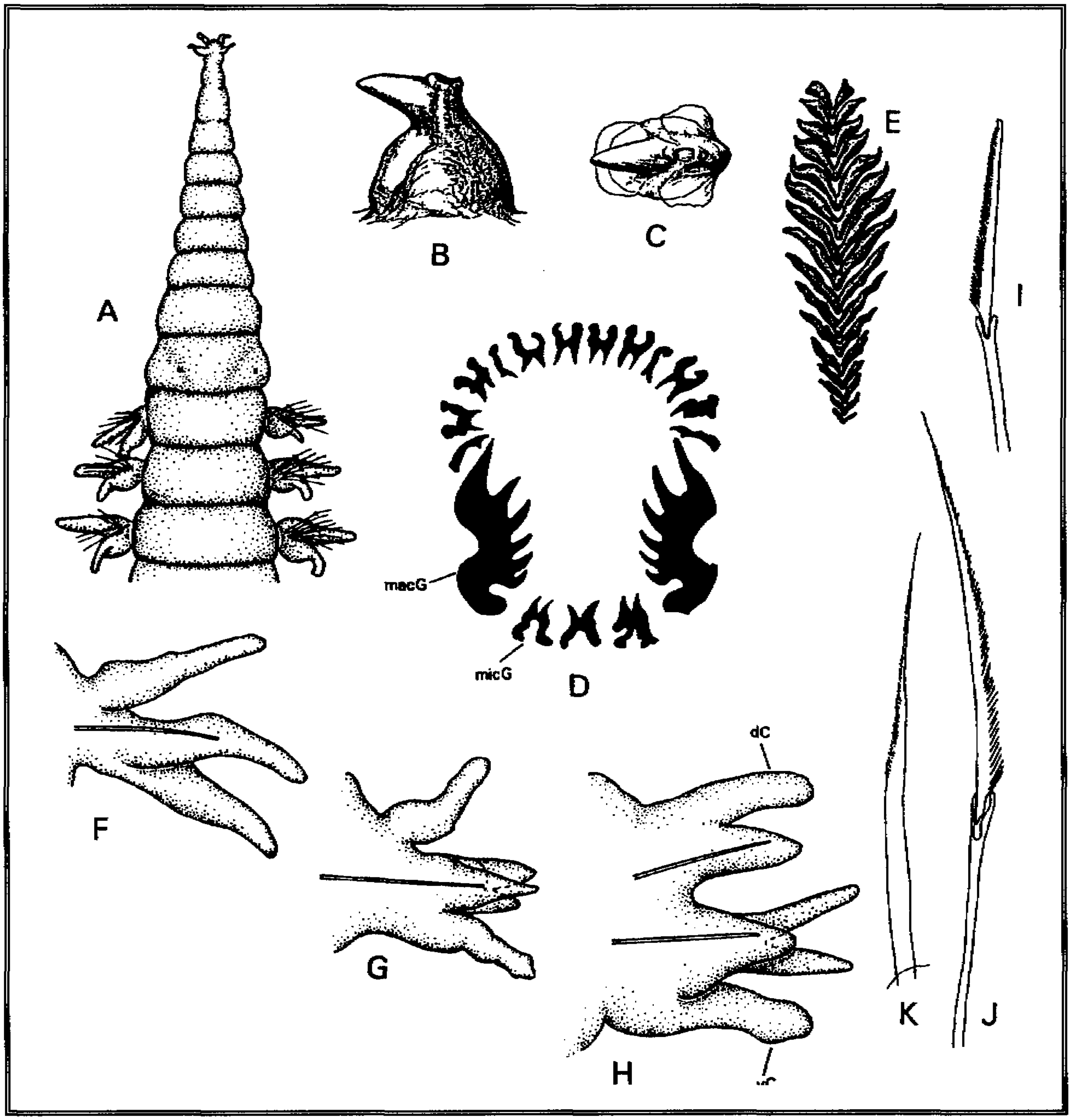

Figure 7.4. *Goniada littorea*: A, anterior end, dorsal view; B-C, proboscideal organ, lateral view and from above; D, micro- and macrognaths *in situ*, anterior view; E, chevrons; F, anterior parapodium, anterior view; G, middle parapodium, anterior view; H, posterior parapodium, anterior view; I, falciger, anterior setiger; J, spiniger, posterior setiger; K, notoseta. (A-E, G after Hartman, 1950; F, I-K after Gilbert, 1984).

lobes. Neurosetae in first 2 to 3 parapodia with inferior group of about 5 compound falcigers with short blades and superior fascicle of long-bladed, slender compound spinigers; subsequent parapodia with very long, slender, compound spinigers only (Fig. 7.4I, J). Notosetae finely serrated capillaries, about 10 to 12 per fascicle (Fig. 7.4K).

Pygidium with two long, slender anal cirri, often broken off in preserved specimens.

Remarks. *G. littorea* differs from its congeners by possessing a large number of micrognaths in the dorsal arc and a pointed, rather than blunt, prostomium. In addition, it is characterized by beaked proboscideal organs.

Type locality and type specimens. Southern California; LACM-AHF.

Habitat. The species is found in medium to fine sand and sands mixed with mud or shell fragments.

Distribution. North Carolina; Gulf of Mexico; southern California; intertidal to 160 m.

Goniada maculata Oersted, 1843

Figure 7.5

Goniada maculata Oersted, 1943:33.—Okuda, 1939:233, fig. 8.—Hartman, 1950:20, pl.1, fig. 7, 8.—Pettibone, 1963:225, fig. 58.—Gardiner, 1976:167, fig. 19c-f.—Uschakov and Wu, 1979:50.—Gilbert, 1984:33-11, figs. 33-7, 33-8.—Lissner *et al.*, 1986:D-11.
Goniada brunnea: Hartman, 1940:251

Material examined. California: Santa Maria Basin, off Point San Luis, Sta. 21 (1); Gulf of the Farallones, Sta. 40-3 (1), Sta. 41-5 (1), Sta. 42-6 (1), Sta. 43-3 (1), Sta. 44-6 (1). —New England: Georges Bank, Sta. 7 (1), Sta. 13 (2).

Description. Length to 100 mm, width to 1 mm, segments to 200. Body slender, gradually tapering toward both ends; cylindrical in short, anterior region, somewhat depressed in posterior region. Neural eyespots present on all biramous segments. Color in alcohol light tan with light to dark brown pigment spots; body darkest in posterior region.

Prostomium bluntly conical, with up to 10 short rings; terminal annulus with four biarticlulate antennae; eyes absent. Basal annulus only slightly wider than preceding ring and not much narrower than first segment (Fig. 7.5A). Proboscis short, reaching back to setiger 12 in Santa Maria Basin specimen; covered with minute, flat, heart-shaped proboscideal organs that may be hard to see (Fig. 7.5B). Terminal jaws surrounded by 18 papillae, consisting of 2 to 4 minute, X-shaped dorsal micrognaths and 1 to 4 larger ventral ones, and macrognaths with 4 to 8 fangs (Fig. 7.5C). Chevrons numbering 8 to 10 on each side, narrowly V-shaped, largest pieces in middle of group (Fig. 7.5D).

Parapodia long, conspicuous, about twice as long as body width in posterior part of body; uniramous through setiger 23 to 45, with single presetal lobe and single, much shorter postsetal lobe (Fig. 7.5E); last uniramous parapodia with very small accessory ventral presetal lobe, developing into second presetal lobe in biramous parapodia (Fig. 7.5 F, G); notopodia with digitiform presetal lobe, postsetal lobe lacking. Dorsal and ventral cirri of subequal length, digitiform and flattened. Neurosetae compound spinigers with short and long blades, longest in posterior setigers (Fig. 7.5 H, I); in anterior parapodia few falcigers present in superior group (Fig. 7.5J). Notosetae short, simple, serrated capillaries, relatively numerous in posterior setigers (Fig. 7.5K). Sexually mature specimens with simple natatory setae in neuropodial fascicles from about setiger 30.

Pygidium small, with 2 short anal cirri.

Remarks. This species is easily confused with *Goniada brunnea* in that both species have blunt prostomia, and show overlapping variablity in the number of uniramous setigers. However, *G. maculata* is

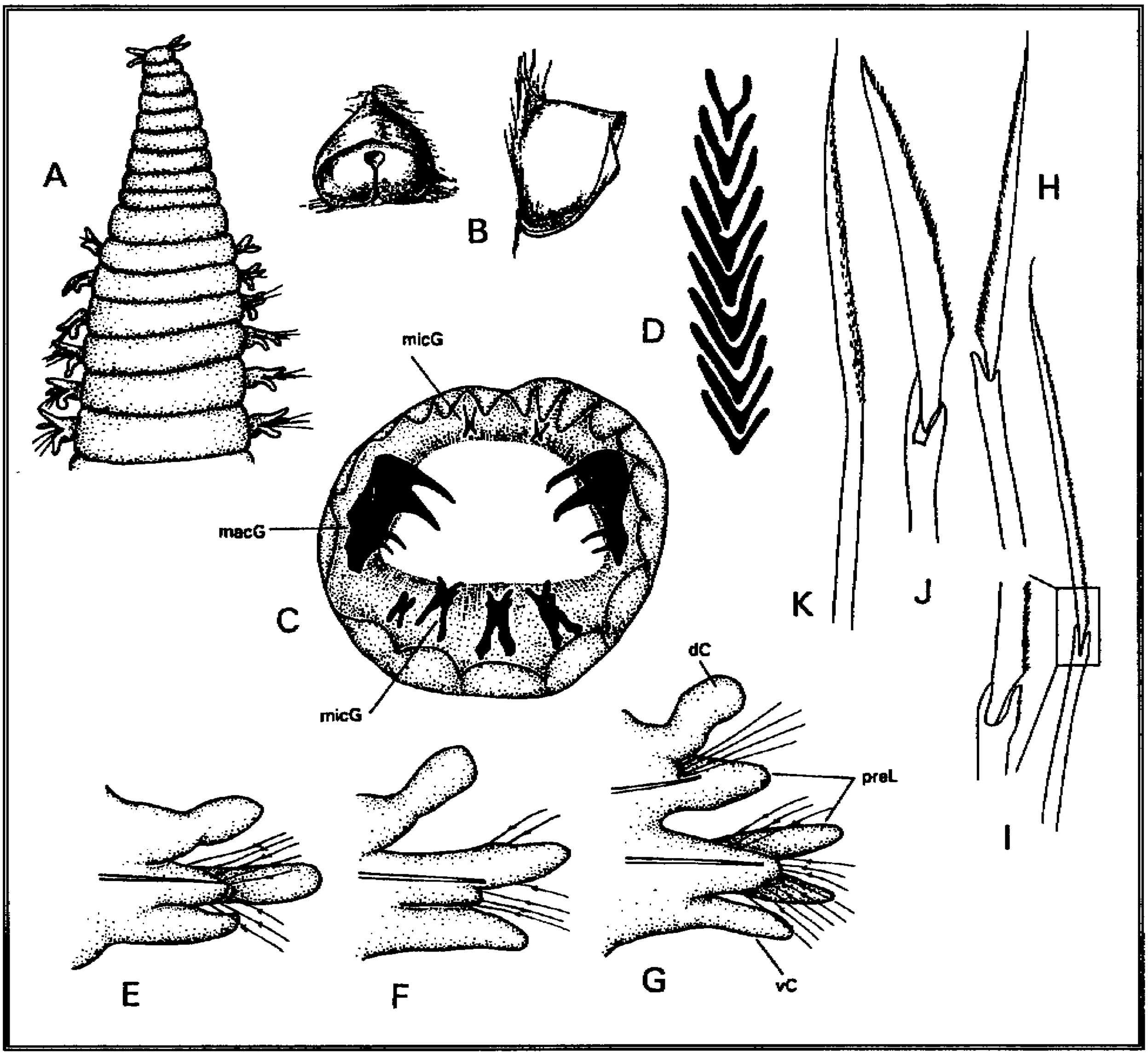

Figure 7.5. *Goniada maculata*: A, anterior end, dorsal view; B, proboscideal organ from above and lateral view; C, micro- and macrognaths *in situ*, anterior view; D, chevrons; E-F, anterior parapodium, posterior and anterior view; G, posterior parapodium, posterior view; H-I, spinigers, anterior and posterior setiger; J, falciger, anterior setiger; K, notoseta (B after Hartman, 1950; D-G after Gardiner, 1975; H-K after Gilbert, 1984).

a gracile, slender species, whereas *G. brunnea* can reach considerable size and has a more stout appearance. The body widens abruptly behind the prostomium in the latter species, whereas it widens very gradually in the former. Furthermore, *G. maculata* lacks a postsetal lobe in the notopodia, whereas it is present in *G. brunnea*. For final species discrimination, the proboscis should be examined to determine the shape of the proboscideal organs and the shapes and distribution of the micrognaths between the dorsal and ventral arcs. If only juvenile specimens are available from areas where both of these species co-occur, species names should be given with caution.

Type locality. Denmark.

Habitat. *G. maculata* occurs in silt, sand, and shelly sand.

Distribution. Arctic Ocean: Greenland, Davis Strait; Atlantic Ocean: western Europe and Gulf of St. Lawrence, and U.S. American east coast to North Carolina; Pacific Ocean: Alaska to California; Japan; Gulf of Iran; South Africa; intertidal to 3020 m.

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8. FAMILY SPHAERODORIDAE MALMGREN, 1867

by

Jerry D. Kudenov[1]

Introduction

The Sphaerodoridae is a relatively small family of deposit feeding benthic polychaetes that are more commonly encountered in deep-sea habitats than in shallow coastal waters. Sphaerodorids have small bodies that typically bear rows of epidermal tubercles or papillae over their dorsal and ventral surfaces.

Morphology

The bodies of sphaerodorids are either short and grublike for around 30 segments, or long and slender for up to 50 or more segments. The prostomium, peristomium and anterior body segments are not obviously separated from one another. The prostomium bears an unpaired median antenna plus two or three pairs of lateral antennae; eyes may be present or absent. The peristomium typically has one pair of cirri. The pharynx is unarmed, and a muscular proventriculus is present. Parapodia are uniramous and are supported by a single acicula. Dorsal cirri are absent, whereas ventral cirri are present. Setae are either simple or compound; usually only one kind of seta is represented. Simple curved hooks may be present in the anteriormost segments.

Terminology describing epithelial protuberances has been clarified by Fauchald (1974), whose work is central to understanding the systematics of this family. Three kinds of epidermal protuberances are recognized. Macrotubercles are conspicuous bulbous structures that may be sessile or stalked. A small distal terminal papilla may sometimes be present on sessile macrotubercles. Microtubercles are recognized by the presence of a basal collar surrounding a terminal papilla. All known species that have microtubercles have sessile macrotubercles that possess terminal papillae. This includes all taxa that have only two longitudinal rows of macrotubercles, and one other known species with four such rows. Papillae are conical, cylindrical, cap-shaped or hemispherical; all are invariably simple.

Principal taxonomic characters include the presence, form and number of rows of macrotubercles; the degree to which macrotubercles are fused with microtubercles; the relative development of the median and lateral antennae; the presence or absence of eyes; the distribution of body papillae; the presence and development of superior presetal and postsetal lobes; the number and distribution of parapodial papillae; the relative lengths of the ventral cirri and acicular lobes; and the presence of simple hooks on anterior setigers.

Taxonomic History

The most important review of the Sphaerodoridae was by Fauchald (1974), who completely revised and redefined the genera, provided a key to all known species, and described 12 new species. Fauchald (1974; 1977) recognized nine genera: *Clavodorum, Commensodorum, Ephesiella, Ephesiopsis, Levidorum, Sphaerodoridium, Sphaerodoropsis, Sphaerodorum,* and *Sphaerephesia*. Perkins (1987) subsequently removed *Levidorum* from the Sphaerodoridae and placed it into a separate family, the Levidoridae. An additional genus from Alaska, *Amacrodorum,* was described by Kudenov (1987a). This

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new genus, lacks macropapillae, and is strongly isolated in the family. New species are continuing to be described. For example, Kudenov (1987a-b) describes eight new species from Alaska and the Gulf of Mexico. Approximately 73 species have been described to date.

Most of the common genera and species were well described by Fauchald (1974). Desbruyères (1980) and Kudenov (1984, 1987a-b) provided descriptions of species from the northeast Atlantic, Gulf of Mexico and Alaska. Four genera and five species (one new) were discovered in the samples from the Santa Maria Basin.

Biology

Given the relatively low number of species and the low frequency with which they are encountered, little information pertaining to sphaerodorid biology is available. Most sphaerodorids have been recorded either from polar seas or deep water, and commonly inhabit sandy or muddy sediments; some species inhabit hard bottoms in shallow depths. They are thought to be free-living surface deposit feeders (Fauchald and Jumars, 1979). At least one species produces large ova and demersal larvae (Pettibone, 1963). One species is suspected of being hermaphroditic (Schroeder and Hermans, 1975). The habitat of sphaerodorids is not fully understood because benthic samples contain so few specimens. Lützen (1961) described an interesting commensal relationship between a sphaerodorid (*Commensodorum commensalis*) and a terebellid polychaete.

Key to the Genera and Species of Sphaerodoridae

1A. Macrotubercles sessile, with terminal papillae (Fig. 8.1D) 2

1B. Macrotubercles sessile, without terminal papillae (Fig. 8.3C): .... Genus *Sphaerodoropsis* 4

2A. Macrotubercles present in 4 rows; microtubercles absent; setiger 1 without simple hooks .... Genus *Sphaerephesia*[2]

2B. Macrotubercles present in 2 rows; microtubercles present in 2 rows (Fig. 8.1C); setiger 1 with large simple hooks (Fig. 8.1E) 3

3A. All other setae simple .... *Sphaerodorum papillifer*

3B. All other setae composite .... *Ephesiella brevicapitis*

4A. Macrotubercles present in 4 rows .... *Sphaerodoropsis biserialis*

4B. Macrotubercles present in more than 4 rows 5

5A. Macrotubercles present in 7-8 rows, forming a transverse row on adjacent segments; prostomial antennae without accessory papillae (Fig. 8.3A); eyes absent .... *Sphaerodoropsis sphaerulifer*

5B. Macrotubercles present in 10-11 rows, forming a zig-zag pattern on adjacent segments; prostomial antennae with retractable accessory papillae (Fig. 8.4D); eyes present. .... *Sphaerodoropsis sexantennella*

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[2] The genus *Sphaerephesia* is not represented in the present materials. It is included in the key because it will probably be encountered in the area.

Descriptions of Species

The Sphaerodoridae is a small family. The fauna of the Santa Maria Basin contained five species, including one species that was new to science; no sphaerodorids were found in the Western Santa Barbara Channel. The species treated in this chapter are listed below.

Ephesiella brevicapitis (Moore, 1909)
Sphaerodoropsis biserialis (Berkeley and Berkeley, 1944)
Sphaerodoropsis sphaerulifer (Moore, 1909)
Sphaerodoropsis sexantennella Kudenov, 1993
Sphaerodorum papillifer Moore, 1909

Ephesiella brevicapitis (Moore, 1909)

Figure 8.1

Sphaerodorum brevicapitis Moore, 1909:335-336, pl. 15, figs. 13-14.—Hartman, 1968:607-608, figs 1-2.
Ephesiella brevicapitis: Fauchald, 1972:96, pl. 19; 1974:267-268.

Material examined. California: Santa Maria Basin, off Point Estero, Sta. 2 (1); off Port San Luis, Sta. R-1 (1).

Description. A moderately large species, measuring up to 40 mm long, 1.6 mm wide, with 100 segments. Prostomium with a median antenna plus 2 pairs of similarly sized lateral antennae; with a pair of dark eyespots in segments 2-3 (Fig. 8.1A). Tentacular cirri small, digitate. Parapodia each with conical acicular, short digitate presetal, and longer digitate postsetal lobes (Fig. 8.1B); parapodial papillae numbering 4, including 1 proximal dorsal and 3 distal papillae on anterior parapodial surfaces (Fig. 8.1B); ventral cirri distally digitate, not projecting beyond parapodial lobes. Macrotubercles and microtubercles each arrayed in 2 rows on dorsum; macrotubercles sessile, each with terminal papilla; microtubercles each with digitate terminal papillae surrounded by a basal collar (Fig. 8.1C, D). Setae include 2 large simple recurved hooks in each parapodium of setiger 1 (Fig. 8.1E), and 2 kinds of compound falcigers (Fig. 8.1F-G); one kind represented by thick shafts terminating in enlarged sockets for short and strongly falcate blades, the other by thin shafts with slim sockets for slender and longer blades.

Biology. *Ephesiella brevicapitis* is reported from muddy sediments in shelf and canyon depths.

Remarks. This species is rarely encountered. Although Moore (1909) described the presence of terminal papillae on macrotubercles, he incorrectly illustrated the terminal papilla emerging from a region near the base of the macropapilla (Fauchald, 1972). Anterior segments are herein illustrated, apparently for the first time.

Type locality and type specimens. California: Santa Catalina Island, Sta. 4395, 31 March, 2045 fathoms; blue-gray mud. Holotype: USNM.

Distribution. Central California, western Mexico; deep basin, slope and canyon depths.

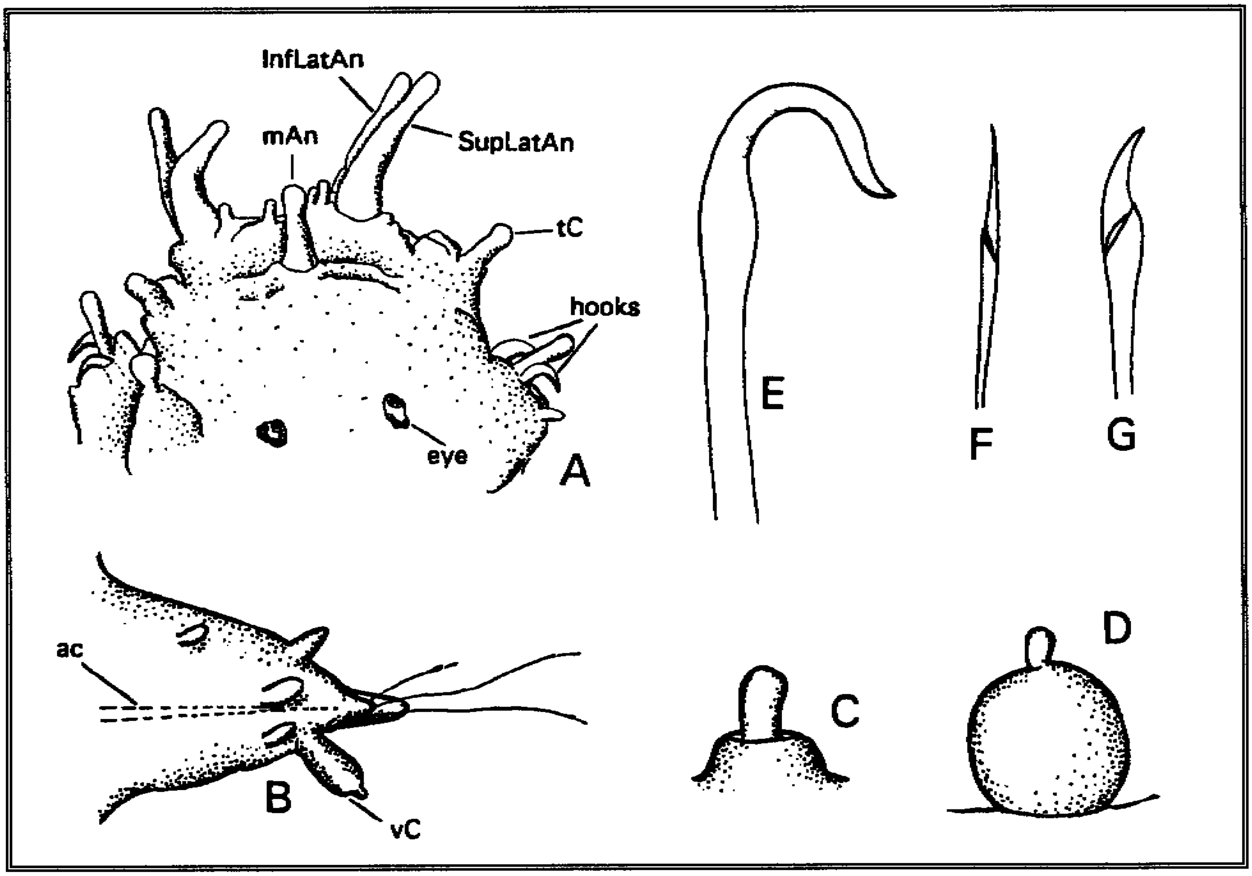

Figure 8.1. *Ephesiella brevicapitis*: A, anterior end, dorsal view; B, median parapodium, anterior view; C, microtubercle; D, macrotubercle; E, simple hook, setiger 1; F-G, compound setae. (B-G after Fauchald, 1972).

Sphaerodoropsis biserialis (Berkeley and Berkeley, 1944)

Figure 8.2

Sphaerodorum biserialis Berkeley and Berkeley, 1944:3, figs. 1-3.
Sphaerodoridium biserialis: Lützen, 1961:415.—Hartman, 1968:601.—Imajima, 1969:154-155, figs. 3 a-d.
Sphaerodoropsis biserialis: Banse and Hobson, 1974:76, Fig. 20a (cited in key only).—Fauchald, 1974:272, fig 3.17.

Material examined. California: Santa Maria Basin, off Point Sal, Sta. R-8 (2).

Description. A relatively small species, measuring up to 3-4 mm long, 0.3-0.5 mm wide, with 23-24 setigers. Prostomium with a median antenna plus 2 pairs of lateral antennae; eyes absent (Fig. 8.2A). Tentacular cirri digitiform. Parapodia each with bluntly conical acicular, and large clavate presetal lobes (Fig. 8.2B). Parapodial papillae numbering 4, including 1 basal papilla on each of the anterior and posterior parapodial surfaces, plus 2 dorsal superior papillae of which distalmost papilla largest, truncate;

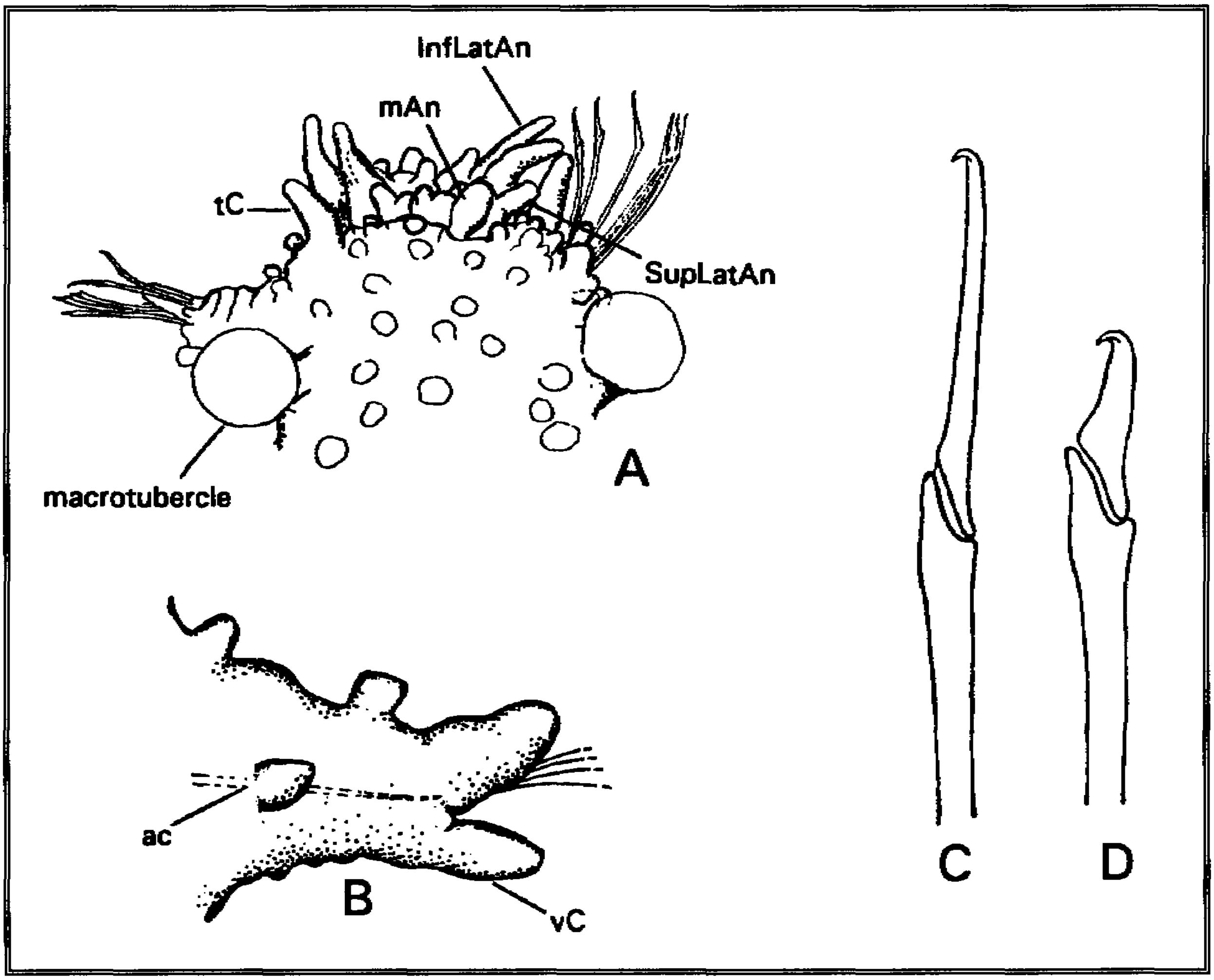

Figure 8.2. *Sphaerodoropsis biserialis:* A, anterior region, dorsal view; B, median parapodium, anterior view; C, D, compound setae. (B after Fauchald, 1974; C from Berkeley and Berkeley, 1944).

proximal papilla small. Ventral cirri similar to acicular lobes, smaller; projecting between acicular and presetal lobes. Macrotubercles arrayed in 4 rows on dorsum. Macrotubercles sessile, lacking terminal papillae. Papillae short, scattered over ventrum. Setae entirely compound, of 1 kind, numbering 15-25 per fascicle, with slightly inflated shafts forming sockets for strongly falcate blades of varying lengths (Fig. 8.2C-D).

Biology. *Sphaerodoropsis biserialis* was originally described from slope depths in the western Canadian Arctic.

Remarks. *Sphaerodoropsis biserialis* is a well-known and widespread species that has been diagnosed by Fauchald (1974). However, the prostomial region has not been well illustrated. Detailed examinations of the present material suggests that three pairs of lateral antennae may be present, of which the superior lateral antennae are smallest, and seem likely to be mistaken for body papillae; each antenna also has a single medial accessory papilla. The type material must be re-examined to determine the number of antennae present.

Type locality and type specimens. Canada, Dease Strait, 69°N, 106°25'W, ~90 m. Holotype: USNM.

Distribution. Canada, Alaska south to California and western Mexico; Japan; in shelf depths.

Sphaerodoropsis sphaerulifer (Moore, 1909)

Figure 8.3

Sphaerodorum sphaerulifer Moore, 1909:336.—Uschakov, 1955:222.
Sphaerodoropsis sphaerulifer: Lützen, 1961:415.—Banse and Hobson, 1968:76, fig. 20e.—Hartman, 1968:605.—Fauchald, 1974:277, fig. 3.1-4.—Kudenov, 1987a:924.

Material examined. California, Santa Maria Basin, off Port San Luis, Sta. 22 (2); off Point Sal, Sta. PJ-1 (3), Sta. PJ-2 (6), Sta. PJ-3 (1), Sta. PJ-4 (2), Sta. PJ-6 (7), Sta. PJ-7 (7), Sta. PJ-8 (4), Sta. PJ-9 (3), Sta. PJ-10 (1), Sta. PJ-11 (2); off Point Arguello, Sta. 58 (3).

Description. A relatively small species, measuring up to 3 mm long, 0.3 mm wide, with 25-26 setigerous segments. Prostomium with a strongly inflated median antenna plus 2 pairs of lateral antennae (Fig. 8.3A); each of the latter short, truncate. Tentacular cirri digitiform. Parapodia each with truncate acicular, and short digitate presetal lobes (Fig. 8.3B); postsetal lobes not defined; parapodial papillae numbering 2, including 1 on each of the anterior and posterior parapodial surfaces; ventral cirri terminal, large, digitiform, projecting beyond parapodial lobes. Macrotubercles arrayed in 7-8 rows on dorsum, sessile, lacking terminal papillae (Fig. 8.3C). Papillae large, spherical (Fig. 8.3D), covering ventrum completely, present in high numbers on prostomium and anterior segments, and between macrotubercles. Setae entirely compound, of 1 kind, with shafts terminating in enlarged sockets for short falcate blades (Fig. 8.3E-F).

Biology. *Sphaerodoropsis sphaerulifer* is reported from silty sand, mud and clay in shelf and slope depths. In the Santa Maria Basin, the species was common is sediments having high silt and low clay inventories.

Remarks. *Sphaerodoropsis sphaerulifer* was originally described from a posterior body fragment. Fauchald (1974) presented the first illustrations of this species. Kudenov (1987a) noted that specimens tentatively identified as *S. sphaerulifer* from Alaska seem to be more similar to those reported by Uschakov (1955), Lützen (1961), and Banse and Hobson (1974) than to those recorded from California by Moore (1909) and Fauchald (1974).

Type locality and type specimens. California: Monterey Bay, 16 July 1902, from a deep-sea fishing line. Type disposition: USNM

Distribution. California, Washington, British Columbia, Alaska, Sea of Japan, Sea of Okhotsk.

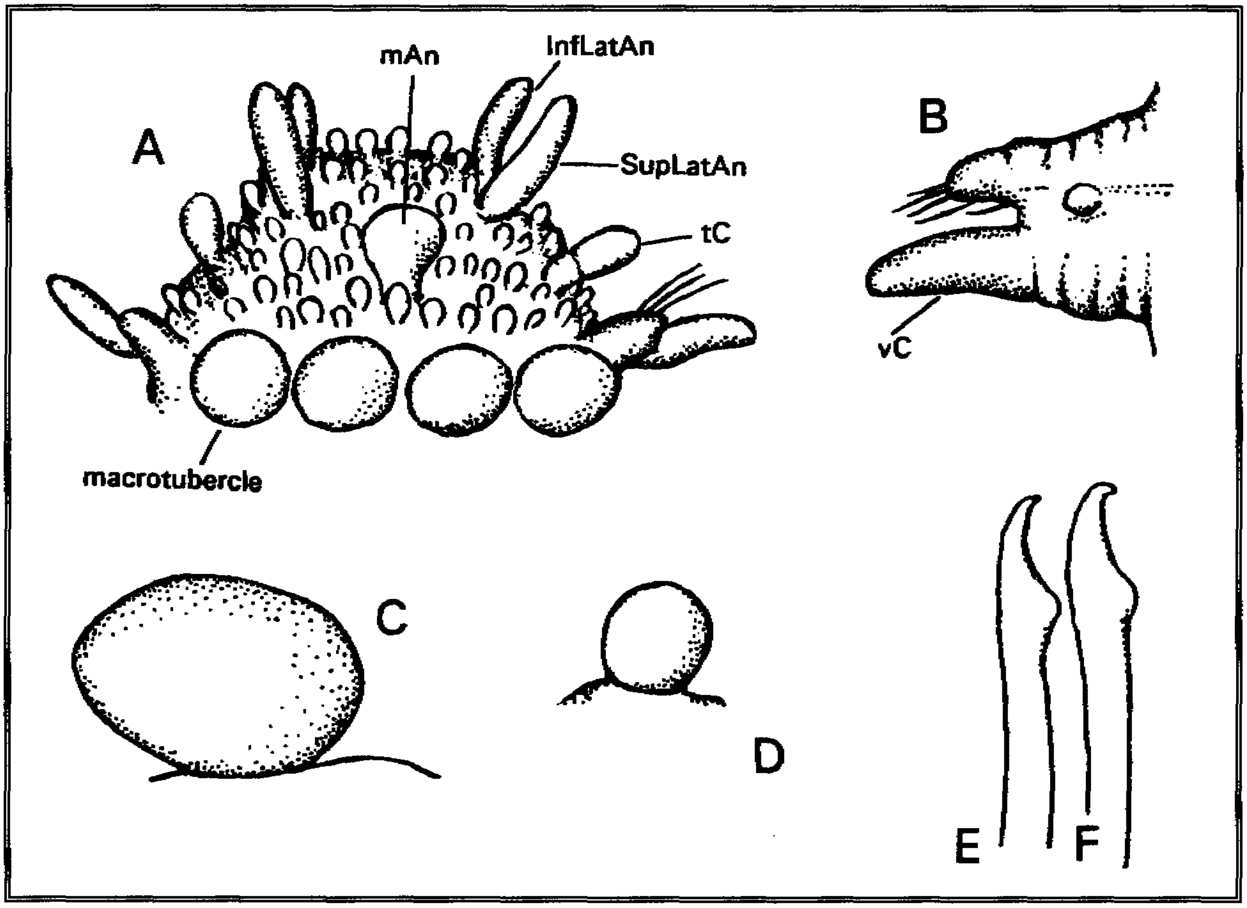

Figure 8.3. *Sphaerodoropsis sphaerulifer*: A, anterior segments, dorsal view; B, median parapodium, anterior view; C, macrotubercle; D, papilla; E-F, simple setae, median segments. (A-D after Fauchald, 1974).

Sphaerodoropsis sexantennella Kudenov, 1993

Figure 8.4

Sphaerodoropsis sp. A: Hyland and Neff, 1988:A-3.
Sphaerodoropsis sexantennella Kudenov: 1993, 582-586.

Material examined. California: Santa Maria Basin, off Point Sal, Sta. PJ-1 (8), Sta. PJ-7 (11), Sta. PJ-8 (6), Sta. PJ-9 (6), Sta. PJ-10 (5), Sta. PJ-11 (3).

Description. A small species, measuring up to 0.5 mm long, 0.2 mm wide excluding setae, with 15 setigerous segments. Prostomium with a short globular median antenna plus 2 pairs of short digitate to globular lateral antennae (Fig. 8.4A-E). Superior lateral antennae apparently lacking accessory papillae; inferior lateral antennae each with 3 retractable accessory papillae on median basal surfaces (Fig. 8.4D, E). Accessory papillae each nipple-shaped, surrounded by a circlet of 6 cirriform appendages. Superior lateral antennae smaller, shorter than inferior antennae. A pair of large medial eyes, deeply embedded in body wall, present on a line behind median antenna at level of setiger 1 (Fig. 8.4D). Tentacular cirri short,

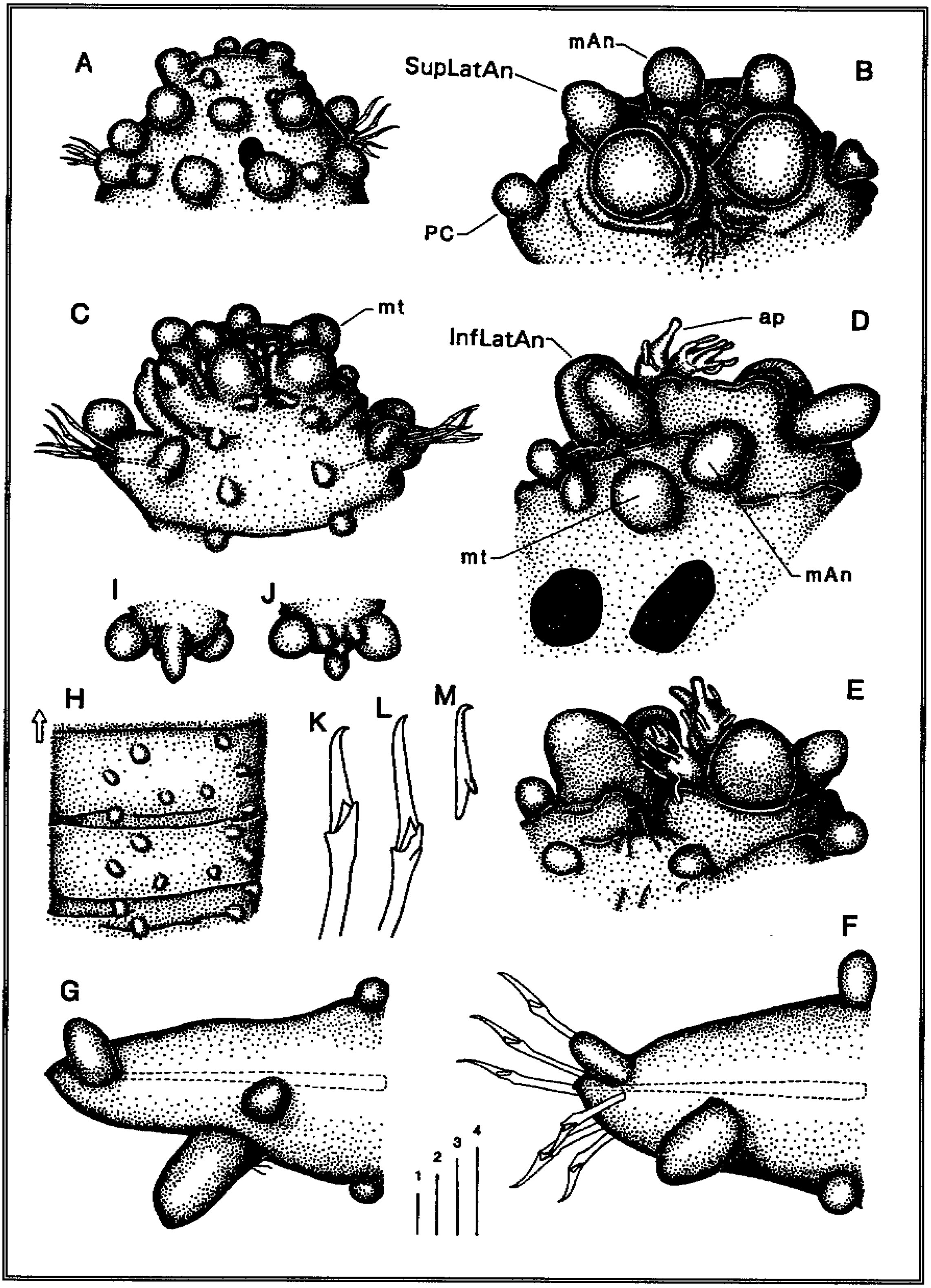

Figure 8.4. *Sphaerodoropsis sexantennella*: A, anterior region, specimen 1, dorsal view; B, prostomium and peristomium, ventral view; C, anterior region, ventral view; D, prostomium, ventral view; E, same, ventral view; F, right parapodium 2, anterior view; G, right parapodium 8, setae omitted; H, ventrum, arrow points anteriorly, ventrolateral view; I, pygidium, dorsal view; J, same ventral view; K, compound falciger from middle of fascicle; L, same, superior; M, blade, showing minute denticles. Scales: 1 = 0.01 mm (A, B, D-G); 2 = 0.05 mm (C, H); 3 = 0.05 mm (I, J); 4 = 0.01 mm (K-M).

papilliform (Fig. 8.4 D). Parapodia each with broad, bluntly conical acicular and long, upright presetal lobes; postsetal lobes absent (Fig. 8.4F, G); parapodial papillae numbering 3, including 1 on anterior parapodial surfaces from setiger 2-3, and 1 each on proximal superior and inferior edges of all parapodia (Fig. 8.4G); papillae otherwise absent from anterior surfaces of first 1-2 parapodia (Fig. 8.4F); ventral cirri large, digitiform, not projecting beyond tip of acicular lobes (Fig. 8.4F-G). Macrotubercles arrayed in 10-11 rows, forming a zig-zag pattern on dorsum, sessile, lacking terminal papillae. Papillae short, blunt, covering ventrum, present between dorsal rows of macrotubercles (Fig. 8.4H). Setae entirely compound, of 1 kind, generally numbering 6 per fascicle (Fig. 8.4F, I-K); shafts inflated, sometimes with an indistinct subdistal spur (Fig. 8.4 1I), forming terminal sockets for long, falcate blades (Fig. 8.4G, H); blades with indistinctly serrated cutting margins and sharp recurved tips (Fig. 8.4K), varying up to 2× longer than the shortest blade in setiger 1 (Fig. 8.4C), becoming nearly equal in length within a fascicle thereafter. Pygidium with short dorsal anal cirrus and longer ventral anal cirrus (Fig. 8.4L-M).

Biology. *Sphaerodoropsis sexantennella* is a continental shelf species, found in sediment with high silt and low clay inventories. Specimens with 12 setigerous segments were ovigerous.

Remarks. *Sphaerodoropsis sexantennella* is unusual in having characteristic and retractable accessory papillae on the inferior lateral antennae. This feature is difficult to observe in that the general size of all prostomial structures is strongly reduced compared to other known species of *Sphaerodoropsis*. Additionally, the prostomium is retracted in most specimens, and distorted in the two illustrated specimens, further compounding observational efforts. *S. sexantennella* is most closely related to *S. oculata* Fauchald, 1974, which was originally described from Antarctica. Both have similar numbers of dorsal macrotubercles dispersed in a zig-zag pattern, large eyes, and generally similar parapodia. However, *S. sexantennella* has three pairs of retractable and characteristic accessory papillae only on inferior lateral antennae, shorter prostomial antennae, papilliform tentacular cirri, no papillae on posterior parapodial surfaces, and blades of compound setae that are both longer and serrated.

Distribution. Southern California, 123-169 m.

Sphaerodorum papillifer Moore, 1909

Figure 8.5

Sphaerodorum papillifer Moore, 1909:333-335, pl. 15, figs. 11-12.—Hartman, 1968:609-610, figs. 1-2.—Banse and Hobson, 1974:76, fig. 20e.

Material examined. California: Santa Maria Basin, off Morro Bay, Sta. 6 (7); off Port San Luis, Sta. 27 (1); off Point Sal, Sta. PJ-1 (1), Sta. PJ-7 (1).

Description. Body long, tapered at both ends, measuring up to 30 mm long, 1 mm wide, with 102 segments. Prostomium with a stout, digitiform median antenna plus 2 pairs of lateral antennae (Fig. 8.5A); inferior lateral antennae each possibly with an accessory papilla. Tentacular cirri digitiform, about as long as median antenna. Two to 3 pairs of V-shaped eyespots typically present on dorsum through segment 2. Parapodia inconspicuous, each with slender, conical acicular, reduced presetal and papilla-like postsetal lobes (Fig. 8.5B); parapodial papillae all small and conical, numbering from at least 12 to over 30 on each anterior and posterior parapodial surfaces; ventral cirri distally digitate, not projecting beyond parapodial lobes. Macrotubercles and microtubercles each arrayed in 2 rows on dorsum. Macrotubercles sessile, each with a terminal papilla (Fig. 8.5A, C). Microtubercles each with a digitate distal papilla surrounded by a basal collar equal in length to distal papilla (Fig. 8.5D). Setae entirely simple, of 2 kinds, including large notopodial hooks in setiger 1 (Fig. 8.5E), and more slender ones with a small lateral boss (Fig. 8.5F), numbering 4-6 per fascicle.

Biology. *Sphaerodorum papillifer* is reported from sand, slate, mud, shell and rocky sediments in shelf and slope depths.

Remarks. This species is highly characteristic in having high numbers of papillae on anterior and posterior parapodial surfaces. The prostomium is characteristically retracted in preserved specimens, and this has historically precluded its illustration. The prostomium of one specimen from Sta. 6 is illustrated, although the prostomium is rather distorted. There appear to be either accessory papillae or an additional pair of prostomial antennae between the median antenna and structures presently interpreted to be the superior lateral antennae.

Type locality and type specimens. California, off San Diego, Sta. 4400, 8 April, 500 fathoms, green mud. Type disposition: USNM.

Distribution. British Columbia, Washington, southern California to western Mexico.

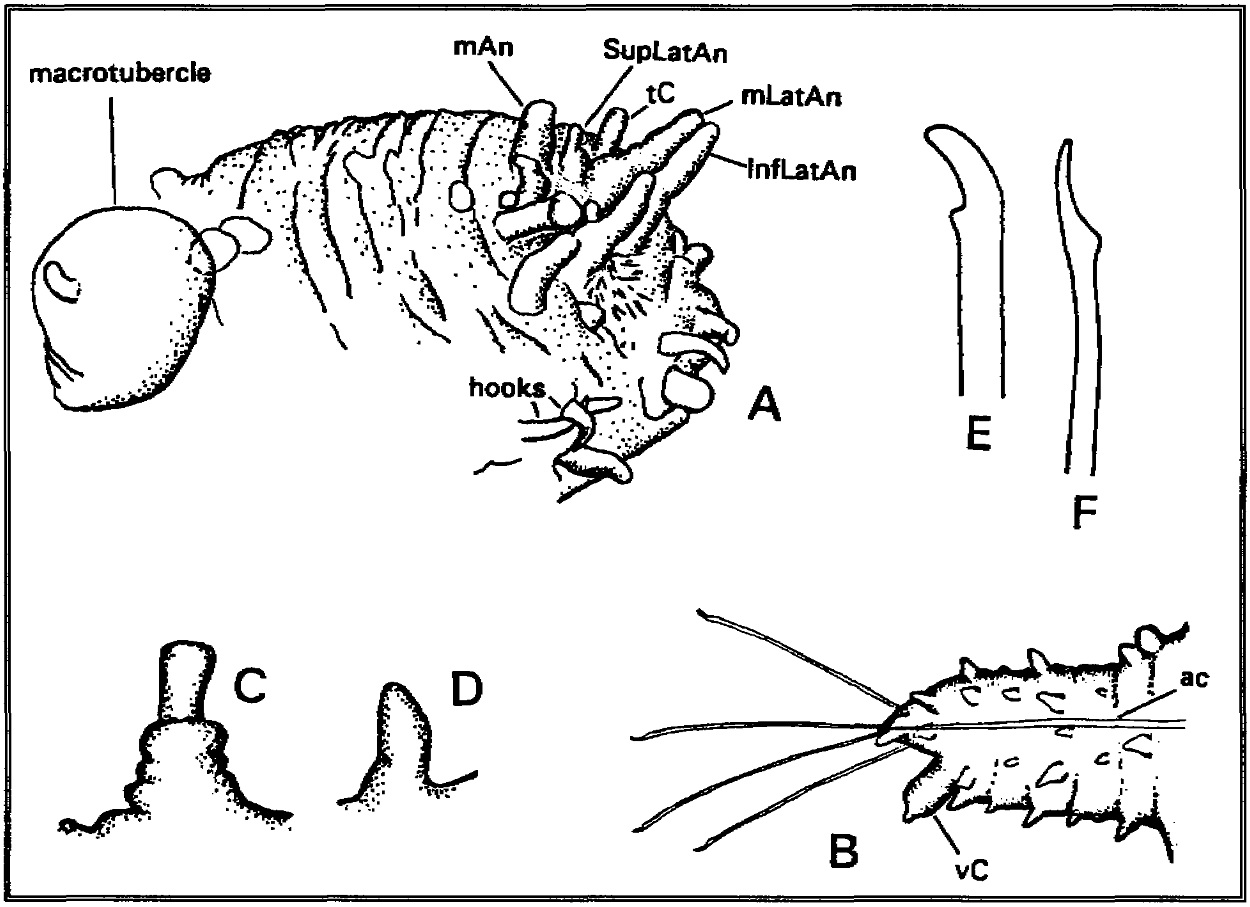

Figure 8.5. *Sphaerodorum papillifer:* A, anterior segments, lateral view; B, median parapodium, anterior view; C, microtubercle; D, papilla; E, simple hook, setiger 1; F, simple seta. (B-F, after Fauchald, 1974).

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9. FAMILY HESIONIDAE SARS, 1862

by

Brigitte Hilbig[1]

Introduction

The hesionids are small to moderate sized worms with a dorsoventrally flattened body of ragged appearance due to well-developed parapodia. Their bodies are typically rather fragile (especially the Hesioninae), and prostomial and parapodial appendages are deciduous. Because of their tendency to fragment, hesionids are often difficult to identify. Reference collections of adult specimens in good condition should therefore be established whenever possible.

Morphology

The prostomium is usually wider than long, oval to quadrangular or pentagonal, and it may be incised posteriorly. It typically bears one to two pairs of lenticular eyes, two or three antennae, and two palps. A pair of nuchal organs may be seen as ciliated ridges or lobes along the posterior margin. A large, more or less muscular proboscis is present, with the margin often equipped with cilia or papillae (very small and crowded papillae are also called fimbriae). Some genera, such as *Hesiolyra* and *Hesiospina*, possess a proboscis with papillae arranged in rings or groups scattered over the entire surface. Small chitinous jaws are present in the genera *Leocrates*, *Hesiospina*, and *Hesiolyra*.

The tentacular segments are fused to the peristomium, ventrally surrounding the mouth, and with each other dorsally. There are two to eight pairs of tentacular cirri that may be distinctly articulated, wrinkled, or smooth. The ventral tentacular cirri are generally shorter than the corresponding dorsal ones.

Parapodia are sesquiramous (notopodium reduced to cirrophore of the dorsal cirrus and a supporting acicula), subbiramous (notopodium much smaller than neuropodium, bearing 1 to very few, usually short and thin setae), or biramous (notopodium almost as large as neuropodium, bearing a well-developed fascicle of often more than one kind of notosetae), but never uniramous (notopodium completely absent). The lack of uniramous parapodia separates hesionids from the syllids. Dorsal and ventral cirri are usually well-developed and may insert on a distinct cirrophore or emerge directly from the parapodial wall. They may be distinctly articulated to smooth. The ventral cirri are generally short, whereas the dorsal cirri vary in length and often extend beyond the parapodia. The first dorsal cirri often resemble the tentacular cirri in length and width and should not be confused. Branchiae are absent.

The notosetae are simple and include capillaries, heavy spines, furcate setae, and pectinate setae. The neurosetae are compound falcigers or spinigers with blades of varying length; sometimes a few simple neurosetae are present. One to four aciculae are present in each parapodial ramus, including the bases of the tentacular cirri, the notopodial ones usually being thinner than the neuropodial ones.

The pygidium is usually small and bears a terminal anal pore and a pair of anal cirri; it may also bear a flat disk or plate (subfamily Microphthalminae).

Important and commonly used generic characters include the number of tentacular cirri, the number and insertion of antennae, and the morphology of the parapodia. The most obvious of these characters is the number of tentacular cirri, because the cirrophores are always clearly visible even if the cirri are broken off. However, several authors (Blake 1975a, Dorsey 1978, Haaland and Schram 1982, 1983, Schram and Haaland 1984) have shown that juveniles start with one pair of tentacular cirri and then add them consecutively during their development, so that different stages can be found with any number of tentacular cirri up to the actual number present in adults. For genera defined as having eight pairs of

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tentacular cirri, Pleijel (1993) proposed to replace the term "number of tentacular cirri" with "absence of notopodia on segment 4" because he discovered some ambiguities in that character.

The antennae tend to break off very easily as well, and it is often difficult to see the scars. The median antenna in particular often inserts in a very shallow depression that may be indiscernible, especially in poorly preserved specimens. The most reliable characters are features associated with the parapodia, such as the development of the notopodia and the shape(s) of the notosetae. The structures on the anterior margin of the proboscis may also be useful, but care should be taken in ensuring that the proboscis is fully extended.

Species-level characters include morphology of the setae, shape of the antennae and palps, length of the tentacular and dorsal cirri, and for the species of *Microphthalmus* the shape of the anal plate. In many keys the annulation of the cirri is also used, but this character may be inconsistent. Fauvel (1923) reported that the annulation of cirri, although present and distinct in live animals, may disappear completely during fixation. Banse and Hobson (1984) observed that regenerating cirri may be smoother than the original ones.

Taxonomic History

The taxonomic and systematic accounts of the Hesionidae are very scattered and quite confusing, with many unclear generic concepts and an ill-defined hierarchy of characters. Only a few authors have attempted a revision of the family (Hessle, 1925; Pettibone, 1963, 1970; O'Connor and Shin, 1983; Perkins, 1984). Newly described hesionids are therefore often assigned to existing genera in inconsistent ways, causing the generic definitions to shift. For example, Hessle (1925) described *Amphidromus*, a genus distinguished from other hesionids with eight pairs of tentacular cirri mainly by having an anteriorly smooth proboscis. Hartman (1959) found *Amphidromus* to be a homonym and replaced it with *Amphiduros*. In the meantime, additional species of *Amphiduros* have been described and to date the genus includes forms with a proboscis bearing either no papillae at all or numerous, very slender papillae called fimbriae. Laubier (1961) established *Podarkeopsis* to accomodate species with eight pairs of tentacular cirri on three visible segments, three antennae, and furcate notosetae. He distinguished the new genus from *Podarke*, but did not discuss differences between *Podarkeopsis* and the much more similar genus *Gyptis* (Hilbig and Dittmer, 1979). Perkins revised these two genera in 1984, providing, for the first time, clear-cut generic diagnoses. Pleijel (1993), in a revision of European species of *Amphiduros* and *Gyptis*, further clarified generic concepts of hesionids with eight pairs of tentacular cirri.

Currently the family Hesionidae consists of 30 genera and about 150 species. New genera and species have recently been described from the deep-sea benthos (Blake, 1985; Blake and Hilbig, 1990), and additional deep-sea taxa await description (Hilbig, unpublished). Larger genera include *Gyptis*, *Podarkeopsis*, *Podarke*, *Nereimyra*, *Ophiodromus*, *Hesione*, and *Microphthalmus*. Other genera, such as *Micropodarke*, *Hesionella*, and *Wesenbergia* contain only one species. In the Santa Maria Basin, six species belonging to three genera were found. Two more species are included in the species descriptions that occur in shallower water, but are among the most common polychaetes of the California coast. Because of the confusion in generic definitions, the key includes several genera that are not represented in the Santa Maria Basin fauna, but are useful to clarify some of the generic concepts as used in this study.

Distribution and Biological Notes

Hesionids occur in soft and hard substrata from the intertidal zone to the deep sea, but are most common in shallow water on hard bottom. They are highly active and non-burrowing, although some species are known to live as commensals with other polychaetes, crustaceans, sipunculans, and echinoderms. The behavior and functional anatomy of these commensal species has been studied repeatedly since the 1950's (Hickok and Davenport, 1957; Storch and Niggemann, 1967; Stewart, 1970). At least the larger species are carnivorous, feeding on small polychaetes and other invertebrates (Shaffer, 1979; Oug, 1980). Shaffer (1979) provided a detailed study of the feeding behavior and function of the gut of *Podarke pugettensis*, one of the most common hesionids along the North American Pacific coast. Some hesionids may be surface deposit feeders (Fauchald and Jumars, 1979).

Little is known about the reproduction because it is difficult to induce spawning in the laboratory. Sexes are usually separate, except for some interstitial forms that are hermaphroditic. Planktonic larvae of hesionids have been described by several authors, the earliest studies being by Treadwell (1897, 1901). Other descriptions of larval stages are provided by Thorson (1946), Casanova (1954), Banse (1956), Rasmussen (1956, 1973), Schram (1968), Bhaud (1971), Blake (1975a), Haaland and Schram (1982, 1983), and Schram and Haaland (1984). Interstitial forms, such as *Microphthalmus*, develop directly (Westheide 1967, 1970), whereas the Hesioninae undergo a more or less prolonged pelagic larval stage that may last no longer than one or two weeks (Blake, 1975a). One of the taxonomically most interesting processes during metamorphosis is the reduction of the anteriormost parapodia and transition of dorsal and ventral cirri into tentacular cirri. An excellent account of this process is given by Haaland and Schram (1982, 1983) for two common European species, *Gyptis rosea* and *Ophiodromus flexuosus*.

Key to the Hesionidae

1A. Parapodia sesquiramous, i.e., notopodia reduced to aciculae and bases of dorsal cirri; notosetae absent (Fig. 9.1A) 2

1B. Parapodia biramous or subbiramous 4

2A. Palps absent; 2 antennae; 8 pairs tentacular cirri on 2 visible segments; proboscis distally smooth (Fig. 9.1B) .... *Hesione*[2]

2B. Palps present; 3 antennae; 8 pairs tentacular cirri on 3 visible segments; proboscis with terminal papillae 3

3A. Neurosetae modified on several anterior setigers; golden, stout, with distally knobbed shafts and short falcigerous blades (Fig. 9.6I, J); 8 pairs tentacular cirri on 3 visible segments; 3 antennae, median one attached frontally; proboscis with 10 papillae .... *Heteropodarke heteromorpha*

3B. Neurosetae not modified; 8 pairs tentacular cirri on 3 visible segments; 2 antennae; proboscis with numerous papillae (Fig. 9.1C) .... *Kefersteinia*[3]

4A. Parapodia biramous, i.e., notopodia and neuropodia subequal in size, notosetae numerous (Fig. 9.2B) 5

4B. Parapodia subbiramous, i.e., notopodia distinctly smaller than neuropodia, notosetae few (may be absent entirely along parts of body) (Fig. 9.7B) 11

5A. Proboscis distally smooth (dissect if not fully everted); 8 pairs tentacular cirri on 1 visible segment; notosetae first present on setiger 1 or 2; 3 antennae, median one attached centrally (Fig. 9.1D) .... *Amphiduros* (in part)[4]

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[2] The genus has not been reported off California, but occurs in the Gulf of California (Hartman, 1940)

[3] Not reported off California, but found further north off Washington and British Columbia (Banse & Hobson, 1974)

[4] *A. pacifica* has been found in shallow water off southern California (Velarde, pers. comm.)

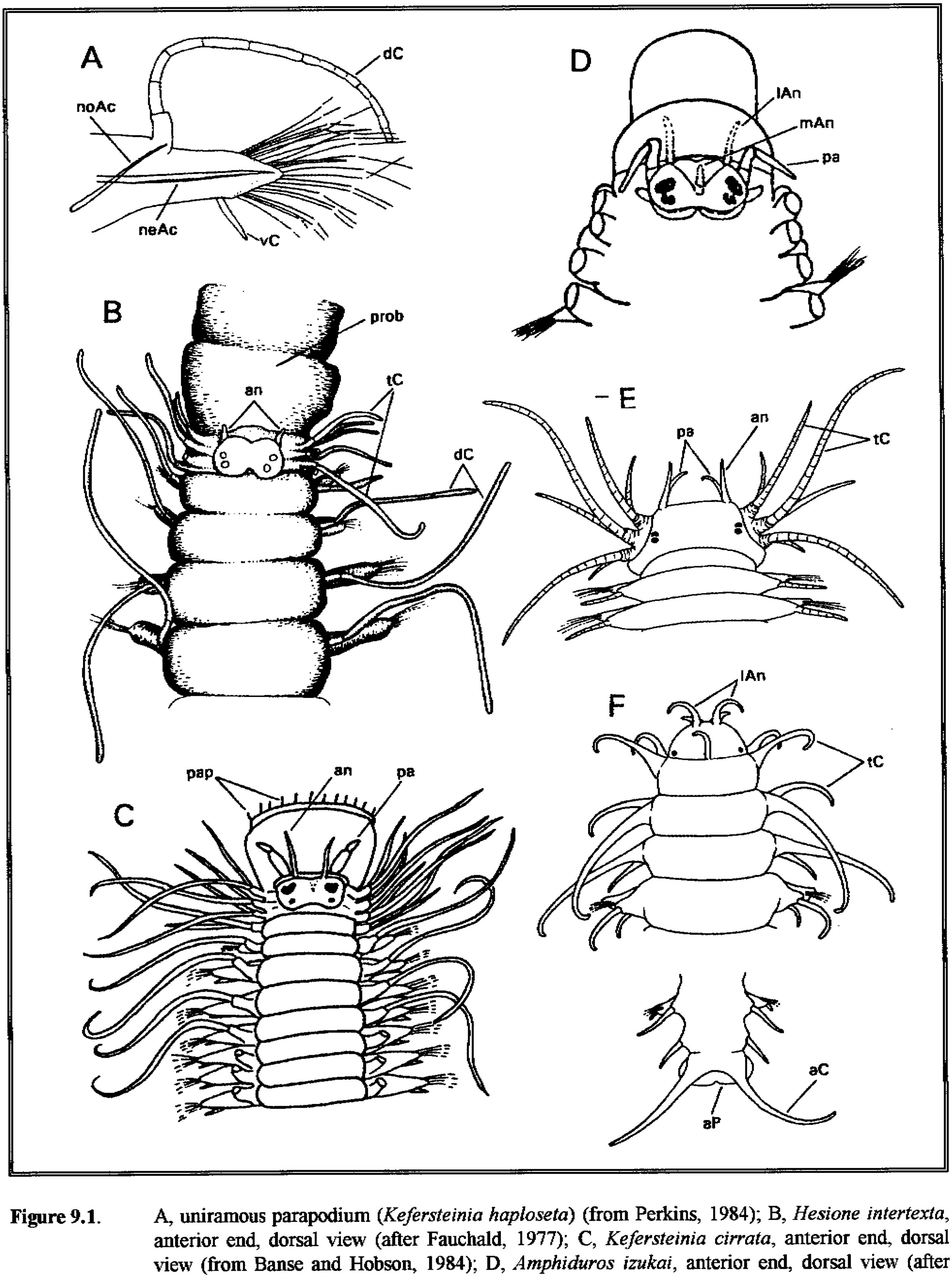

Figure 9.1. A, uniramous parapodium (*Kefersteinia haploseta*) (from Perkins, 1984); B, *Hesione intertexta*, anterior end, dorsal view (after Fauchald, 1977); C, *Kefersteinia cirrata*, anterior end, dorsal view (from Banse and Hobson, 1984); D, *Amphiduros izukai*, anterior end, dorsal view (after Hessle, 1925); E, *Parahesione luteola*, anterior end, dorsal view; F, *Microphthalmus aberrans*, anterior and posterior end, dorsal view (E, F from Pettibone, 1963).

5B. Proboscis with numerous papillae; 6 or 8 pairs tentacular cirri on 1 visible segment 6

6A. Palps simple; 2 antennae, 6 pairs tentacular cirri (Fig. 9.1E) .... *Parahesione*

6B. Palps biarticulate; 3 antennae, 6 or 8 pairs tentacular cirri on 1 visible segment; notosetae first present from setiger 1 or 2; proboscis with numerous papillae 7

7A. Six pairs tentacular cirri; median antenna attached on frontal margin of prostomium (leaving distinct scar if fallen off); prostomium trilobed (Fig. 9.7A) .... *Ophiodromus*[5]

7B. Eight pairs tentacular cirri; median antenna attached medially (leaving indistinct scar if fallen off); prostomium bilobed (Fig. 9.3A): genus *Gyptis* 8

8A. Notosetae of 1 kind, distally serrated, blunt-tipped; dorsal and ventral cirri articulated; distinct brown segmental pigment bands (Fig. 9.2A) .... *Gyptis brunnea*

8B. Notosetae of more than 1 kind, including 1 or 2 spines per fascicle 9

9A. Notosetae including smooth spines and coarsely serrated capillaries 10

9B. Notosetae of 4 kinds, including smooth spines and coarsely serrated, finely serrated, and very slender smooth capillaries (Fig. 9.5B-E) .... *Gyptis plurisetis*

10A. Dorsal and ventral cirri articulated; nuchal organs well-developed, sometimes forming distinct lobes around postectal corners of prostomium; proboscis moderately wide when fully extended; longest blades of neurosetae about twice as long as shortest (Fig. 9.4F) .... *Gyptis lobatus*

10B. Dorsal and ventral cirri smooth; nuchal organs indistinct grooves along posterior margin of prostomium; proboscis very wide and bell-shaped when fully everted (Fig. 9.3A); longest blades of neurosetae 3 times as long as shortest ones (Fig. 9.3E); deep-water form .... *Gyptis hians*

11A. Palps simple; pygidium disk-shaped; tentacular and parapodial cirri smooth, not inserted on cirrophore (Fig. 9.1F); small interstitial forms on sandy beaches .... *Microphthalmus*[6]

11B. Palps biarticulate; pygidium not disk-shaped; tentacular and parapodial cirri smooth to articulated, inserted on cirrophore 12

12A. Notosetae very few, sometimes entirely missing in most setigers; 6 pairs tentacular cirri on 1 visible segment; 2 antennae; proboscis with numerous papillae .... *Nereimyra*[5]

12B. Notosetae present at least from setiger 4 on, usually about 5 per fascicle or more 13

13A. Notosetae including furcate setae; 3 antennae, median one attached frontally 14

13B. All notosetae capillary, present from setiger 1 or 2; 8 pairs tentacular cirri on 1 visible segment; proboscis smooth; 3 antennae, median one attached centrally .... *Amphiduros* (in part)[4]

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[5] Not reported from California

[6] Not included in this Atlas

14A. Six pairs tentacular cirri on 1 visible segment; notosetae first present on setiger 3 or 4; proboscis with numerous terminal papillae .... *Podarke pugettensis*

14B. Eight pairs tentacular cirri on 1 visible segment; notosetae first present on setiger 4 to 6; proboscis with few terminal papillae: genus *Podarkeopsis* 15

15A. Furcate setae with smooth shaft; shallow-water species .... *Podarkeopsis brevipalpa*[7]

15B. Furcate setae with serrations below shorter tine (visible at 400×) 16

16A. Notosetae including smooth spines and furcates; longest blades of neurosetae slightly more than twice as long as shortest ones (Fig. 9.9C, E); anterior and posterior eyes subequal .... *Podarkeopsis glabra*

16B. Notosetae including distally serrated spines, furcates, and smooth, very fine capillaries; longest blades of neurosetae more than 4 times as long as shortest ones (Fig. 9.10F, H, I); posterior eyes much smaller than anterior ones .... *Podarkeopsis perkinsi*

Description of Species

In the Santa Maria Basin and Santa Barbara Channel, seven species of hesionids were found, two of which were only recently described. Two more species are included in this chapter because they may occur in the area or in close proximity. All species described in this chapter are listed below.

Gyptis brunnea (Hartman, 1961)
Gyptis hians Fauchald and Hancock, 1981
Gyptis lobatus (Hessle, 1925)
Gyptis plurisetis Hilbig, 1992
Heteropodarke heteromorpha Hartmann-Schröder, 1962
Podarke pugettensis Johnson, 1901
Podarkeopsis brevipalpa (Hartmann-Schröder, 1959)
Podarkeopsis glabra (Hartman, 1961)
Podarkeopsis perkinsi Hilbig, 1992

Genus *Gyptis* Marion and Bobretzki, 1875

Type species: *Gyptis propinque* Marion and Bobretzki, 1875

Diagnosis. Prostomium with 2 or 3 antennae, median one, if present, attached in central or posterior position; 2 biarticulate palps and usually 2 pairs of lenticular eyes present. Proboscis thin-walled, wide and short when fully extended, with numerous, crowded terminal papillae ("fimbriae" *sensu* Hartman, 1968) in up to 4 rows. Eight pairs tentacular cirri arising from 1 visible segment, smooth to distinctly articulated. Parapodia sesquiramous in setiger 1 in some species, biramous from setiger 2 (or 1 in some species). Notosetae numerous, including 1 or more kinds of capillaries and often 1 or 2 acicular spines per

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[7] This species seems to be restricted to more southern regions; specimens identified as *G. brevipalpa* from Alaska to southern California belong to different species.

fascicle. Neurosetae numerous compound falcigers with long to short blades. Simple setae and shafts of compounds usually cross-striated.

Remarks. The genus *Gyptis* was believed to be a synonym of *Oxydromus* Grube, 1855 (see Hartman, 1959) until Hartman (1965) discovered that *Oxydromus* was preoccupied. The name is therefore no longer valid for hesionids (See Fauchald, 1977). In the Santa Maria Basin, four species of *Gyptis* were found, making this genus the most well-represented hesionid genus in the study area.

Gyptis brunnea (Hartman, 1961)

Figure 9.2

Oxydromus brunnea Hartman, 1961:69-70, pl. 5, figs. 1-4; 1968:365.
Amphiduros brunnea: Lissner *et al.*, 1986:D-8.

Material examined. California: Santa Maria Basin, off Point Estero, Sta. 6 (1).

Description. Length to 6.5 mm, width to 1.5 mm excluding parapodia, segments to 29. Body small, slender, fragile, dorsoventrally depressed. Color in alcohol tan with conspicuous segmental transverse bands of brown pigment. Prostomium with brown pigment band between anterior eyes and along posterior margin (Fig. 9.2A).

Prostomium nearly quadrangular to obcordate, with deep posterior notch; with supposedly 3 deciduous antennae, 2 palps and 2 pairs of eyes; anterior pair further apart and larger than posterior pair. Palpophores short, palpostyles missing. Nuchal grooves along postectal margin. Proboscis wide, slightly bell-shaped when fully extended, with thin muscular layer; with numerous (up to 70) crowded distal papillae, often deciduous.

Eight pairs of tentacular cirri on 1 distinct segment; cirrophores short, cirrostyles missing. Parapodia sesquiramous in setiger 1, biramous in all following setigers; notopodia slightly smaller than neuropodia, both rami with conical pre- and postsetal lobes (Fig. 9.2B). Dorsal and ventral cirri distinctly articulated, ventral cirri somewhat shorter than dorsal ones. Notosetae numerous, first present in setiger 2, cross-striated capillaries with coarse distal serrations (Fig. 9.2C); neurosetae compound falcigers with short to long blades, longest in upper part of fascicle; shafts smooth, blades with serrated cutting edge and distal hood; length/width ratio of blades ranging from 13:1 to 21:1 (Fig. 9.2D, E).

Remarks. *G. brunnea* is distinguished from other co-occurring species of *Gyptis* by the presence of only one type of notosetae instead of two or more kinds. The pigmentation may also be helpful because the pattern is very characteristic, but it may fade in alcohol.

Type locality and type specimens. Southern California; holotype and paratypes: LACM-AHF.

Biology. This species is found on rocky or gravelly substrate in shelf depths. Blake (1975a) collected pelagic larvae that were believed to be *G. brunnea* in September 1974. These larvae were reared to a juvenile benthic stage that had 24 setigers and six pairs of tentacular cirri. The juveniles were maintained in clean sand.

Distribution. Southern and central California, to 200 m.

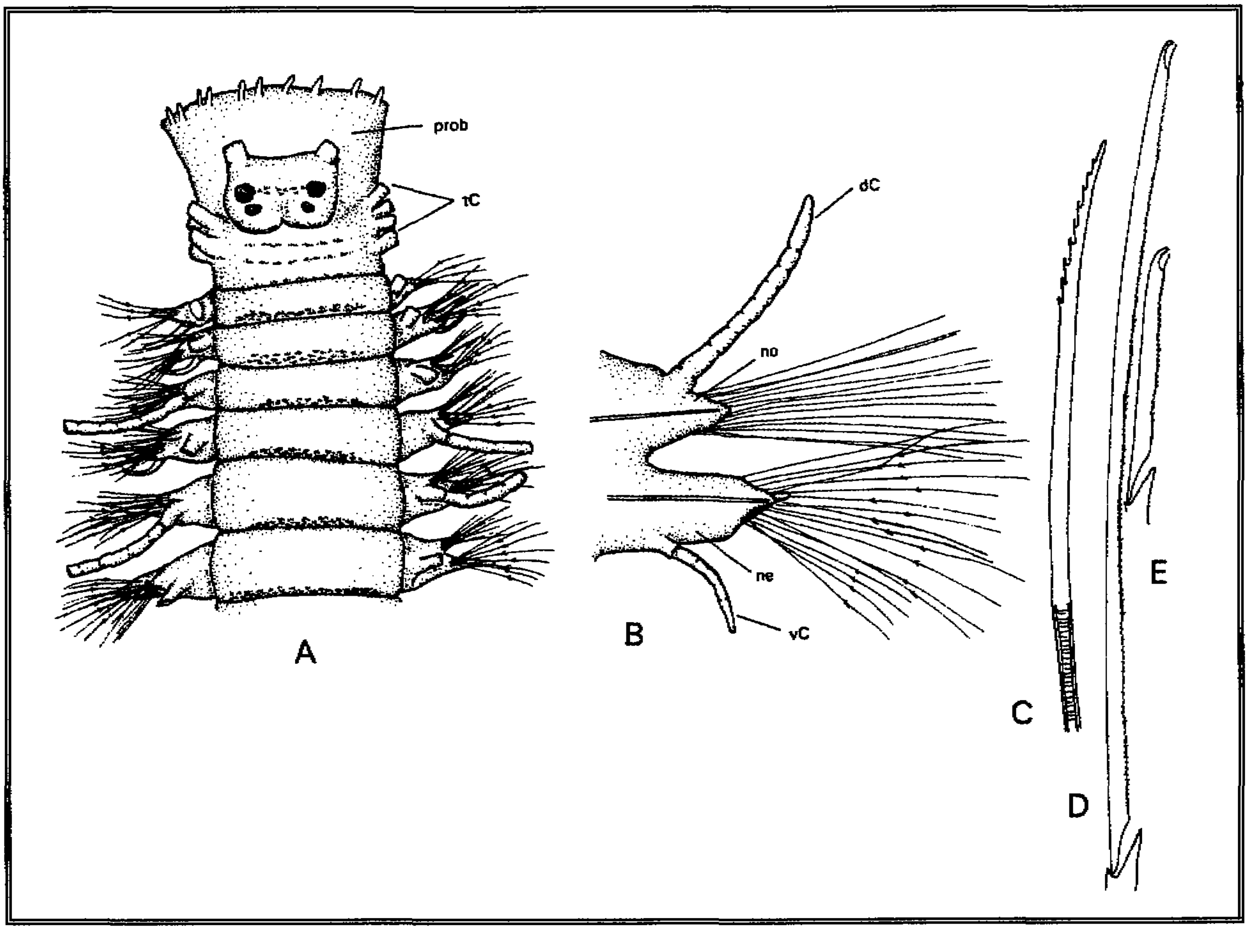

Figure 9.2. *Gyptis brunnea*: A, anterior end, dorsal view; B, parapodium (after Hartman, 1961); C, notoseta; D-E, longest and shortest blade from a neuropodial fascicle.

Gyptis hians Fauchald and Hancock, 1981

Figure 9.3

Gyptis hians Fauchald and Hancock, 1981: 24, pl. 5, figs. a-e.—Hyland *et al.*, 1990:F-1.

Material examined. California: Santa Maria Basin, off Point Sal, Sta. R-7 (4).

Description. All known specimens incomplete with 17 to 29 setigers; length to 17 mm, width to 1.5 mm (excluding parapodia). Body slender fragile, with very long parapodia; segmental furrows not discernible. Color in alcohol uniformly tan.

Prostomium twice as wide as long, rounded anteriorly and deeply notched posteriorly; 3 antennae and 2 palps; lateral antennae slender, median antenna short, papilliform, inserted well behind frontal margin. Palps about as long as lateral antennae, with stout palpophore and slender, digitiform palpostyle. Proboscis short, very wide and bell-shaped when fully extended, with numerous terminal papillae arranged in about 4 rows (Fig. 9.3A).

Eight pairs of slender, smooth tentacular cirri present, most with styles broken off, and length unknown. Parapodia sesquiramous in setiger 1, biramous in all following setigers; notopodia with triangular presetal lobe and shorter postsetal lobe; neuropodia twice as long as notopodia, with presetal

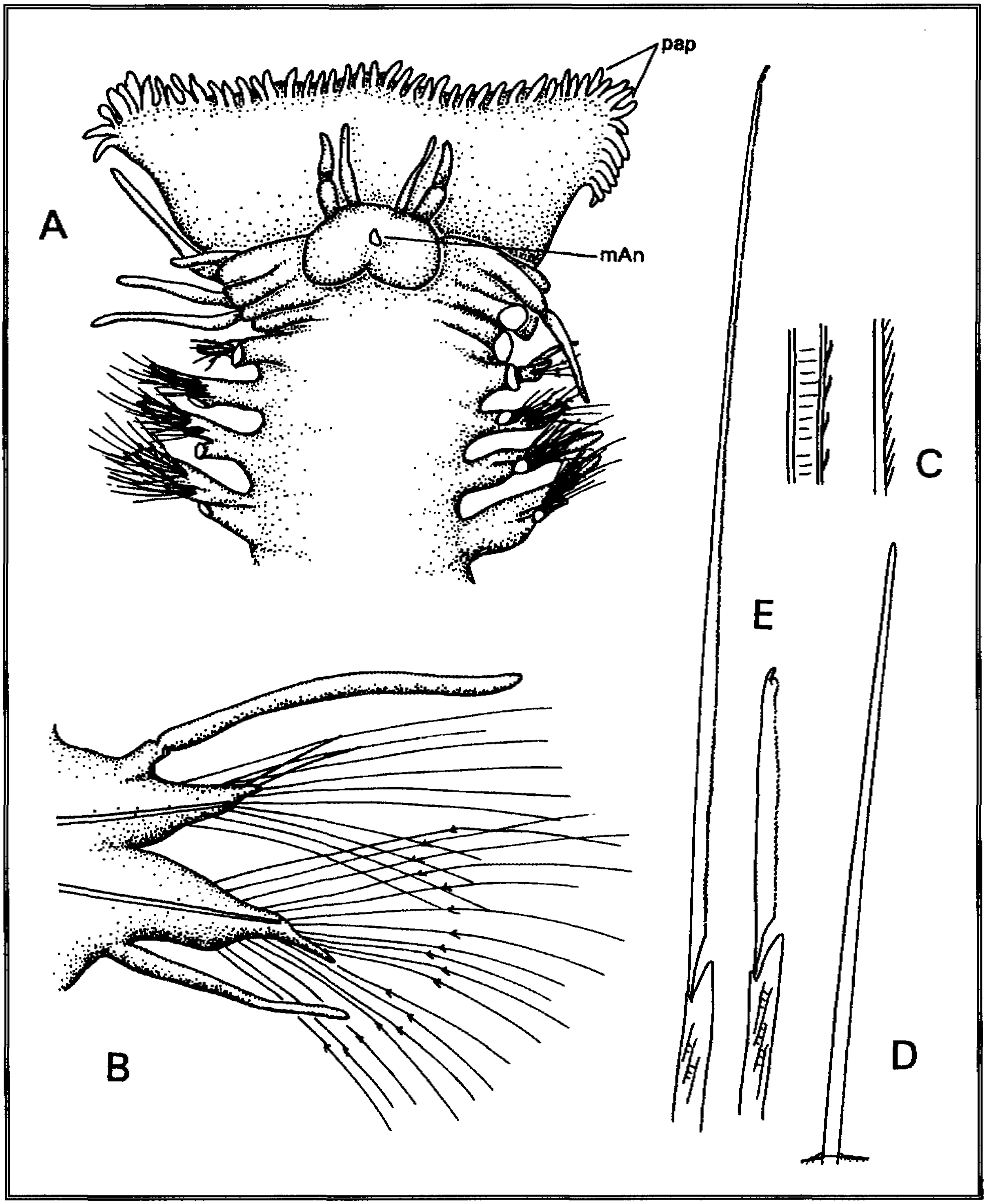

Figure 9.3. *Gyptis hians*: A, anterior end, dorsal view; B, parapodium; C, details from capillaries, proximal part (left) and close to the tip (right); D, notopodial spine; E, longest and shortest blade from a neuropodial fascicle (A, B after Fauchald and Hancock, 1981).

lobe tapering to a long, slender, triangular process. Dorsal cirri slender, smooth to indistinctly annulated, attached somewhat behind setal fascicle; ventral cirri long, slender, extending beyond neuropodial lobe (Fig. 9.3B). Notosetae from setiger 2, of two kinds: (1) numerous long, slender capillaries, cross-striated, coarsely serrated (Fig. 9.3C); (2) 1 or 2 smooth spines in anteriormost position (Fig. 9.3D). Neurosetae compound, with short and long blades; short-bladed setae in small inferior fascicle, with hooked tip and terminal hood; long-bladed setae in superior fascicle, almost spinigerous, with hooked tip; all blades thin, delicate, very finely serrated; shafts cross-striated (Fig. 9.3E); length/width ratio of blades ranging from 10:1 to 56:1. Setae in fascicles as a whole whitish and glistening.

Remarks. This is the first report of *Gyptis hians* off California; the species was described from off Oregon in water depths of 800 to 2800 m. Its occurrence in the Santa Maria Basin represents a geographic and bathymetric range extension. The species is found in muddy bottoms. It is most easily distinguished from other co-occurring species of *Gyptis* by the extremely long and slender blades on some neurosetae.

Type locality and type specimens. Off Oregon, 44°39'N, 124°58'W, 800 m; holotype LACM-AHF Poly 1144, paratype LACM-AHF Poly 1145.

Distribution. Oregon to central California, 500 to 2800 m.

Gyptis lobatus (Hessle, 1925)

Figure 9.4

Oxydromus lobatus Hessle, 1925:24-25, fig. 7
Gyptis nr. *lobatus* Lissner *et al.*, 1986:D-8.—Hyland and Neff, 1988:A-2.—Hyland *et al.*, 1990:F-1.

Material examined. California: Santa Maria Basin, off Point Sal, Sta. PJ-1 (1), Sta. PJ-2 (2), Sta. PJ-3 (2), Sta. PJ-5 (3), Sta. PJ-7 (3), Sta. PJ-8 (1), Sta. PJ-10 (1).

Description. All observed specimens incomplete, up to 39 segments; length to 23 mm, width to 1 mm excluding parapodia. Body small, slender, fragile, with conspicuous parapodia. Color in alcohol uniformly tan.

Prostomium rounded anteriorly, notched posteriorly, almost rectangular; with four eyes, the anterior pair largest and slightly wider apart than posterior pair; nuchal organs large, crescent-shaped, located along postectal margins of prostomium. Two palps and 3 antennae present, the latter broken off in all specimens (Fig. 9.4A). Proboscis wide, bell-shaped when fully extended, with thin muscular layer; distally with numerous crowded papillae in 2 to 4 rows (Fig. 9.4B).

Eight pairs articulated tentacular cirri inserted on 1 visible segment (Fig. 9.4A, B); ventral tentacular cirri shortest. Parapodia sesquiramous in setiger 1, with enlarged dorsal cirrus. All following parapodia biramous, fully developed from setiger 3; dorsal and ventral cirri distinctly articulated, ventral cirri shorter than dorsal (Fig. 9.4C). Notosetae first present from setiger 2; numerous (usually about 20 per fascicle) serrated capillaries, cross-striated; in ventralmost position 1 to 3 (usually 2) smooth, blunt spines with cross-striations (Fig. 9.4D, E). Neurosetae compound falcigers with short to long blades, longest in upper middle, shortest in ventralmost position; length/width ratio ranging from 7:1 to 20:1. Blades finely serrated, distally hooked, with terminal hoodlike structure (Fig. 9.4F, G).

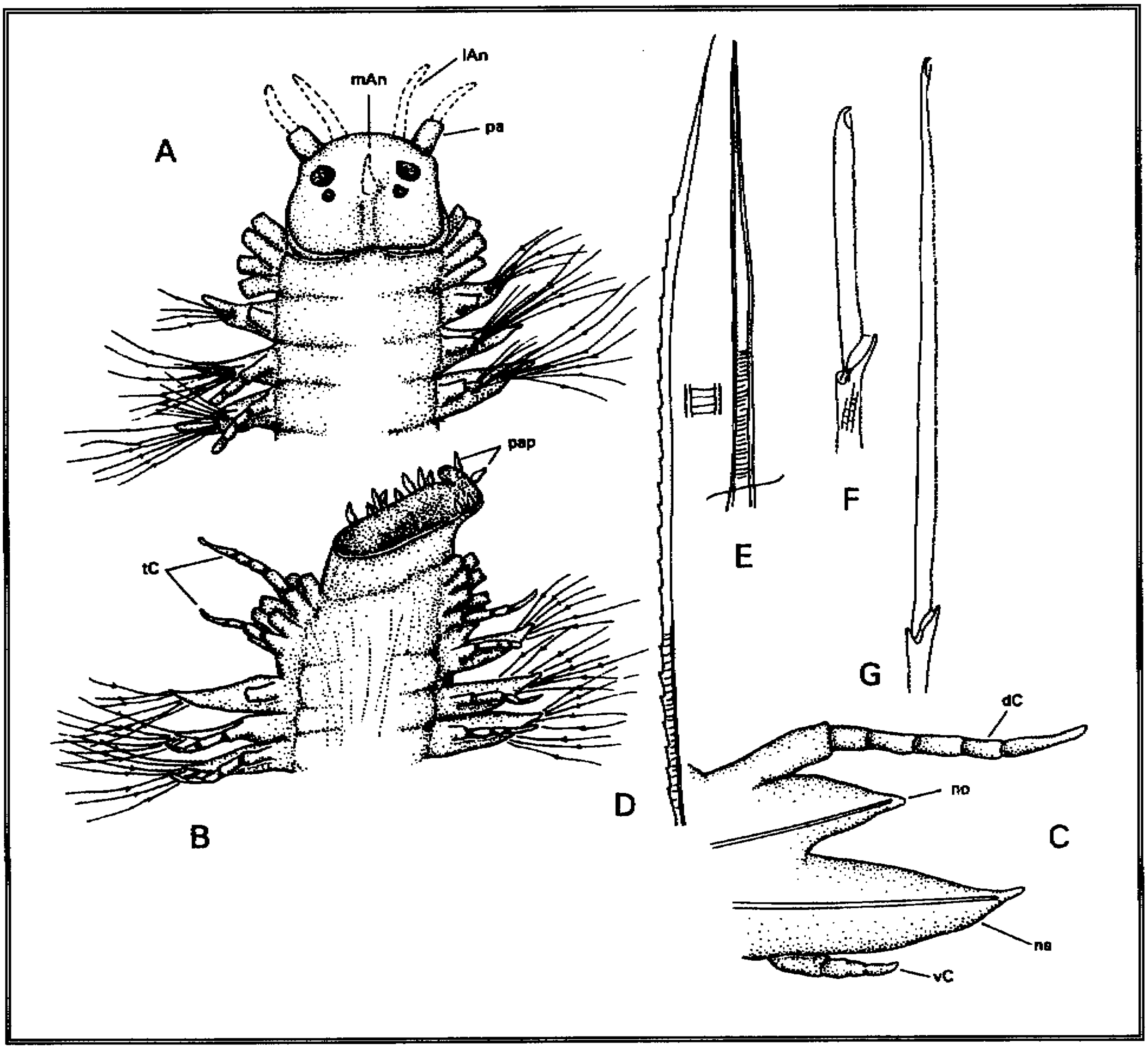

Figure 9.4. *Gyptis lobatus*: A, anterior end, dorsal view; B, same, ventral view, proboscis everted; C, parapodium; D, capillary seta; E, notopodial spine with detail of cross-striation; F-G, shortest and longest blade of a neuropodial fascicle.

Remarks. This species was originally identified as *G.* nr. *lobatus*, supposedly because the structure referred to as prostomial "lobes" by Hessle (1925) is not quite as pronounced in the examined specimens as it is in his drawing. These "lobes", which are obviously the nuchal organs, change their shape changes with muscle tension in prostomium and peristomium. The final appearance in preserved specimens depends on the worm's behavior during fixation. As Hessle mentions in the original description, he examined only one specimen in fairly poor condition. The difference in the shape of the nuchal organs is therefore considered inconsequential. All other characters agree sufficiently with the description to justify the identification of this species.

Type locality and type specimens. Japan; Sagami, Okinose, in 150 m.

Habitat. *G. lobatus* was found in a relatively narrow depth range of about 130 m in substrates with high silt-clay contents.

Distribution. Japan; central California; 120 to 150 m.

Gyptis plurisetis Hilbig, 1992

Figure 9.5

Gyptis plurisetis Hilbig, 1992:712-713, fig. 2.
Hesionidae sp. A Lissner *et al.*, 1986:D-9.—Hyland and Neff, 1988:A-2.—Hyland *et al.*, 1990.
Amphiduros sp. A Uebelacker, 1984:28-34, fig. 28-30.

Material examined. California: Santa Maria Basin, off Point San Luis, Sta. R-1: 1 paratype (USNM 148702).—Gulf of Mexico, southern Florida: holotype (USNM 75314) and 1 paratype (USNM 75315); off Texas: 1 paratype (USNM 75212).

Description. Only anterior ends present, length to 2 mm, width to 1.3 mm, 5 to 8 setigers. Color in alcohol uniformly tan.

Prostomium oval to pentagonal, distinctly wider than long, with 2 long palps and 3 antennae, the median one located just anterior to eyes and about half as long as lateral ones. Two pairs of large, subequal, round eyes, the anterior pair further apart than posterior pair. Nuchal organs developed as crescentic, ciliated grooves along postectal margin of prostomium. Proboscis cylindrical, with numerous deciduous distal papillae (Fig. 9.5A, B).

Eight pairs of tentacular cirri present on 1 or 2 visible segments, most with styles broken off, remaining ones smooth to indistinctly articulated. Parapodia sesquiramous in setiger 1, biramous from setiger 2. Notosetae of four kinds: (1) blunt, short acicular spines, 2 per fascicle; (2) long, coarsely serrated capillaries, about as thick as spines, 5 per fascicle; (3) finely serrated capillaries, as long as coarsely serrated ones, but slightly thinner, about 5 per fascicle; and (4) 1 or 2 very thin, smooth capillaries of about same length as spines (Fig. 9.5C-F). Neurosetae compound falcigers, with long, very delicate, finely serrated blades and smooth shafts. Length/width ratio of blades ranging from 4:1 to 6:1. All notosetae and shafts of neurosetae cross-striated.

Remarks. This species was described as *Amphiduros* sp. A by Uebelacker (1984) from the Gulf of Mexico. Examination of the specimens deposited at the U.S. National Museum of Natural History proved that the single specimen of Hesionidae sp. A collected during Phase I belongs to the same species. Both taxa were assigned to the genus *Gyptis* because *Amphiduros* is characterized by a smooth rather than papillated or fimbriated proboscis (Hessle, 1925 as *Amphidromus*).

Type location and type specimens. Gulf of Mexico; holotype USNM 75314, paratypes USNM 75212, 75315, 148702.

Habitat. The species occurs in low densities in silty clay and coarse to fine sands.

Distribution. Gulf of Mexico: Florida to Texas; central California; 40 to 100 m.

Genus *Heteropodarke* Hartmann-Schröder, 1962

Type species: *Heteropodarke heteromorpha* Hartmann-Schröder, 1962

Diagnosis. Prostomium with 3 antennae, median one attached frontally; 2 simple palps; 2 pairs of rounded, subequal eyes present. Proboscis cylindrical, with 9 or 10 terminal papillae. Six or 8 pairs of tentacular cirri arising from 3 indistinctly marked segments. Parapodia sesquiramous throughout, notosetae usually absent. Neurosetae compound falcigers, modified in several anterior setigers, and occasionally single delicate spiniger.

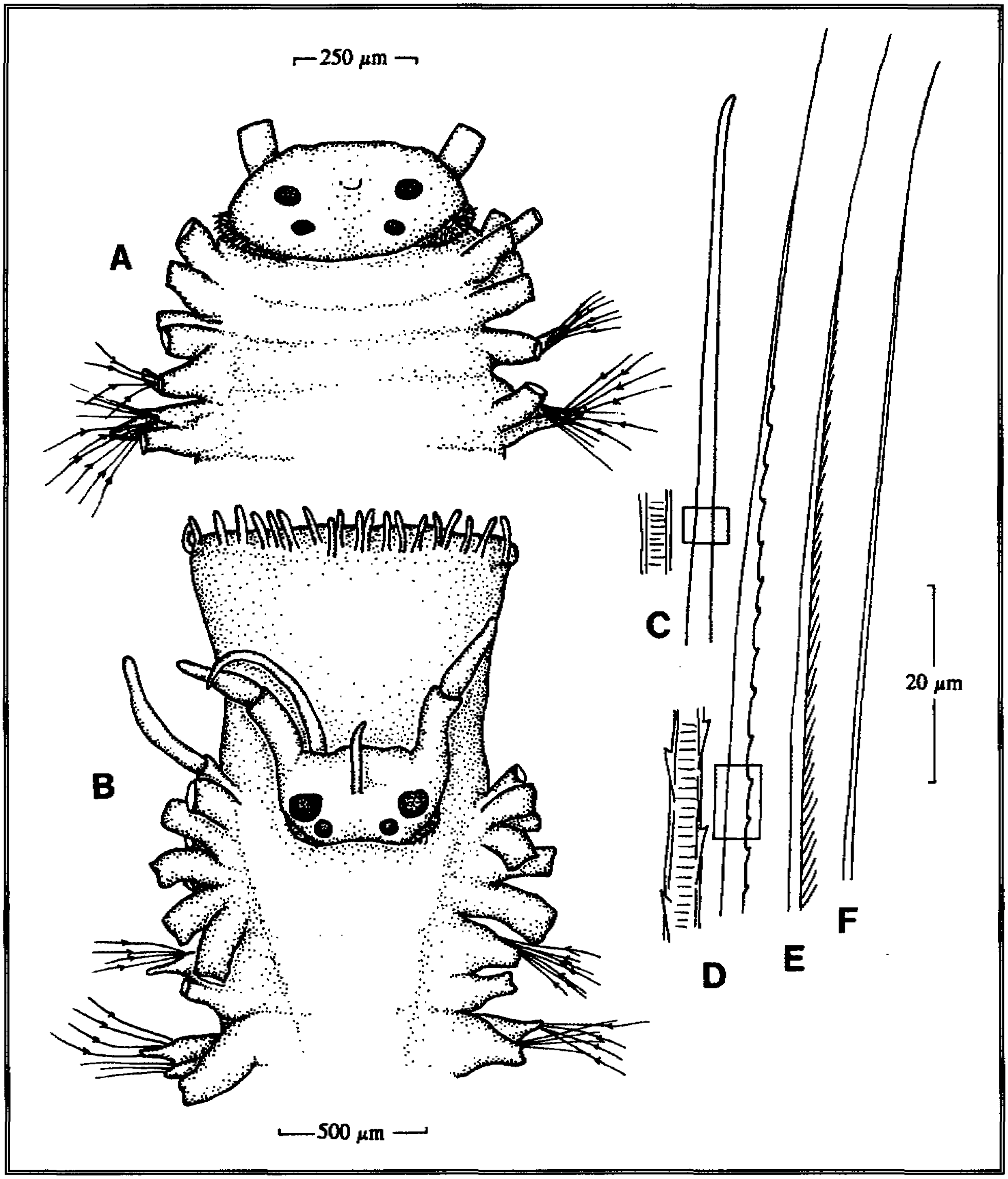

Figure 9.5. *Gyptis plurisetis*: A, anterior end, dorsal view Californian specimen; B, same, specimen from the Gulf of Mexico (after Uebelacker, 1984); C, notopodial spine with detail of cross-striation; D, coarsely serrated capillary with detail of cross-striation and serrations; E, finely serrated capillary; F, smooth capillary (from Hilbig, 1992).

Remarks. One unusual feature of the genus is the apparent variability of the number of tentacular cirri (Hartmann-Schröder, 1962, 1964; Dorsey, 1978; Perkins, 1984). It seems that all known species generally have up to 6 pairs, but occasionally specimens are found with 8 pairs. Hartmann-Schröder (1974) suggested that the last pair of tentacular cirri might be added at a relatively late life stage when the animals are already 30 to 40 setigers long. However, Perkins (1984) never found any specimens with more than 6 pairs in his material even though he examined numerous specimens with up to 200 segments. If indeed the number of tentacular cirri is variable within a species or a subspecies level character, *Heteropodarke* would be unique within the Hesionidae.

Heteropodarke heteromorpha Hartmann-Schröder, 1962

Figure 9.6

Heteropodarke heteromorpha Hartmann-Schröder, 1962:118-120, pl. 5, fig. 30, pl. 6, figs. 31-34. —Lissner *et al.*, 1986:D-8.

Material examined. California: Bodega Bay, shallow subtidal, Coll. 1975, J. Blake, Sta. 1B (6), Sta. 4B (4).

Description. Length to 8 mm, width to 0.15 mm excluding parapodia, setigers to 95. Body long, threadlike, narrowest in region with modified setae, somewhat inflated in posterior half of body. Color in alcohol uniformly tan.

Prostomium rounded, with 3 subequal, clavate antennae attached frontally. Palps appearing simple, inserting on short palpophores, with palpostyle similar to antennae. Two pairs of rounded, moderately large, reddish, lentigerous eyes arranged in trapezoid. Up to 6 or 8 pairs of tentacular cirri arising from 1 visible segment; each articulated, with the dorsal ones reaching back about 6 setigers; ventral tentacular cirri shorter (Fig. 9.6A).

Parapodia sesquiramous throughout, with notopodium reduced to slender, tapering notoacicula projecting into base of dorsal cirrus. Dorsal cirri with about 10 articles, distinctly longer than body width; ventral cirri with about 7 articles, about as long as body width (Fig. 9.6B). Notosetae absent except for rarely occurring, slightly curved acicular spines in posterior setigers (observed on two animals) (Fig. 6.9C); neurosetae in setigers 1 and 2 unmodified compound falcigers with distally knobbed shafts and short, blunt, smooth blades (Fig. 6.9D, E); unmodified falcigers in posterior setigers mostly with blunt, serrated blades (Fig. 6.9F, G); single, very fine spiniger in some anterior setigers (Fig. 6.9H). Falcigers modified in setigers 4 to maximally 23 (usually about 15 to 18), intermediate in setiger 3 (Fig. 6.9I); shafts of modified falcigers golden, twice as wide as unmodified setae, ending in knoblike hinge almost surrounding blade; blades smooth, very short, spherical, with two low, very blunt teeth, often barely extending beyond articulation with shaft (Fig. 9.6J). Spiniger occurring in at least all modified fascicles, occasionally also in about 5 to 20 subsequent parapodia, especially in large specimens.

Pygidium small, surrounding terminal anus, bearing two long, slender anal cirri that break off easily.

Remarks. The specimens from Bodega Bay generally agree quite well with Hartmann-Schröder's original description of *H. heteromorpha*, although some characters were found that were described as species-specific for *H. lyonsi* Perkins, 1984. These characters include the presence of spinigers beyond the setigers with modified setae and the presence of emergent acicular spines in the notopodia of some posterior setigers. The distribution of the spinigers seems to be mostly age-dependent, because they were found in unmodified setigers of large specimens only. Occasionally, two setigers with a spiniger were separated by a setiger without a spiniger. In two of the examined specimens, a spine was found in one of the far

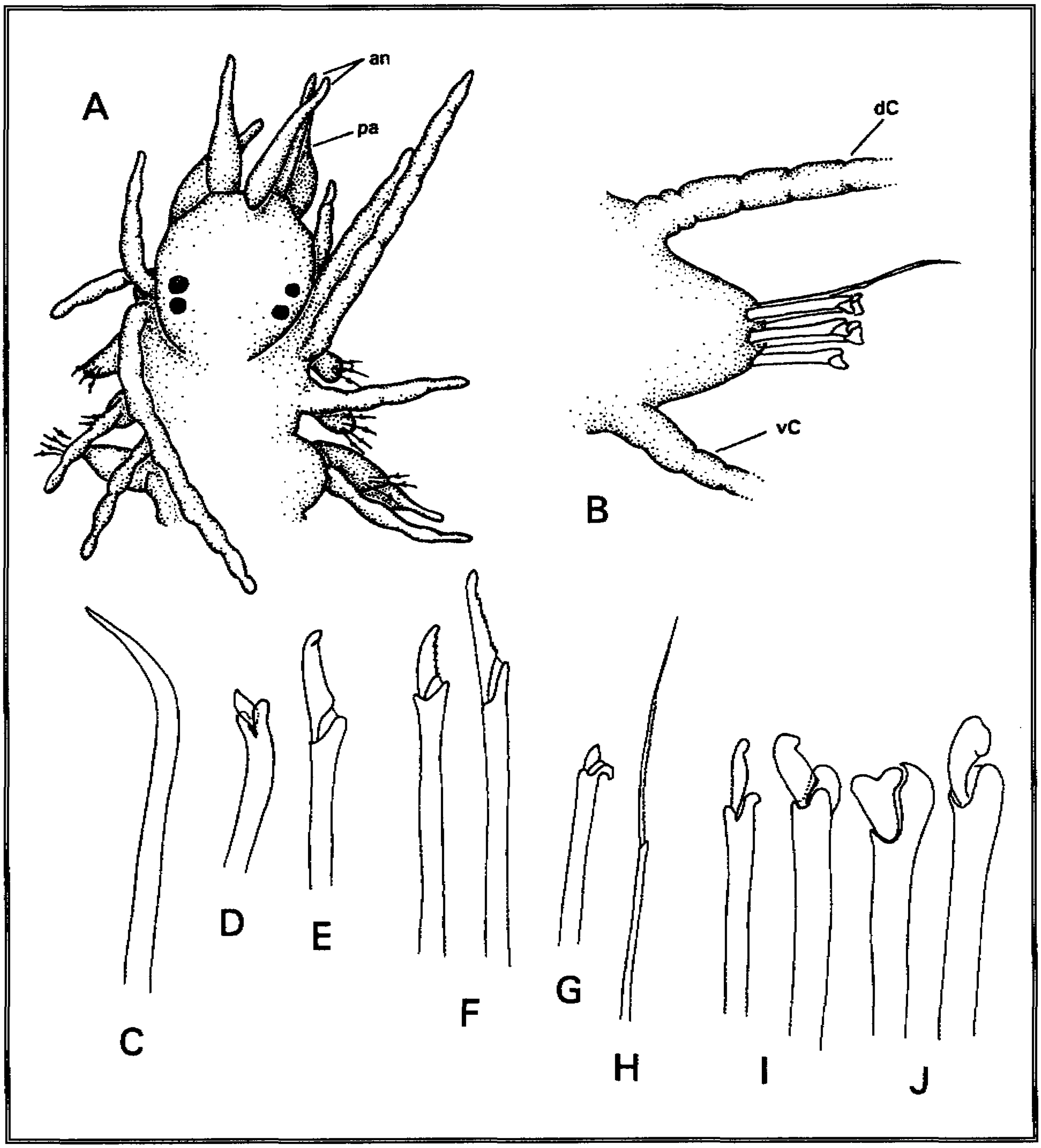

Figure 9.6. *Heteropodarke heteromorpha*: A, anterior end, dorsal view (after Hartmann-Schröder, 1962); B, parapodium (after Dorsey, 1978); C, notopodial spine, far posterior setiger; D, ventralmost seta, setiger 1; E, dorsalmost seta, setiger 2; F, ventralmost (left) and dorsalmost seta, middle segment; G, short-bladed seta, far posterior segment; H, spiniger; I, ventralmost (left) and dorsalmost seta, setiger 3; J, modified setae (left after Dorsey, 1978).

posterior setigers. However, *H. lyonsi* is not considered a synonym of *H. heteromorpha* because of other differences, such as the length of the dorsal and ventral cirri and details in setal morphology.

Type location and type specimens. Peru: Callao, 3 m, in sand with shell fragments and some pebbles; holotype (ZMH P-14155) and 19 paratypes (ZMH P-14156, P-15401).

Habitat. *H. heteromorpha* is found in sandy sediments.

Distribution. New Caledonia; Peru to California, 3 to 98 m.

Genus *Podarke* Ehlers, 1864

Type species: *Podarke agilis* Ehlers, 1864

Diagnosis. Prostomium with 3 antennae, median one attached in middle of prostomium; 2 biarticulate palps and usually 2 pairs of lentigerous eyes present. Proboscis cylindrical, muscular, with many crowded terminal papillae or papillae absent. Six pairs of tentacular cirri arising from 1 to 3 visible segments. Parapodia sesquiramous in setigers 1 and 2, subbiramous from setiger 3. Notosetae few, including furcate setae and occasionally capillaries. Neurosetae numerous compound falcigers.

Remarks. The status of *Podarke*, especially in relation to the quite similar genus *Ophiodromus*, has been confused for many years (see, e.g., Fauchald 1977). One of the reasons for the confusion was certainly Ehlers's discrimination of *Podarke* from *Ophiodromus*. He erroneously considered the palps of the newly erected genus *Podarke* to be additional antennae and made this character the main diagnostic feature to separate the two genera. Hessle (1925) commented on this error and synonymized *Podarke* and *Ophiodromus*. The only difference between the genera that he could detect was the development of the neuropodial lobes, and he rightfully doubted that this was a generic character. With respect to the notosetae, Hessle believed that *P. pugettensis* was intermediate between *P. agilis* that had highly reduced notopodia bearing a single fine notoseta, and *Ophiodromus flexuosus* with numerous notosetae. Fauvel (1923), however, thought that the difference between biramous and subbiramous parapodia was a generic level character. His generic definition of *Podarke* (sesquiramous or subbiramous parapodia with few notosetae) and *Ophiodromus* (biramous parapodia with numerous notosetae) was adopted by Hartman (1959) and is followed here. According to that definition, *Ophiodromus* contains 5 species, all but one described from Europe; *Podarke* consists of about 10 species, the only Pacific species being *P. pugettensis* (U.S. Pacific coast) and *P. angustifrons* from the Philippines.

***Podarke pugettensis* Johnson, 1901**

Figure 9.7

Podarke pugettensis Johnson, 1901:397-398, pl. 3, figs. 23-25.—Berkeley and Berkeley, 1948:56, figs. 83-84.
Ophiodromus pugettensis: Hessle, 1925:20-21.—Hartman, 1961:67-68 (synonymy); 1968:369.—Blake, 1975b:183, fig. 91.—Lissner *et al*., 1986:D-8.
Ophiodromus (Podarke) pugettensis: Blake, 1975a:49-54, figs. 13-15.

Material examined. California: Tomales Bay (4).

Description. Length to 40 mm, width to 5 mm, segments to 65. Body short, wide, dorsoventrally depressed, tapering towards pygidium and less distinctly toward prostomium. Color in alcohol pale; color in life dark reddish, purple, or almost black with pale cirri and prostomial appendages.

Prostomium wider than long, almost quadrangular, trilobed, with 3 antennae, median one attached frontally. Two biarticulate palps, slender, subequal in length to lateral antennae; median antenna about half as long. Two pairs of large, subequal, lentigerous eyes arranged in rectangle (Fig. 9.7A).

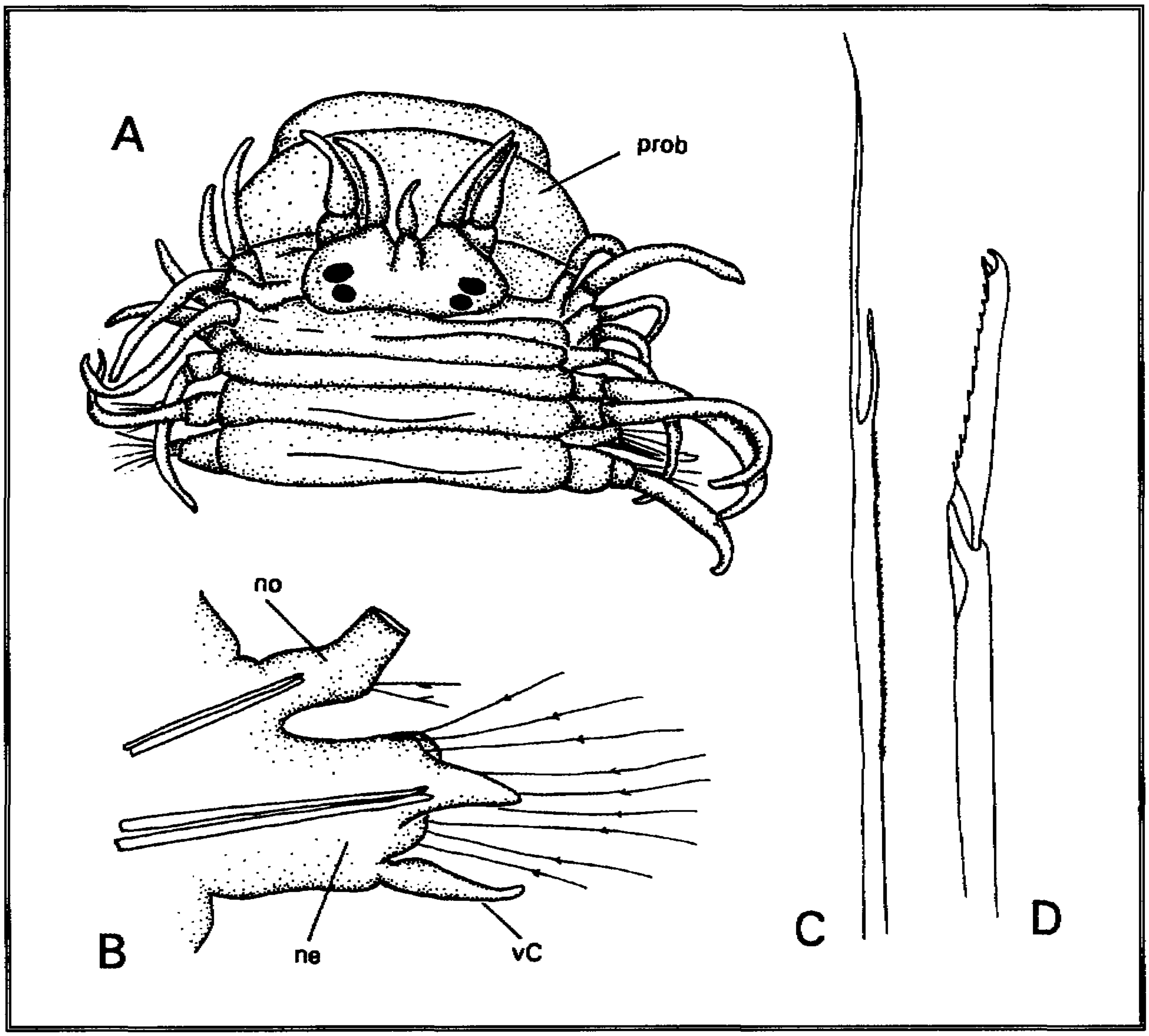

Figure 9.7. *Podarke pugettensis*: A, anterior end, dorsal view (after Johnson, 1901); B, parapodium; C, notoseta; D, neuroseta.

Six pairs smooth tentacular cirri arising from 2 visible segments (1 in very large specimens), smooth; ventral cirri shorter than dorsal ones. Parapodia sesquiramous in setigers 1 and 2, rarely 3, subbiramous from setiger 3 or 4; notopodia strongly reduced to small lateral projection of dorsal cirrophore, with 2 aciculae; neuropodia well developed, with conical presetal lobe and rounded, low postsetal lobe (Fig. 9.7B). Dorsal and ventral cirri smooth and slender, the latter much shorter than the former. Notosetae furcate, long and slender, with subdistal serration under short tine; long tine at least 4 times as long as short tine; usually 2 per fascicle (Fig. 9.7C). Neurosetae numerous compound falcigers with moderately long blades (length/width ratio 5.5:1 to 23:1), with the shortest blades on inferior and superior setae and the longest in middle of fascicle (Fig. 9.7D). Pygidium small, ring-shaped, with terminal anus. Anal cirri not observed.

Remarks. Large specimens of *P. pugettensis* may differ slightly from the generic characters described from the type species *P. agilis* Ehlers, 1864, in that the tentacular cirri arise from one visible segment instead of three, and the habitus resembles that of *Ophiodromus flexuosus* more than that of

Podarke agilis because of its proportions and the indistinct segmental borders. However, the development of the notopodia indicates clearly that this species belongs to *Podarke*.

Biology. This species has been subject of several studies because of its commensal way of life (Hickok and Davenport, 1957; Storch and Niggemann, 1967; Stewart, 1970). Stewart (1970) discovered three physiologically distinct populations, two of them living on the starfish *Patiria miniata* and *Petalaster foliolata*, respectively, and one living freely. The population associated with *Patiria* was the most selective in choosing a host and was attracted by a two-component substance produced by the starfish. Free-living individuals showed no attraction to any host. His results confirmed findings of Hickok and Davenport (1957), who conducted a number of choice experiments with different populations of *P. pugettensis* and several species of starfish. Storch and Niggemann (1967) described a new subspecies of *P. pugettensis* from the Red Sea and studied interactions with its sand dollar host. Shaffer (1979) provided an excellent account of the feeding biology, rejecting earlier theories that *P. pugettensis* might be a herbivore. His experiments showed clearly that the species is a carnivore that feeds on both living and dead prey. Living prey organisms are selected primarily by size-related vibrations, whereas dead organisms are evaluated with chemical senses. The proboscis functions as a pump to seize the prey. The larval development was described by Blake (1975a). The development is lecithotrophic, with settlement occuring at the 6-setiger stage. Development of juveniles proceeds rapidly to animals resembling adults.

Distribution. Washington to central California, shallow intertidal.

Genus *Podarkeopsis* Laubier, 1961

Type species: *Podarkeopsis galangaui* Laubier, 1961

Diagnosis. Prostomium with 3 antennae, with median one attached frontally between lateral ones; with 2 biarticulate palps and 2 pairs of lenticular eyes. Proboscis cylindrical, with thick muscular layer and 10 terminal papillae that may alternate with tufts of cilia. Eight pairs tentacular cirri arising from 3 visible segments, smooth to distinctly articulated. Parapodia sesquiramous in setigers 1 to 5, biramous thereafter. Notosetae few, including furcate setae, acicular spines and occasionally some capillaries, smooth or serrated, with or without cross-striations. Neurosetae numerous compound falcigers.

Remarks. This genus was established by Laubier (1961) to accomodate a species that resembled *Podarke* in having furcate notosetae, but possessed eight rather than six pairs of tentacular cirri. In subsequent years, the presence of furcate setae was not considered a genus-level character, but rather a species character, and *Podarkeopsis* was synonymized with *Gyptis*. Perkins (1984), however, reestablished the genus and referred a number of *Gyptis* species with furcate setae to *Podarkeopsis*. The genus now includes a well-defined group of species with eight pairs of tentacular cirri.

In the Santa Maria Basin, two species of *Podarkeopsis* were found, one of which is new to science. *Podarkeopsis brevipalpa*, formerly a "catch-all species" for specimens with furcate notosetae and 8 pairs of tentacular cirri (as *Gyptis brevipalpa*) appears to be restricted to intertidal and shallow subtidal depths and was not found in California material available to the author, but is included here because it may co-occur with *P. glabra* in California. The species was originally described from El Salvador (Hartmann-Schröder, 1959) and has been reported from Oregon and Washington (confirmed by the author).

Podarkeopsis brevipalpa (Hartmann-Schröder, 1959)

Figure 9.8

Oxydromus brevipalpa Hartmann-Schröder, 1959:105-107.
Gyptis brevipalpa: Banse and Hobson, 1968: 12-13, fig. 3B-E.
Podarkeopsis brevipalpa: Perkins 1984:579.

Description. Body slender, fragile, without pigmentation. Prostomium almost rectangular, slightly wider than long, with 3 antennae attached frontally; median antenna very short, about one-fourth as long as lateral ones. Two biarticulate palps, somewhat shorter than lateral antennae, and 2 pairs of large eyes arranged in trapezoid, the anterior pair further apart than posterior pair and very close to the latter. Proboscis cylindrical, muscular, with 10 or 11 large terminal papillae.

Eight pairs tentacular cirri arising from 3 visible segments (Fig. 9.8A). Parapodia sesquiramous in setigers 1-3 or 4, subbiramous from setiger 4 or 5 (Fig. 9.8B); notopodium very small, conical, usually with 3 setae; notosetae including 1 smooth capillary, 1 distally serrated spine, and 1 furcate seta with smooth shaft and unequal tines (Fig. 9.8C-E). Neuropodia well developed with conical presetal lobe and low, broadly triangular acicular lobe; neurosetae compound falcigers with short to long blades, with setae having longest blades located in middle of fascicle. All dorsal cirri missing; ventral cirri slender, smooth, about as long as neuropodial lobe. Pygidium unknown.

Remarks. *Podarkeopsis brevipalpa* (as *Oxydromus brevipalpa* Hartmann-Schröder) has traditionally accomodated hesionids with eight pairs of tentacular cirri and furcate notosetae; it was synonymized with *P. glabra* (as *Oxydromus arenicola glabra* Hartman) by Banse and Hobson (1968). However, a closer examination of the notosetae of specimens from several locations off California revealed that those specimens possess furcate setae with serrations under the shorter tine and thus do not belong to *P. brevipalpa* which is characterized by smooth furcate setae (Hartmann-Schröder in Banse and Hobson, 1968). Although Banse and Hobson noted this conflict, they did not recognize *P. brevipalpa* and *P. glabra* as separate species.

Podarkeopsis glabra (Hartman, 1961)

Figure 9.9

Oxydromus arenicolus glabrus Hartman, 1961:68.
Gyptis arenicola glabra: Hartman, 1968:363.—Banse and Hobson, 1968:12, fig. 3b-h.
Podarkeopsis glabrus: Perkins, 1984 (synonymy).—Lissner *et al*., 1986:D-9.—Hyland and Neff, 1988: A-2.—Hyland *et al*., 1990:F-1.
Gyptis brevipalpa: Blake, 1975b:183. *Not* Hartmann-Schröder, 1959.

Material examined. California: Santa Maria Basin, off Purisima Point, Sta. 42 (1); off Point San Luis, Sta. R-1 (3); off Point Conception, Sta. 77 (1); Bodega Harbor (1); Gulf of the Farallones, ca. 30 m, Jul. 1973 - Feb. 1974 (5).

Description. Length to 15 mm, width to 1 mm, segments to 30. Body short, wide, depressed except for nearly cylindrical pharyngeal region. Color in alcohol uniformly tan.

Prostomium nearly quadrangular, slightly wider than long, with 2 palps and 3 antennae; outer antennae about as long as palps, median antenna only one-third as long, inserted at frontal margin of prostomium. Four subequal eyes present in posterior half, moderately large, arranged in a rectangle. Two

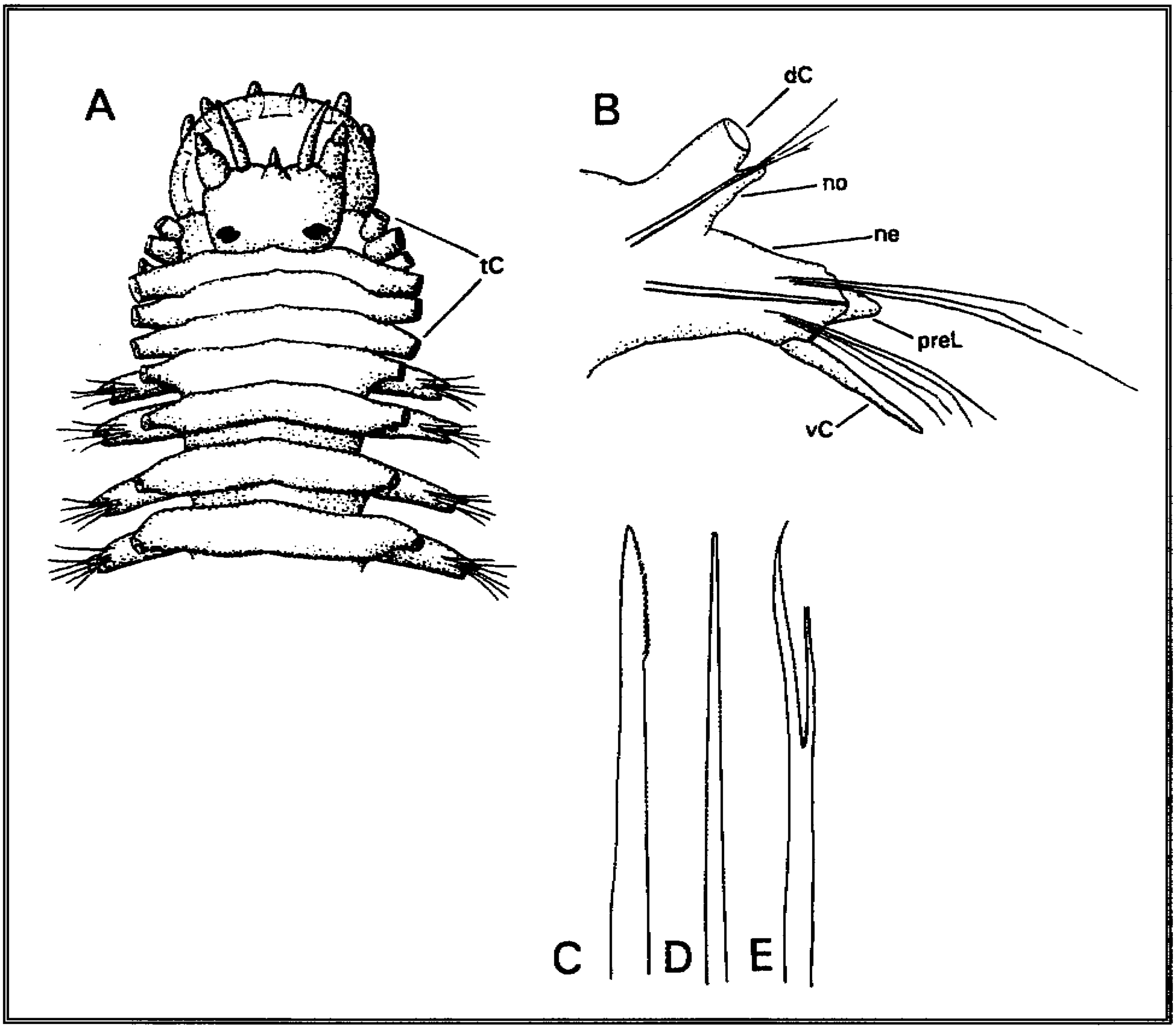

Figure 9.8. *Podarkeopsis brevipalpa*: A, anterior end, dorsal view; B, parapodium, posterior view; C, notopodial spine; D, smooth capillary; E, furcate notoseta (A, B from Hartmann-Schröder, 1959; C-E after Hartmann-Schröder in Banse and Hobson, 1968).

large nuchal grooves along postectal margin of prostomium (Fig. 9.9A). Proboscis wide, smooth, with 10 distal papillae.

Eight pairs of tentacular cirri on 3 distinct segments; each smooth to indistinctly articulate, the dorsal cirri much longer than the corresponding ventral ones. Parapodia sesquiramous in setigers 1 to 4 (rarely 5), biramous after that; dorsal cirri long, slender, indistinctly articulated; ventral cirri much shorter, exceeding just beyond the neuropodial presetal lobe, smooth or indistinctly articulated (Fig. 9.9B). Notosetae first present from setiger 5; consisting of 2 to 5 acicular spines with weak subdistal serrations (large animals) and 2 to 5 furcate setae with unequal tines; shorter tine with basal serrations, longer tine open-ended, appearing broken off (Fig. 9.9C, D). Neurosetae compound falcigers with long and short blades, longest blades in middle of fascicle; shaft smooth, blade finely serrated, tapering to hook-shaped tip and often with short distal hood (Fig. 9.9E).

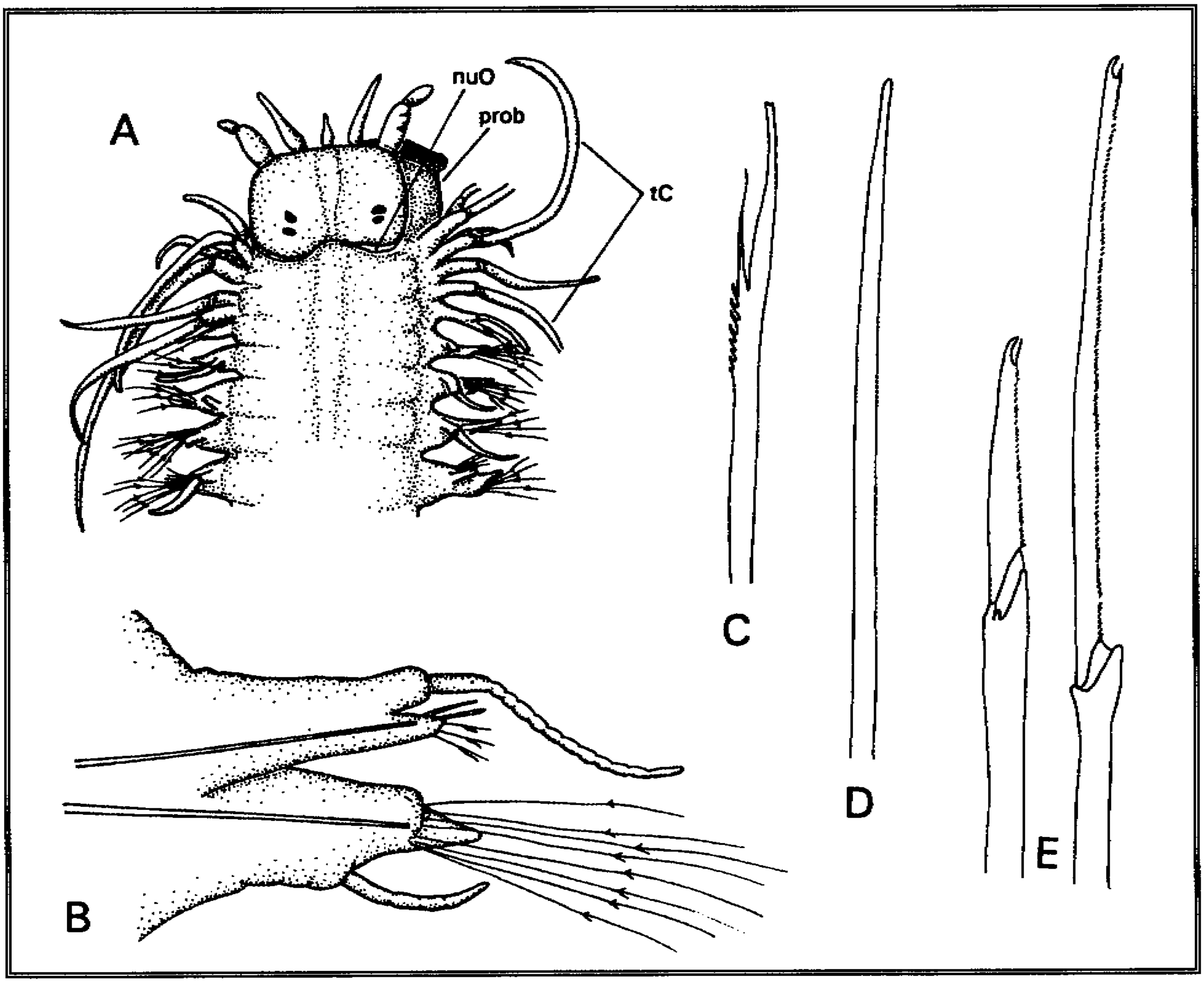

Figure 9.9. *Podarkeopsis glabra*: A, anterior end, dorsal view; B, parapodium; C, furcate notoseta; D, notopodial spine; E, longest and shortest blade from a neuropodial fascicle.

Habitat. *P. glabra* occurs in mixed mud and silt.

Remarks. There has been considerable confusion about the genus to which this species should be assigned. After a careful revision of several hesionid genera by Perkins (1984), the species was moved from *Gyptis* to *Podarkeopsis*. Banse and Hobson (1968) were the first to point out some confusion concerning the very similar *Gyptis brevipalpa*, a widely distributed hesionid along the North American west coast. It appears that what has been called *G. brevipalpa* is often is *Podarkeopsis glabra*, due to differences in the furcate setae. An examination of the type by Hartmann-Schröder (in Banse and Hobson, 1968) revealed that the furcate setae of *G. brevipalpa* are smooth, whereas in *P. glabra* they are serrated at the base of the shorter tine. None of the specimens from numerous locations along the U.S. Pacific shelf observed by the author had smooth furcate setae; *G. brevipalpa* may be restricted to intertidal and shallow subtidal water from where it was described (Hartmann-Schröder, 1959).

Distribution. Central America; California to Alaska, in shallow waters.

Podarkeopsis perkinsi Hilbig, 1992

Figure 9.10

Podarkeopsis perkinsi Hilbig, 1992:715-716, fig. 3.
Podarkeopsis sp. A Lissner *et al.*, 1986:D-9.
Podarkeopsis sp. B Lissner *et al.*, 1986:D-9.—Hyland and Neff, 1988:A-2.—Hyland *et al.*, 1990:F-1.

Material examined. California: Santa Maria Basin, off Purisima Point, Sta. R-6: holotype (USNM 148703); off Point San Luis, Sta. 26: 1 paratype (USNM 148704), Sta. 28: 1 paratype (USNM 148705), Sta. R-3: 2 paratypes (SBMNH 35619); off Point Arguello, Sta. 61: 1 paratype (LACM-AHF Poly 1617); off Point Conception, Sta. 76: 1 paratype (LACM-AHF Poly 1618); off Point Sal, Sta. R-9: 1 paratype (SBMNH 35620); off the Farallon Islands, continental slope north and south of Pioneer Canyon (2).

Description. Length to 18 mm, width to 2 mm, segments to 51. Body slender, widest in pharyngeal region, gradually tapering toward pygidium. Color in alcohol uniformly tan.

Prostomium pentagonal, with 3 antennae, 2 palps, and 2 pairs of eyes (occasionally faded in alcohol); anterior pair as far apart as posterior pair, moderately large, kidney-shaped; posterior pair minute rounded spots. Lateral antennae about as long as palps, median antenna about half as long; palps directed toward ventrum. Two heavily ciliated nuchal organs along postectal margins of prostomium (Fig. 9.10A). Proboscis with 10 large terminal papillae and ciliary band (Fig. 9.10C).

Eight pairs of tentacular cirri on 3 visible segments; first 2 pairs on segment 1. Second pair longest, all ventral tentacular cirri considerably shorter than corresponding dorsal ones (Fig. 9.10A, B). Parapodia sesquiramous in setigers 1 to 3, biramous thereafter; notopodia about half as long as neuropodia, with conical presetal lobe; dorsal cirri extending to tip of neuropodium, indistinctly articulated or wrinkled, attached to wide cirrophore. Neuropodia with long, conical presetal lobe; ventral cirri short, slender, smooth, inserted subdistally (Fig. 9.10D).

Notosetae first present in setiger 4; including up to 6 furcate setae in dorsalmost position, up to 14 finely serrated, very slender capillaries in middle position, and up to 6 distally coarsely serrated spines in ventralmost position; ventralmost setae in juveniles appearing as cultriform setae with flattened and serrated tip (Fig. 9.10E-G). Neurosetae compound, arranged in two groups: dorsal fascicle of numerous, very long-bladed and slender falcigers and ventral fascicle of few short-bladed falcigers (Fig. 9.10H, I).

Pygidium small, surrounding terminal anus, with 2 slender ventrally inserting anal cirri (Fig. 9.10J).

Remarks. *P. perkinsi* is easily recognized by the occurrence of the first notopodia in setiger 4 (rather than 5 as is typical for the genus) and the setal morphology. The serrations on the notopodial spines and the extremely long-bladed upper neurosetae are diagnostic for this species. *P. perkinsi* differs from *P. glabra* most obviously by the presence of capillary setae in the notopodial fascicle and the occurrence of notosetae from setiger 4 rather than 5.

Habitat. The species was found in silt and sand on the upper and middle slope.

Distribution. Known only from off central California, 385 to 1020 m.

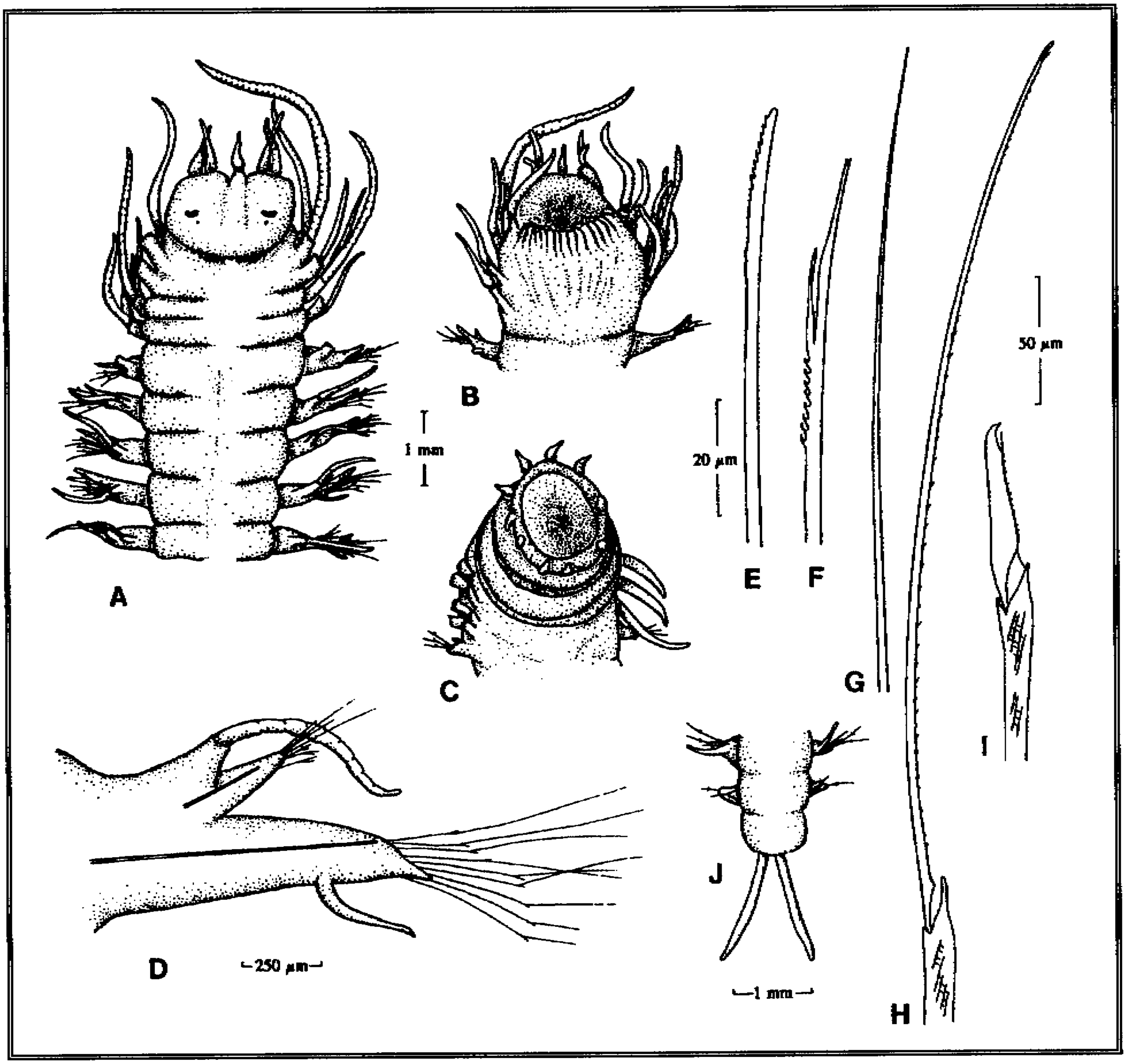

Figure 9.10. *Podarkeopsis perkinsi*: A, anterior end, dorsal view; B, same, ventral view; C, proboscis, anteroventral view; D, parapodium; E, notopodial spine; F, furcate notoseta; G, capillary notoseta; H, long-bladed neuroseta; I, short-bladed neuroseta; J, posterior end, dorsal view (from Hilbig, 1992).

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10. FAMILY PILARGIDAE SAINT JOSEPH, 1899

by

James A. Blake[1]

Introduction

The pilargids are a small group of carnivorous or omnivorous polychaetes, only rarely encountered in casual collections. Most species are subtidal and require careful sieving to remove them from the muds and muddy sands which they inhabit. Pilargids are related to the hesionids and syllids but are easily differentiated from them by the absence of aciculae in tentacular segments, the absence of compound setae, and the unarmed proboscis. Several of the genera have characteristic notopodial spines which are shaped like boat hooks.

Morphology

Pilargids are elongate worms with somewhat flattened, ribbonlike bodies (e.g., *Sigambra, Ancistrosyllis,* and *Pilargis*) or bodies that are cylindrical (e.g., *Cabira, Synelmis,* and *Parandalia*). The body surface may be smooth or distinctly papillated. The prostomium, tentacular segments and the first setiger are more or less fused. The prostomium is typically small, inconspicuous and has 0-3 antennae; eyes are normally lacking. The brain is visible on the dorsal side of the prostomium in some genera. This structure is divisible into forebrain, midbrain, and hindbrain. The shape of the brain and its component regions may be diagnostic at the generic level. The median antenna, when present, is on the posterior part of the prostomium. Antennae may be short (e.g., *Pilargis*) or quite long (e.g., *Sigambra*). Palps are biarticulate and usually set off from the prostomium by large palpophores bearing small (or no) palpostyles. The proboscis is unarmed, bulbous and usually bears a circlet of papillae around the distal opening. The anterior end of the animal often appears enlarged due to the contained proboscis. The tentacular segment is achaetous and usually bears two pairs of tentacular cirri (rarely absent).

Parapodia are subbiramous, with the notopodia reduced to embedded notoaciculae in the cirrophores of the dorsal cirri. Additional capillary setae, large curved hooks, or straight spines may be present. Neuropodia are somewhat conical with embedded neuroaciculae and simple neurosetae; compound setae are always lacking. Dorsal and ventral cirri are present, with the ventral smaller than the dorsal or both cirri subequal. The pygidium bears a terminal anus and a pair of anal cirri; a pygidial plaque may be present (e.g., *Parandalia*).

The most important taxonomic characters include the presence and structure of the notopodial spines, degree of flattening of the body, presence/absence of the antennae and tentacular cirri, and the form of these same structures if present. More recently, the gross morphology of the brain has been suggested as a useful taxonomic character (Fitzhugh and Wolf, 1990).

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Taxonomic History

The most important taxonomic treatments of the Pilargidae are by Hartman (1947) and Pettibone (1966). Hartman (1947) generally agreed with the earlier concept of pilargids established by Hessle (1925) and was the first modern systematist to define and establish the position of the Pilargidae within the polychaetes. She emphasized that pilargids should be kept separate from hesionids because they completely lacked compound setae. As part of Hartman's review, several genera including *Pilargis, Ancistrosyllis*, and *Loandalia* were revised or emended. A more extensive revision of the genera and species of pilargids was completed by Pettibone (1966). Among the important results of Pettibone's work was a review of the species of *Ancistrosyllis*, revision of *Cabira*, reestablishment of the genus *Sigambra*, a review of the species of *Synelmis*, and description of three new species. Additional contributions to the family organization have been made by Pearson (1970), Emerson and Fauchald (1971), and Fitzhugh and Wolf (1990).

Descriptions and/or keys to the genera and species from the eastern Pacific can be found in Hartman (1968), Emerson and Fauchald (1971), Fauchald (1972), and Salazar-Vallejo (1986). Other works that have recently dealt with generic problems or regional faunas include Pearson (1970), Katzmann *et al.*, (1974), Wolf (1984; 1986), Britaev and Saphronova (1981), Imajima (1987), and Salazar-Vallejo (1990). Fauchald (1977) provides useful keys and diagnoses of the genera. Fitzhugh and Wolf (1990) discuss systematic relationships of the genera using a cladistic analysis. Among other things, these authors demonstrated that the subfamilies established by Salazar-Vallejo (1986) were not appropriate.

Depending upon how one cares to interpret and define generic level characters, 10-13 genera are currently recognized. Four genera and about 12 species are found in California; six species have been found in the MMS collections.

Biology

Pilargids are considered to be carnivores or omnivores (Day, 1967), although there is little observational evidence on feeding habits (Fauchald and Jumars, 1979). The eversible proboscis should be capable of capturing prey items despite its lack of armature.

According to Day (1967), pilargids with well-developed head appendages creep over surfaces, while species with reduced head appendages, such as *Pilargis*, are burrowers. At least one species, *Ancistrosyllis commensalis* Gardiner, has been reported from the burrows of a capitellid polychaete (Gardiner, 1976). Similar commensal relationships are likely owing to the nature of the large recurved hooks found in many of the genera.

Very little is known concerning reproduction in pilargids. Sexes are separate (Pettibone, 1982). The most complete account of larvae is by Cazaux (1970) who described the larval development of *Pilargis verrucosa*. Descriptions of isolated planktonic larvae of *Ancistrosyllis groenlandica, Ancistrosyllis* sp., and *Cabira* sp. have been presented by Bhaud (1972), Blake (1975), and Britaev (1981), respectively.

Key to the Genera and Species

1A. With stout, often recurved notopodial hooks (Fig. 10.1C) in addition to internal notoaciculae 2

1B. With internal notoaciculae only, no emergent notosetae (Fig. 10.4B) 9

2A. Stout emergent notosetae straight, not hooked (Fig. 10.8C). Body subcylindrical, with parapodia sharply demarcated (Fig. 10.8A) 12

2B. Stout emergent notosetae hooked (Fig. 10.1C) 3

3A. Body subcylindrical, parapodia poorly developed; notopodial lobe very small, with internal notoaciculae and stout emergent hooked notosetae from setiger 7 .... Genus *Cabira*[2]

3B. Body elongate, dorsoventrally flattened, with parapodia well developed; dorsal and ventral cirri distinct 4

4A. Prostomium reduced, inconspicuous, antennae shorter than palps (Fig. 10.1A); tentacular cirri short; dorsal cirri short, with those of setiger 1 similar to or slightly longer than those following .... Genus *Ancistrosyllis* 5

4B. Prostomium larger, antennae longer than palps (Fig. 10.6A); tentacular cirri long; dorsal cirri long and slender, with those of setiger 1 unusually long .... Genus *Sigambra* 7

5A. Ventral cirri from setiger 1; prostomium with 3 antennae (Fig. 10.1A); tentacular segment distinctly separated from prostomium; dorsal cirri elongate, fusiform or cirriform 6

5B. Ventral cirri from setiger 3; prostomium with 2 lateral antennae and no median antenna (Fig. 10.3A); tentacular segment not distinctly separated from prostomium; dorsal cirri short, conical .... *Ancistrosyllis hamata*

6A. Notopodial hooked setae present from setigers 4-6; neuropodial lobe short (Fig. 10.1C) .... *Ancistrosyllis groenlandica*

6B. Notopodial hooked setae present from setigers 13-18; neuropodial lobe long (Fig. 10.2C) .... *Ancistrosyllis breviceps*

7A. Hooked notosetae from setiger 3-4; with or without accompanying straight notosetae; median antenna subequal to or longer than lateral antennae (Fig. 10.6A) 8

7B. Hooked notosetae from setiger 11-15; hooked setae sometimes accompanied by single emergent, straight or slightly curved notoseta; median antenna approximately twice as long as lateral antennae (Fig. 10.7A) .... *Sigambra bassi*

8A. Hooked notosetae accompanied by 1-2 accessory straight or curved, thin spines (Fig. 10.8B); median antenna longer than lateral antenna (Fig. 10.8A); proboscis with 8 distal papillae .... *Sigambra setosa*

8B. Hooked notosetae not accompanied by accessory spines (Fig. 10.6B); median antenna subequal to lateral antennae; proboscis with 14-16 distal papillae .... *Sigambra tentaculata*

9A. Prostomium without antennae; tentacular cirri present or absent 11

9B. Prostomium with 2 antennae; pair of tentacular cirri present .... Genus Pilargis 10

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[2] No species of *Cabira* are known from the eastern Pacific.

10A. Papillae cover all surfaces of body (Fig. 10.4A-B) .... *Pilargis berkeleyae*

10B. Papillae limited to prostomium, tentacular cirri, and parapodia (Fig. 10.5A-B) ... *Pilargis maculata*

11A. Tentacular cirri absent; palps free, not fused .... Genus *Loandalia*[3]

11B. Tentacular cirri present; palps long, narrow, fused dorsally .... Genus *Litocorsa*[4]

12A. Prostomium with antennae; tentacular cirri present; parapodia sharply set off from body by deep intersegmental grooves .... Genus *Synelmis*[5]

12B. Prostomium without antennae (Fig. 10.9A); tentacular cirri absent; parapodia distinct, but without deep intersegmental grooves .... Genus *Parandalia* 12

13A. Eyes present (Fig. 10.9A); emergent notopodial spine first present from setiger 9; posterior neuropodia with setae in a single row, with up to 7 setae per fascicle .... *Parandalia ocularis*

13B. Eyes absent; emergent notopodial spine first present from setiger 7-8; 12-15 neuropodial setae in each parapodium .... *Parandalia fauveli*[6]

Descriptions of Species

Six species and four genera have been encountered in the MMS collections. However, nine species are expected to occur in the offshore environment adjacent to the study area and are all included in the keys, descriptions, and illustrations presented in this chapter. These species are listed below. Notes are also presented on additional pilargid genera that might eventually be encountered.

Ancistrosyllis groenlandica McIntosh, 1879
Ancistrosyllis breviceps Hartman, 1963
Ancistrosyllis hamata (Hartman, 1960)
Pilargis berkeleyae Monro, 1933
Pilargis maculata Hartman, 1947
Sigambra tentaculata (Treadwell, 1941)
Sigambra bassi (Hartman, 1945)
Sigambra setosa Fauchald, 1972
Parandalia ocularis Emerson and Fauchald, 1971

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[3] No species of *Loandalia* have been reported from California. Salazar-Vallejo (1986) has described *L. riojai* from western Mexico, but this species differs from an earlier generic definition by having notopodial spines.

[4] The genus *Litocorsa* was erected by Pearson (1970) for *L. stremma*, discovered in Scotland. The same species was reported from the Mediterranean by Katzmann *et al*, (1974). A second species was described by Wolf (1986) from the Gulf of Mexico. No species of *Litocorsa* have been reported from the eastern Pacific.

[5] No species of *Synelmis* have been found in the Santa Maria Basin and western Santa Barbara Channel. However, *S. albini* (Langerhans) has been reported from intertidal sediments at La Jolla by Hartman (1947) as *Ancistrosyllis rigida (fide,* Pettibone, 1966).

[6] *Parandalia fauveli* has been reported from intertidal mud flats in southern California and western Mexico. The species has not been found in the Santa Maria Basin.

Genus *Ancistrosyllis* McIntosh, 1879

Type species: *Ancistrosyllis groenlandica* McIntosh, 1879

Diagnosis. Body elongate, depressed, with lateral parapodia deeply cut. Prostomium small, inconspicuous, bearing 3 short antennae; 2 biarticulate palps present with large palpophores and small palpostyles. Proboscis cylindrical, globular, with or without papillae. Tentacular segment more or less fused with prostomium, achaetous, with 2 pairs of short tentacular cirri. Parapodia subbiramous. Notopodia inflated, with notoaciculae curved distally, with stout emergent hooks from setigers 3-13. Neuropodia with conical to truncate setigerous lobes, with neuroaciculae and simple neurosetae. Dorsal and ventral cirri short. Neurosetae with smooth blades or blades finely to coarsely serrated, usually with hooked tips. Pygidium with paired short anal cirri. Integument with scattered papillae.

Remarks. *Ancistargis* Jones, 1961 was separated from *Ancistrosyllis* by having two antennae instead of three. Pettibone (1966) preferred to combine the two genera because the critical median antenna, when present, was small to minute and sometimes difficult to detect. Emerson and Fauchald (1971) preferred to keep the then five known species of *Ancistargis* separate because they appeared to represent a well-defined group of species. This separation has been followed by Fauchald (1972, 1977) and Salazar-Vallejo (1986), but not by Wolf (1984). I consider the presence or absence of a small median antenna to represent a species rather than a generic level character and prefer to retain the synonymy as proposed by Pettibone (1966).

Three species are found in the eastern Pacific: *Ancistrosyllis groenlandica* McIntosh, *A. hamata* (Hartman), and *A. breviceps* Hartman. Only *A. groenlandica* has been found in the samples from the Santa Maria Basin. The other two species are known from adjacent canyons and basins in southern California and probably occur in deeper locations off the central California coast. For this reason, all three species are treated

Ancistrosyllis groenlandica McIntosh, 1879

Figure 10.1

Ancistrosyllis groenlandica McIntosh, 1879:502, pl. 65, figs. 3, 20.—Pettibone, 1963:110-111, fig. 30; 1966:166-168, fig. 3.—Hartman, 1965:71.—Bhaud, 1972:263-272, figs. 1-3.—Katzmann *et al.*, 1974:3-7, figs. 1-2.—Imajima, 1987:153-155, fig. 2.—Salazar-Vallejo, 1986: 193-209, pl. 1, figs. 5-6.

Material examined. California, Santa Maria Basin, Sta. R-9 (3); western Santa Barbara Channel, Sta. 86 (1); Sta. 97 (1).

Description. A moderate sized species, Santa Maria Basin specimens up to 20 mm long and 1 mm wide for about 80 segments. Body dorsoventrally flattened, widest in middle, tapering both anteriorly and posteriorly; parapodia deeply cut; body surface and parapodia with numerous short papillae. Color in alcohol: tan with conspicuous rust-colored glandular areas dorsally and ventrally on parapodia [not well developed in California specimens]; irregular lateral pigmented areas sometimes present throughout body.

Prostomium with large palpophores and small button-like palpostyles anteroventrally; 3 small subequal antennae, shorter than palps (Fig. 10.1A); eyes lacking. Proboscis short, cylindrical, with few scattered papillae. Tentacular segment distinct from prostomium, with 2 pairs of short, subequal tentacular cirri, similar to antennae (Fig. 10.1B). Dorsal cirri of setiger 1 about twice as large as on following

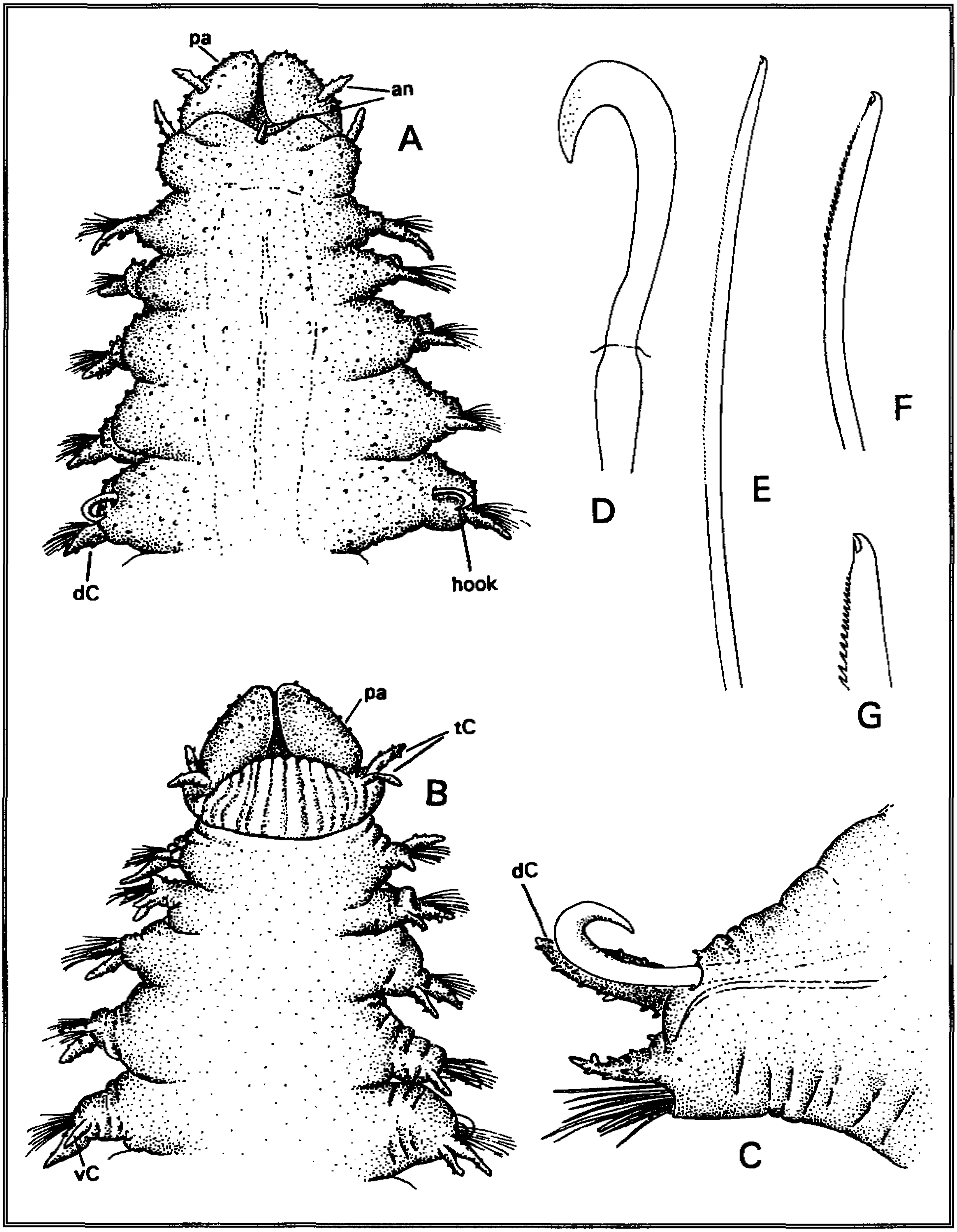

Figure 10.1. *Ancistrosyllis groenlandica.* A, anterior end, dorsal view; B, same end, ventral view; C, posterior parapodium, anterior view; D, notopodial hook; E-G, serrated neurosetae.

segments (Fig. 10.1A). Dorsal cirri short, fusiform, extending somewhat beyond neuropodial lobes (Fig. 10.1C). Notopodia with inflated notoacicular lobes and emergent recurved hooked setae from setiger 4-6; individual hooks with roughened tips (Fig. 10.1D). Neuropodial lobes conical, with neuroaciculae and 2 types of neurosetae: 1) longer and short, slender setae with fine serrations, and slightly hooked tips (Fig. 10.1E); 2) short, broad, sabre-like setae with coarse serrations, with bifid tips (Fig. 10.1E-G). Ventral cirri from setiger 1, each cirrus narrow, elongate, shorter than dorsal cirri (Fig. 10.1C). Pygidium conical, rounded terminally, bearing 2 short anal cirri with scattered papillae.

Biology. Pearson (1970) reported maximal densities of 35 individuals per m^2 at depths of 18-128 m in two Scottish lochs, where the species occurred in soft muds to muddy sands. Salinities in the lochs ranged from 25-31‰ and temperatures from 6-13°C. Planktonic larvae have been described by Bhaud (1972). Eleven-setiger larvae with well-developed ventral cirri on setiger 1 and hooked notosetae from setiger 10. The species is found on bottoms of mud, mixed silt-mud and mud with gravel and shell fragments.

Remarks. There are reported differences in the distribution of the curved notopodial hooks of adults. They are said to begin on setiger 4-5 (Pettibone, 1963), 4-6 (Pettibone, 1966), 4-7 (Hartman, 1965) and 3-5 (Katzmann *et al.*, 1974; Imajima, 1987). The broad, thickened neurosetae were illustrated clearly by Katzmann *et al.* (1974) and Imajima (1987). In the Santa Maria Basin specimens, these setae were mostly broken near the point where they emerge from the podial lobe. The heavily pigmented glandular pigment frequently reported for this species are not well-developed in the California specimens. An examination of specimens from the U.S. Atlantic slope revealed that this pigment is considerably more intense.

Type locality and type specimens. Davis Strait, off Greenland, 750 m (BMNH).

Distribution. Eastern Pacific, California to Mexico; West Greenland, Britain, Gulf of St. Lawrence to off North Carolina, off NE South America, Mediterranean. Subtidal, 45-2950 m.

Ancistrosyllis breviceps Hartman, 1963

Figure 10.2

Ancistrosyllis breviceps Hartman, 1963:13, fig. 1a-d; 1968:375, figs. 1-10.—Pettibone, 1966: 168, fig. 4a-d.

Description. A moderate sized species, up to 32 mm long and 4 mm wide (including parapodia). Body depressed, with parapodia longer than width of body. Body with minute papillae on body surface and dorsal and ventral cirri.

Prostomium small, with large palpophores and small palpostyles (Fig. 10.2A-B); with 3 antennae, each very short (Fig. 10.2A); lateral antennae not extending beyond palps; median antenna located at posterior border of prostomium. Tentacular segment distinct from prostomium, bearing 2 pairs of subequal tentacular cirri, each longer than antennae (Fig. 10.2A-B). Dorsal cirri on setiger 1 slightly longer than on following segments. Notopodia low with slender notoaciculae and prominent emergent hooked seta (Fig. 10.2F) first present from about setiger 13; earlier segments may have imbedded curved setae. Dorsal cirri short, cirriform, not extending beyond neuropodial lobe (Fig. 10.2C). Neuropodia elongate, with neuroaciculae and fascicle of 4-7 simple setae. Neurosetae variable in length with each having curved, hooked (?bifid) tips (Fig. 10.2D-E). Ventral cirri from setiger 1, each short, subulate, beginning on setiger 1. Pygidium unknown.

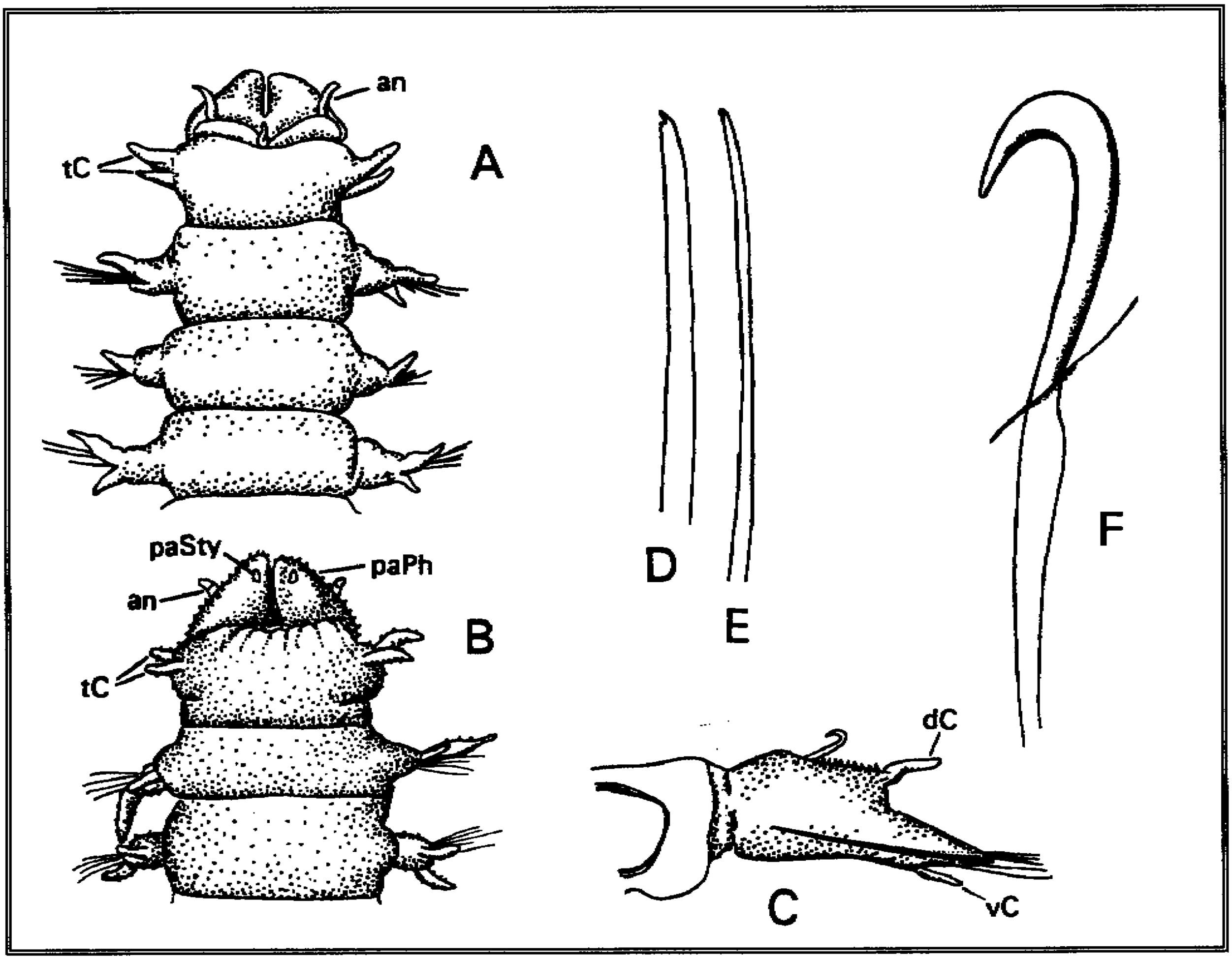

Figure 10.2. *Ancistrosyllis breviceps.* A, anterior end, dorsal view; B, same, ventral view; C, posterior middle parapodium; D-E, neurosetae; F, notopodial hook. (A, C, F, after Hartman, 1947; B, D-E, after Pettibone, 1966).

Biology. *Ancistrosyllis breviceps* has not been reported since its original discovery in submarine canyons off southern California. The species should be considered an upper continental slope species.

Remarks. *Ancistrosyllis breviceps* may be readily distinguished from *A. groenlandica,* its closest relative in the eastern Pacific, in having hooked setae first present from setiger 13-18 instead of 4-6 and by having elongate neuropodial lobes instead of ones that are short and conical.

Type locality and type specimen. California, Santa Monica Canyon, 706 m. Holotype: LACM-AHF.

Distribution. Southern California, 171-740 m.

Ancistrosyllis hamata (Hartman, 1960)

Figure 10.3

Pilargis hamatus [sic] Hartman, 1960:88, pl. 7, figs. 4-6; 1963:16.—Reish, 1968:76.
Ancistrosyllis hamata: Pettibone, 1966:168-169, fig. 5a-d.—Hartman, 1963:16; 1968:377, figs. 1-3.
— Katzmann *et al.*, 1974:8-12, figs. 3-4, 10B.
Ancistargis hamata: Salazar-Vallejo, 1986:198, pl. 1, figs. 1-2.

Description. Up to 30 mm long and 2 mm wide for 100 segments. Body dorsoventrally flattened, widest in middle, tapering both anteriorly and posteriorly; parapodia deeply cut. Body surface and dorsal and ventral cirri lightly papillated. Posterior segments dark reddish brown, covered with dark specks.

Prostomium with large palpophores and small palpostyles, with low conical lateral antennae, shorter than palps; median antenna absent; eyes lacking (Fig. 10.3A). Tentacular segment not visibly separated from prostomium, with 2 pairs of short subequal tentacular cirri. Dorsal cirri of setiger 1 slightly longer than on following segments. Notopodia with low inflated notoacicular lobes, with very short, conical dorsal cirri (Fig. 10.3B); stout curved emergent hooks (Fig. 10.3C) from setiger 4-7. Neuropodial lobes short, truncate, with retractile conical neuroacicular lobes, with bundle of about 7 simple neurosetae of 2 kinds: slender capillaries and thicker distally bifid setae (Fig. 10.3D). Ventral cirri small, conical, beginning on setiger 3 (Fig. 10.3B). Pygidium unknown.

Biology. Although collected from shallow continental shelf depths, *Ancistrosyllis hamata* has been reported by Hartman (1960) from the Santa Catalina Basin, San Pedro Basin, and Tanner Basin. On the continental slope, Hartman (1963) reported the species from several submarine canyons in depths of 420-976 m. The species should probably be considered an upper slope species.

Remarks. *Ancistrosyllis hamata* is readily distinguished from other California species in having two antennae instead of three, by having short, conical dorsal and ventral cirri instead of ones that are elongate and fusiform or cirriform, and by having the ventral cirri first present from setiger 3 instead of 1.

Type Locality and type specimens. California, deep basins. Holotype and paratypes: LACM-AHF.

Distribution. Southern California to western Mexico, 50-1500 m; Mediterranean, 20-50 m.

Genus *Pilargis* Saint-Joseph, 1899

Type species: *Pilargis verrucosa* Saint-Joseph, 1899

Diagnosis: Body long, flattened, ribbonlike, with parapodia deeply cut. Prostomium reduced, biarticulate palps with large ovoid palpophores and small papillar palpostyles, paired short lateral antennae, without median antennae. Tentacular segment with 2 pairs of tentacular cirri. Parapodia subbiramous. Notopodia with inflated cirrophores with internal notoaciculae, without notosetae; conical dorsal cirri more or less set off from dorsal cirrophores. Neuropodia conical lobes with stout neuroaciculae; neurosetae simple, variable in length; ventral cirri short, conical. Pygidium with or without short anal cirri. Proboscis unarmed, globular. Integument minutely papillated.

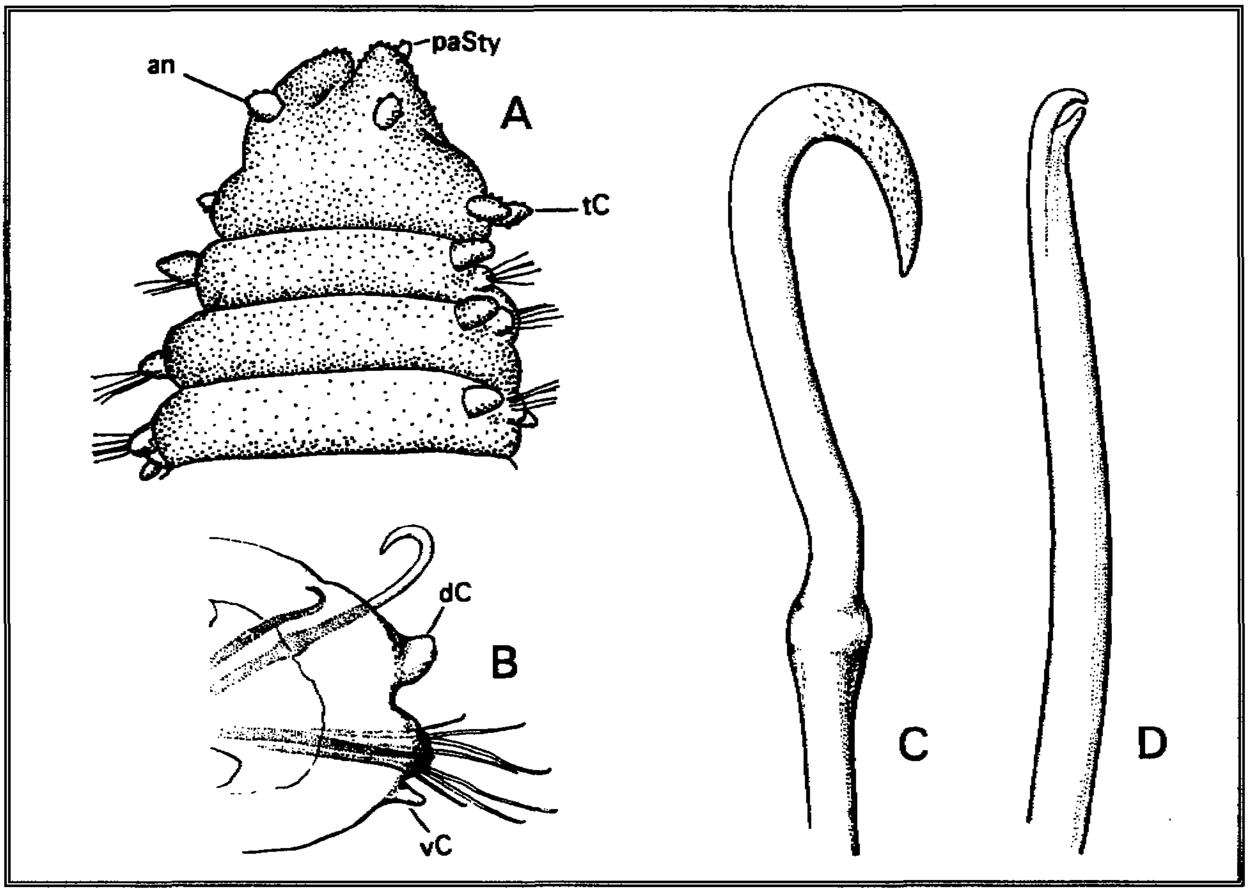

Figure 10.3. *Ancistrosyllis hamata*: A, anterior end, dorsal view; B, middle parapodium; C, notopodial hook; D, neuroseta. (A, after Pettibone, 1966; B-D, after Hartman, 1960).

Remarks. Three species of *Pilargis* have been reported from the eastern Pacific. *Pilargis berkeleyae* Monro (1933) and *P. maculata* Hartman (1947) were both described and compared by Hartman (1947). Pettibone (1966) synonymized *P. maculata* with *P. berkeleyae* with no explanation, but apparently considered that the parapodial differences emphasized by Hartman (1947) were due to contraction during preservation. However, in addition to the parapodial differences, *P. berkeleyae* has a heavily papillated body surface, whereas *P. maculata* has papillae limited to the prostomium, tentacular cirri, and structures associated with the parapodia, the body essentially lacks papillae. Both species are therefore retained in the present review. This point of view was also followed by Wolf (1984). The third species of *Pilargis* to be described from the eastern Pacific was *P. mirasetis* Fauchald, 1972 from deep-water off western Mexico. The holotype of this species has been reexamined and referred to a new genus in the family Nautiliniellidae (Blake, 1993; Chapter 11, this volume).

Pilargis berkeleyae **Monro, 1933**

Figure 10.4

Pilargis berkeleyi [sic] Monro, 1933:673, figs. 1-10.—Hartman, 1947:491, pl. 59, figs. 1-8; 1963:16; 1968:383, figs. 1-5.

Pilargis berkeleyae: Pettibone, 1966:161-164, (In Part), fig. 1 only.—Imajima, 1987:162-164, Fig. 7.—Wolf, 1984: 29-26 to 29.28, fig. 29.210.

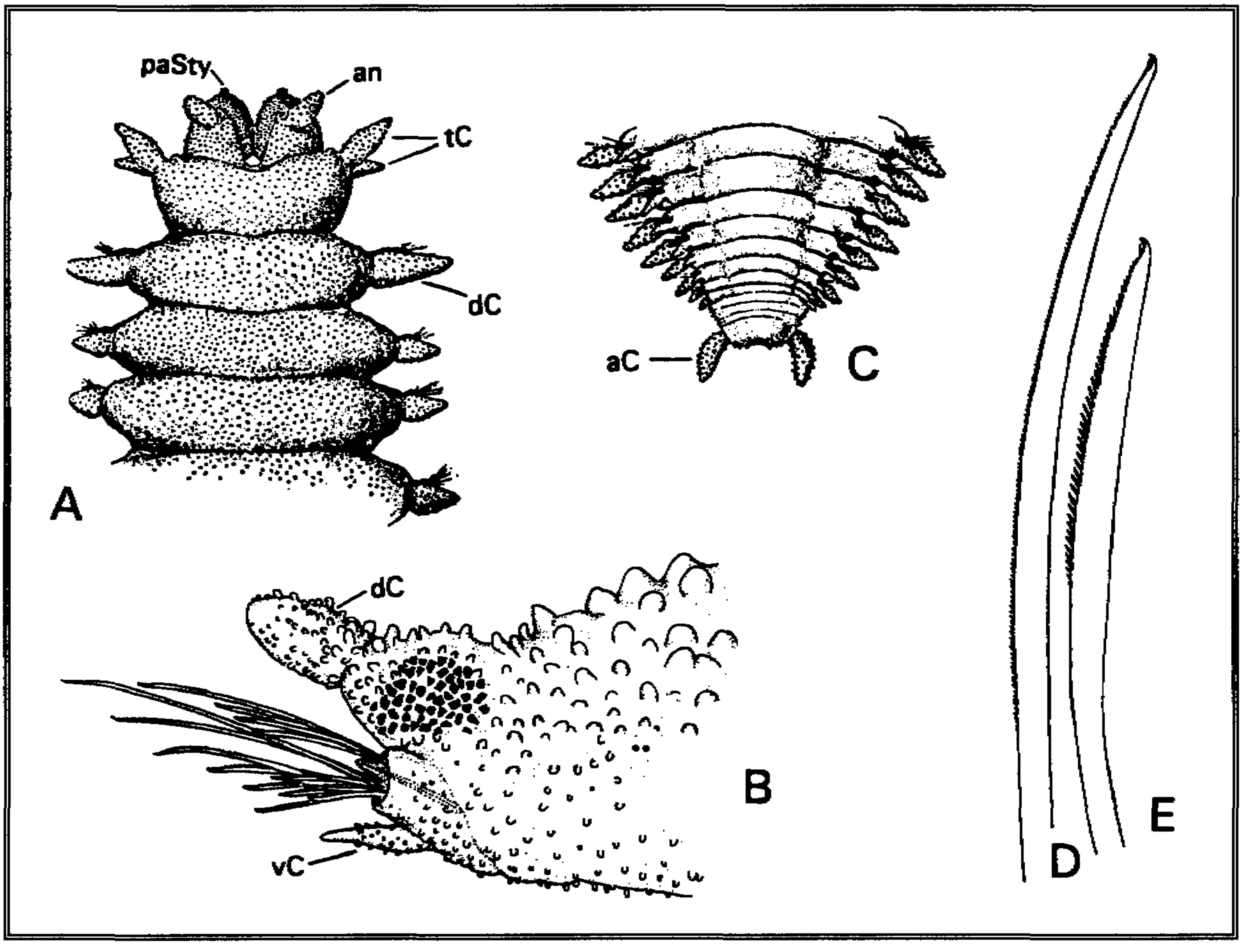

Figure 10.4. *Pilargis berkeleyae*. A, anterior end, dorsal view; B, middle parapodium, anterior view; C, posterior end, dorsal view; D, superior neuroseta; E, inferior neuroseta. (A, C, after Hartman, 1947; B, D-E, after Imajima, 1987).

Material examined. California, Santa Maria Basin, off Point Buchon, Sta. 12 (2); off Point Sal, Sta. PJ-23 (1); western Santa Barbara Channel, Sta. 85 (1).

Description. A large species, up to 300 mm long and 4 mm wide for about 500 segments. Body flattened, ribbonlike, tapering anteriorly and posteriorly; integument with papillae on body surfaces and parapodia; papillae of mid-dorsal region sometimes larger, more conspicuous. Color in alcohol: tan with darkly pigmented dorsal cirrophores and dark pigment on ventrum and scattered on prostomium and some anterior dorsal surfaces.

Prostomium small, with indistinct oval palpophores and minute palpostyles, with 2 short, club-shaped lateral antennae (Fig. 10.4A). Tentacular segment distinct, bearing 2 pairs of short papillated tentacular cirri, dorsal pair slightly longer than ventral pair (Fig. 10.4A). Dorsal cirri of setiger 1 larger than those of following segments; dorsal cirri from setiger 5-6 with thickened cirrophores with dark pigment. Notopodia with inflated dorsal cirrophores, somewhat variable in shape depending upon location along body and state of preservation; dorsal cirri oval to somewhat conical in shape (Fig. 10.4B); with notoaciculae, notosetae lacking (Fig. 10.4B). Neuropodia conical, bearing short cirriform ventral cirrus on all segments; with stout neuroaciculae and bundle of simple neurosetae; neurosetae variable in length, with finely serrated blades and hooked, sometimes bifid tips (Fig. 10.4D-E). Pygidium ringlike, with 2 heavily papillated anal cirri (Fig. 10.4C).

Biology. *Pilargis berkeleyae* has been reported from intertidal to continental shelf depths in California. The species appears to be best adapted to sediments with higher sand content.

Remarks. *Pilargis berkeleyae* is closely related to *P. maculata*, with which it has sometimes been considered a synonym. *P. berkeleyae* has papillae densely concentrated over the entire body, whereas, in *P. maculata*, the papillae are limited to the prostomium, tentacular cirri, and the parapodia. See additional comments under *P. maculata* (below).

Type locality. Washington, Friday Harbor, intertidal.

Distribution. Eastern Pacific, Washington to Southern California; western Pacific, Sea of Japan, Japan; Gulf of Mexico; West Africa; intertidal to 450 m.

Pilargis maculata Hartman, 1947

Figure 10.5

Pilargis maculata Hartman, 1947:494-496, pl. 60, figs. 1-5; 1968:385, 4 figs.
Pilargis berkeleyae: Pettibone, 1966:161-164, (in part), fig. 2 only. Not Monro, 1933.

Material examined. California, Santa Cruz, Oct. 1992, coll. Kinnetics Laboratories, Inc., as part of sewage outfall survey (1)

Description. A large species, recorded up to 140 mm in length for about 350 segments on an incomplete fragment by Hartman (1947). Body broad, flattened, ribbonlike, tapering anteriorly to small prostomium and posteriorly to narrow pygidium; integument with papillae limited to prostomium, palps, and parapodia, mostly lacking on rest of body (Fig. 10.5A-B). Color in alcohol: tan with dark glandular mass located on notopodium (Fig. 10.5C); this structure said to be red in life (Hartman, 1947), and nearly black when preserved; in Santa Cruz specimen, this structure completely surrounding cirrophore in Santa Cruz specimen; a similar, but considerably smaller spot is present ventrolaterally on the same parapodia.

Prostomium small, with 2 lateral lobes, each bearing short papillated antennae; palps consisting of oval palpophores, each bearing short, minute palpostyles (Fig. 10.5A-B). Tentacular segment distinct, bearing 2 pairs of short papillated and subequal tentacular cirri. Notopodia with thick conical, papillated dorsal cirri and bearing internal acicula. Dorsal cirri of setiger 1 larger than those of following segments; dorsal cirri consisting of thickened cirrophore with short papillate tip; dorsal cirri of remaining segments short, cirriform. Neuropodia conical, bearing short cirriform ventral cirrus on all segments; with stout neuroaciculae and bundle of simple neurosetae; neurosetae with finely serrated blades and hooked, sometimes bifid tips (Fig. 10.5D). Pygidium ringlike, probably with 2 anal cirri.

Biology. *Pilargis maculata* was originally reported from San Mateo County from rock crevices in intertidal sandstone outcrops. The species is probably associated with cryptic habitats among rocks or other types of hard substrates.

Remarks. *Pilargis maculata* is readily distinguished from *P. berkeleyae* by the lack of papillae over most of the body surfaces. The pigment spot on the ventral side of the parapodia may be diagnostic; the heavy glandular pigment surrounding the cirrophore is variable in its degree of development, but apparently similar in both species.

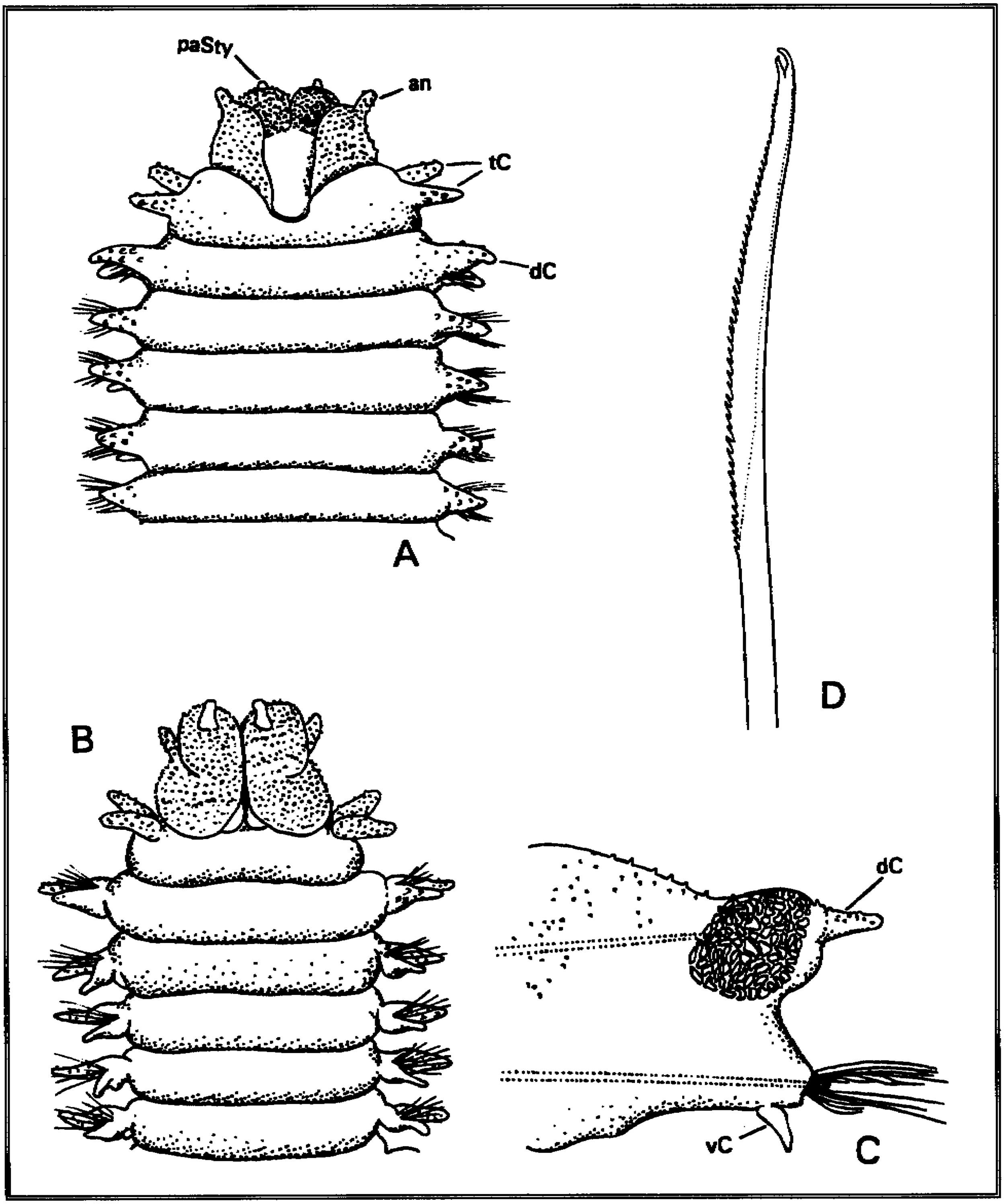

Figure 10.5. *Pilargis maculata*. A, anterior end, dorsal view; B, same, ventral view; C, middle parapodium; D, neuroseta. (all after Hartman, 1947).

Type locality. California, San Mateo County. Holotype: LACM-AHF Poly No. 74.

Distribution. Central California, intertidal to shallow subtidal.

Genus *Loandalia* Monro, 1936

Diagnosis. Body elongate, cylindrical, with some parapodia deeply cut; integument smooth, not papillated, may be areolated. Prostomium with a pair of palps bearing small, button-like palpostyles; antennae absent. Tentacular segment achaetous, distinct from prostomium and setiger 1; tentacular cirri absent. Parapodia subbiramous. Notopodia reduced, notopodial spines and aciculae absent or aciculae and slender setae present. Neuropodia well developed, with short ventral cirrus present or absent. Neurosetae including slender bristled setae; sometimes with heavy dark spines in anterior setigers. Ventral branchiae present in posterior segments. Pygidium large plaque with 2 anal cirri. Proboscis with distal papillae and proximal papillae present or absent.

Remarks. The status of *Loandalia* is confused. Emerson and Fauchald (1971) considered the genus to be monotypic based upon an examination of the holotype of the type-species, *L. aberrans* Monro, 1936, from west Africa. This species had dark neuropodial spines in two anterior setigers, ventral branchiae, and no antennae or tentacular cirri. Two additional species have since been described: *L. maculata* Intes and LeLoeuff (1975) also from west Africa and *L. riojai* Salazar-Vallejo (1986), from western Mexico. *Loandalia maculata* has anterior neuropodial spines and ventral branchiae, but also has emergent notopodial spines. *Loandalia riojai*, lacks anterior neuropodial spines, but has emergent notopodial spines and ventral branchiae. Salazar-Vallejo (1986) considered that the presence of the ventral branchiae was a character unique to *Loandalia* and apparently considered the neuropodial spines to be a species level character. As a further departure from the type species, *L. riojai* has notopodial spines, while *L. aberrans* lacks these setae. Because the presence or absence of emergent notopodial spines is a generic level character in pilargids, a definition which includes the presence or absence of this character in one genus is inconsistent. Regardless, the species which compose *Loandalia* differ as a group from *Parandalia* Emerson and Fauchald in having instead of lacking ventral branchiae and in the presence instead of absence of heavy neuropodial spines in setigers 1-2. No species of *Loandalia* have been reported from California, but Salazar-Vallejo's (1986) *L. riojai* is from western Mexico.

Genus *Litocorsa* Pearson, 1970

Diagnosis. Body elongate, slender, cylindrical, parapodia not deeply cut; integument smooth. Prostomium elongate, narrow, with palps fused dorsally; antennae present or absent. Tentacular segment achaetous, not distinctly separated from prostomium; 2 pairs of small tentacular cirri present. Parapodia biramous; notopodia each with emergent straight acicular spine and slender internal aciculum; neuropodia with 1-2 stout emergent spines and slender serrated setae with fine tips. Pygidium with pair of slender anal cirri.

Remarks. Only two species of *Litocorsa* are known: *L. stremma* Pearson, the type species, originally recorded from the west coast of Scotland and later from the Mediterranean (Katzmann *et al.*, 1974), and *L. antennata* described by Wolf (1986) from Puerto Rico and the Gulf of Mexico from Florida to Texas. To date, the genus has not been reported from the Pacific.

Wolf (1986) was the first describe the true structure of the prostomium of *Litocorsa* and determined that the pointed prostomium first described by Pearson (1970) was in fact the result of the dorsal fusion of the palps. This structure is unique in the Pilargidae.

Genus *Sigambra* Müller, 1858

Type species. *Sigambra grubii* Müller, 1858

Diagnosis. Body long, flattened, with deeply cut parapodia; integument smooth, not papillated, may be areolated or wrinkled. Prostomium with 2 biarticulate palps and 3 antennae, each longer than palps. Proboscis cylindrical, with distal circlet of large conical papillae or indistinctly papillate. Tentacular segment achaetous, more or less fused to prostomium and setiger 1; bearing 2 pairs of tentacular cirri. Parapodia subbiramous. Notopodia with aciculae and stout emergent hooked setae. Dorsal cirri long, slender, or flattened leaflike, extending beyond neuropodia. Neuropodia conical, with neuroaciculae and simple neurosetae; neurosetae capillary, smooth and spinous. Ventral cirri shorter than dorsal cirri, subulate. Pygidium with paired long anal cirri.

Remarks. This genus was resurrected and defined by Pettibone (1966). Four species are known from the eastern Pacific, of which three occur in the Santa Maria Basin. Most of the species in this genus were formerly assigned *Ancistrosyllis*. Species of *Sigambra* are readily distinguished from *Ancistrosyllis* by having long, well-developed antennae and tentacular cirri instead of ones that are reduced and short.

***Sigambra tentaculata* (Treadwell, 1941)**

Figure 10.6

Ancistrosyllis tentaculata Treadwell, 1941:1, figs. 1-3.—Hartman, 1960:88; 1961: 15; 1963:13; 1965:71.

Sigambra tentaculata: Pettibone, 1966: 182-186, figs. 14-15. —Hartman, 1968:391, figs. 1-3.—Banse and Hobson, 1974:50.—Katzmann *et al.*, 21.—Gardiner, 1976:121, fig. 9c—Wolf, 1984:29-8 to 29-10, fig. 29-6.—Salazar-Vallejo, 1986:202.

Material examined. California: Santa Maria Basin, Sta. R-8 (8), Sta. 21 (12); western Santa Barbara Channel, Sta. 91 (2).

Description. A moderate sized species, up to 15 mm long and 2 mm wide for about 90 segments. Body slightly inflated anteriorly, gradually tapering posteriorly; dorsoventrally flattened, with parapodia deeply cut; integument smooth, papillae lacking. Color in alcohol: light tan.

Prostomium somewhat variable, recessed to different degrees into tentacular segment and inflated or shrunken probably depending upon preservation; palps biarticulate, with large palpophores vaguely separated from prostomium, with small digitiform palpostyles; antennae long, smooth, filiform, with median antenna located on posterior part of prostomium and extending posteriorly to about setiger 6; lateral antennae positioned somewhat more anteriorly, and about one-half length of median antenna (Fig. 10.6A); eyes absent, but sometimes pigmented areas present lateral and posterior to antennae. Proboscis with 14-16 papillae around distal opening, with additional basal papillae irregularly distributed. Tentacular segment longer than following segment, with 2 pairs of thin, subequal, cirriform tentacular cirri (Fig. 10.6A). Dorsal cirri of setiger 1 about twice as long and considerably thinner than dorsal cirri on subsequent segments, almost appearing to be an additional tentacular cirrus; subsequent dorsal cirri widest basally, tapering distally to pointed tips. Notopodia low, conical, with notoaciculae curving distally; recurved notopodial hooks from setiger 4 (Fig. 10.6B-C); sometimes with an additional emergent tapering seta (Wolf, 1984). Neuropodia conical, with neuroaciculae and numerous simple neurosetae; ventral cirri slender, subulate, shorter than setal lobes (Fig. 10.6B); ventral cirri absent from setiger 2. Neurosetae

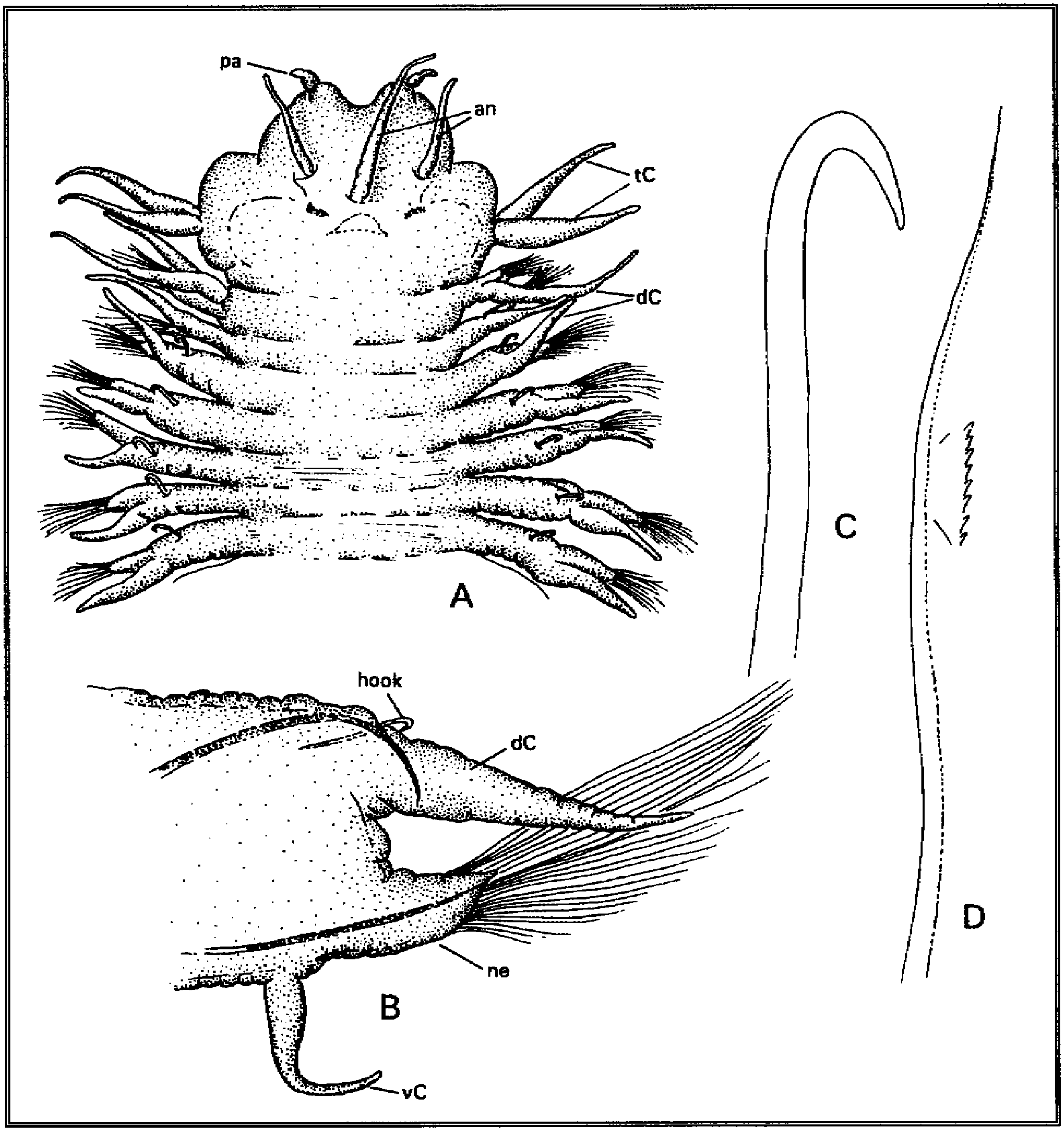

Figure 10.6. *Sigambra tentaculata*: A, anterior end, dorsal view; B, middle parapodium, posterior view; C, notopodial hook; D, neuroseta.

variable in length, with longest ones smooth to finely serrated capillaries (Fig. 10.6D) and shortest ones with prominent serrations. Pygidium rounded, with 2 long anal cirri.

Biology. Recorded from intertidal depths to the deep sea; in mud, sand, and sand mixed with mud and shell fragments (Wolf, 1984).

Remarks. Records from great depths should be critically re-examined. According to Hartmann-Schröder (1974), *S. parva* Day, 1963 and perhaps *S. hanokai* Kitamori, 1960 are synonyms of *S. tentaculata*. These possibilities are also discussed by Katzmann *et al.* (1974).

Among the eastern Pacific species, *S. tentaculata* is distinguished by having three antennae that are subequal, or the median antenna is only slightly larger than the lateral ones. In contrast, both *S. bassi* and *S. setosa* have a median antenna which is considerably longer than the lateral ones. Hooked setae begin in setiger 3-4 in *S. tentaculata* and *S. setosa* and in setiger 11-15 in *S. bassi*. *S. tentaculata* differs from *S. setosa* in lacking extra straight or curved spines accompanying the curved notopodial spines.

Type locality and type specimen. Long Island, New York. Holotype: AMNH 2893.

Distribution. Eastern Pacific, California continental shelf; off New England, 400-2900 m; Virginia, Chesapeake Bay to North Carolina; Northern Gulf of Mexico, 15-117 m; NE South America; Mediterranean; ?Japan. Intertidal to 5120 m.

Sigambra bassi (Hartman, 1945)

Figure 10.7

Ancistrosyllis bassi Hartman, 1945:15; 1947:501, pl. 61, figs. 1-7; 1951:36, pl. 11, figs. 1-6.
Sigambra bassi: Pettibone, 1966:186, fig. 16a-f.—Hartman, 1968:389, figs. 1-5.—Gardiner, 1976:123, fig. 9d-f.—Wolf, 1984:29-10 to 29-12, fig. 29-8.

Material examined. California: western Santa Barbara Channel, Sta. 85 (1).

Description. A moderate sized species, up to 40 mm long, 2 mm wide, for about 145 segments. Body wide anteriorly, tapering posteriorly, dorsoventrally flattened, with parapodia deeply cut; integument smooth, papillae lacking. Color in alcohol: light tan; color in life: greenish yellow (Pettibone, 1966).

Prostomium with biarticulate palps with large palpophores vaguely separated from prostomium, bearing small digitiform palpostyles; median antenna long, arising from posterior part of prostomium, extending for 9-12 segments; lateral antennae shorter, arising more anteriorly than median one, extending only to about first segment (Fig. 10.7A). Proboscis with circlet of 14 conical papillae (Fig. 10.7B). Tentacular segment larger than following setigers, bearing 2 pairs of cirriform tentacular cirri, each about same length as lateral antennae (Fig. 10.7A-B). Dorsal cirri of setiger 1 long, similar to median antenna (Fig. 10.7A). Parapodia subbiramous. Notopodia low, bearing heavy curved hooks from about setiger 11-15 (Fig. 10.7D-E); sometimes with emergent aciculae (Fig. 10.7D), these either straight or slightly curved; dorsal cirri long, extending far beyond setal lobes. Neuropodia conical, with neuroaciculae and numerous slender capillary neurosetae, shorter ones with fine serrations; ventral cirri extending slightly beyond setal lobes (Fig. 10.7D), lacking on setiger 2. Pygidium with pair of long anal cirri.

Biology. The species is known from intertidal to shallow subtidal depths (to 113 m, present record) in sandy sediments.

Remarks. *Sigambra bassi* is readily distinguished from other eastern Pacific congeners by having the notopodial hooks first present from setiger 11-15 instead of 3-10.

Type locality and type specimens. Southern Florida, intertidal, sandy shore. Holotype and paratypes LACM-AHF.

Distribution. Central and southern California; Gulf of Mexico, Texas to Florida; North Carolina, intertidal to 113 m.

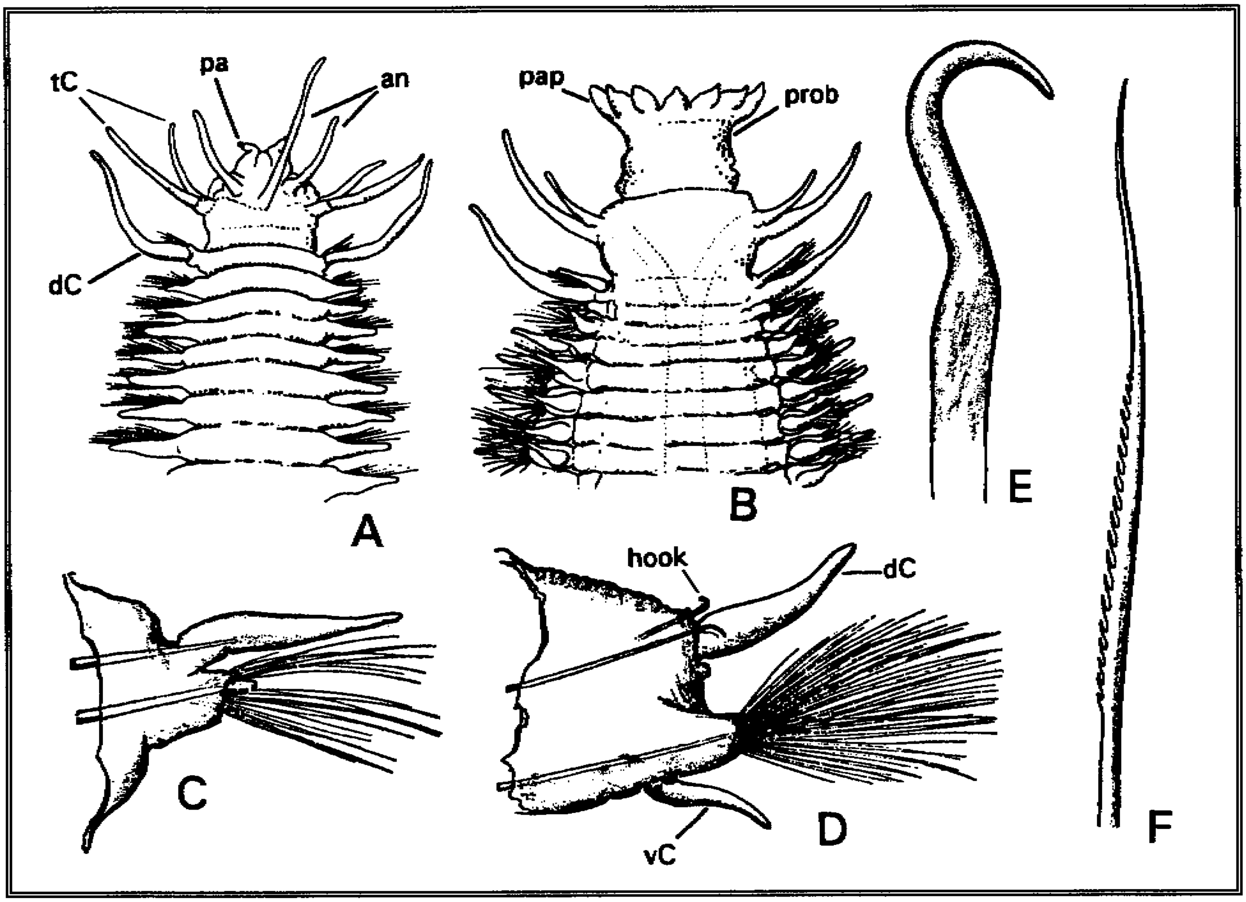

Figure 10.7. *Sigambra bassi*: A, anterior end, dorsal view; B, same, ventral view with proboscis everted; C, parapodium of setiger 2; D, posterior parapodium; E, notopodial hook; F, neuroseta. (from Hartman, 1947).

Sigambra setosa **Fauchald, 1972**

Figure 10.8

Sigambra setosa Fauchald, 1972:62-64, pl. 7, figs. a-c.—Salazar-Vallejo, 1986:201, pl. 2, figs. 15-16.

Material examined. California: Santa Maria Basin, Sta. 10 (1); western Santa Barbara Channel 102, (1); off San Francisco, Gulf of the Farallones, 2830-2855 m (5).

Description. A relatively small species, up to about 20 mm long, 1 mm wide, for about 60 segments. Body widest anteriorly, cylindrical, then tapering posteriorly becoming dorsoventrally flattened, with parapodia deeply cut; integument smooth, papillae lacking. Color in alcohol: light tan, with some dusky pigment on prostomium, including 2 deeply imbedded pigment spots resembling eyes.

Prostomium recessed to varying degrees into peristomium, probably due to preservation; with biarticulate palps with large palpophores distinctly separated from prostomium, bearing small digitiform palpostyles (Fig. 10.8A); median antenna arising from posterior part of prostomium, extending for twice length of prostomium; lateral antennae also arising from posterior part of prostomium, shorter than median antenna. Proboscis with 8 papillae around distal opening. Tentacular segment and first setiger longer than

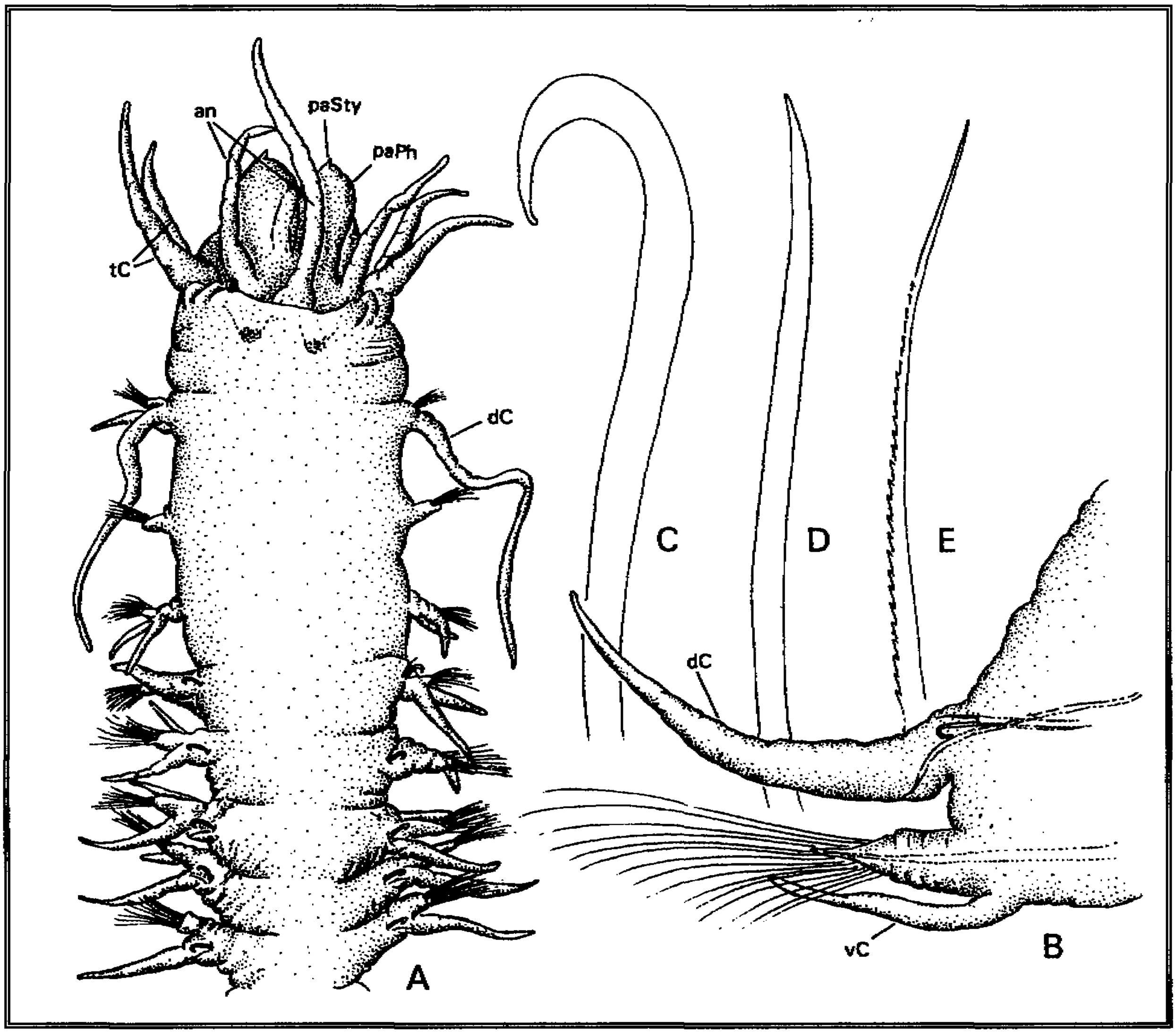

Figure 10.8. *Sigambra setosa*: A, anterior end, dorsal view; B, parapodium, anterior view; C, notopodial hook; D, straight, pointed notoseta; E, neuroseta.

following segments. Tentacular segment bearing 2 pairs of cirriform tentacular cirri, each about same length as lateral antennae (Fig. 10.8A). Dorsal cirri of setiger 1 extremely long, similar to median antenna (Fig. 10.8A). Parapodia subbiramous to biramous. Notopodia bearing heavy curved hooks from setiger 4 (Fig. 10.8C); accompanied by 1-2 thickened pointed setae (Fig. 10.8D) and single imbedded aciculum (Fig. 10.8B); pointed setae present on majority of segments especially in middle and posterior regions, usually lacking anteriorly. Dorsal cirri long, extending far beyond setal lobes (Fig. 10.8B). Neuropodia tapering to acute tip, bearing neuroaciculae and fascicle of numerous slender, finely serrated capillary neurosetae (Fig. 10.8E); ventral cirri extending beyond setal lobes, lacking on setiger 2. Pygidium with pair of long anal cirri.

Biology. This species occurs in outer continental shelf to lower slope depths in fine silty muds.

Remarks. *Sigambra setosa* appears to be intermediate between *S. bassi* and *S. tentaculata* in the distribution of characters. *S. setosa* and *S. bassi* both have a long median antenna, although it is longest in *S. bassi; S. tentaculata* has all three antennae subequal. *S. setosa* and *S. tentaculata* have notopodial hooks first present on an anterior setiger (3-4), while in *S. bassi,* these hooks begin on setiger 11-15. Extra emergent notosetae have been reported for all three species. In *S. bassi*, the occasional extra notosetae are emergent aciculae according to Pettibone (1966); in *S. tentaculata*, the emergent setae are rare, but may include an occasional capillary; in *S. setosa*, there is usually an extra 1-2 stiff pointed emergent setae with the hooks along with an imbedded acicula.

California specimens of *S. setosa* differ from the original account of *S. setosa* by Fauchald (1972) from deep-water off western Mexico in that the median antenna is clearly longer than the lateral ones. In contrast, the antennae on Fauchald's specimens were reported to be subequal. The consistent appearance of extra notosetae is here considered to be a more important taxonomic character than the length of the antennae, and the species determination is based upon this feature.

Type locality and type specimen. Western Mexico, Gulf of California, 1823 m. Holotype: LACM-AHF.

Distribution. Eastern Pacific, Mexico, in the Gulf of California 1784-2449 m; Santa Maria basin, 99-591 m; off San Francisco, 2830-2855 m.

Genus *Synelmis* Chamberlin, 1919

Diagnosis. Body long, subcylindrical, with parapodia sharply separated from body. Integument smooth, iridescent. Prostomium small, with paired biarticulate palps bearing small digitiform palpostyles; 3 antennae present. Proboscis cylindrical. Tentacular segment with 2 pairs of tentacular cirri. Parapodia subbiramous. Notopodia with notoaciculae and stout, emergent, straight or slightly curved acicular spine; dorsal cirri short, subulate. Neuropodia subcylindrical, with neuroaciculae and simple neurosetae; neurosetae including smooth, straight acicular spines or spines with teeth or serrations, furcate setae, and serrated setae that taper to entire or bifid tips. Pygidium with paired short anal cirri.

Remarks. Pettibone (1966) redefined *Synelmis* and proposed several species-level synonymies as part of her description of *S. albini*. The most recent account of this genus is by Wolf (1986) who described a new species from Puerto Rico and another from Texas and Florida. Wolf considered that Pettibone's materials included several species. *Synelmis albini* (Langerhans, 1881) has been reported from intertidal sediments at La Jolla in southern California by Hartman (1947) as *Ancistrosyllis rigida* (*fide* Pettibone, 1966). No specimens have been taken in the study area of this Atlas.

Genus *Parandalia* Emerson and Fauchald, 1971

Diagnosis. Body elongate, cylindrical, with deeply cut parapodia; integument smooth to areolated or wrinkled. Prostomium small, indistinct, with a pair of well-developed biarticulate palps bearing button-shaped palpostyles; antennae entirely absent. Eyes present or absent; when present, located dorsally on an anterior segment, not prostomium. Proboscis cylindrical, with several distal sensory papillae; proximal surface smooth. Peristomial segment indistinctly separated from prostomium; tentacular cirri entirely absent. Parapodia uniramous anteriorly, and subbiramous to biramous posteriorly. Notopodia with thick, straight, crystal-clear spine emerging from median and posterior segments, accompanied by 1-2 capillary setae; dorsal cirri absent. Neuropodia tapering to bluntly rounded tips, each bearing fascicle of geniculate, pointed setae; ventral cirri present as small, papillar lobes. Pygidium expanded, inflated, bearing 2-3 short, blunt anal cirri.

Remarks. *Parandalia* was separated from *Loandalia* on the basis of the presence of notopodial spines in the former and their absence in the latter (Emerson and Fauchald, 1971). However, new species of *Loandalia* described by Intes and LeLeouf (1975) and Salazar-Vallejo (1986) have dorsal spines.

According to these authors *Loandalia* is a distinct genus because it has ventral branchiae and heavy neuropodial spines on setigers 1-2.

As presently defined, *Parandalia* contains seven species, of which four occur in the eastern Pacific. *Parandalia ocularis*, the type species, is present in the Santa Maria Basin.

Parandalia ocularis Emerson and Fauchald, 1971

Figure 10.9

Parandalia ocularis Emerson and Fauchald, 1971:19-21, figs. 1-5.—Salazar-Vallejo, 1986:205.

Material examined. California: Santa Maria Basin, Sta. R-1 (1); off Point Arguello, Sta. 64, 59 m (1).

Description. A moderate sized species, up to 41 mm long and 0.5 mm wide for about 40 setigerous segments. Body widest anteriorly (first 6 segments), then narrowing after about 20 segments and tapering to posterior end. Body cylindrical throughout, with anterior region areolated and somewhat dorsolaterally compressed. With pair of subcutaneous eyes present dorsally between setigers 2-3. Color in alcohol: light tan, with some reddish brown pigment on parapodia.

Prostomium inconspicuous, with pair of dorsally directed biarticulate palps (Fig. 10.9A); each palp with palpophore tipped with single minute, knoblike palpostyle. Peristomium inconspicuous; tentacular cirri entirely lacking. Proboscis large, cylindrical, muscular, with 4 small distal papillae (Fig. 10.9B).

Setigers 1-2 uniramous, subsequent parapodia biramous; first 3 notopodia on setigers 3-5 reduced relative to following segments, each bearing 1-2 simple setae; notopodia becoming fully developed by about setiger 9 where a single large, clear acicula (?or spine) begins to protrude, becoming more exposed and prominent in following segments; each protruding acicular seta accompanied by 1-2 simple geniculate capillaries throughout (Fig. 10.9C). Anterior neuropodia reduced, becoming fully developed by setigers 6-7; small papillate ventral cirrus present from setiger 8. Neurosetae number 4-7 per fascicle; each seta with blade provided with transverse rows of slender teeth, resembling camerated setae of orbiniids (Fig. 10.9E). Pygidium a rounded anal plaque, bearing 3 short anal cirri (Fig. 10.9D).

Biology. Reported from continental shelf depths in coarse sands to fine silts, 50-150m.

Remarks. The genus *Parandalia* has recently been reviewed by Salazar-Vallejo (1990). Out of seven valid species, *Parandalia ocularis* belongs to a group of five species that have some anterior uniramous parapodia. In this group, the species has somewhat reduced fascicles of neurosetae in that only seven setae in a single series are present. In contrast, four related species have up to 16 setae in a double series. Four species of *Parandalia* are known from the eastern Pacific: *P. bennei* Solís-Weiss, 1983 from Mazatlan Bay, Mexico, 3-25 m; *P. gracilis* (Hartmann-Schröder, 1959) from estuarine areas of El Salvador; *P. fauveli* (Berkeley and Berkeley, 1941), recorded from southern California to Alaska in intertidal to shallow water, in mud; and *P. ocularis* from western Mexico to central California, from shallow subtidal to outer shelf depths. *P. ocularis* is the only eastern Pacific species having eyes.

Type locality and type specimens. California, Santa Barbara Channel, 45 m. Holotype: LACM-AHF.

Distribution. Eastern Pacific, southern and central California continental shelf, 50-150 m.

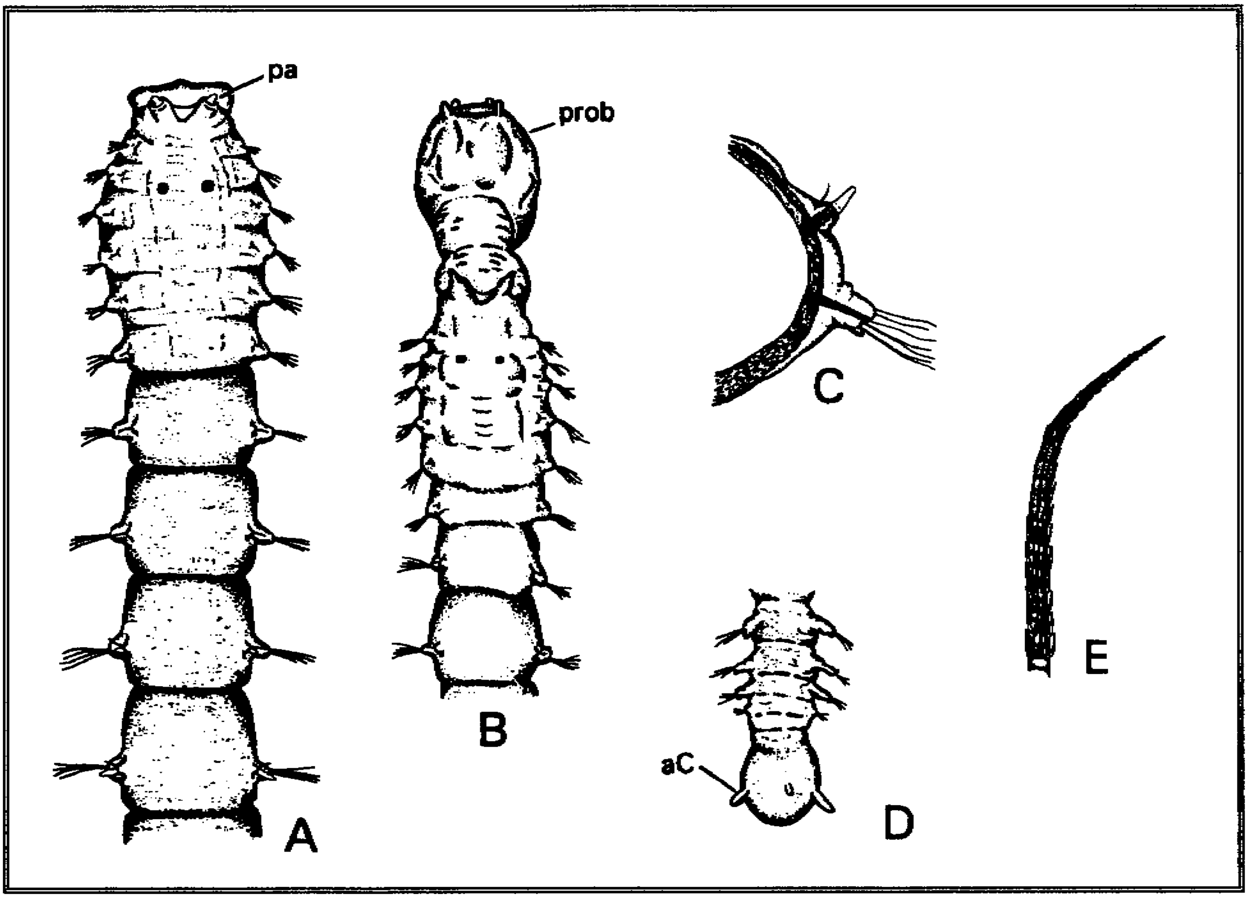

Figure 10.9. *Parandalia ocularis*: A, anterior end, dorsal view; B, same, with proboscis everted; C, middle parapodium, anterior view; D, posterior end, dorsal view; E, neuroseta. (from Emerson and Fauchald, 1971).

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11. FAMILY NAUTILINIELLIDAE MIURA AND LAUBIER, 1990

by

James A. Blake[1]

Introduction

The nautiliniellids are a small group of pilargid-like polychaetes that live as commensals or parasites of deep-sea bivalve molluscs. Although only first described in 1989, nine species have already been identified, and there are probably many additional species awaiting discovery. Individual species tend to be small and have probably been overlooked by biologists owing to their relationship with molluscs. The morphology of the prostomium and types of setae have proven to be quite variable and the status of this new group is not fully understood.

Morphology

The bodies of nautiliniellids are elongate, cylindrical, and smooth. The prostomium is variable and may have one to two pairs of antennae, a median antenna, or antennae may be entirely absent; eyes are absent. Distinct palps are lacking. The foregut is expanded into a muscular pharynx that has been termed a proventriculus by Miura and Laubier (1989, 1990); this pharynx is partially eversible (Blake, 1990). The peristomial segment is well developed with distinct tentacular cirri in two genera (*Santelma* and *Flascarpia*), reduced in three genera (*Petrecca, Laubierus*, and *Miura*), and lacking in three other genera (*Nautiliniella, Shinkai*, and *Natsushima*). Parapodia are subbiramous to sesquiramous with reduced notopodia usually having an imbedded acicula; neuropodia have internal aciculae and one to several simple hooked spines. The pygidium is simple and lacks appendages.

Taxonomic History

The taxonomic history is the Nautiliniellidae is very recent. The first published description was by Miura and Laubier (1989) who described *Nautilina calyptogenicola* from a deep-sea vesicomyid clam collected from the Japan Trench at a depth of 5960 m. This species was characterized by having two pairs of small antennae, short dorsal and ventral cirri, and a single, large protruding neuropodial hooked spine. The authors assigned this new genus to a new family, the Nautilinidae. In a subsequent paper, the same authors renamed the genus and subfamily *Nautiliniella* and Nautiliniellidae, because the earlier names were preoccupied in the Cephalopoda (Miura and Laubier, 1990). In this same paper, the authors described two additional new genera and species: *Shinkai sagamiensis* Miura and Laubier from the bivalve, *Calyptogena soyoae*; and *Natsushima bifurcata* Miura and Laubier from *Solemya* sp. Both of the latter species were collected at the Hatsushima cold-seep site off Japan in depths of 1130-1170 m. The genus *Shinkai* was superficially similar to *Nautiliniella*, but differed in having up to 8 hooks per neuropodium instead of one and in having only a single antenna instead of two. *Natsushima* differed from the other two genera in having two types of neuropodial spines instead of one. Blake (1990) described another genus and species, *Petrecca thyasira,* from the mantle cavity of a thyasirid clam, *Thyasira insignis* collected from seep-like communities off Newfoundland. *Petrecca* differed from the previously described genera in having greatly

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elongated notopodia and a single, achaetous tentacular segment. Miura and Ohta (1991) described *Shinkai longipeda* from the mantle cavity of *Calyptogena* sp. collected at active hydrothermal vents in the Okinawa Trough in 1400 m. This species appears to be transitional between the genera *Shinkai* and *Petrecca* in the development of the notopodia.

Four additional species and genera were described from the Gulf of Mexico and the eastern Pacific by Blake (1993). These North American taxa were considerably different the previously described genera and serve to confuse the status of this heterogenous group of species. All of the new genera have an achaetous peristomial segment with either small or well-developed tentacular cirri. *Miura spinosa* was collected as part of the MMS Phase II Monitoring program. This species lacks antennae, has a thickened achaetous notopodial lobe, and a fascicle of small neuropodial spines. *Pilargis mirasetis* Fauchald, 1972, was reexamined and referred by Blake (1993) to a new genus *Santelma*. *S. miraseta* comes from deep water off western Mexico. This species has three antennae, two pairs of tentacular cirri, a single large protruding acicula, and a fascicle of very fine bidentate setae. *Laubierus mucronatus* comes from mussels at the methane seep communities on the Florida Escarpment in about 3300 m. This new taxon has two small antennae, a long notopodial lobe with large acicula, and both large and small types of neuropodial spines. The fourth genus and species described by Blake (1993) was *Flascarpia alvinae*, also from the methane seep community on the Florida Escarpment. This species has two antennae, two well-developed tentacular cirri, a reduced notopodium that may function as a gill, and a fascicle of heavy neuropodial spines.

Blake (1993) acknowledged the heterogeneity of the eight genera now assigned to the Nautiliniellidae and it is likely that considerable revision will be in order once additional specimens become available for study. Blake identified two distinct groups of species: (1) Genera lacking a peristomial segment (*Nautiliniella, Shinkai*, and *Natsushima*) and (2) genera having a peristomial segment or achaetous segment (*Petrecca, Miura, Laubierus, Flascarpia,* and *Santelma*). All of these taxa are united in the absence of notosetae, presence of simple spinous neurosetae, absence of anal cirri, and lack of palps. They are closely allied to the pilargids, but cannot be assigned to that family because of the lack of palps. Further, other more subtle aspects such as the nature of the setae differ considerably from those of the Pilargidae.

Biology

Members of the Nautiliniellidae are all believed to be associated with the mantle cavities of deep-sea bivalve molluscs. There is insufficient data to determine if the worms are commensals or parasites with the clams. Five species have been described from cold-seep communities (Miura and Laubier, 1989, 1990; Blake, 1990, 1993), while a sixth comes from active hydrothermal vents (Miura and Ohta, 1991). The Santa Maria Basin species, *Miura spinosa*, was found at an upper slope or sea valley station at a depth of 565 m. The specimen was not associated with a bivalve when it was sorted from the mud, but may have been washed from a bivalve in the same sample. Infestation rates of nautiliniellids may be fairly high when they are present. For example, out of 10 specimens of *Thyasira insignis* collected from off Newfoundland, five were found with a specimen of *Petrecca thyasira*. These clams were each relatively small, ranging from 29 × 30 cm to 37 × 43 cm in width × length. The worms themselves were up to 16 mm long and thus occupied a considerable space among the gill filaments of the clams. Infestation data is not available for other species.

Description of Species

Genus *Miura* Blake, 1993

Diagnosis: Body oval in cross section, widest anteriorly, tapering posteriorly. Prostomium rounded; antennae and eyes lacking. Pharynx weakly muscularized, prominent in first 3 segments. Peristomial segment achaetous, smaller than following setigers with 2 pair of short lobes present. Parapodia sesquiramous, with thickened notopodial lobe, acicula not observed; neuropodium with fascicle of 5-6 simple hooks and internal acicula; ventral cirrus lacking. Pygidium unknown.

Remarks: The genus *Miura* differs from other nautiliniellids in lacking antennae and notopodial aciculae. A single species, *Miura spinosa*, is known and occurs in the Santa Maria Basin.

Miura spinosa Blake, 1993

Figure 11.1

Miura spinosa Blake, 1993:148-149, fig. 1.

Material examined. California: Santa Maria Basin, off Point Sal, Sta. R-7 (holotype, USNM 148677).

Description. A small species, holotype an anterior fragment measuring 1.5 mm long, 0.7 mm wide for 10 setigers. Color in alcohol: light tan with scattered orange pigment spots. Body subcylindrical to oval in cross section, widest through first 6-7 setigers, then tapering posteriorly.

Prostomium twice as wide as long, broadly rounded anteriorly (Fig. 1A); antennae and eyes lacking. Mouth with broad ventral lip (Fig. 1B); pharynx weakly muscularized, prominent in first 3 segments (Fig. 1A). Peristomial segment achaetous, smaller than following setigers, with 2 pairs of small lateral lobes. Parapodia sesquiramous, with thickened notopodial lobe lacking internal acicula; neuropodium with fascicle of 4-6 simple hooks; each hook sharply pointed, with subapical notch and boss (Fig. 1D); acicula present, with distal end slightly protruding on some setigers; ventral cirrus thick, rounded lobe. Pygidium unknown.

Biology. *Miura spinosa* was collected at a depth of 565 m in a sea valley in the Santa Maria Basin that has very fine silty sediments with high clay content. Station R-7 was also recorded to have low dissolved oxygen concentrations in the near bottom water of $\overline{x}$=0.898 ml/L, SD=±0.152. At present, it is not known if this animal might be associated with bivalves.

Remarks. The shape of the setae of *Miura spinosa* is similar to those of *Santelma miraseta*, with which this species was identified in the Phase II monitoring program. Originally described as a species of *Pilargis*, Blake (1993) determined that *P. miraseta* was more similar to the nautiliniellid genera and named the new genus and transferred the species. *S. miraseta* differs from *M. spinosa* in having short notopodial lobes instead of ones that are large and thick, in having long protruding neuropodial aciculae instead of lacking them, and in having two distinct tentacular cirri instead of two pair of short, stubby lobes.

Distribution. California, upper continental slope depths, 565 m.

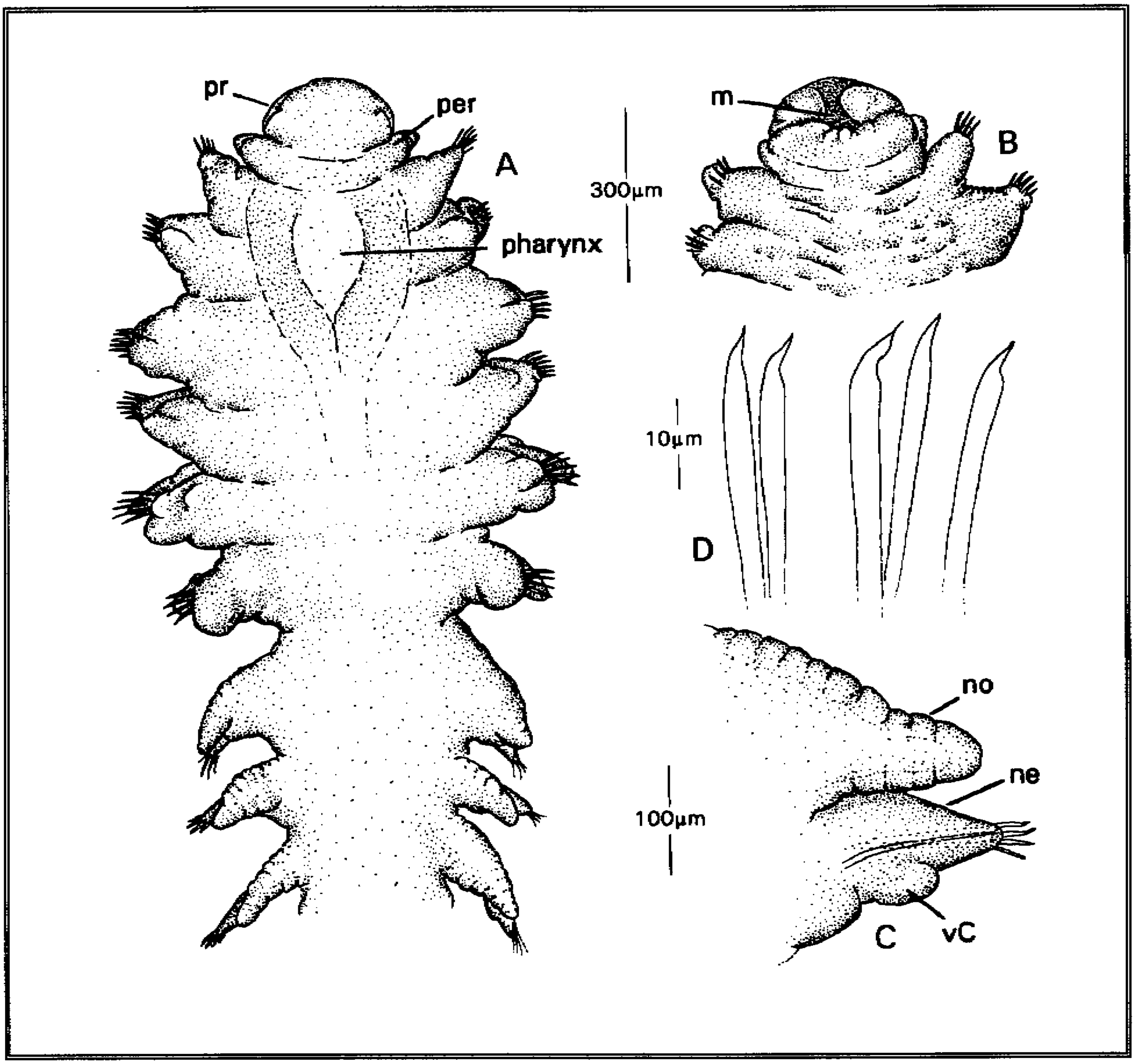

Figure 11.1. *Miura spinosa*: A, anterior end, dorsal view; B, same, ventral view; C, tenth parapodium, posterior view; D, setae.

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12. FAMILY NEREIDIDAE JOHNSTON, 1845

by

Brigitte Hilbig[1]

Introduction

Nereidids are cylindrical worms of greatly varying lengths ranging from only a few millimeters to more than 20 centimeters; they are usually quite robust and preserve well, except for the far posterior part of large specimens and occasionally deciduous tentacular cirri. Although the family contains a great number of genera and species with quite variable morphologic features, nereidids are easily recognized by the presence of two often massive palps on the prostomium and four pairs of tentacular cirri arising from the anterolateral corners of the peristomium.

Morphology

The prostomium is either pyriform or rounded and may be cleft anteriorly; it bears two antennae (rarely one), two biarticulate palps (Fig. 12.2A), and two pairs of eyes, which may be absent in deep-sea forms. The pharynx is eversible to form a proboscis that is adorned with a pair of fang-shaped, often serrated terminal jaws. It consists of two rings, a proximal or oral ring and a distal or maxillary ring; these rings may be equipped with groups of papillae or hardened paragnaths of various sizes, shapes, and distributional patterns that are of great taxonomic importance (Fig. 12.1A-D). It is therefore often necessary to dissect the proboscis to identify species. The incision should be made ventrally, slightly off to one side to keep median structures intact, from the mouth down to about the 6th or 7th setiger. Care should be taken not to break the jaws in attempting to spread the often very muscular and rigid proboscideal wall. In some species, e.g., *Nereis diversicolor*, the number of paragnaths seems to be quite variable, especially on the ventral side of the proboscis (Takahasi, 1933; Barnes and Head, 1977; Gillet, 1990), and it may be necessary to examine several specimens to assess that variability. According to investigations by Barnes and Head (1977), the paragnaths of the maxillary ring are used for seizing prey; whereas those on the oral ring are mainly used for browsing and burrowing.

The peristomium is apodous and bears four pairs of smooth or moniliform tentacular cirri on the anterior margin. Exceptions are the genera *Micronereides* with only two pairs of tentacular cirri and no apparent peristomium, and *Cheilonereis* with a greatly expanded peristomium that forms a collar around the prostomium.

Parapodia are uniramous in the first two setigers with only a dorsal cirrus and an upper ligule present above the neuropodium (Fig. 12.6D), and distinctly biramous in all subsequent setigers (except for a small group of genera that are characterized by absent or reduced notopodia throughout). Both parapodial rami possess an often minute acicular lobe and 1 to 3 conspicuous lobes above and below the acicula that are called ligules (Fig. 12.6E). The dorsal cirri insert either at the base, in the middle, or near the tip of the upper notopodial ligule (Fig. 12.5B, C); whereas the ventral cirri always arise from the base of the lower neuropodial ligule. Branchiae are usually absent except in the genera *Dendronereis* and *Dendronereides*, which possess pectinate dorsal branchiae. However, many species use vascularized and enlarged parapodial ligules or dorsal cirrophores for respiration (Fig. 12.2E). The proportions of the parapodia, especially the ligules, differ greatly among species and are very reliable taxonomic characters.

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[1] Science Applications International Corporation, 89 Water Street, Woods Hole, Massachusetts 02543.

Because the parapodial shape often changes from anterior to posterior on one animal, an anterior, middle, and posterior parapodium should be dissected for identification.

Setae are generally compound except for some singly occurring simple falcigers in the subgenus *Hediste*. The articulation between shaft and blade is either symmetrical (homogomph) or asymmetrical (heterogomph; slightly asymmetrical articulations are also called hemigomph). The blades may be distally blunt (falcigerous) or drawn out to a very fine, hairlike tip (spinigerous) (Fig. 12.1E-H). Typically, the shafts are distinctly camerated, and the blades often show serrations or very fine, long hairs along the cutting edge. The distribution of setal types is more important for species identifications than the setal morphology, and is best recorded when parapodial lobes are examined. Specialized setae, such as the simple setae characterizing *Hediste*, may be hard to find, and more than one parapodium should be examined.

The pygidium is small, encircles the terminal anus, and usually bears two ventrolaterally inserted anal cirri. It is often missing especially in large animals because the posterior part of the body has a very thin integument and cuticle and disintegrates more easily than the muscular anterior body.

Taxonomic History

The history of the nereids is as confusing as it is interesting. The largest genus of the family, *Nereis*, is one of the two genera erected by Linné in 1758 to accommodate essentially all marine worms without scales. Well into the second half of the 19th century, the name was used for a wide variety of polychaetes, including many nephtyids, syllids, phyllodocids, and eunicids that are part of the European polychaete fauna described by Müller, Fabricius, Pallas, Dalyell, delle Chiaje and others. The discovery of epitokous forms added to the confusion because they were often described as separate species and sometimes placed in a different genus, *Heteronereis* Oersted, 1843. The term heteronereid is still used for swarming stages with greatly modified morphological features. At the same time, a number of genera that were synonymized later with *Nereis* were erected by Kinberg and others. Solid generic concepts and the division of the large family of Nereididae into subfamilies have only been established within the last 20 years or so; important contributions have been made by Pettibone (1971), Imajima (1972), Banse (1977), and Hartmann-Schröder (1985).

Currently, the Nereididae contain about 37 genera and approximately 400 species. The largest genera are *Nereis* (134 species), *Perinereis* (60 species), *Ceratonereis* (53 species) and *Neanthes* (50 species); most of the remaining genera consist of no more than two species. Historically, much of the generic definition relied on the features associated with the proboscis. Pettibone (1971) introduced the morphological details of the parapodia as additional taxonomic characters.

Distribution and Biological Notes

Nereidids are typically shallow-water organisms, but are found anywhere from intertidal to abyssal depths. Some species live in brackish and fresh water and even in moist habitats on land. A particularly rich nereidid fauna is found in the Indopacific. A wealth of literature on physiology, development, and ultrastructures of nereidids is available, probably because the worms are easy to obtain in the field and maintain in the laboratory, and many of them reach large body sizes.

Generally, nereidids live in mucous tubes from which they emerge to grasp food; actual feeding takes place within the tube. The tubes are rapidly reconstructed if the animal is forced out of the old one by some disturbance (Goerke, 1971) and is most likely produced by the often very conspicuous glands located at the parapodial bases.

The feeding modes have been shown to vary greatly among species, but also among populations of the same species (ZoBell and Feltham, 1938; Harley, 1950; Goerke, 1966, 1971; Fauchald and Jumars, 1979). Some species seem to be clearly carnivorous, as may be expected due to the presence of jaws and paragnaths in the proboscis, but many others feed on algae, bacteria, detritus, and sediments. Direct uptake of dissolved organic matter also plays a role, especially during larval and juvenile stages when the surface/volume ratio is still large (Chapman and Taylor, 1968; Taylor, 1968; Bass, Chapman and Chapman, 1969). Harley (1950) and Goerke (1966) reported a filter-feeding mechanism for *Nereis diversicolor*.

Sexes are usually separate, although some species are hermaphrodites (Reish, 1957). Most nereids show swarming behavior following great morphological changes into epitokous forms that are called heteronereids. Typically, the palps and eyes are enlarged, and the parapodia develop wide, flattened additional lobes and paddle-shaped natatory setae to facilitate swimming. Most nereidids do not swim during the atokous phase. During this phase, the coelomic cavity is filled with gametes, the body wall loses much of its muscular layer, and feeding stops. Gametes are either shed into the water or kept in a tube and brooded. Heteronereids of the common Pacific species *Platynereis bicanaliculata* were found from May through August (Blake, 1975a) in California.

Key to the Nereididae

1A. Proboscis without soft papillae or hard paragnaths; notosetae homogomph spinigers, neurosetae homogomph spinigers and heterogomph spinigers and falcigers; tentacular cirri long, moniliform (Fig. 12.9A) .... *Nicon moniloceras*

1B. Proboscis with papillae or paragnaths in at least some areas (Fig. 12.1A), tentacular cirri smooth... 2

2A. Peristomium collarlike, greatly expanded anteroventrally; notosetae homogomph spinigers, neurosetae homogomph spinigers and heterogomph falcigers; notopodia with large, foliose superior ligules .... Genus *Cheilonereis*[2]

2B. Peristomium not enlarged 3

3A. Proboscis without paragnaths, but with soft papillae; anterior setigers with bushy fascicles of very numerous setae; ventral cirri double on some anterior parapodia (Fig. 12.2C) 4

3B. Proboscis with paragnaths; setal fascicles of anterior parapodia not bushy; ventral cirri single throughout 6

4A. Dorsal cirri double in first 2 setigers (Fig. 12.4C), single and arising from elongate, vascularized and ciliated cirrophores in subsequent setigers; two pairs of eyes; all setae homogomph spinigers.... .... *Gymnonereis crosslandi*

4B. Dorsal cirri single throughout; eyes absent 5

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[2] Genus not represented in Phase I and Phase II material, but reported from off California; see Hartman (1968).

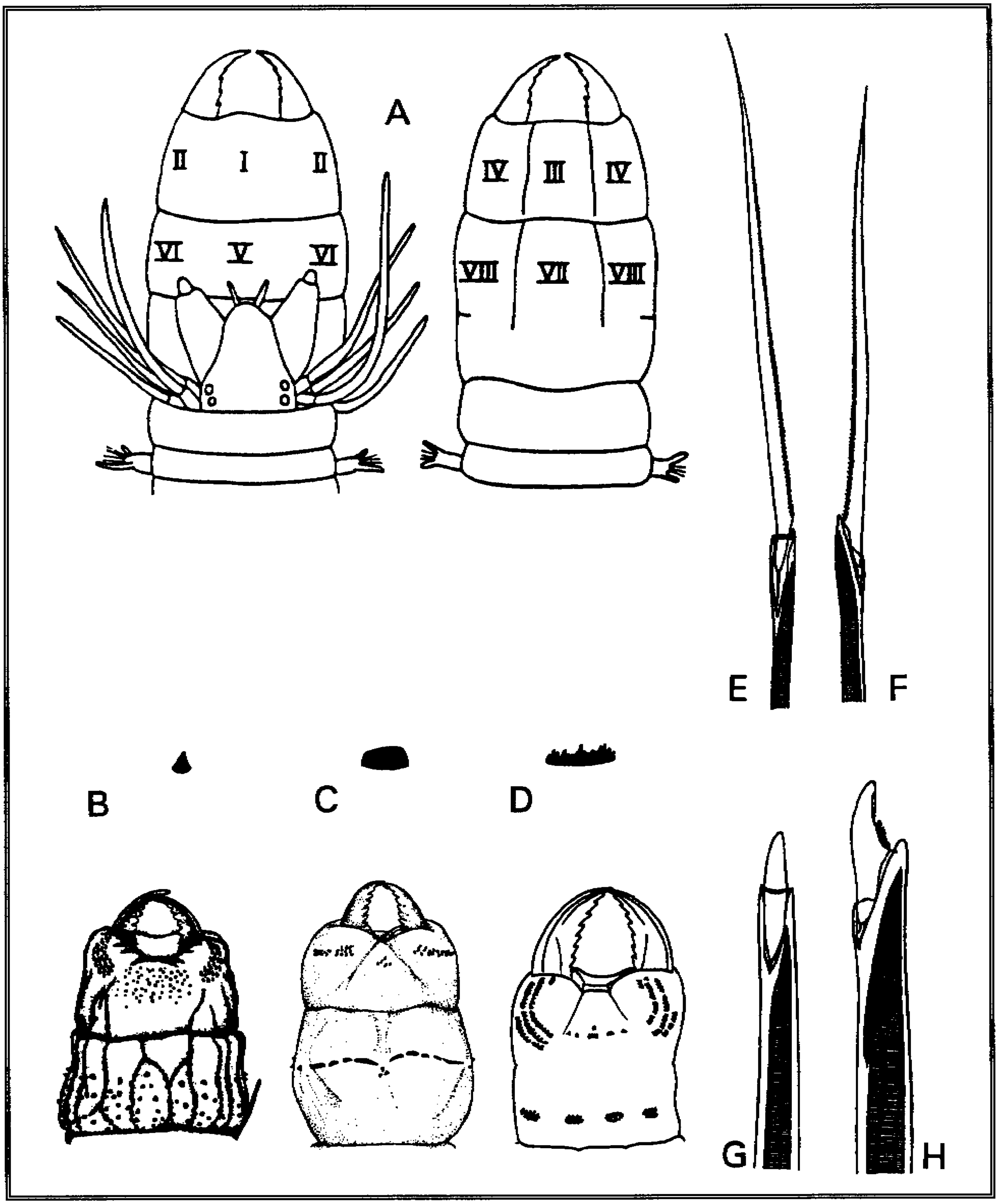

Figure 12.1. Morphological features of the Nereididae: A, areas of proboscis; B, conical paragnath, single and on proboscis; C, transverse paragnath, single and on proboscis (lower row); D, pectinate paragnath, single and on proboscis; E, homogomph spiniger; F, heterogomph spiniger; G, homogomph falciger; H, heterogomph falciger. (from various sources).

5A. Ventral cirri double from setiger 1 (accessory cirrus often tiny in first 2 to 3 parapodia); setal fascicles bushy in setigers 4 through 8-10 .... *Ceratocephale pacifica*

5B. Ventral cirri double from setiger 3; setal fascicles bushy in setigers 2 through 10-13 .... *Ceratocephale loveni*

6A. Paragnaths present on both proboscideal rings 8

6B. Paragnaths present on only one proboscideal ring 7

7A. Paragnaths present on oral ring, absent from maxillary ring .... Genus *Eunereis*[2]

7B. Paragnaths present on maxillary ring, absent from oral ring .... Genus *Ceratonereis*[2]

8A. All paragnaths conical (Fig. 12.1B) 10

8B. Some paragnaths pectinate or transverse (Fig. 12.1C, D) 9

9A. Some pectinate paragnaths present in addition to conical ones .... Genus *Platynereis*[2]

9B. Some transverse paragnaths present in addition to conical ones .... Genus *Perinereis*[2]

10A. Setae including homogomph spinigers and heterogomph spinigers and falcigers (Fig. 12.1E, F, H); homogomph falcigers absent 11

10B. Homogomph falcigers present in middle and posterior parapodia (Fig. 12.1G, 12.6I, J): genus *Nereis (Nereis)* 12

11A. Posterior neuropodia with single or very few heterogomph falcigers with blades fused or nearly fused to shaft .... Genus *Nereis (Hediste)*[2]

11B. Heterogomph falcigers with free blades; mostly estuarine species .... Genus *Nereis (Neanthes)*[2]

12A. Eyes absent; parapodia long relative to body width, with foliaceous upper notopodial ligule especially in posterior setigers 13

12B. Eyes present; parapodia not elongate 14

13A. Jaws with 7 teeth; area I with 1-3 paragnaths, area II with 4 large cones; homogomph falcigers with 5 coarse teeth on blade .... *Nereis anoculis*[3]

13B. Jaws with 15-16 teeth; area I with no paragnaths, area II with 5 to 8 cones in small cluster; homogomph falcigers with 3 coarse teeth on blade .... *Nereis ligulata*

14A. Anterior parapodia with rounded ligules; area VI with 4 large cones in diamond; all tentacular cirri of subequal length, reaching back to about setiger 3; large, robust species reaching 14 mm body width .... *Nereis pelagica*

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[3] Species was not found in Phase I or Phase II material, but is likely to occur in adjacent areas; see Hartman (1968).

14B. Ligules of all parapodia pointed and conical; paragnaths in area VI small, usually not arranged in diamond; small species, reaching only a few mm width 15

15A. All paragnaths very small, sparse in most areas; posterior dorsal tentacular cirri much longer than others, reaching back to setiger 4-12 (usually 6-8) (Fig. 12.8A); body reaching great length in relation to width .... *Nereis procera*

15B. Some paragnaths large and conspicuous; areas VII and VIII with anterior row of large cones and several irregular posterior rows of small cones; all tentacular cirri of subequal length, reaching back to setiger 2 or 3; body moderately long .... *Nereis zonata*[3]

Description of Species

Hartman (1968) listed more than 20 nereidid species belonging to about 10 genera, indicating that the nereidid fauna off California is quite diverse. Most of the species described in this chapter are included in Hartman's Atlas, with the exception of one species present in the MMS Phase I material was new to science. The following species were found in samples from the Santa Maria Basin and Western Santa Barbara Channel:

Ceratocephale loveni Malmgren, 1867
Ceratocephale pacifica (Hartman, 1960)
Gymnonereis crosslandi (Monro, 1933)
Nereis ligulata Hilbig, 1992
Nereis pelagica Linné, 1758
Nereis procera Ehlers, 1868
Nicon moniloceras (Hartman, 1940)

Genus *Ceratocephale* Malmgren, 1867

Type species: *Ceratocephale loveni* Malmgren, 1867

Diagnosis. Prostomium deeply cleft anteriorly, with 2 antennae and 2 palps; eyes present or absent. Proboscis with soft papillae on oral ring; maxillary ring smooth, bearing toothed jaws; paragnaths absent. Four pairs of tentacular cirri present. First few setigers crowded, with dense fascicles of very numerous, delicate setae. Dorsal cirri simple throughout, arising from long, inflated, vascularized cirrophores (at least on middle setigers); ventral cirri double in anterior setigers, simple thereafter. Setae all homogomph spinigers. Dorsum of anterior setigers with segmental ciliary ridge, sometimes rising to a middorsal flap.

Remarks. There is considerable confusion about this generic name in the literature, *Ceratocephala* being used at the same time as *Ceratocephale*. Both names were coined by Malmgren in 1867, but Banse (1977a) established that *Ceratocephale* was published earlier and therefore has priority. Chamberlin (1919) proposed *Chaunorhynchus* as a replacement for *Ceratocephala* because it was discovered that *Ceratocephala* was preoccupied. When *Ceratocephala* proved to be invalid, Banse (1977a) synonymized *Chaunorhynchus* with *Ceratocephale*. He also established a new subfamily, the Gymnonereidinae, for nereidids that lack paragnaths and possess bifid ventral cirri on at least some segments.

Ceratocephale loveni Malmgren, 1867

Figure 12.2

Ceratocephale loveni Malmgren, 1867a:61, pl. 5, fig. 33.—Pettibone, 1963:152-154, fig. 42a, b. —Hartmann-Schröder, 1974:200, figs. 19-22.—Blake *et al.*, 1986.—Maciolek *et al.*, 1987a, b.
Ceratocephale fauveli Hartman, 1967:62. *Not C. sibogae fauveli* Hartmann-Schröder, 1962. *Not* Gallardo, 1967.
Ceratocephale hartmanae Banse, 1977:617-619, fig. 2b-f.—Lissner *et al.*, 1986:D-10.—Hyland and Neff, 1988:A-2.
Ceratocephala loveni: Malmgren, 1867b:176.—Wesenberg-Lund, 1951:39.—Uschakov, 1958:82, fig. 3.—Hartman, 1959: 237.—Eliason, 1962:252.
Chaunorhynchus loveni: Hartman, 1942:49, figs. 83-84.

Material examined: California: Santa Maria Basin, off Point Estero, Sta. 10 (1); off Point San Luis, Sta. 26 (1); Gulf of the Farallones, Sta. E-19, 2955 m (1), Sta. EPA-1, 1263 m (2).—Mexico: Gulf of California, Guaymas Basin hydrothermal vents, *Alvin* dive 1175 (1).—New England: Georges Bank Benthic Infaunal Monitoring Program, Sta. 14A (3); U.S. North Atlantic Slope and Rise Program, Sta. N4 (3).

Description. Length to 60 mm, width to 7 mm, segments more than 80. Body wide and cylindrical in pharyngeal region (about 6 setigers), somewhat depressed and much narrower after about 10th setiger; anterior 10-13 parapodia crowded, large, with characteristic thick, fascicles of very numerous, delicate setae; parapodia in middle and posterior segments slender, longer than body width, giving ragged appearance to animal. Dorsal ridges present in anterior half of body, connecting bases of dorsal cirrophores, with 1 or 2 rows of cilia; occasionally raised to middorsal papilla ("flap" *sensu* Banse, 1977) after setiger 10. Color in alcohol uniformly tan with light greenish blood in dorsal cirrophores.

Prostomium wider than long, deeply cleft anteriorly, with 2 slender, tapering antennae and palps with short, wide palpophores and tapering palpostyles; palps and antennae of approximately same length. Eyes absent. Proboscis with amber-colored jaws with about 11 to 13 pointed teeth and soft papillae on margin of oral ring; 3 papillae across regions V and VI, and 7 papillae across regions VII and VIII; occasionally 3 additional ventral papillae below the marginal row; maxillary ring smooth (Fig. 12.2A, B).

Peristomium slightly shorter than subsequent setigers, with 4 pairs of tentacular cirri; first dorsal tentacular cirri in adults clearly longest; ventral tentacular cirri subequal in length, shorter than corresponding dorsal cirri. Parapodia in setigers 1 and 2 uniramous, biramous in all following segments; notopodia slender, with long presetal lobe; dorsal cirri filiform in anteriormost segments, from about setiger 7 through about 20 (3 to 10 in small individuals) arising from elongate, inflated, vascularized and heavily ciliated cirrophore (Fig. 12.2C-E). Cirrophores in posterior setigers slender, not distinguishable from styles, but still vascularized and ciliated; dorsal cirri reaching up to 4 times length of podial lobe, distinctly longer than body width. Neuropodia with long, slender presetal lobe and small ventral ligule diminishing in size in middle segments, absent in posterior third of body. Ventral cirri simple in first 2 setigers, bifid from setiger 3 through about 35 (20 in small specimens); secondary ventral cirrus often minute in setigers 3 and 4, subequal to primary cirrus in middle setigers and diminishing in size along last 10 parapodia of its occurrence.

All setae homogomph spinigers; in first 10 to 13 parapodia setae very numerous, arranged in dense fascicles; in subsequent setigers about 10 notosetae and 25 neurosetae per fascicle; shafts cross-striated, blades usually smooth to very finely serrated (serrations visible at 400×) (Fig. 12.2F); occasionally small group of upper subacicular neurosetae with very long, fine hairs along cutting edge (Fig. 12.2G); blade length varying, shortest usually in inferiormost neurosetae.

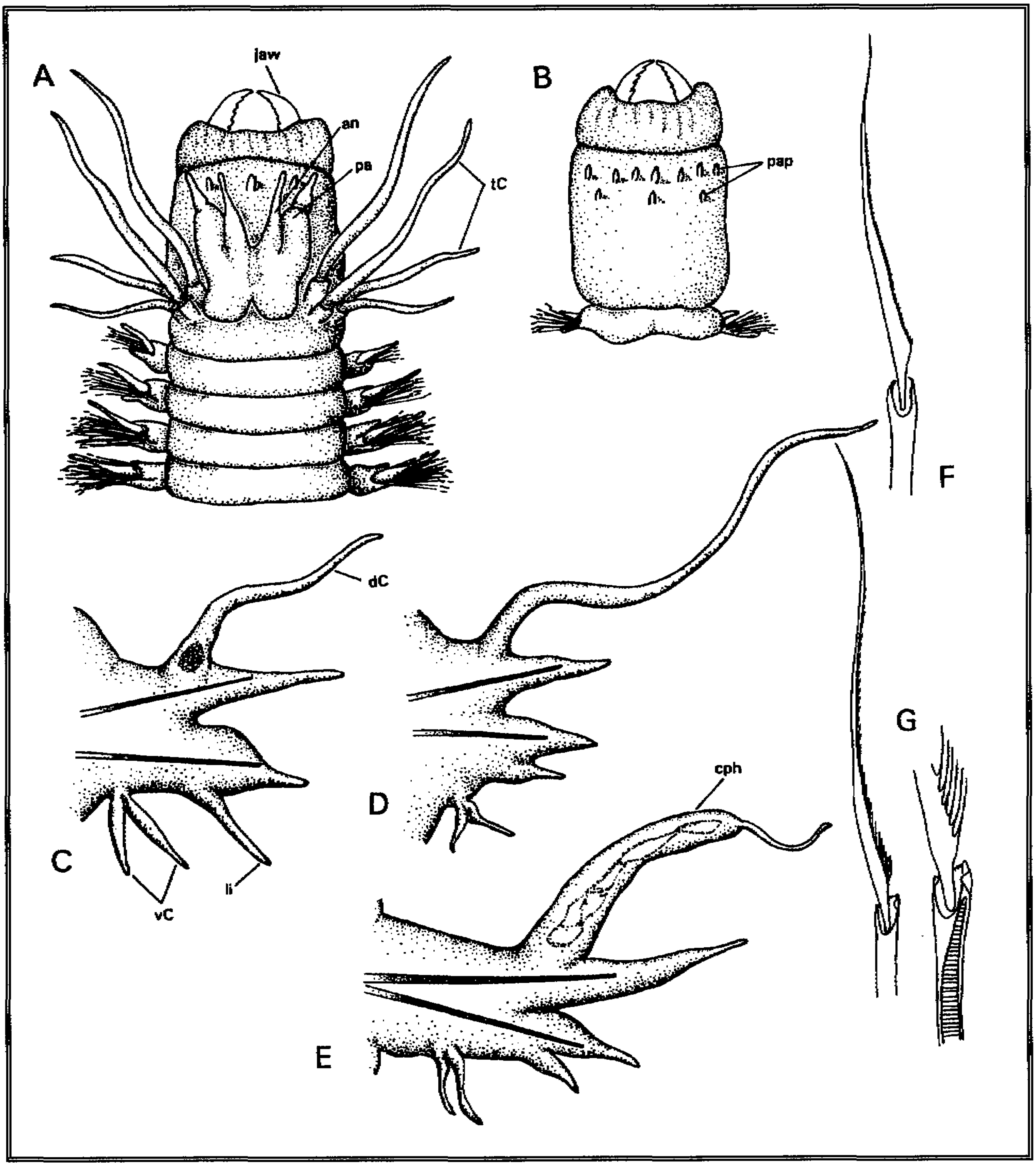

Figure 12.2. *Ceratocephale loveni*: A, anterior end, dorsal view; B, proboscis, ventral view; C, 10th parapodium, anterior view; D, 37th parapodium, anterior view; E, 12th parapodium, specimen from Santa Maria Basin, anterior view; F, lower subacicular neuroseta; G, upper subacicular neuroseta; detail: hinge. (A-D after Malmgren, 1867a).

Pygidium small, bearing 2 slender, tapering anal cirri about as long as last 7 segments, inserted ventrolaterally; anus terminal, surrounded by low, rounded papillae.

Remarks. Banse (1977) described *Ceratocephale hartmanae* from a single anterior end that was in fairly poor condition, but had distinct middorsal "flaps" arising from the ciliated dorsal ridges after setiger 10. Although he noted that *C. loveni* shows a tendency to develop these flaps, he felt that the considerable size of the flaps in the new specimen was a justification for a new species. *C. hartmanae* is synonymized here because middorsal papillae, or flaps, were observed on specimens of *C. loveni* (ventral cirri double from setiger 3) as well as *C. pacifica* (ventral cirri double from setiger 1). Blake (1985) made the same observation and believed the status of *C. hartmanae* to be questionable. After examination of additional material, it appears that middorsal papillae are not a species-specific character. They may be size or sex dependent.

Type locality and type specimens. Skagerrak (Sweden), soft bottom, 180 m; Swedish State Museum of Natural History, syntypes (type coll. No. 367 and 2449-2451).

Habitat. The species occurs in silt and fine sand.

Distribution. Mexico to California; North Sea; North Atlantic: Scandinavia, Greenland; Nova Scotia to Virginia; Sea of Okhotsk; Northern Pacific; 50 to 5000 m.

Ceratocephale pacifica (Hartman, 1960)

Figure 12.3

Ceratocephala loveni pacifica Hartman, 1960:94-96, pl. 8.
Ceratocephale loveni pacifica: Hartman, 1968:501.
Ceratocephale pacifica: Banse, 1977:617, fig. 2a.—Blake, 1985:85, 87.

Material examined. California: Gulf of the Farallones, Sta. S-19, 2580 m (1), Sta. E-7, 2462 m (1).—Mexico: Gulf of California, Guaymas Basin hydrothermal vents, *Alvin* dive 1175 (2).

Description. Length to 8 mm, width less than 1 mm, segments to 24. Body slender, somewhat depressed, in pharyngeal region slightly inflated and cylindrical. Anterior 10 parapodia crowded, with large fascicles of fine, brassy setae. Dorsum with transverse, ciliated ridges in anterior third of body, connecting dorsal cirrophores; occasionally forming middorsal papillae on few segments around setiger 10. Color in alcohol uniformly tan.

Prostomium wider than long, deeply incised between antennae; antennae slender, tapering, about as long as palps; palpophores short, almost spherical, palpostyles tapering; eyes absent (Fig. 12.3A). Proboscis with amber-colored jaws, each with 12 teeth (Fig. 12.3B); maxillary ring smooth; oral ring with 3 conical dorsal papillae (areas V and VI) and 7 ventral papillae (areas VII and VIII) in a more or less regular marginal row (as in Fig. 12.2A, B); 3 additional ventral papillae located proximal to that row, often difficult to see unless proboscis fully everted.

Peristomium short, with 4 pairs of tentacular cirri; dorsal tentacular cirri of similar length, about 1.5 times as long as corresponding ventral ones. Parapodia of setigers 1 and 2 uniramous, biramous on all following setigers. Notopodia with long, conical presetal lobe and low, rounded acicular and postsetal lobes; dorsal cirri filiform in few anterior setigers, arising from inflated, elongate, vascularized and heavily ciliated cirrophores from about setiger 8 to 30 (largest specimen) (Fig. 12.3C); in subsequent segments

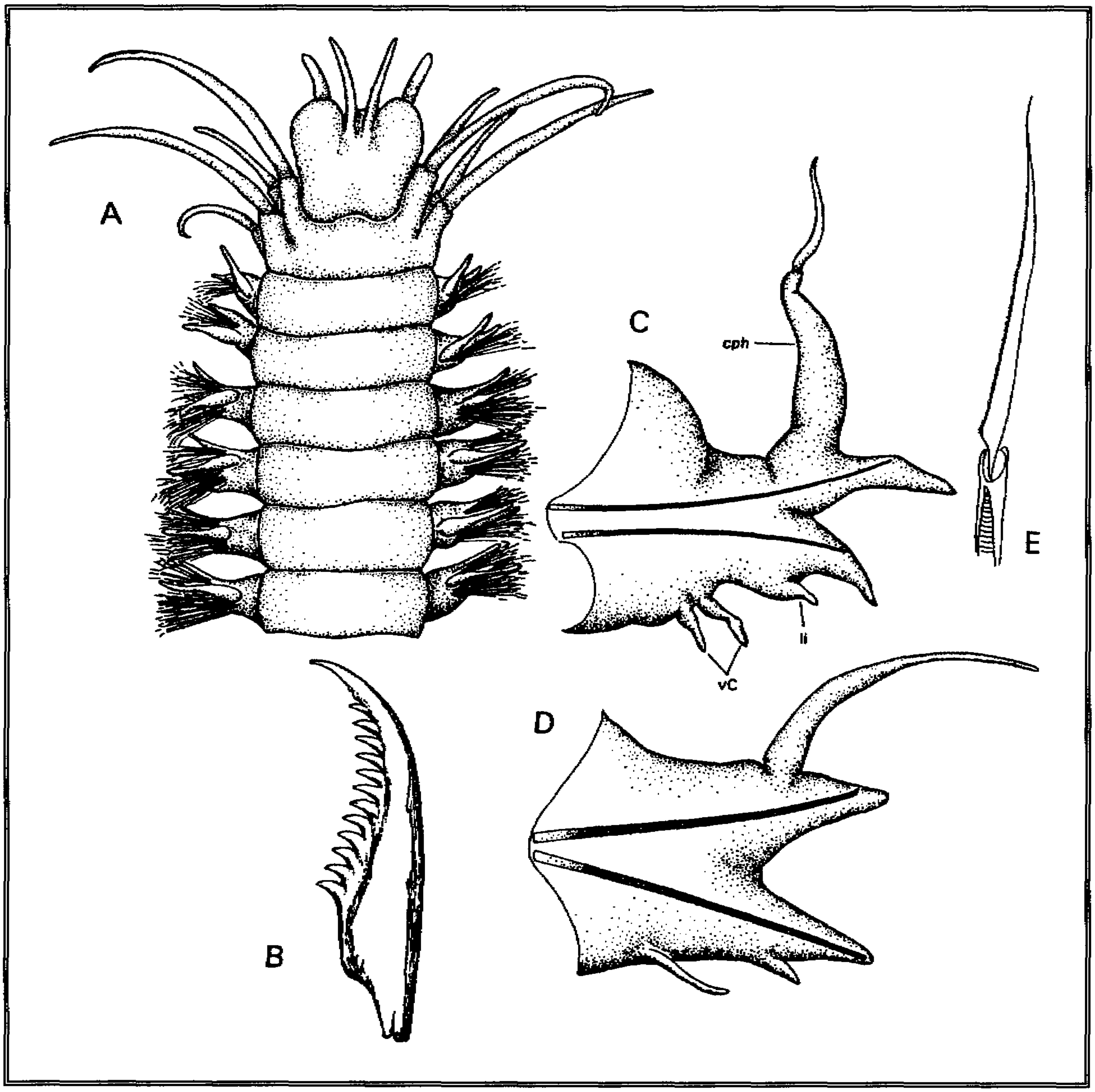

Figure 12.3. *Ceratocephale pacifica*: A, anterior end, dorsal view; B, jaw; C, anterior parapodium, anterior view; D, posterior parapodium, anterior view; E, neuroseta. (B, C after Hartman, 1960).

dorsal cirri slender, about as long as body width; cirrophores discernible only by ciliation, not inflated (Fig. 12.3D). Neuropodia with slender, long presetal lobe and much shorter, rounded acicular and postsetal lobes; small ventral ligule present. Ventral cirri double from setiger 1 (rarely 2) to about 25, secondary ventral cirrus sometimes minute in first 1 to 3 setigers, generally about as large as primary ventral cirrus, diminishing in size in last 5 to 7 setigers of its occurrence.

All setae delicate homogomph spinigers, in dense fascicles on setigers 4-8 or 10; blades of similar length except for small group of inferiormost neurosetae with short blades and occasionally distinctly longer blades on some upper neurosetae; blades smooth or finely serrated, occasionally with long hairs on some upper or lower neurosetae (Fig. 12.3E). Aciculae single in each ramus, black except for light brown to colorless bases and tips.

Remarks. Banse (1977) stated that in *C. pacifica* "flaps are certainly absent", whereas Blake (1985) found middorsal flaps on specimens from the Guaymas Basin. One of Blake's specimens was reexamined and the presence of these flaps confirmed. Another noteworthy finding is the variability in one of the most important specific characters, the distribution and development of double ventral cirri (starting on setiger 1 or 2, subequal from setiger 1 or minute in anterior 1 to 3 segments). However, the secondary ventral cirrus is always present by setiger 2, thus distinguishing this species from *C. loveni* in which the double ventral cirri begin in setiger 3.

Type locality and type specimens. California, West Cortes Basin; LACM-AHF Poly 0847 (holotype).

Distribution. Western Mexico to central California, 840 to 2580 m.

Genus *Gymnonereis* Horst, 1919, emended Banse, 1977

Type species: *Gymnorhynchus sibogae* Horst, 1918

Diagnosis. Prostomium cleft anteriorly, with 2 antennae and 2 palps; eys present or absent. Proboscis with soft papillae on oral ring; maxillary ring smooth, bearing smooth jaws; paragnaths absent. Four pairs of tentacular cirri present. Anterior setigers crowded, with dense fascicles of fine setae. Dorsal cirri bifid in some anterior setigers, simple thereafter, arising from elongated, vascularized cirrophores in middle setigers; ventral cirri bifid on most or all setigers. Setae usually homogomph spinigers, occasionally few falcigerous neurosetae present.

***Gymnonereis crosslandi* (Monro, 1933)**

Figure 12.4

Chaunorhynchus crosslandi Monro, 1933:46-49, fig. 20.
Ceratocephala crosslandi: Hartman, 1952:16. *Not* Uschakov, 1958:84.
Ceratocephala crosslandi americana: Hartman, 1952:16, pl. 4, figs. 1-3.
Ceratocephale crosslandi americana: Hartman, 1968:499; Hartmann-Schröder, 1977.
Gymnonereis crosslandi: Banse, 1977:623.—Taylor, 1984:31-4, fig. 31-2.—Lissner *et al.*, 1986: D-10.—Hyland and Neff, 1988:A-2.—Hyland *et al.*, 1990:F-1.

Material examined. California: Santa Maria Basin, off Point Conception, Sta. 73 (3); off Point San Luis, Sta. R-1 (1).

Description. Length to 40 mm, width to 2 mm, segments at least 40. Body inflated in pharyngeal region (setigers 1 to 6), tapering in subsequent setigers, narrower than parapodial length, and fragile in posterior region. Color in alcohol uniformly tan.

Prostomium wider than long, deeply cleft betweeen antennae; antennae about as long as palps, long, slender, tapering; palps with long, cylindrical palpophores (present as distinct features along lateral prostomial margin to about eye level), and short, slender palpostyles; eyes large, rounded to oval, arranged in rectangle (Fig. 12.4A). Maxillary ring of proboscis without papillae, with smooth, amber jaws; oral ring with 3 marginal papillae dorsally (areas V and VI) and 7 ventrally (areas VII and VIII); 3 pairs of very low, oval papillae located subterminally on ventral surface (Fig. 12.4B). Peristomium as long as following

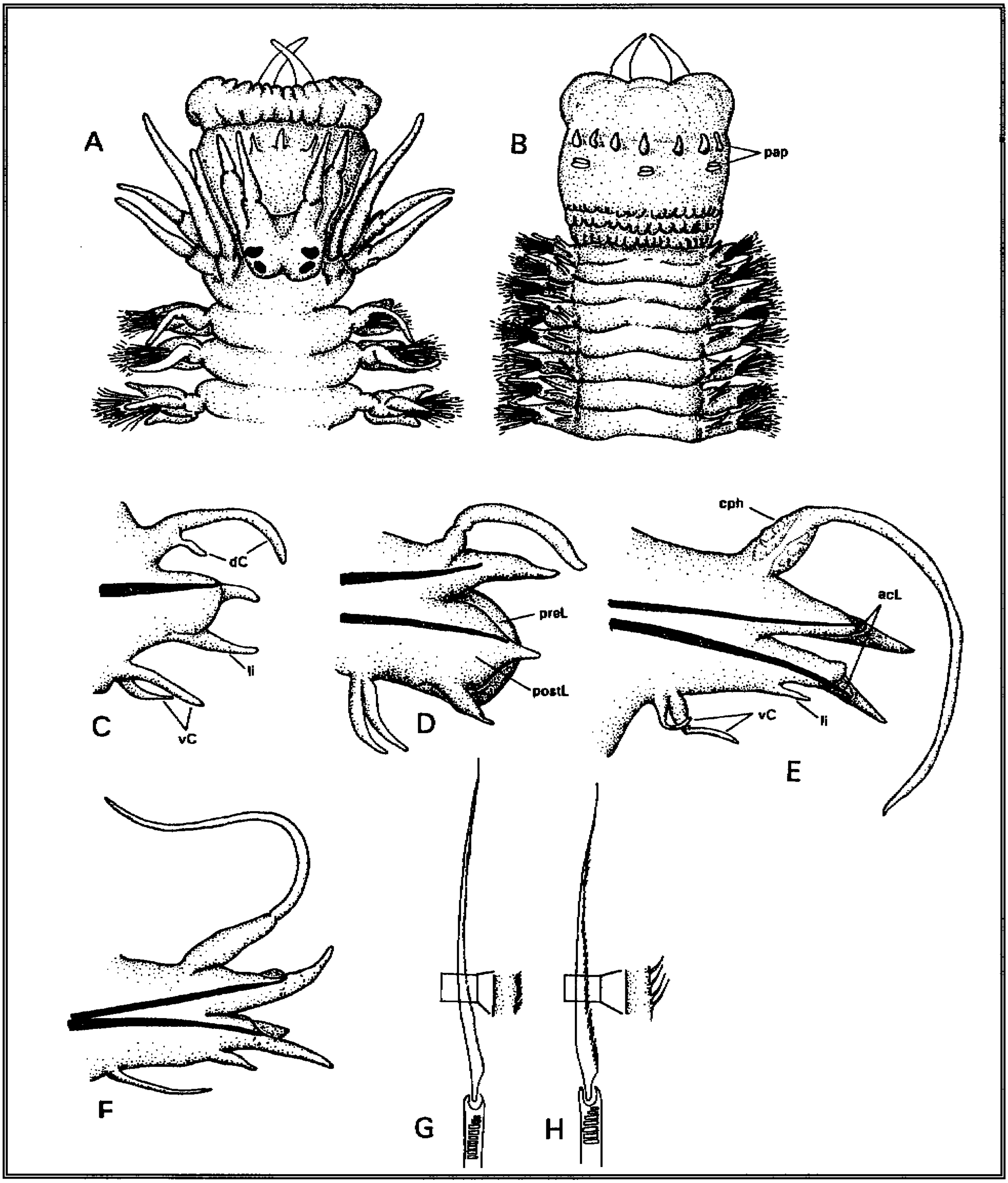

Figure 12.4. *Gymnonereis crosslandi*: A, anterior end, dorsal view; B, same, ventral view; C, second parapodium, posterior view; D, middle parapodium, posterior view; E, posterior parapodium, posterior view; F, far posterior parapodium, anterior view; G, lower neuroseta; detail: fine serrations; H, upper neuroseta; detail: long serrations. (A, D after Monro, 1933; B after Hartman, 1952; C after Taylor, 1984).

setigers; ventral tentacular cirri shorter than the corresponding dorsal pairs; anterior pair well separated from posterior pair, arising from long ceratophores.

Parapodia uniramous in first 2 setigers, biramous in all following setigers (Fig. 12.4C-F). Notopodia with low presetal and acicular lobes and long, conical postsetal lobe; dorsal cirri long, slender, with small accessory cirri attached basally in first 2 setigers; cirrophores in posterior setigers slightly inflated, with large empty vesicles in epidermis. Neuropodia with lobes similar to notopodia and short, conical ventral ligule inferior to parapodial lobes; ventral cirri double from setiger 1 through at least setiger 36, becoming simple in following setigers, arising from parapodial base. One acicula in each ramus, equal in size, black.

Setae very numerous, arranged in several rows in noto- and neuropodial fascicles of first 12 to 15 parapodia, present in moderate numbers in subsequent parapodia; all setae homogomph spinigers; notosetae with very finely serrated blades, neurosetae with fine, but long serrations on blades in upper part of fascicle, similar to notosetae in lower part of fascicle (Fig. 12.4G, H). Shafts of all setae strongly cross-barred.

Pygidium small, surrounding terminal anus, bearing single anal cirrus. Gut often filled with sediment.

Remarks. This species may be superficially confused with *Ceratocephale pacifica* (see above) because the accessory dorsal cirri on setigers 1 and 2 are sometimes very small and invisible if the whole animal is viewed from above. It may be helpful to dissect the proboscis for examination of the jaws which are smooth in *Gymnonereis*, but toothed in *Ceratocephale*. The dorsal cirrophores with vesicular epidermis may function as gills.

Type locality and type specimens. Gulf of Panama; BMNH 1932:12:24:106 (holotype), LACM-AHF Poly 0846 (holotype of *Ceratocephale crosslandi americana*).

Habitat. *G. crosslandi* occurs in mixed sediments ranging from clay to sand.

Distribution. Gulf of Mexico; Gulf of Panama; Baja California; southern and central California; 43 to 478 m.

Genus *Nereis* Linné, 1758

Type species: *Nereis pelagica* Linné, 1758

Diagnosis. Prostomium pyriform, widest posteriorly, with 2 antennae, 2 palps, and 4 eyes. Proboscis with hard, conical paragnaths on at least some areas of both rings; maxillary ring with toothed jaws. Four pairs of tentacular cirri present. Parapodia biramous from setiger 3; dorsal and ventral cirri simple throughout. Notosetae homogomph spinigers in anterior setigers, gradually replaced by few short-bladed homogomph falcigers; neurosetae including homogomph and heterogomph spinigers and heterogomph falcigers.

Remarks. Due to the long history of this genus, it is treated differently among authors. *Nereis sensu strictu* includes species with spinigerous notosetae in the anterior half of the body and falcigerous notosetae posteriorly, either exclusively or in addition to spinigers. Species with only spinigerous notosetae only are referred to the genus *Neanthes* Kinberg, 1866, and species with homogomph falcigers in some neuropodia are assigned to *Hediste* Malmgren, 1867. *Nereis sensu lato* includes *Nereis s. str.* as *Nereis* (*Nereis*), and *Neanthes* and *Hediste* as additional subgenera (see, for example, Pettibone (1963)). In this chapter, the genus *Nereis* is used *sensu lato* (see also key).

Nereis ligulata Hilbig, 1992

Figure 12.5

Nereis ligulata Hilbig, 1992:709-711, fig. 1.
Nereis nr. *anoculis* Lissner *et al.*, 1986:D-10.

Material examined. California: Santa Maria Basin, off Point San Luis, Sta. 27 (holotype).

Description. Holotype incomplete, in 6 parts; length 121 mm, width 2.5 mm without parapodia in anterior segments, segments about 190, only last few segments and pygidium absent. Body slender, gradually tapering towards pygidium behind pharyngeal region, appearing ragged because of elongate parapodia. Color in alcohol uniformly tan; integument wrinkled in anterior segments.

Prostomium longer than wide, roughly hexagonal, with slender, filiform antennae and palps of about the same length, with short conical styles and massive, long palpophores; eyes absent (Fig. 12.5A). Proboscis with light brown jaws, each with 15 to 16 pointed teeth; paragnath pattern: Area I: none; II: 5 to 8 in cluster; III: 5 in 1 irregular row; IV: 6 to 7 in arc; largest paragnaths of entire proboscis; V: none; VI: 2 to 3 in a row or triangle; VII and VIII: 3 in widely spaced row.

Peristomium about as long as prostomium, 3 times as wide; with 4 pairs tentacular cirri, about as long as peristomium except for second dorsal tentacular cirrus, which reaches back to setiger 6 or 7. Parapodia uniramous in first 2 setigers, biramous thereafter; notopodia with dorsal cirri arising from base of upper ligule in anteriormost segments, gradually moving to middle and subdistal positions in mid-body and posterior segments; upper notopodial ligule pointed, about as long as lower notopodial ligule in first 20 segments (Fig. 12.5B); in subsequent segments tip becoming glandular and ligule greatly increasing in length (Fig. 12.5C). Neuropodia with small acicular lobe and slender, foliaceous lower ligule inserting between ventral cirrus and tip of acicular lobe in anterior and middle setigers, close to tip of acicular lobe in posterior setigers; ventral cirri slender, about as long as dorsal cirri.

Notosetae slender homogomph spinigers from setiger 3 through about 28; homogomph falcigers first appearing in setiger 25, present throughout remaining segments, in posteriormost setigers embedded alongside acicula; blades short, with 3 coarse teeth (Fig. 12.5E). Upper fascicle of neurosetae with slender homogomph spinigers and, from setiger 16, 1 or 2 heterogomph falcigers; lower fascicle with heterogomph spinigers, from setiger 16 or 17 also with about 5 to 7 heterogomph falcigers; the latter occurring singly in posterior segments and entirely absent in about last 20 segments. All spinigers with finely serrated blades; neuropodial falcigers with blades of varying length, in anterior and middle segments with long serrations and distally forming blunt hook; in far posterior segments finely serrated, distally curved and ending in fine point (Fig. 12.5F-J).

Remarks. *Nereis ligulata* resembles *N. anoculis* Hartman, 1960 in the shape of the elongated parapodia with foliaceous upper notopodial ligules. The species belongs to a deep-sea group having elongate parapodia (Blake, 1985; Blake and Hilbig, 1990), but differs in the number of teeth on the jaws, the overall paragnath pattern, the shape of the parapodia, and the shape and distribution of the different setal types.

Type locality and type specimens. Santa Maria Basin; holotype: USNM 148701.

Distribution. Known only from the type locality, 611 m, mixed sand and silt/clay.

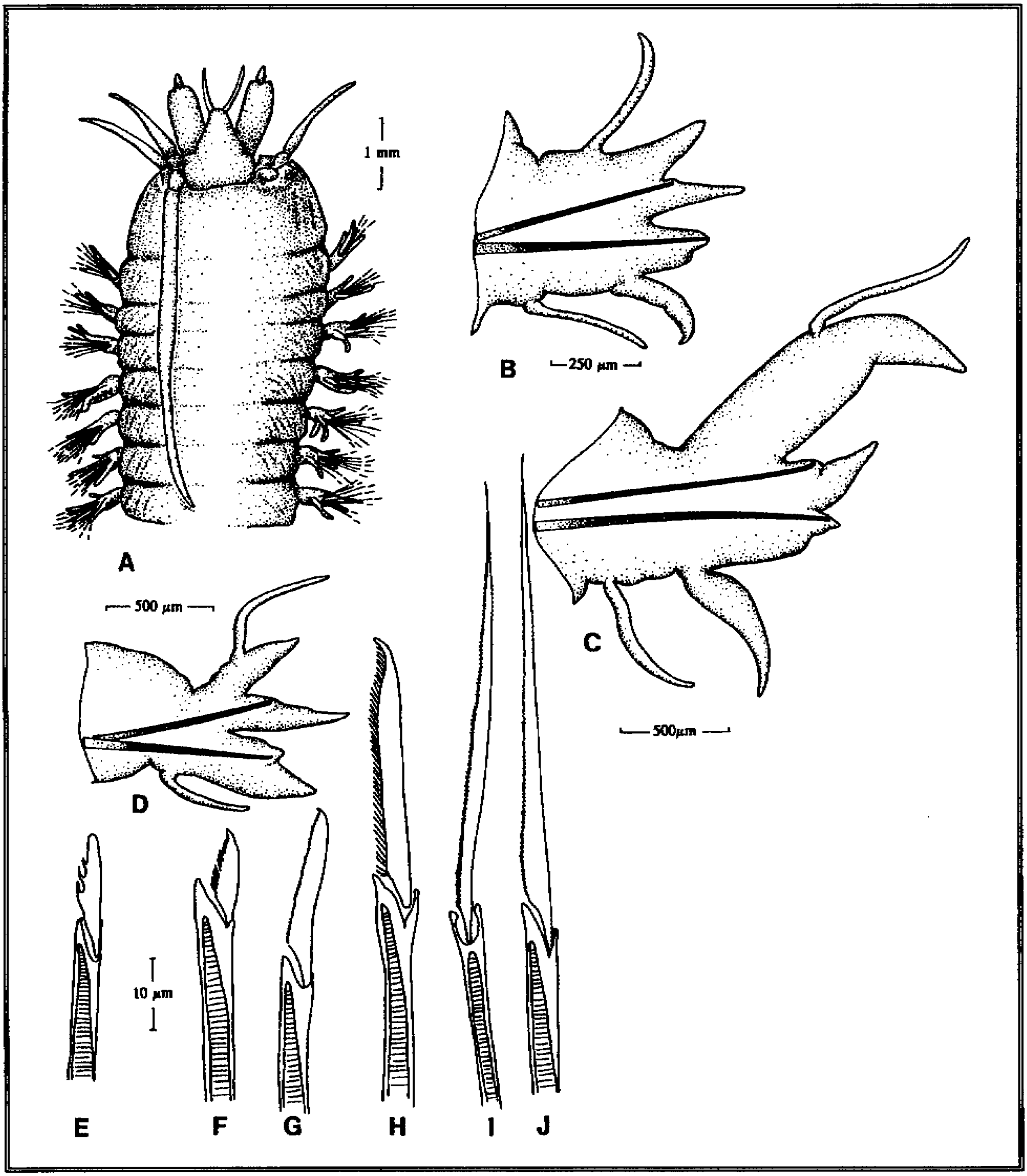

Figure 12.5. *Nereis ligulata*: A, anterior end, dorsal view; B-D, anterior, middle, and posterior parapodium, anterior view; E, notopodial homogomph falciger; F, supraacicular neuroseta, anterior parapodium; G, same, far posterior parapodium; H, subacicular neuroseta, anterior parapodium; I, neuropodial homogomph spiniger; J, neuropodial heterogomph spiniger (from Hilbig, 1992).

Nereis pelagica Linné, 1758

Figures 12.6, 12.7

Nereis pelagica Linné, 1758:654.—Fauvel, 1923:336, fig. 130a-f.—Hartman, 1940:225, pl. 35, fig.52. —Imajima, 1972:142-146, figs. 48, 49.—Taylor, 1984:31-42, fig. 31-40.
Nereis (Nereis) pelagica: Pettibone, 1963:179, fig. 42d-h.
Nereis pelagica neonigripes: Lissner *et al.*, 1986:D-10.

Material examined. California: Santa Maria Basin, off Point Estero, Sta. 1 (1); off Point Buchon, Sta. 16 (1).

Description. Length to 160 mm, width to 14 mm including parapodia, segments more than 100. Body slender, cylindrical, tapering toward pygidium. Color in alcohol uniformly tan to dark purplish, with iridescent cuticle; occasionally tips of parapodial lobes and ligules darkened; color in life yellowish to green, brown, or violet.

Prostomium pyriform, with 2 slender, tapered antennae and 2 slightly longer, massive palps with long palpophore and short, conical palpostyle; 2 pairs of eyes, large, lentigerous, in trapezoidal arrangement (Fig. 12.6A). Proboscis with dark brown to black jaws with 7-8 teeth each; paragnath distribution: Area I: 2 (rarely 1 or 3) in tandem; II: 12 to 14 in 2 or 3 arched rows; III: 10 to 15 in cluster; IV: 20 to 30 of various sizes in 3 to 5 arched rows; Area V: none (rarely 1 to 3); Area VI: 4 large cones in diamond-shaped arrangement; VII and VIII: 1 transverse distal row of large cones and 2 or 3 irregular proximal rows of smaller cones (Fig. 12.6B, C).

Peristomium nearly twice as long as subsequent setigers, bearing 4 pairs of tentacular cirri of subequal length, reaching back to about setiger 3 (young specimens occasionally with unequal tentacular cirri). Parapodia of first 2 setigers uniramous, all following parapodia biramous; notopodia with upper and lower ligule, neuropodia with lower ligule and acicular lobe; dorsal cirri blunt, about as long as upper ligule in first setiger, then gradually increasing in length and becoming slender and tapered in posterior part of body; clearly surpassing length of podial lobes in posterior setigers. Ventral cirri slender, tapering, somewhat shorter than neuropodial ligule throughout. All ligules subequal, bluntly rounded in anterior parapodia, becoming conical and more pointed in middle and posterior setigers, particularly in juveniles (Fig. 12.6D-G); upper notopodial ligules occasionally diminishing in size in posterior segments of juveniles.

Notosetae delicate homogomph spinigers in anterior 20 to 40 setigers, homogomph falcigers in remaining setigers; blades with serrated cutting edge, in posterior setigers smooth (Fig. 12.6H-J). Neurosetae homogomph spinigers and heterogomph falcigers in supraacicular fascicle and heterogomph falcigers and spinigers in subacicular fascicle (Fig. 12.6K-M); aciculae black except for colorless proximal part, occurring singly in each ramus.

Sexually mature epitokes (heteronereids) with greatly enlarged eyes and palps, and with modified parapodia and setae in natatory region (Fig. 12.7A); parapodia flattened, with additional lobes at bases of dorsal and ventral cirri and on neuropodia (Fig. 12.7B); males with crenulated dorsal cirri. Setae hemigomph, with wide, paddle-shaped, finely serrated blades (Fig. 12.7C). Males with 14 to 16 pre-epitokous setigers, with modified dorsal cirri in first 7 and modified ventral cirri in the first 5 to 6 setigers; females with 15 to 19 pre-epitokous setigers, with modified dorsal cirri in first 5 and modified ventral cirri in first 4 setigers (Fig. 12.7D).

Remarks. The specimens from Phase I were originally identified as *N. pelagica neonigripes*, but upon reexamination were placed into the stem species because they agreed with the description of a small specimen identified as ?*Nereis pelagica* by Hartman (1940). She considered the identification doubtful

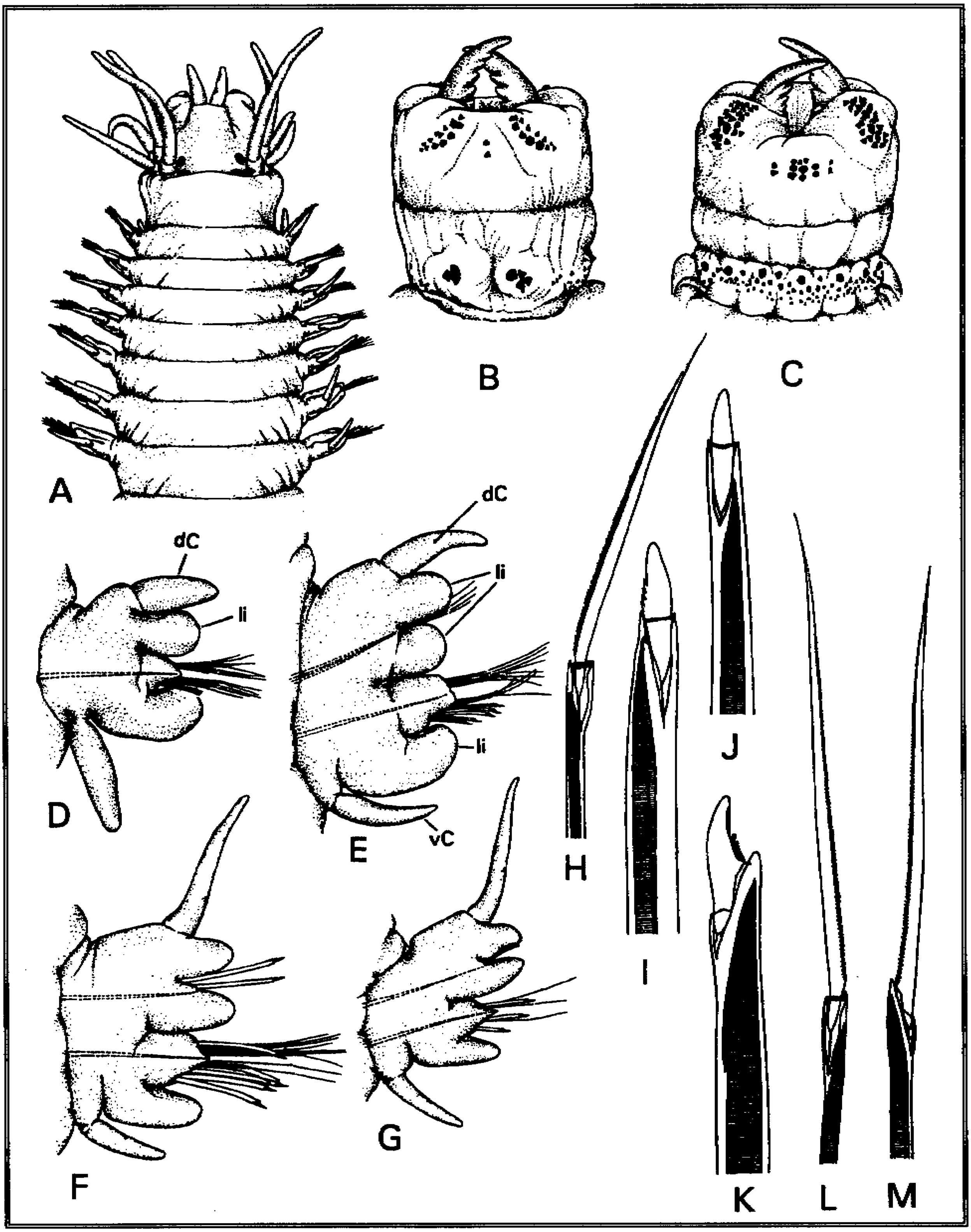

Figure 12.6. *Nereis pelagica*: A, anterior end, dorsal view; B, proboscis, dorsal view; C, same, ventral view; D-G, first, 5th, middle, and posterior parapodium, anterior view; H, homogomph spiniger, anterior notopodium; I-J, homogomph falcigers, middle and posterior notopodium; K, heterogomph falciger, neuropodium, supraacicular; L, homogomph spiniger, neuropodium, supraacicular; L, heterogomph spiniger, neuropodium, subacicular. (from Imajima, 1972).

because of the reduction of the dorsal ligules in posterior segments, but this same reduction was seen on the Phase I specimens, and it seems to be a juvenile character. No color pattern was apparent in either of the specimens, although it may have faded in alcohol. Even if a pigment pattern had been present, it is doubtful if the subspecies *N. pelagica neonigripes* should be recognized. While Hartman changed the status of *N. neonigripes* from that of a species to a subspecies of *N. pelagica*, Pettibone (1963) included *N. pelagica neonigripes* with the stem species—without explicitly stating it—by mentioning the darkened parapodial lobes and also variability in the paragnath pattern in her description of *N. pelagica*.

Type locality. Western Europe.

Biology. *Nereis pelagica* is found in a wide variety of substrata ranging from soft sandy bottoms (rarely mud) to rocks, encrusting animals, and algal holdfasts. According to Pettibone (1963), the species prefers clean, circulating water. Epitokous specimens are found in surface waters year-round, most often in spring and summer. *N. pelagica* was observed in stomach contents of haddock, Atlantic cod, and herring (Pettibone, 1963). The Phase I specimens are from rocks and muddy bottoms at 60 to 650 m depth.

Distribution. Cosmopolitan; Arctic; Norway to Mediterranean Sea; West Africa; New England to Florida; Bering Sea to Panama; Japan; South Pacific; intertidal to 1200 m.

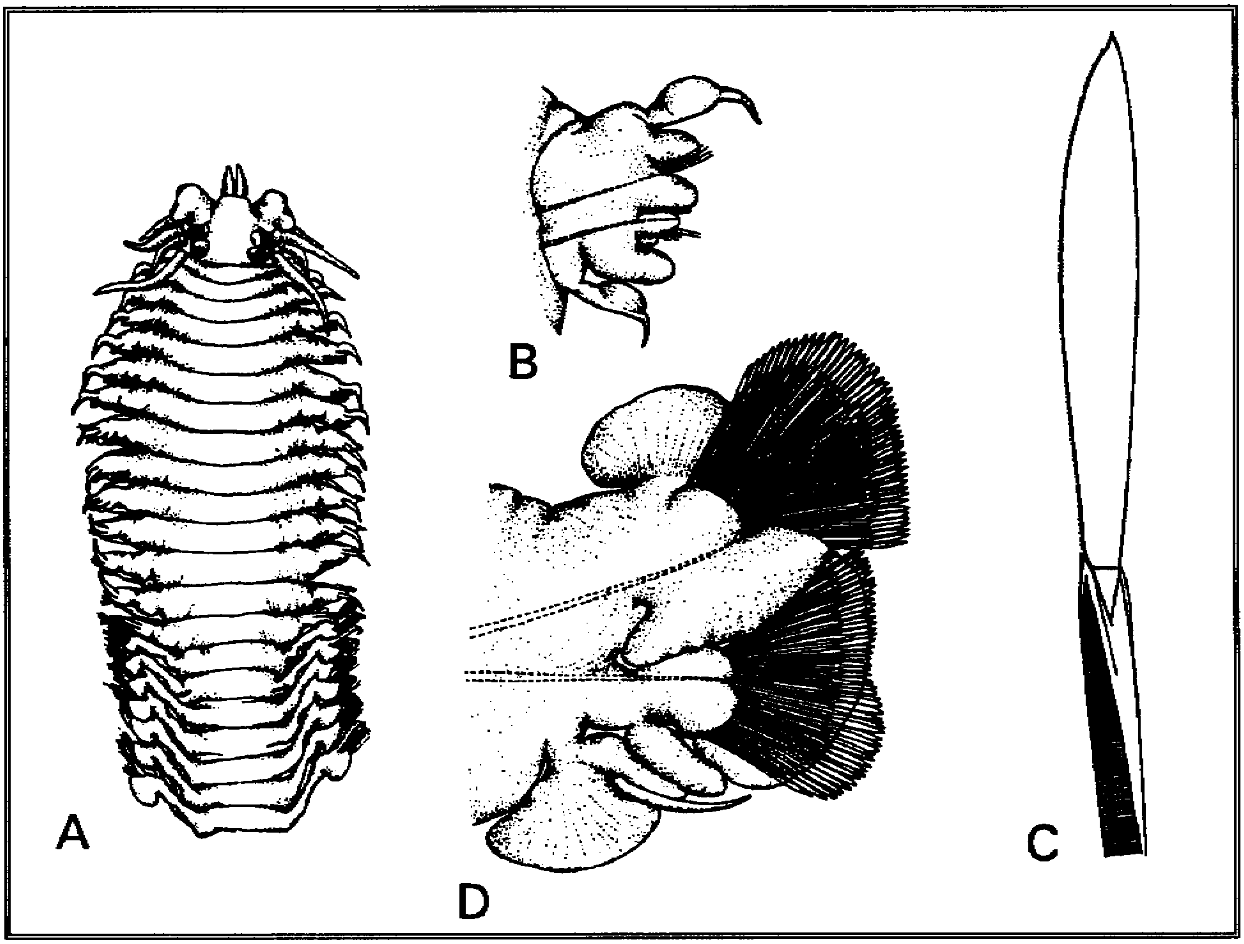

Figure 12.7. *Nereis pelagica*: A, male heteronereid, anterior end, dorsal view; B, anterior parapodium, anterior view; C, natatory seta; D, middle parapodium, anterior view. (from Imajima, 1972).

Nereis procera Ehlers, 1868

Figure 12.8

Nereis procera Ehlers, 1868:557, pl. 23, fig. 2.—Johnson, 1901:400-401, pl. 4, fig. 47, pl. 5, figs. 53-59.—Moore, 1911:244-246, pl. 15, fig. 18.—Lissner *et al.*, 1986:D-10.—Hyland and Neff, 1988:A-2.—Hyland *et al.*, 1990:F-1.
Nereis nr. *procera* Lissner *et al.*, 1986:D-10.—Hyland *et al.*, 1990:F-1.
Nereis sp. B Lissner *et al.*, 1986:D-10.

Material examined. California: Santa Maria Basin, off Point Buchon, Sta. 13 (1); off Point San Luis, Sta. 21 (2); off Purisima Point, Sta. 52 (1); off Point Arguello, Sta. 60 (1); off Point Sal, Sta. R-8 (1); western Santa Barbara Channel, Sta. 80 (1).

Description. Length to 125 mm, width to 4 mm without parapodia, segments to 180. Body slender, very long, widest in pharyngeal region and gradually tapering towards pygidium; posterior half appearing ragged because of increasing length of parapodia relative to body width. Color in alcohol uniformly tan, occasionally with dark pigmentation on prostomium behind eyes and anterior segments.

Prostomium about as long as wide, pyriform, with slender antennae and massive palps; palpophores slightly shorter than antennae, palpostyles short and conical. Two pairs of relatively small eyes in rectangular arrangement (Fig. 12.8A). Proboscis with light to dark brown jaws, each with 8 to 9 teeth, and small, often inconspicuous paragnaths: Area I: none, II: 3 to 5 in transverse row or small cluster, III: 4 to 12 in 1 or 2 transverse rows, often widely spaced, IV: 6 or 7 in small cluster and 3 or 4 additional ones in arched row, V: none, VI: 4 to 6 in diamond or 2 parallel rows (rarely only 1 cone), VII and VIII: several irregular rows of often widely spaced, generally small cones (Fig. 12.8B, C).

Peristomium about twice as long as subsequent setigers, bearing 4 pairs tentacular cirri; posterior dorsal tentacular cirri longest, reaching back to setiger 4 to 12 (usually 7 or 8); other tentacular cirri subequal, reaching back to setiger 1 or 2 (rarely 3). First 2 parapodia uniramous, all remaining parapodia biramous. Dorsal cirri long, tapering, arising from notopodial base in anterior setigers and from middle of upper notopodial ligule in posterior setigers, transition gradual; notopodia with upper and lower ligule, neuropodia with short acicular lobe and lower ligule; all parapodial ligules conical, of similar length, proportions of parapodia not changing from anterior to posterior except for slight prolongation of notopodia and more filiform dorsal cirri in far posterior setigers. Ventral cirri slender, tapering, slightly shorter than dorsal cirri, arising from neuropodial base throughout (Fig. 12.8D-F).

Notosetae delicate homogomph spinigers with finely serrated blades in first 20 to 35 setigers, replaced by 1 or 2 homogomph falcigers with very short, proximally serrated blades (Fig. 12.8G); upper neurosetae homogomph spinigers and 1 or 2 heterogomph falcigers; lower neurosetae heterogomph spinigers and falcigers, spinigers sometimes absent from far posterior setigers; falcigerous blades of varying lengths, finely serrated and distally hooked (Fig. 12.8H, I). Aciculae light brown (juveniles) to black, occurring singly in each ramus.

Intestine in posterior half of body frequently filled with sediment. Pygidium of atokous form not known.

Sexually mature epitokous males with 54 to 67 setigers, the first 14 being pre-natatory (Moore, 1911); dorsal cirri modified in anterior 7 setigers, ventral cirri modified in anterior 5 setigers. Prostomium with slightly enlarged eyes and palps pointing ventral rather than lateral; parapodia in natatory region with enlarged ligules and additional lobes at bases of dorsal and ventral cirri and on neuropodial acicular lobe; dorsal cirri crenulated to about setiger 50. Pygidium small, with 2 anal cirri and several papillae surrounding anus.

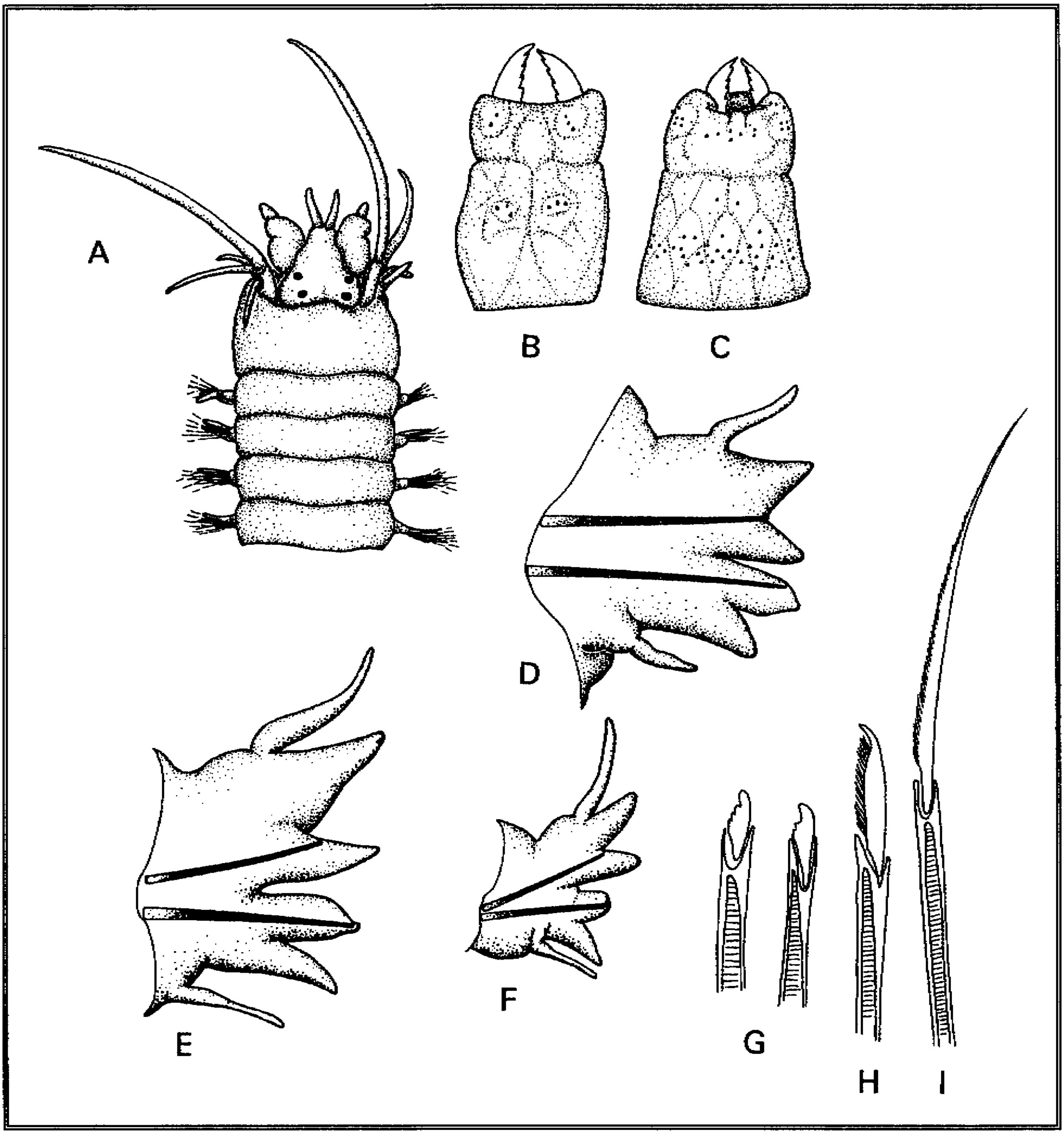

Figure 12.8. *Nereis procera*: A, anterior end, dorsal view; B, proboscis, dorsal view; C, same, ventral view; D, middle parapodium, anterior view; E, posterior parapodium, anterior view; F, far posterior parapodium, anterior view; G, notopodial homogomph falcigers, left from juvenile; H, neuropodial heterogomph falciger; I, notopodial homogomph spiniger. (A, D-F after Johnson, 1901).

Remarks. *N. procera* exhibits considerable variability in the paragnath pattern. Paragnaths are generally sparse, widely spaced, small, and absent from areas I and V; the differences in numbers in the other areas seem to be partly size-related.

Type locality and type specimens. Gulf of Georgia, Washington; MCZ.

Habitat. In the Santa Maria Basin and Western Santa Barbara Channel, the species was found in depths between 55 and 300 m in silt and silt mixed with sand.

Distribution. Western Canada to Southern California, intertidal to 1200 m, in silt, sand and on rocks.

Genus *Nicon* Kinberg, 1866

Type species: *Nicon pictus* Kinberg, 1866

Diagnosis. Prostomium pyriform, widest posteriorly, with 2 antennae, 2 palps, and 4 eyes. Proboscis smooth, paragnaths and papillae absent; maxillary ring bearing toothed jaws. Four pairs of tentacular cirri present. Parapodia biramous after setiger 2, with 2 notopodial ligules, neuropodial acicular lobe, and neuropodial ligule. Dorsal and ventral cirri simple throughout. Notosetae homogomph spinigers, neurosetae homogomph and heterogomph spinigers, and heterogomph falcigers.

Remarks. The only known Californian species, *N. moniloceras*, is easily recognized by the moniliform tentacular cirri; however, the systematically more important diagnostic character is the smooth proboscis. It may be helpful to examine the proboscis in poorly proserved or broken specimens.

***Nicon moniloceras* (Hartman, 1940)**

Figure 12.9

Leptonereis glauca moniloceras Hartman, 1940:217, pl. 34, figs. 42-46
Nicon moniloceras: Hartman, 1959:274; 1968:555.—Imajima and Hartman, 1964:150-151, pl. 35, figs. a-c.—Uschakov and Wu, 1965:60.—Imajima, 1972:53-55, fig.8a-j.—Taylor, 1984:31-13, fig. 31-10.—Lissner *et al.*, 1986:D-10.

Material examined. California: Santa Maria Basin, off Point Estero, Sta. 1 (26).

Description. Length to 30 mm, width to 2 mm including parapodia, segments to 64. Body slender, cylindrical, tapering toward pygidium; with characteristic pigment pattern on prostomium between antennae and across dorsum, the latter fading in alcohol. Anterior 5 segments with scattered dorsal epithelial glands staining with methyl green.

Prostomium pyriform, longer than wide, with slender, filiform antennae and massive palps with palpophores about as long as antennae and papilliform palpostyles; two pairs of large eyes in rectangular or slightly trapezoidal arrangement, posterior pair smallest (Fig. 12.9A). Proboscis smooth, lacking any papillae or paragnaths; jaws amber-colored to transparent, with about 8 or 9 blunt teeth.

Peristomium with four pairs of moniliform tentacular cirri arising from short cirrophores (articles sometimes seen only under compound microscope); posterior dorsal pair longest, reaching back to setiger 7 (9 in large specimens); ventral tentacular cirri much shorter, reaching back to about setiger 2. Parapodia in

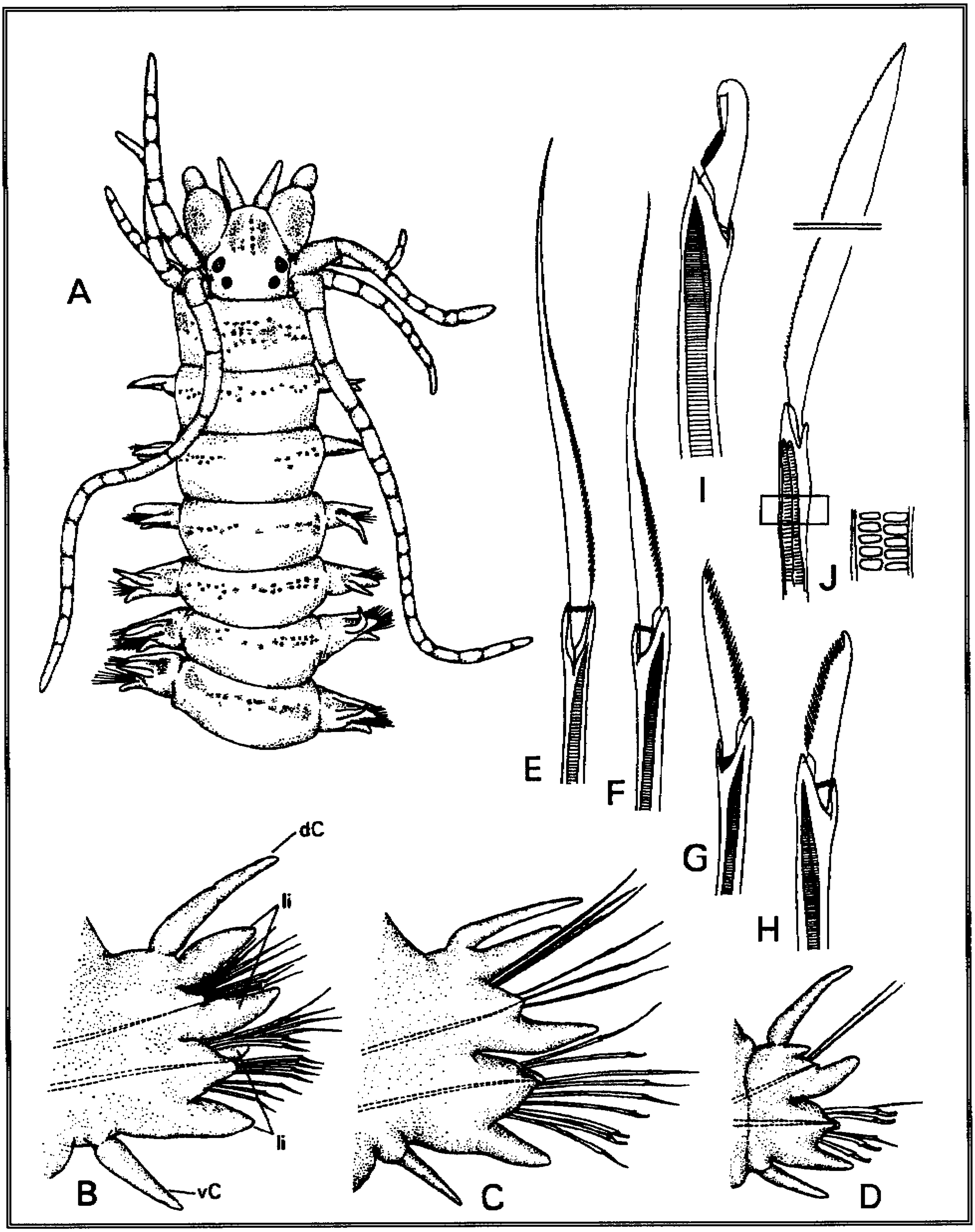

Figure 12.9. *Nicon moniloceras*: A, anterior end, dorsal view; B-D, anterior, middle and posterior parapodium, anterior view; E, notopodial homogomph spiniger; F, neuropodial subacicular heterogomph spiniger; G, neuropodial heterogomph falciger, subacicular fascicle; H, same, supraacicular fascicle; I, neuropodial heterogomph falciger, median parapodium; J, neuropodial natatory seta, blade shortened; detail: internal structure. (A-I from Imajima, 1972).

setigers 1 and 2 uniramous, biramous in all following setigers; notopodia with upper and lower ligule; upper ligule equal to lower ligule through mid-body, diminishing to minute structure in posterior segments; dorsal cirri long, indistinctly articulated, extending beyond notopodial ligules. Neuropodium with low, triangular pre-and postsetal lobes and lower ligule subequal to notopodial ligules; ventral cirri shorter than dorsal cirri, not exceeding neuropodial ligule in length (Fig. 12.9B-D). Distinct glands visible through body wall at notopodial bases in middle and posterior segments.

Notosetae slender, delicate homogomph spinigers; supraacicular neurosetae homogomph spinigers and heterogomph falcigers, subacicular neurosetae heterogomph falcigers (anterior setigers) or heterogomph falcigers and spinigers (posterior setigers). Blades of spinigers of similar length, finely serrated; in posterior setigers subacicular neuropodial spinigers with relatively coarse serrations along proximal part of blade. Blades of falcigers serrated and slightly bent in anterior segments, recurved inwards with tendon in posterior segments (Fig. 12.9E-I). Epitokous specimens with natatory setae in setigers 26 through 45 (Fig. 12.9J); notosetae delicate, homogomph, neurosetae thick, heterogomph. Pygidium small, with 2 tapering ventrolateral anal cirri about as long as last five segments; anus terminal.

Remarks. *Nicon moniloceras* is the only species of the genus known from California. Specimens in good condition are usually easy to identify because of the moniliform tentacular cirri.

Type locality and type specimens. Off Catalina Island, 80 m, in brachiopod colony; holotype: LACM-AHF Poly 0023.

Biology. The species prefers coarse sediments and hard substrata and is usually found in low densities. Females become epitokous at a relatively small body size (16 to 17 mm); large eggs were observed nearly filling the entire body cavity, including parapodial bases, except for the first and last 3 to 4 segments. An ovigerous female with transitional parapodia (few natatory setae, atokous setae still all present) was collected between October and January.

Distribution. Western Mexico to California; Gulf of Mexico; Yellow Sea; Japan; intertidal to 200 m.

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13. FAMILY NEPHTYIDAE GRUBE, 1850

by

Brigitte Hilbig[1]

Introduction

Nephtyids are among the more conspicuous and familiar polychaetes found in marine soft sediment. These worms are long, strongly muscular, and have a cylindrical anterior region containing the proboscis and a tapering middle and posterior region that is roughly rectangular in cross section. While the smallest species are less than 10 mm long when reaching sexual maturity, other species can grow to considerable size, reaching 20 cm in length and 1 cm in width. The most striking feature of this family is the shape of the parapodia. The widely separated rami and the usually dense, fan-shaped setal fascicles pointing diagonally outward from the "corners" of each segment are characteristic for all nephtyids. Members of this family preserve well and are easy to identify because taxonomically important characters remain intact; only the posterior end or the anal cirrus will occasionally break off during fixation.

Morphology

The prostomium is typically quadrangular to pentagonal with a thin, spatulate anterior margin; it bears two pairs of short, conical to cirriform antennae (the posterior pair is missing in *Inermonephtys*). The anterior pair arises from the anterior margin, points forward or to the sides, and is sometimes continuous with that margin; the second pair is inserted ventrolaterally, either directly behind the anterior pair or at some distance, and usually points to the sides. A pair of nuchal organs is located at the posterior corners of the prostomium; they are heavily ciliated and appear as short, rounded papillae when protruded (long and cirriform in *Inermonephtys*) and as slits or grooves when retracted. Eyes are subdermal and can often be seen in juveniles and in adults of small species, but are obscured by the thick body wall in large specimens. Posteriorly, the prostomium is usually indistinctly separated from the first segment; the outline of the large brain often appears as a narrow posterior extension reaching over the middorsum of the first 2 or 3 segments. Ohwada (1985) noted that the prostomial shape is defined very early during postlarval development, so that it can be used as a reliable character in the identification of juveniles.

The pharynx is eversible and forms a large, cylindrical to clavate proboscis. The anterior margin is surrounded by a circlet of 14 to 22 long, proximally fused, bifid papillae; the subdistal region is covered with as many longitudinal rows of 2 to 8 smaller, conical to cirriform papillae, and occasionally a single middorsal and a single midventral papilla arise between the distal and subdistal papillae (*Inermonephtys* lacks proboscideal papillae). Proximally the proboscis is either smooth or covered with minute, wartlike structures. At the inside wall about halfway down the proboscis there is a single, roughly conical, chitinous paragnath on either side. *Dentinephtys* possesses two lateral trepans of hard teeth that are located above the paragnaths.

There is no visible peristomium; the mouth is surrounded by the first few setigers. The first parapodia are usually directed forward and somewhat reduced, especially in the notopodia. The ventral cirri may be slightly enlarged and are called tentacular cirri by some authors. All subsequent parapodia are essentially similar except for changes in proportions. Notopodia and neuropodia are slender, elongate, and widely separated; a single acicula supports each ramus, projecting into an acicular lobe that may be

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conical, rounded, or incised. The shape of the acicular lobe is of great taxonomic importance. For species identification, parapodia from the middle region of the body should be examined because incised or rounded acicular lobes tend to become conical in posterior segments. Anterior and posterior to the acicular lobe, there are pre- and postacicular lamellae; the preacicular lamellae are usually shorter than the acicular lobes and broadly rounded, whereas the postacicular lamellae are often much longer than the acicular lobes, at least in the middle region of the body (lamellae are rudimentary in *Micronephtys*). Like the acicular lobes, parapodial lamellae are important taxonomic characters at the species level and should be examined on middle parapodia. Dorsal cirri arise from the inferior margin of the postacicular lamella; ventral cirri insert on the inferior neuropodial wall and are usually larger than the dorsal cirri. An interramal cirrus (also called branchia), inserted just underneath the dorsal cirrus, is present on almost all parapodia, starting from setiger 3, 4, or between 5 and 10 and lacking on the last 10 to 20 setigers. Generally, interramal cirri are slender and digitiform, but they may be basally inflated or foliaceous; they are either short and straight or long and curved outward (recurved) or inward (involute).

Setae are simple and typically numerous, arranged in thick, fan-shaped fascicles arising in front of and behind the acicular parapodial lobes. Preacicular setae are short, stiff, pointed, usually crossbarred (also called "laddered"), but are replaced with smooth capillaries in posterior parapodia in a small group of *Nephtys* species, including *N. cornuta*. Postacicular setae are flowing and silky, typically much longer than preacicular setae and include capillaries that may be smooth, spinulose (finely serrated in side view), or spinose (coarsely serrated in side view); *Aglaophamus*, *Inermonephtys* and *Micronephtys* also possess lyrate setae. The distribution of setal types within a fascicle varies greatly and can be used for species discrimination. Aciculae are single in each parapodial ramus, usually colorless, sometimes amber-colored in large specimens, and distally straight or bent to a fine, hook-shaped tip.

The posterior region of the body consists of very narrow segments with parapodia much longer than the body width. The pygidium is a small, narrow ring surrounding a terminal anus that is pushed slightly dorsad by the base of the single, long, filiform, ventral anal cirrus.

Taxonomic History

Nephtyid descriptions go back as far as 1780, and many of the nephtyids that are presently considered valid species were described by polychaete taxonomists of the 19th century, including Ehlers, Augener, McIntosh, Malmgren, Grube, Quatrefages, Savigny, and others. The oldest species were first placed in the genus *Nereis* which, according to Linné's "Systema Naturae", accommodated essentially all polychaetes except for scale worms. Cuvier established the genus *Nephtys* in 1817, and the family Nephtyidae was erected in 1850 by Grube (as Nephthydea). There are now about 50 valid species in this genus. *Aglaophamus* was established by Kinberg (1866) to include nephtyids with lyrate setae; at the same time he described *Aglaopheme*, a genus that differed in morphological details of the paragnaths, but was later synonymized with *Aglaophamus*. Paragnaths have not been commonly used as taxonomic characters because there are sufficient characters for genus and species discrimination that are more readily accessible than paragnaths, which are visible only after dissection. Friedrich (1939) established the genus *Micronephtys* for species with reduced morphological features such as parapodial lobes and ligules and the presence of only a few small interramal cirri. Fauchald (1967) described two nephtyids from Vietnam that were characterized by only one pair of antennae and the absence of proboscideal papillae, and he placed them in a new genus, *Inermonephtys*. Very recently, Imajima and Takeda (1987) added a fifth genus, *Dentinephtys*, for a species described by Hartman (1950) that was found to possess trepans with large chitinous teeth inside the proboscis.

The most widely used diagnostic generic characters include the shape of the interramal cirri (involute in *Aglaophamus*, recurved in *Nephtys*) and the number of rows of papillae on the proboscis (14 in *Aglaophamus*, 22 in *Nephtys* and *Micronephtys*, none in *Inermonephtys*). Fauchald (1967) added characters such as the presence or absence of lyrate setae, the shape of the acicular tip, and also reestablished the shape of the paragnaths as a generic character, but emphasized that no single character is sufficient to define a genus. Proper placement of a species in a genus requires examination of a combination of characters because some of them are variable and even overlap among genera. For example, there are several species of *Nephtys* whose interramal cirri are straight rather than recurved; some species of *Aglaophamus* possess 22 rather than 14 rows of subterminal papillae; two of the three species of *Aglaophamus* described in this atlas do not have lyrate setae. Important revisions and monographs of nephtyids were provided by Hartman (1938, 1950), Rainer and Hutchings (1977), and Imajima and Takeda (1985, 1987).

Distribution and Biological Notes

Nephtyids are typical inhabitants of sandy sediments and are therefore most often found in depths to about 100 m, although they occur over a wide depth range from the intertidal zone to the deep sea. They are very active swimmers and burrowers, but do not construct permanent tubes in the sediment. Species occurring together in a geographical area tend to be separated to a degree by preferences of different grain sizes (Clark and Haderlie, 1962; Clark *et al.*, 1962). Although nephtyids are present in many areas, knowledge about their biology is poor; Fauchald and Jumars' (1979) review of feeding biology contains only very few remarks on nephtyids. Traditionally they are considered carnivores because gut contents were found to consist of molluscs, crustaceans, and polychaetes. However, Sanders (1956, 1960) reported subsurface deposit feeding in dense assemblages of *N. incisa*, and sediments were seen in the guts of *N. cornuta* (Noyes, 1980, as *Aglaophamus neotenus*). Clark (1962) examined gut contents of two Atlantic species of *Nephtys* and found mostly animal remains, including setae of several polychaete families, along with only a few sand grains. According to Clark (1962), the fact that nephtyids seem to avoid sediments that normally have a high organic carbon content indicates that nephtyids typically do not deposit feed, unless they are forced into fine sediments by competition (see also Redmond and Scott, 1989). No data are available on feeding behavior.

Sexes are separate; gametes are released freely into the water and after fertilization develop into planktonic larvae. Metamorphosis takes place in the sediment (Noyes, 1980). Because of difficulties in rearing larvae beyond a metatrochophore stage in the laboratory, there are no complete accounts of the reproduction and development of nephtyids, although larvae have been found frequently in plankton samples. At least some species may become epitokous and develop additional long setae (Garwood and Olive, 1981), but data to support that assumption are sparse.

Key to the Nephtyidae

1A. Interramal cirri curved inward, free end pointing toward parapodial wall (involute): genus *Aglaophamus* 2

1B. Interramal cirri curved outward, free end pointed away from parapodium (recurved), or interramal cirri straight 4

2A. Some neuropodia with erect lobe resembling interramal cirrus 3

2B. Neuropodia without erect lobe; interramal cirri first present on segment 8 or 9; proboscis with 14 rows of subterminal papillae; postacicular setae smooth and spinulose (finely serrated); lyrate setae absent .... *Aglaophamus paucilamellata*

3A. Neuropodial erect lobe up to 8 times as long as wide (Fig. 13.3E); interramal cirri first present on segment 5 to 8; proboscis with 22 rows of subterminal papillae; postacicular setae spinulose and lyrate .... *Aglaophamus verrilli*

3B. Neuropodial erect lobe up to 3 times as long as wide (Fig. 13.1D); interramal cirri first present on segment 8 or 9; proboscis with 14 rows of subterminal papillae; postacicular setae smooth and spinose, lyrate setae absent .... *Aglaophamus erectans*

4A. Interramal cirri first present on segment 3 or 4 5

4B. Interramal cirri first present on segments 5 to 11 9

5A. Interramal cirri first present on segment 4, recurved; acicular lobes in middle parapodia incised; prostomium and first few segments pigmented (Fig. 13.6A-D) .... *Nephtys caecoides*

5B. Interramal cirri first present on segment 3 (may be very small in first few segments) 6

6A. Anterior end dorsally pigmented (Fig. 13.9A); acicular lobes of middle parapodia incised; proboscis with 22 terminal papillae, 22 rows of subterminal papillae, and middorsal papilla .... *Nephtys ferruginea*

6B. Anterior end unpigmented; acicular lobes incised, conical, or rounded; proboscis with or without middorsal papilla 7

7A. Interramal cirri recurved; acicular lobes incised; proboscis with 22 terminal papillae and 22 rows of subterminal papillae; middorsal papilla absent .... *Nephtys californiensis*

7B. Interramal cirri straight, somewhat flattened 8

8A. Acicular lobes of middle parapodia conical; proboscis with 22 terminal papillae; middorsal papilla as long as largest subterminal papillae .... *Nephtys simoni*

8B. Acicular lobes of middle parapodia incised; proboscis with 20 terminal papillae; middorsal papilla much longer than largest subterminal papillae .... *Nephtys signifera*

9A. Both pairs of antennae pointing forward, posterior pair bifid or with lateral boss; proboscis with 14 terminal papillae, 16 rows of subterminal papillae, and middorsal papilla; interramal cirri first present on segment 5 or 6; body reaching maximally 15 mm length .... *Nephtys cornuta*

9B. All antennae simple; proboscis with at least 20 terminal papillae and 20 rows of subterminal papillae; interramal cirri first present on or after segment 6; body reaching distinctly more than 15 mm length 10

10A. Interramal cirri first present on segment 6 11

10B. Interramal cirri first present on or after segment 7 12

11A. Interramal cirri basally inflated where best developed and filled with many small vessel loops; neuropodial postsetal lamellae long, truncate; proboscis with 22 terminal papillae and 22 rows of subterminal papillae; middorsal papilla absent .... *Nephtys assignis*

11B. Interramal cirri slender; all parapodial lamellae reduced; anterior parapodia with preacicular setae at least as long as postacicular setae; proboscis with 22 rows of only 1 to 3 subterminal papillae and large middorsal papilla; inside proboscis two trepans with 8 or 9 conspicuous, hard teeth (Fig. 13.4B, C) .... *Dentinephtys glabra*

12A. Interramal cirri first present on segment 7 or 8, broadly foliaceous where best developed, straight; all parapodial lamellae rudimentary, acicular lobes rounded; proboscis proximally smooth, middorsal papilla absent .... *Nephtys schmitti*

12B. Interramal cirri first present on segment 8 to 11, slender, recurved; acicular lobes incised; proboscis proximally rough, middorsal papilla present; anterior end sometimes with pigment spots at notopodial bases .... *Nephtys punctata*

Description of Species

The nephtyid fauna of the Californian shelf is diverse, with roughly one-quarter of all known species of *Nephtys* occurring in the area. Seventeen species belonging to 3 genera are reported; this chapter deals with 12 of these species and one additional species that was described recently (Hilbig, 1992):

Aglaophamus erectans Hartman, 1950
Aglaophamus paucilamellata Fauchald, 1972
Aglaophamus verilli (McIntosh, 1885)
Dentinephtys glabra (Hartman, 1950)
Nephtys assignis Hartman, 1950
Nephtys caecoides Hartman, 1938
Nephtys californiensis Hartman, 1938
Nephtys cornuta Berkeley and Berkeley, 1945
Nephtys ferruginea Hartman, 1940
Nephtys punctata Hartman, 1938
Nephtys schmitti Hartman, 1938
Nephtys signifera Hilbig, 1992
Nephtys simoni Perkins, 1980

Genus *Aglaophamus* Kinberg, 1866

Type species: *Agalophamus lyratus* Kinberg, 1866

Diagnosis. Prostomium rectangular to pentagonal, with 2 pairs of small antennae; anterior pair inserted dorsally at anterior corners of prostomium, posterior pair inserted ventrolaterally (also referred to as palps). Occasionally two subdermal eyes present on prostomium or on one of the first segments. One pair of nuchal organs at posterior corners of prostomium. Proboscis proximally smooth, distally with circlet of 14 (sometimes 22) bifid papillae, subdistally covered with 14 rows of soft papillae (species with more than 14 terminal papillae also have more than 14 rows of subdistal papillae); single middorsal and midventral papillae sometimes arising betweeen subdistal and distal papillae. Two paragnaths inside proboscis, base triangular. Parapodia usually with conical acicular lobes; interramal cirri involute, present on most segments; preacicular setae crossbarred, postacicular fascicles composed of spinulose or spinose capillaries and usually lyrate setae.

Remarks. Kinberg (1866) separated *Aglaophamus* from *Nephtys* not only based on the presence of lyrate setae, but also the shape of the paragnaths which he describes as being "fusiform, not hooked (nec ungulatae)." He does not mention the interramal cirri at all; curiously, they seem to be the only feature representing an invariable generic character, whereas the lyrate setae may be present or absent. The shape of the paragnaths has proven to be inconsistent as well because they may be conical and gently rounded at the tip or sharply pointed and clawlike ("ungulate").

Aglaophamus erectans Hartman, 1950

Figure 13.1

Aglaophamus erectans Hartman, 1950:125-127, pl. 19, figs. 1-10; 1968:569.—Lissner *et al*., 1986:D-10. —Hyland and Neff, 1988: A-2.—Hyland *et al*., 1990:F-1.

Material examined. California: Santa Maria Basin, off Point Sal, Sta. 33 (1); off Point San Luis, Sta. R-3 (1).

Description. Length to 56 mm, width to 4 mm excluding parapodia, segments to 93. Body stout, tapering toward pygidium; color in alcohol: tan with scattered dark pigment on prostomium (one large specimen with triangular orange pigment spot covering posterior two-thirds of prostomium) and along midventral line.

Prostomium slightly longer than wide, subrectangular (widest in front), with 2 pairs of antennae,the ventral ones largest; eyes absent (Fig. 13.1A). Proboscis with 14 bifid terminal papillae and 14 rows of 10 to 13 subterminal papillae, decreasing in size toward mouth; midventral and middorsal papillae absent (Fig. 13.1B).

First parapodia large, directed forward, with neurosetae projecting beyond prostomium. Subsequent parapodia directed laterally, with well-separated rami (Fig. 13.1C); notopodium with low presetal lamella, triangular acicular lobe, and foliaceous postsetal lamella directed slightly upward; dorsal cirri present from segment 1, small throughout, conical; interramal cirri first present from segment 8 or 9, smaller than dorsal cirri through about setiger 14, fully developed and curving inward from about setiger 17 (Fig. 13.1D), decreasing again to small papilliform appendage within last 25 setigers. Neuropodia with low presetal lamella, conical acicular lobe and rounded postsetal lamella of about the same length as acicular lobe; from segment 16 or 17 on small papilliform upper neuropodial lobe present, best developed on mid-body segments, up to 3.5 times as long as wide. Ventral cirri larger than dorsal cirri, clavate. Aciculae transparent, distally curved.

Setae of three kinds; preacicular setae short, crossbarred in lower notopodial and upper neuropodial position, about 10 to 20 per fascicle (Fig. 13.1E); in upper notopodial and lower neuropodial position small fascicles of 3 to 10 capillary setae covered with widely spaced rows of minute spines (Fig. 13.1F). Postacicular setae in both rami about twice as long as preacicular setae, longest and most numerous in notopodium; capillary, spinose along middle third, with coarsely serrated appearance at low magnification (Fig. 13.1G); large specimens with additional smooth, thin capillaries in uppermost and lowermost positions of both fascicles; lyrate setae absent.

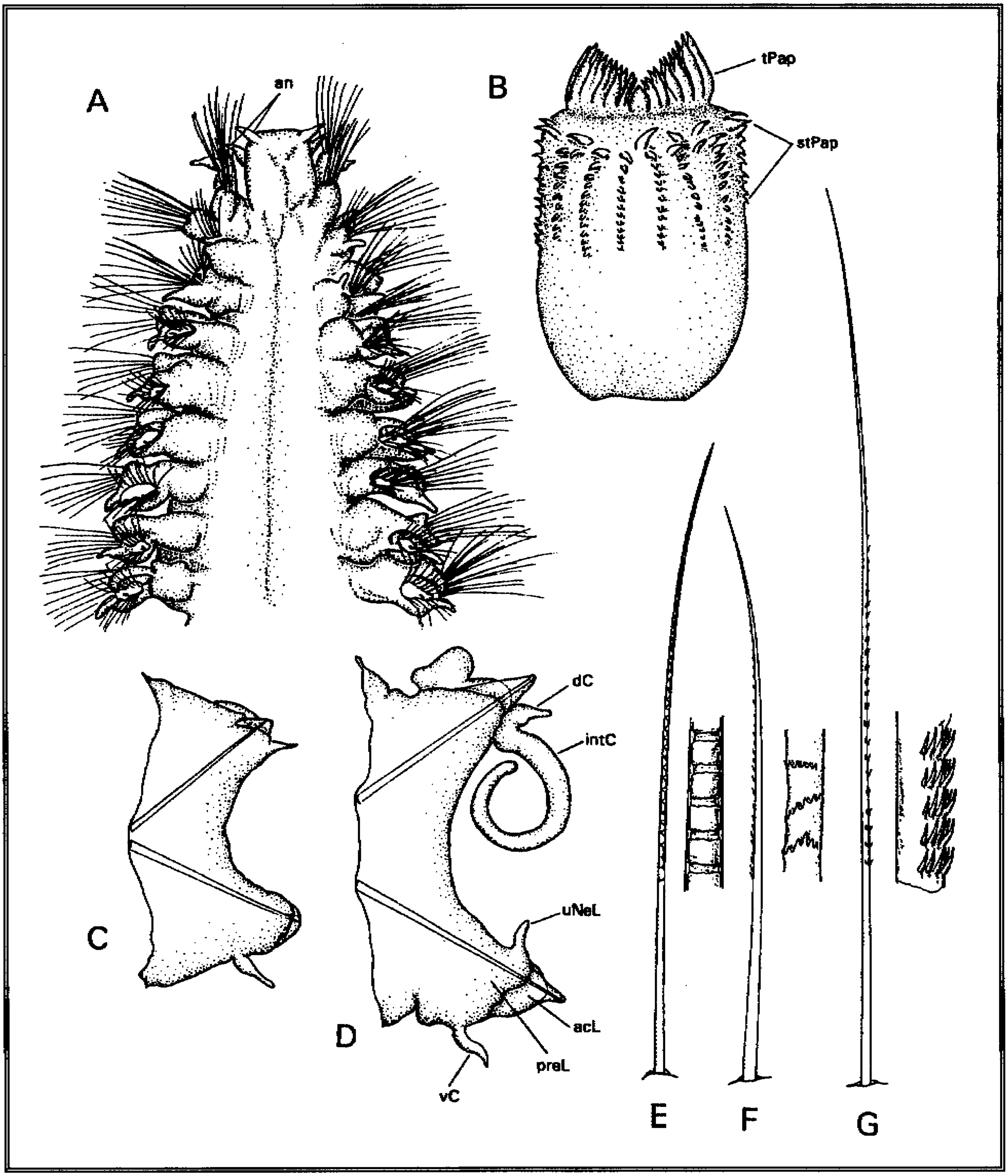

Figure 13.1. *Aglaophamus erectans*: A, anterior end, dorsal view; B, proboscis, anterior view; C, anterior parapodium, anterior view; D, middle parapodium, anterior view; E, crossbarred seta with detail; F, spinulose preacicular seta, detail: rows of surficial spines; G, postacicular seta, detail: spines (A-D, after Hartman, 1950; details of E and G from Hartman, 1950).

Remarks. *A. erectans* resembles *A. verrilli* somewhat in the presence of a superior neuropodial lobe; however, this lobe is up to 8 times as long as wide and cirriform in the latter species, whereas in the former it is papilliform and only up to 3.5 times (usually about twice) as long as wide. In addition there are differences in the setal types, the most obvious being the presence or absence of lyrate setae; and in the number of papillae on the proboscis (22 versus 14 rows).

Type locality and type specimens. SW of Santa Catalina Island, 81 m; holotype and paratypes: LACM.

Habitat. The species occurs in mud and silt.

Distribution. Mexico to California, 37 to 440 m.

Aglaophamus paucilamellata Fauchald, 1972

Figure 13.2

Aglaophamus paucilamellata Fauchald, 1972:86-87, pl. 16, figs. a-f.—Lissner *et al.*, 1986:D-10.

Material examined. California: Santa Maria Basin, off Point Estero, Sta. 7 (1); off Point San Luis, Sta. 27 (1).

Description. Longest fragment (holotype) 15 mm long, 4 mm wide including setae for 32 segments. Body slender, without pigmentation.

Prostomium longer than wide, anteriorly rounded, nearly quadrangular; antennae subequal, ventral ones largest, inserted closely behind the dorsal ones; eyes absent (Fig. 13.2A). Proboscis with 14 rows of 8 to 10 papillae; no middorsal papilla.

First parapodia directed forward, with neuropodia extending almost as far as prostomium and neurosetae projecting well beyond antennae. Subsequent parapodia directed laterally, with well-separated rami. Notopodia and neuropodia with low, rounded presetal lamellae, conical acicular lobes and short, rounded postsetal lamellae, shorter than acicular lobes. Dorsal and ventral cirri small, clavate; interramal cirri first present in segment 8 or 9, large and curved inward throughout, present to end of body except for the last 3 or 4 segments (Fig. 13.2B). Aciculae transparent, relatively thick, distally curved.

Preacicular setae in both rami short, tapering to fine tip, crossbarred except for basal 1/4 (Fig. 13.2C); notopodia with about 10 setae per fascicle, neuropodia with 6. Postacicular setae of 2 kinds: (1) 2 to 4 very fine, smooth capillaries in upper notopodial and lower neuropodial position; (2) 20 to 30 spinulose capillaries in lower notopodial and upper neuropodial position (Fig. 13.2D); all postacicular setae about twice as long as preacicular ones. Lyrate setae absent.

Remarks. The species was originally known only from Baja California; its occurrence in the Santa Maria Basin is a northward range extension.

Type locality and type specimens. Bahia de San Cristobal, Western Mexico; holotype and paratypes: LACM.

Habitat. *A. paucilamellata* is found in mixed sediments.

Distribution. Western Mexico to central California, 220 to 680 m.

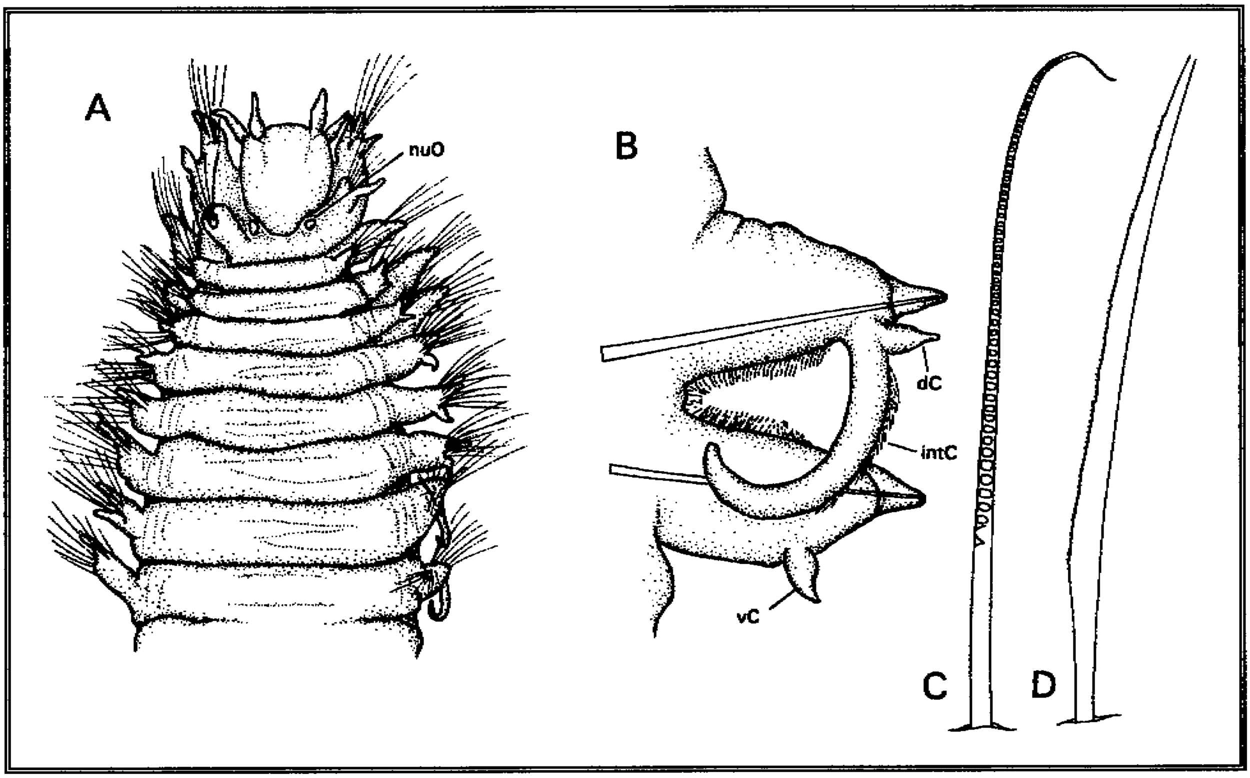

Figure 13.2. *Aglaophamus paucilamellata*: A, anterior end, dorsal view; B, middle parapodium, anterior view; C, preacicular seta; D, postacicular spinulose seta.

Aglaophamus verrilli (McIntosh, 1885)

Figure 13.3

Nephthys verrilli McIntosh, 1885:163-164, pl. 26, figs. 6-7, pl. 32A, fig. 8.
Nephthys dibranchis: Hartman, 1938:146 (in part); 1940:237 (in part). *Not* Augener, 1922.
Aglaophamus dicirris Hartman, 1950:122-124, pl. 18, figs. 1-8 (synonymy).—Lissner *et al.*, 1986:D-10.—Hyland and Neff, 1988:A-2.—Hyland *et al.*, 1990:F-1.
Aglaophamus erectans: Lissner *et al.*, 1986:D-10 (in part).
Aglaophamus verrilli: Knox, 1960:115.—Pettibone, 1963:190-191, fig. 48c, d.—Rainer and Hutchings, 1977:316-320, figs. 7-11 (synonymy).—Taylor, 1984:35-15 - 35-17, fig. 35-12.—Imajima and Takeda, 1985:80-81, fig.11.

Material examined. California: Santa Maria Basin, off Point San Luis, Sta. 22 (3); off Purisima Point, Sta. 42 (1); off Point Arguello, Sta. 58 (2); off Point Sal, Sta. PJ-7 (2), Sta. PJ-8 (1), Sta. PJ-11 (2), Sta. R-8 (4).

Description. Length to 55 mm, width to 4 mm excluding parapodia, segments to 87. Body stout, short, tapering toward pygidium, with crowded segments and conspicuous parapodia. Color in alcohol uniformly tan.

Prostomium slightly longer than wide, rectangular, bearing 2 pairs of subequal antennae anteriorly and a pair of minute but conspicuous black eyes in posterior half (Fig. 13.3A, B). Proboscis cylindrical to clavate, distally strongly muscular, with 22 marginal papillae; proximally inflated, with 22 rows of 3 to 9 papillae; middorsal papilla usually absent; rarely 1 or 2 papillae slightly displaced medially, but equal to other papillae, not elongate (Fig. 13.3C).

Parapodia biramous, with well-separated rami of equal size except for setiger 1 with reduced neuropodium (Fig. 13.3D). Notopodia with low presetal lamella, conical acicular lobe, and rounded, foliaceous postsetal lamella; interramal cirri first present on segment 5 to 8, continuing to near end of body; each interramal cirrus involute (curved inward), long and slender, much longer than corresponding dorsal cirri from about third setiger of their appearance. Neuropodia with lobes similar to notopodia and clavate ventral cirri, postsetal lamellae slightly shorter than notopodial ones; upper neuropodial lobe slender, cirriform, longer than ventral cirri, first appearing in setiger 14 to 23 and continuing almost to end of body. Aciculae yellow, distally tapering and curved (Fig. 13.3E). Preacicular setae in both rami arranged in widely scattered, fanlike fascicles, short, tapering to fine tip, crossbarred along distal two-thirds to three-fourths of length; postacicular setae of 3 kinds: (1) long, flowing, very slender capillaries covered with minute surficial spines at least along basal third, often hard to see; (2) lyriform furcate setae with subequal prongs, scattered among numerous capillaries, about 5 to 8 per fascicle in median parapodia; (3) smooth capillaries in setiger 1 (Fig. 13.3F-H).

Anal cirrus filiform, about as long as last 10 segments.

Remarks. This species was originally identified as *A. dicirris*; however, Knox (1960) synonymized *A. dicirris* with *A. verrilli*; the synonymy has since been adopted by Pettibone (1963) and Rainer and Hutchings (1977) among others, and is followed here. The species is easily recognized by the neuropodial cirriform lobes that are present even in very small juveniles.

Type locality and type specimens. Piñas Bay, Panama; holotype of *A. dicirris*: LACM-AHF Poly 0786; lectotype of *A. verrilli*: BMNH 1885: 12:1:127.

Biology. *A. verrilli* has been reported from sand mixed with mud or shell fragments; in the Santa Maria Basin, it occurs in sediments with high silt-clay content at about 100 to 140 m depth. One large voucher specimen collected during Phase I (fall/winter 1973/74) is ovigerous.

Distribution. California to Panama; Gulf of Mexico; Maryland to Georgia; New Zealand, Australia; Japan; India; intertidal to 200 m.

Genus *Dentinephtys* Imajima and Takeda, 1987

Diagnosis. Prostomium suboval to trapezoidal, with 2 pairs antennae; dorsal pair directed anteriorly, inserted on anterior margin of prostomium; ventral pair directed laterally, arising from anteroectal margins of prostomium; eyes absent; nuchal organs present at postectal prostomial margins. Proboscis with 22 bifid terminal papillae and 22 rows of only 1 to 3 subterminal papillae; large middorsal papilla. Proboscis internally armed with two trepans, each with 8 or 9 hard, whitish teeth pointing sharply backward, located just inside the circlet of terminal papillae; trepans usually not visible unless dissected, even in fully everted proboscis. Parapodia with recurved interramal cirri and capillary setae; lyrate setae absent.

Remarks. *Dentinephtys* is very similar to *Nephtys* except for the trepans located inside the proboscis; to date only one species is known, but additional species may be moved from *Nephtys* to *Dentinephtys* after reexamination of the dissected proboscis.

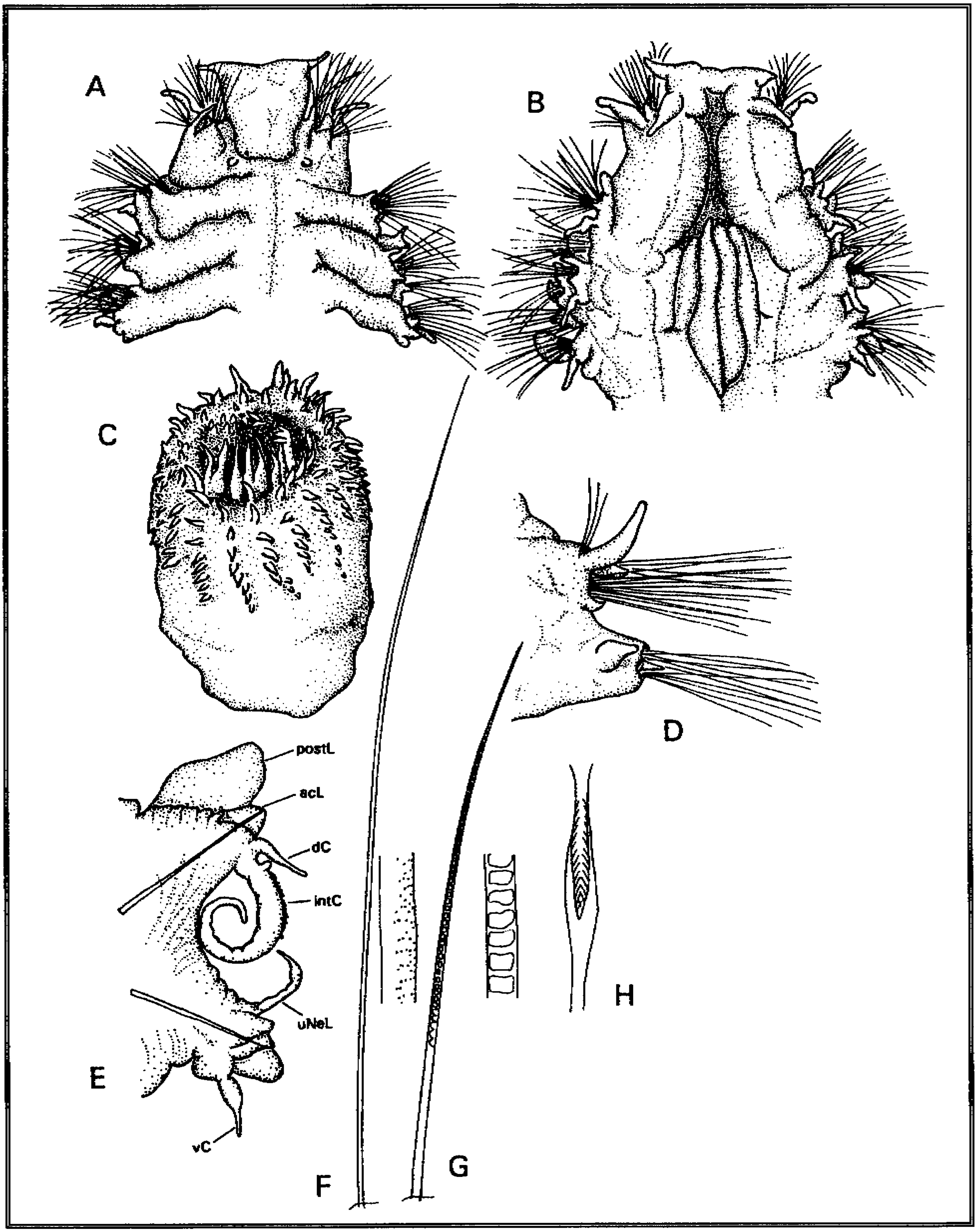

Figure 13.3. *Aglaophamus verrilli*: A, anterior end, dorsal view; B, same, ventral view; C, proboscis, ventrolateral view; D, first parapodium, posterior view; E, middle parapodium, anterior view; F, postacicular seta; detail: surficial spines; G, preacicular seta; detail: crossbars; H, lyrate seta (A-E, H, and details of F and G after Imajima and Takeda, 1985).

Dentinephtys glabra (Hartman, 1950)

Figure 13.4

Nephtys glabra Hartman, 1950:109-110, pl. 13, figs. 1-9; 1968:585.
Dentinephtys glabra Imajima and Takeda, 1987:43-46, figs. 2-3.—Hyland and Neff, 1988:A-2.

Material examined. California: Santa Maria Basin, off Purisima Point, Sta. R-5 (1).

Description. Length more than 115 mm, width to 8 mm including parapodia, segments more than 120. Body unpigmented, setae and acicular tips dusky. First 5 segments crowded, with parapodia directed forward on segments 1 and 2, gradually turning laterally in next 3 segments.

Prostomium suboval to pentagonal, anterior margin slightly wider than posterior. Antennae small, conical; dorsal ones arising from anterior prostomial margin, ventral ones from anterior corners (Fig. 13.4A). Proboscis smooth and glistening proximally, with 22 rows of only 1 to 3 papillae subterminally; lateral papillae larger than dorsal and ventral ones; large, conspicuous middorsal papilla. Terminal circlet with 22 relatively short bifid papillae; 2 trepans with 8 or 9 whitish, hard, basally fused teeth just below terminal papillae on inside of proboscis; teeth pointing sharply backward (Fig. 13.4A-C).

First parapodia large, flattened, with subequal rami; pre- and postacicular lamellae low and rounded, acicular lobes bluntly conical; dorsal and ventral cirri subequal. Subsequent parapodia with well-separated rami; preacicular lamellae low and rounded throughout, postacicular lamellae rounded, slightly longer than acicular lobe, pointing slightly upward in neuropodia and toward dorsum in notopodia; acicular lobes bluntly rounded; in posterior parapodia all lamellae reduced. Interramal cirri first present on segment 6 or 7 and continuing through end of body; distinctly recurved and heavily ciliated throughout; small through about segment 13, occupying one-third of interramal space; fully developed around segment 22, filling out entire interramal space (Fig. 13.4D-F). Setae very numerous, between 20 and 30 preacicular setae and 50 or 60 postacicular setae in each fascicle; preacicular setae crossbarred along distal half (Fig. 13.4G); in anterior segments 1.5 times as wide as in middle and posterior segments, stiff, amber-colored; postacicular setae in anterior segments slender, not much longer than preacicular setae, smooth; in middle and posterior segments more than 3 times as long and almost twice as wide as preacicular setae, silky, flowing; covered with very regular rows of large spines along proximal third in middle of fascicle (Fig. 13.4H); spines gradually diminishing in upper and lower setae of each ramus. Aciculae yellow, with blunt tips appearing dusky when seen from above.

Remarks. The examined specimen differs slightly from the description of Imajima and Takeda (1987) in that the trepan has 9 instead of 8 teeth on each side. Although the trepan can only be seen after dissection even when the proboscis is fully everted, the characteristic look of the anterior end caused by the proportions of the setae distinguishes this species from all *Nephtys* occurring in the area.

Type locality and type specimens. California, off Anacapa Island; holotype: LACM 0793.

Habitat. The species lives in sand and sand mixed with silt.

Distribution. Central and southern California; Japan; 68 to 154 m.

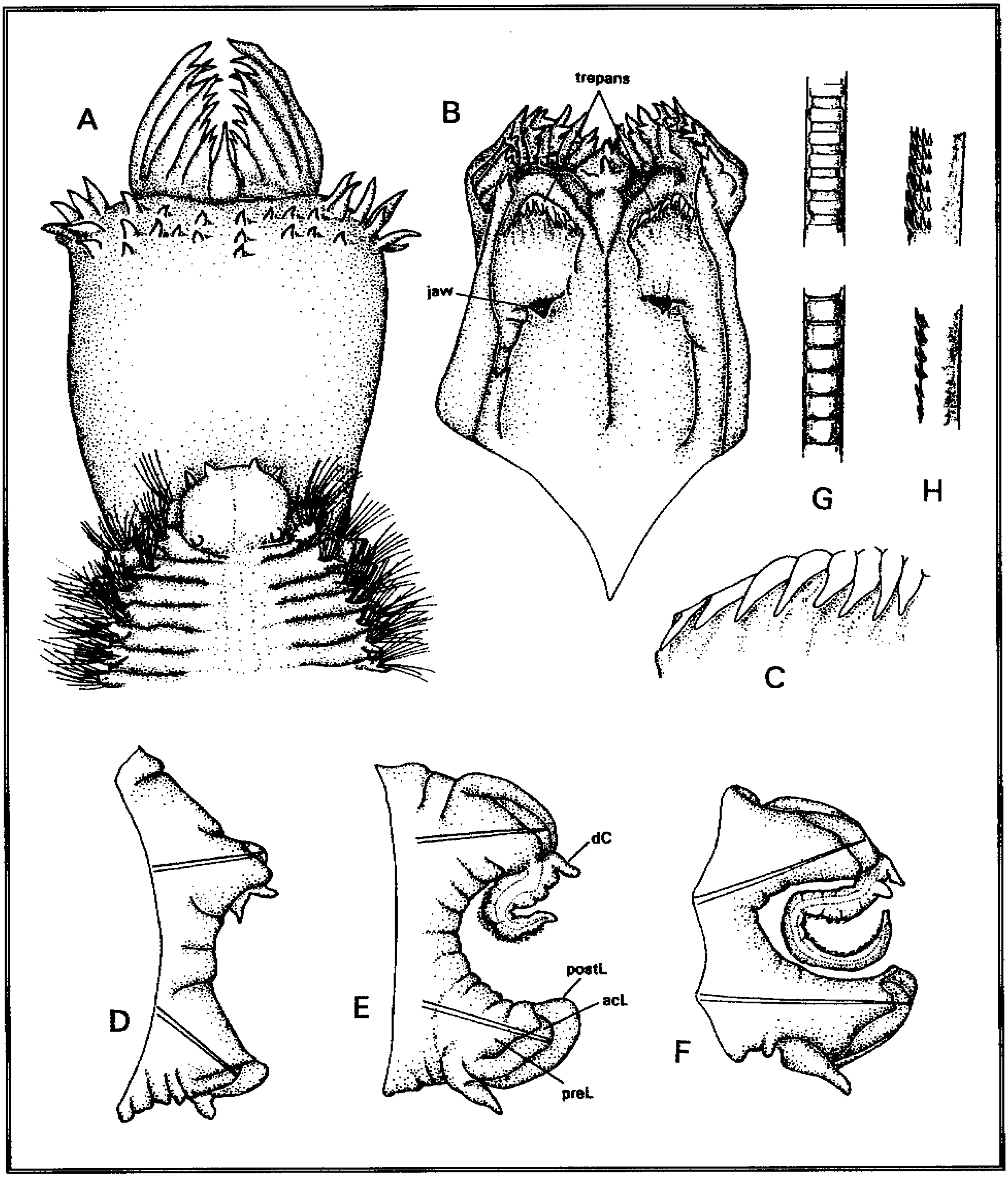

Figure 13.4. *Dentinephtys glabra*: A, anterior end, dorsal view; B, proboscis, dissected; C, trepan; D, 6th parapodium, anterior view; E, 32nd parapodium, anterior view; F, 63rd parapodium, anterior view; G, basal and middle part of preacicular seta; H, basal and middle part of postacicular seta (A, F after Hartman, 1950; B-E after Imajima and Takeda, 1987; G-H from Hartman, 1950).

Genus *Nephtys* Cuvier, 1817 in Audouin and Milne Edwards, 1833

Type species: *Nephtys hombergii* Savigny, 1818

Diagnosis. Prostomium quadrangular, pentagonal, or rounded; with 2 pairs antennae inserted anterolaterally and laterally, and a pair of nuchal papillae at postectal margins. Proboscis with terminal circlet of 14, 20, or 22 bifid papillae and 16 or 22 rows of subterminal papillae, with or without middorsal and midventral papilla. Proximal part of proboscis smooth or rough, covered with minute wartlike papillae.

Parapodia with widely separated rami (except for first one); acicular lobes conical, rounded, or incised; pre- and postacicular lamellae low and rounded to well-developed and foliaceous; interramal cirri recurved or straight, starting on segment 3, 4, or between segments 5 and 11. Dorsal and ventral cirri present, conical to digitiform. Preacicular setae short, crossbarred, at least in anterior segments; postacicular setae long, smooth, spinulose (finely serrated), or spinose (coarsely serrated); lyrate setae absent. Aciculae single in each ramus, with fine curved tips or straight and blunt.

Pygidium small, narrow, surrounding terminal anus, with ventrally inserted, long, filiform anal cirrus.

***Nephtys assignis* Hartman, 1950**

Figure 13.5

Nephtys assignis Hartman, 1950:112-113, pl. 14, figs. 1-6; 1968:573.—Banse and Hobson, 1968:17.—Hyland and Neff, 1988:A-2.—Hyland *et al.*, 1990:F-1.

Material examined. California: Santa Maria Basin, off Point Sal, Sta. PJ-10 (2). Washington: Puget Sound (10).

Description. Length to 200 mm, width to 10 mm excluding parapodia, segments to 145. Body wide, with large parapodia, tapering toward pygidium within middle and posterior thirds of body. Color in alcohol uniformly tan, sometimes with slightly dusky dorsum in anterior few setigers.

Prostomium roughly rectangular, about as long as wide when proboscis retracted; antennae widely spaced, the ventral ones being largest; eyes absent (Fig. 13.5A). Proboscis large, rigid, proximally smooth, with 22 rows of about 5 subdistal papillae and terminal circlet of 22 papillae; middorsal papilla absent (Fig. 13.5B).

First parapodia directed forward, with conspicuous notopodium bearing enlarged, conical dorsal cirrus, and small neuropodium. Subsequent parapodia directed laterally; both rami without preacicular lamellae; acicular lobes weakly incised, with acicula projecting into pointed tip; notopodial postacicular lamellae truncate, foliaceous; neuropodial postacicular lamellae much larger than notopodial ones, almost rectangular, pointing slightly upward, foliaceous, with blisterlike accessory gill in large specimens; lobes of both rami best developed in setigers 20 to 65, diminishing in size within following 10 setigers, absent in posterior setigers. Interramal cirri first present on segment 6, minute through segment 12 to 20 (Fig. 13.5C), on subsequent segments starting to recurve, best developed in parapodia with largest lobes, small and straight in posterior segments; proximally inflated where well-developed, filled with numerous small vessel loops similar to those in neuropodial gills; distally slender and digitiform (Fig. 13.5D, E). Dorsal and ventral cirri slender in anterior and middle parapodia, tending to become wider and conical in posterior parapodia (Fig. 13.5F).

Setae short, dusky, and not very numerous compared to size of animal; preacicular setae short, stiff, crossbarred along distal half (Fig. 13.5G), in large fascicles in anterior 10 to 12 parapodia, fewer in

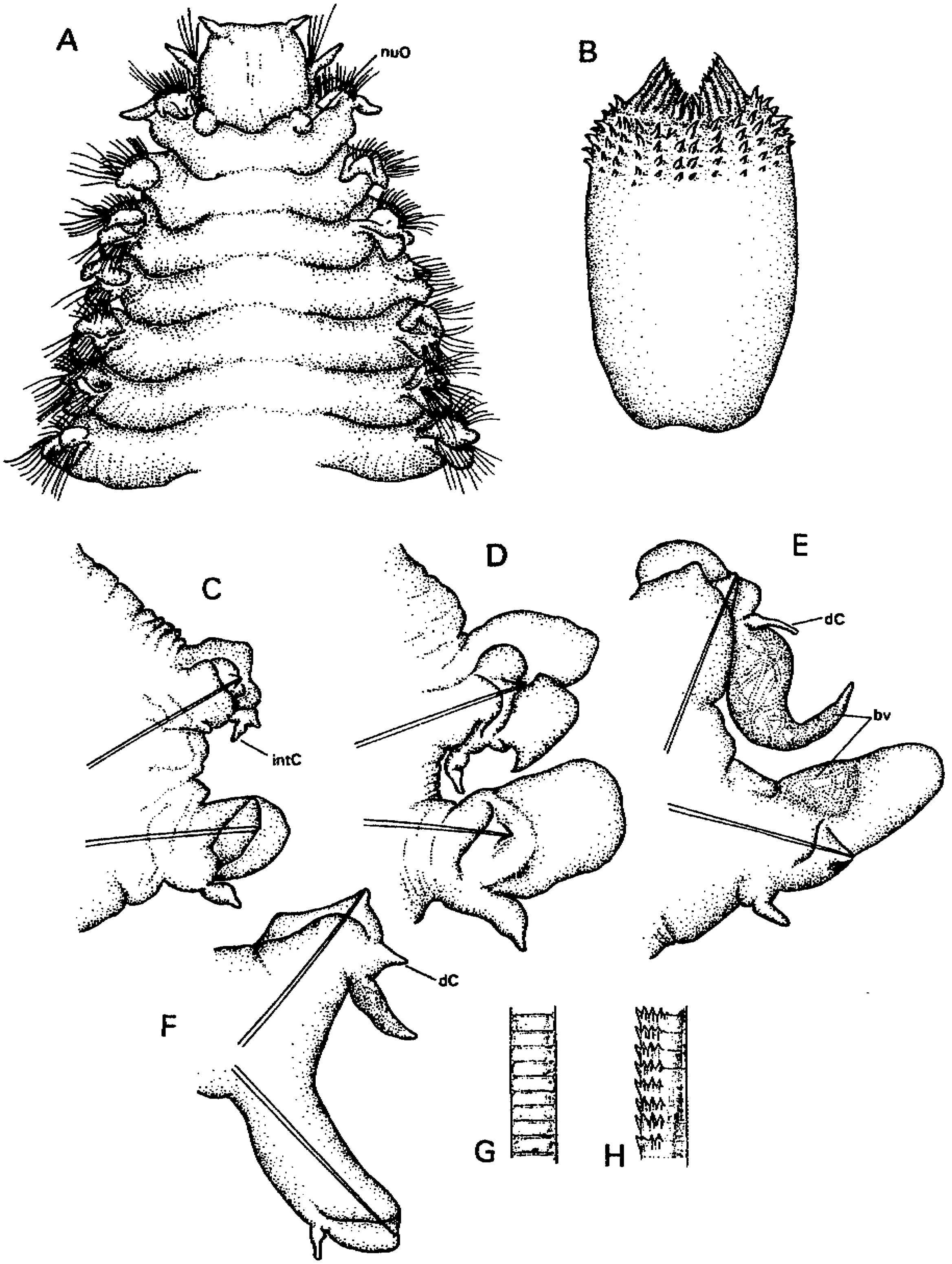

Figure 13.5. *Nephtys assignis*: A, anterior end, dorsal view; B, proboscis, dorsal view; C, anterior parapodium, anterior view; D-E, middle parapodia, anterior view; F, posterior parapodium, anterior view; G, detail of preacicular seta; H, detail of postacicular seta (A-D after Hartman, 1950; G-H from Hartman, 1950).

subsequent setigers; postacicular setae longer than preacicular ones, relatively stiff as well, with regular rows of surficial spines creating a coarsely serrated appearance (Fig. 13.5H). Aciculae single in each ramus, distally straight, blunt, dark amber colored.

Anal cirrus filiform, about as long as last 13 segments.

Remarks. One interesting feature, the presence of an additional gill, has not been observed before; the presence of numerous coiled vessel loops in that gill and in the interramal cirrus (rather than one large loop as seen in other species) may be an adaptation for increasing respiratory efficiency.

Type locality and type specimens. Santa Catalina Channel, California, 160 to 180 m; holotype and paratypes: LACM-AHF.

Habitat. *N. assignis* is found in sand and mud.

Distribution. Washington to California; Mexico, Guatemala; 4 to 200 m.

Nephtys caecoides Hartman, 1938

Figure 13.6

Nephtys caecoides Hartman, 1938:148-149, fig. 63; 1950:101-102 (synonymy); 1968:577.—Blake, 1975b:197, pl. 39, figs. 165-166.—Lissner *et al.*, 1986:D-10.—Hyland and Neff, 1988:A-2. —Hyland *et al.*, 1990:F-1.

Nephtys parva Clark and Jones, 1955:143-146.—Hyland and Neff, 1988:A-2.—Hyland *et al.*, 1990:F-1.

Nephtys sp. B: Lissner *et al.*, 1986:D-10.

Material examined. California: Santa Maria Basin, off Point San Luis, Sta. 21 (3), Sta. R-2 (8); off Point Arguello, Sta. 58 (1), Sta. 64 (1); off Point Sal, Sta. R-8 (1); Western Santa Barbara Channel, Sta. 79 (1); San Francisco Bay, paratype, USNM 26465.

Description. Length to 100 mm, width to 8 mm, segments to 129. Body stout and wide in anterior third (pharyngeal region), tapering, slender and more flexible in middle and posterior region. Color in alcohol tan with variable pigmentation on prostomium and first few setigers (Fig. 13.6A-D).

Prostomium rounded to trapezoidal depending whether probscis is retracted or everted, bearing 2 pairs of widely separated antennae and a pair of nuchal organs on postectal margin (Fig. 13.6C); eyes absent (may be present in juveniles on one of the first 3 setigers). Proboscis wide and relatively short, with 22 rows of 3 to 5 subdistal papillae and 22 long, bifid distal papillae; long middorsal and slightly shorter midventral pailla present (Fig. 13.6E).

First parapodium directed forward, enlarged, with setae projecting well beyond prostomium; all subsequent parapodia pointing laterally, with widely separated rami. Notopodia with low preacicular lamella, incised acicular lobe (conical in juveniles), and broad postacicular lamella of slightly greater length than acicular lobe (shorter than acicular lobe in juveniles); dorsal cirri small, digitiform; interramal cirri first present in setiger 4, continuing to near end of body; short and almost straight in juveniles (Fig. 13.6F), recurved and occupying about half of space between rami in adults (Fig. 13.6G). Neuropodia with low preacicular lamella, incised acicular lobe (conical in juveniles) and bluntly triangular postacicular lamella pointing slightly upward. Setae of 4 kinds; preacicular setae short, stiff, crossbarred along distal half; postacicular notosetae consisting of small upper fascicle of spinulose capillaries, large middle fascicle of wide spinose setae and 1 or 2 thin, smooth capillaries in lowermost position; neurosetae consisting of 1 or 2 thin, smooth capillaries in uppermost position, numerous spinose setae in middle fascicle, and few

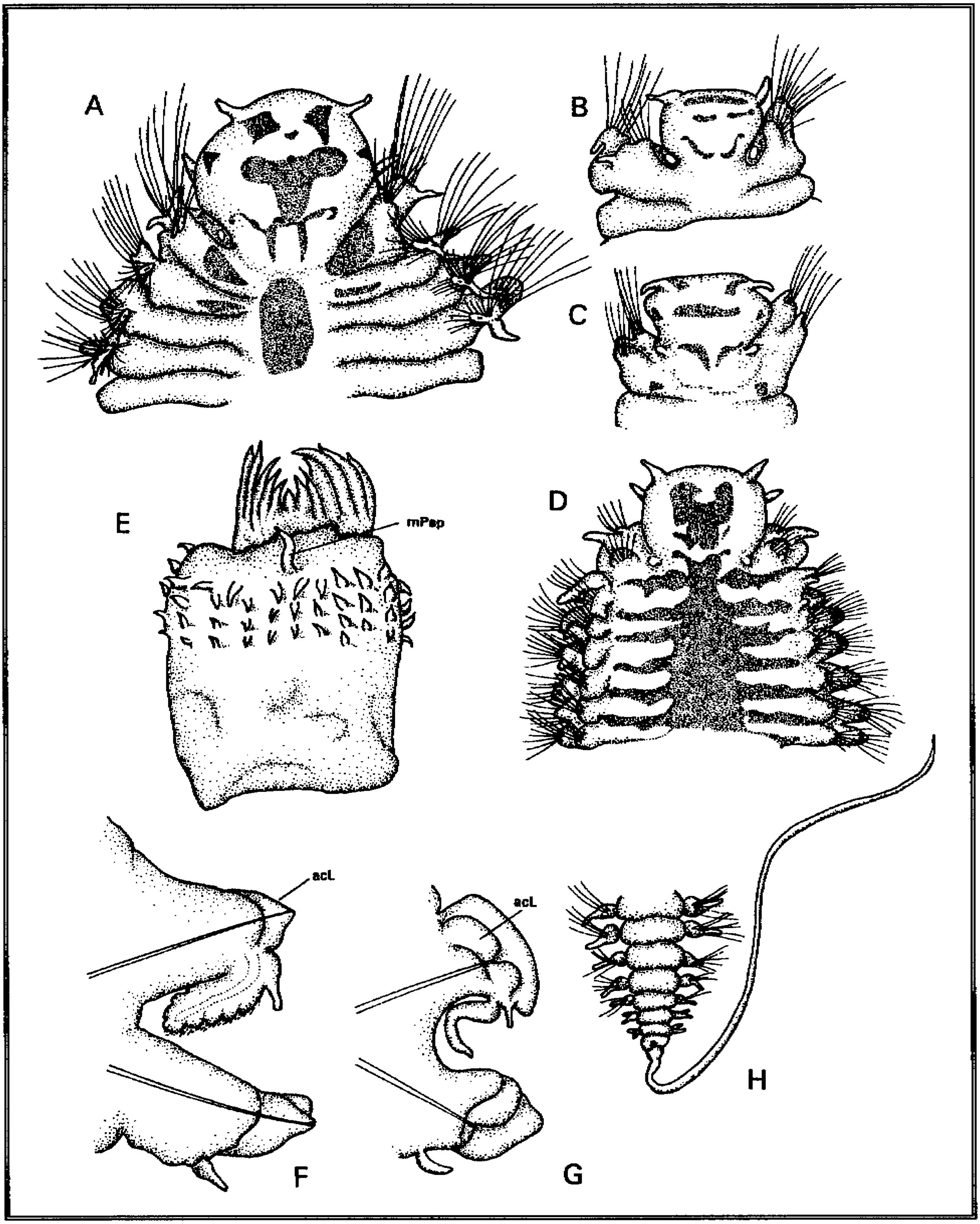

Figure 13.6. *Nephtys caecoides*: A, anterior end, dorsal view; B-D, same, showing variation of pigment patterns; E, proboscis, dorsal view; F, middle parapodium, juvenile; G, middle parapodium, adult; H, posterior end, dorsal view (D, G after Blake, 1975).

spinulose capillaries in lowermost fascicle. Aciculae single in each ramus, transparent to yellow, distally tapering to fine, curved tip.

Pygidium small, surrounding terminal anus, bearing long, filiform anal cirrus inserted midventrally, reaching back about 13 segments (Fig. 13.6H).

Remarks. This species was described from shallow water and is a common littoral form in the eastern Pacific. Its occurrence in depths between 50 and 110 m is an extension of its depth range. The specimens originally identified as *Nephtys* sp. B were recognized as juveniles of *N. caecoides* based on the occurrence of the interramal cirri and the distribution of the different setal types. *N. parva* is considered a synonym of *N. caecoides*, as was already suspected by Clark and Jones in their original description (Clark and Jones, 1953). During examination of the paratype, it was noted that the preacicular setae are crossbarred along almost the entire length except for the basal part, rather than in the proximal two-thirds as reported by Clark and Jones.

Type locality and type specimens. Tomales Bay, California; holotype: USNM 20319.

Habitat. According to an ecological study by Clark and Haderlie (1962), *Nephtys caecoides* prefers muddy sediments. In the intertidal zone, it is therefore typically found on sheltered beaches. In the Santa Maria Basin, the species occurred in 50-110 m depth on sand, sand mixed with silt, and silt.

Distribution. Western Mexico to British Columbia, in bays and lagoons and the open shelf, intertidal to 110 m.

Nephtys californiensis Hartman, 1938

Figure 13.7

Nephtys californiensis Hartman, 1938:150-151, fig. 64; 1940:240; 1950:103; 1968:579.—Uschakov and Wu, 1962:8-9, fig. 3A-D.—Blake, 1975b:197.—Lissner *et al*., 1986:D-10.—Imajima and Takeda, 1987:68-70, figs. 13-14 (synonymy).

Material examined. California: Santa Maria Basin, off Point San Luis, Sta. 23 (3); off Point Sal, Sta. 104 (1).

Description. Length to 300 mm, width to 10 mm, segments to 160. Body wide, stout and rigid in anterior third, gradually tapering toward pygidium and more flexible in middle and posterior part. Color in life iridescent pearl-grey to pale whitish, in alcohol uniformly tan; with "spread-eagle" pigment pattern across back of prostomium and central reddish spot resembling an eye (Fig. 13.7A, B); sometimes only the latter present.

Prostomium rounded anteriorly, trapezoidal, about as long as wide when proboscis everted, longer than wide when proboscis retracted; bearing 2 widely spaced pairs of antennae of roughly equal size; eyes absent; nuchal papillae small, located at postectal margin of prostomium (Fig. 13.7B, C). Proboscis with 22 rows of about 6 to 8 subdistal papillae; middorsal papilla absent; anterior margin of proboscis with 22 bifid distal papillae (Fig. 13.7A).

Parapodia biramous, with well-developed rami except for first pair with slightly reduced neuropodia. Notopodia of all subsequent setigers with low preacicular lamella, incised acicular lobe (conical in far posterior setigers) and low, broadly rounded postacicular lamella; dorsal cirri small and cirriform throughout. Interramal cirri first appearing in segment 3, minute in first 2 or 3 segments, then increasing and becoming recurved; continuing to end of body except for last few segments. Neuropodia

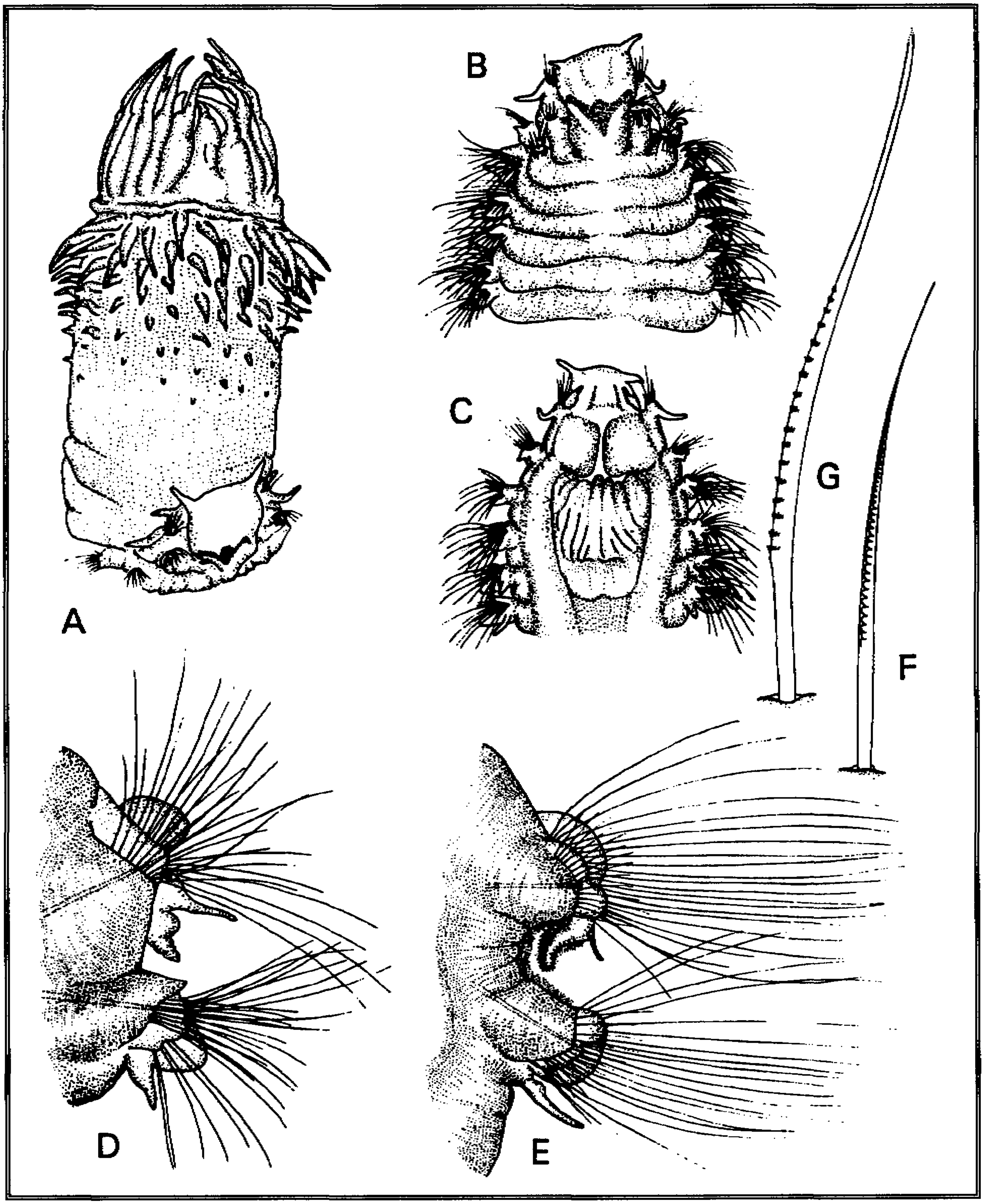

Figure 13.7. *Nephtys californiensis*: A, anterior end and proboscis, dorsolateral view; B, anterior end, dorsal view; C, same, ventral view; D, third parapodium, anterior view; E, middle parapodium, anterior view; F, preacicular seta; G, postacicular seta from middle of fascicle (A-E from Imajima and Takeda, 1987).

with lobes resembling those of notopodia; postacicular lamellae directed slightly upward and somewhat longer than notopodial ones. Ventral cirri conical to cirriform, somewhat larger than corresponding dorsal cirri (Fig. 13.7D, E). Setae of both rami similar; preacicular setae short, stiff, crossbarred along distal half (Fig. 13.7F); postacicular setae at least 3 times as long as preacicular ones, flowing, silky; those in middle position spinose (coarsely serrated in side view) and twice as wide as preacicular setae, those in lower and upper position smooth to spinulose (finely serrated in side view) and as wide as preacicular setae, in small fascicles of 3 to 6 setae (Fig. 13.7G).

Remarks. This species is closely related to *N. caecoides*, and the two species are easily confused if examined superficially. Hartman (1950) remarked that although *N. caecoides* and *N. californiensis* are distinguished by the difference of the first appearance of the interramal cirri (segment 3 in *N. californiensis*, segment 4 in *N. caecoides*), there seemed to be some variability in this character. She also reported the presence or absence of the middorsal papilla to be inconsistent ("usually absent", Hartman (1938)). It is possible that she confused *N. californiensis* with juvenile *N. ferruginea* which are unpigmented or show pigmentation just on the prostomium, but are characterized by possessing a middorsal papilla on the proboscis and interramal cirri from setiger 3. Some of those specimens may also be *N. signifera*, a species that resembles *N. ferruginea* except for the pigmentation. In disagreement with Hartman, *N. caecoides* and *N. californiensis* are therefore considered clearly separated.

Type locality and type specimens. Dillon Beach, California; holotype: USNM 20320.

Habitat. *N. californiensis* tends to co-occur with *N. caecoides* (see above), although Clark and Haderlie (1962) noted a clear separation of those two species by the grain size of the substatum in the intertidal zone. The authors found *N. californiensis* on exposed beaches with sandy sediment, whereas *N. caecoides* occurred in sheltered, muddy areas, and there was not much overlap between the optimal habitats of the two species. In the Santa Maria Basin and Santa Barbara Channel, *N. californiensis* was found in sand and silt.

Distribution. Mexico to California; Gulf of Mexico; Yellow Sea; Japan; intertidal to 330 m.

Nephtys cornuta Berkeley and Berkeley, 1945

Figure 13.8

Nephtys cornuta Berkeley and Berkeley, 1945:328-330, figs. 2-4.—Hartman, 1950:106-107; 1968:581.—Fauchald, 1972:90.—Hyland and Neff, 1988:A-2.—Hyland *et al.*, 1990:F-1.

Nephtys cornuta franciscana Clark and Jones, 1955:146, fig. 2.—Lissner *et al.*, 1986:D-10.—Hyland and Neff, 1988:A-2.

Nephtys sp. A: VTN Consolidated, 1980. *Not* Lissner *et al.*, 1986.

Aglaophamus neotenus Noyes, 1980:106-108, figs. 1-2. New synonymy.

Nephtys neotena: Ohwada, 1985:58, fig. 1D.

Material examined. California: Santa Maria Basin, off Point Estero, Sta. 10 (4); off Point Sal, Sta. 33 (8), Sta. PJ-2 (3), Sta. PJ-6 (3), Sta. PJ-7 (21), Sta. PJ-8 (26); off Point San Luis, Sta. R-2 (81); holotype of *N. cornuta franciscana* (USNM 26466).—Alaska: Boca de Quadra (43) (*Nephtys* sp. A).—Maine: Mear's Cove flats, Damariscotta River, low water line (8); Walpole (27) (*Aglaophamus neotenus*).

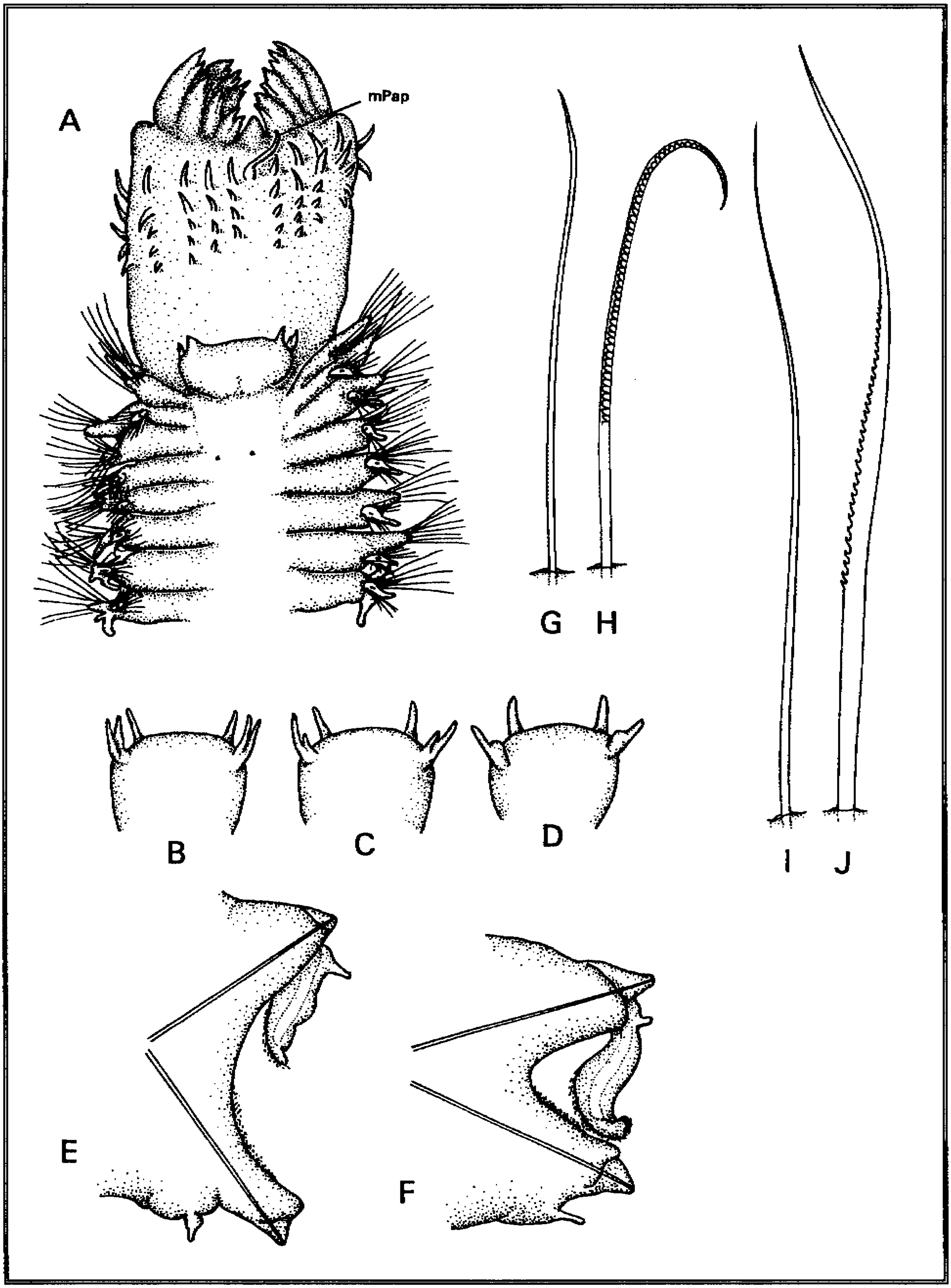

Figure 13.8. *Nephtys cornuta*: A, anterior end, dorsal view; B-D, prostomia, ventral view, to show variability of ventral antennae; E, parapodium 5, anterior view; F, posterior parapodium, anterior view; G, smooth preacicular seta; H, crossbarred preacicular seta; I, smooth postacicular seta; J, spinose postacicular seta.

Description. Length to 15 mm, width to 1 mm excluding parapodia, segments to 35. Body slender, fragile, breaking easily especially in posterior region; most examined specimens incomplete. Color in alcohol uniformly tan or mottled brown on prostomium, dorsum of first 10 segments, and pygidium; usually with rust-colored to black subdermal eyes in setiger 3, sometimes accompanied by crescents of black subdermal pigment.

Prostomium rounded, slightly longer than wide when proboscis retracted and much wider than long when proboscis fully everted (Fig. 13.8A). Both pairs of antennae inserted anterolaterally, directed forward, of subequal size; ventral ones bifid or at least with basal lateral extension (Fig. 13.8B-D). Proboscis with 16 rows of about 5 long, slender subdistal papillae and 14 bifid terminal papillae; middorsal papilla present (Fig. 13.8A).

First parapodia small, elongate, directed forward (pointing laterally when proboscis is everted), extending as far as prostomium. Subsequent parapodia directed laterally, with widely separated rami; pre- and postacicular lamellae in both rami rudimentary, acicular lobes prominent, conical; dorsal cirri small, tapering; ventral cirri somewhat larger, in posterior segments with inflated base (Fig. 13.8E, F). Interramal cirri first present from setiger 5 or 6; straight and short through about setiger 10, occupying most of the space between rami and slightly recurved in following setigers. Both interramal cirri and upper neuropodial wall heavily ciliated. Preacicular setae short, stiff, crossbarred at least through setiger 10 to 19, replaced by smooth setae in following setigers; occasionally both setal types occurring together or preacicular setae crossbarred throughout (Fig. 13.8G, H). Postacicular setae coarsely serrated and smooth capillaries, longer than preacicular setae (Fig. 13.8I, J). Aciculae transparent, with fine, curved, sometimes deep amber-colored tips.

Remarks. The subspecies *Nephtys cornuta franciscana* is considered invalid because it does not seem to be a well-defined group within the species *N. cornuta*; while Clark and Jones (1955) separated *N. c. franciscana* from the stem species based on the distribution of crossbarred setae, among other characters, examination of more than 100 specimens of both subspecies showed that intermediate forms exist, typically with crossbarred preacicular setae reappearing in one or few posterior setigers following a number of setigers with smooth preacicular setae only. Ellis and Ronaldson (1988) noted that other characters, such as the presence of subdermal eyes and body length of sexually mature specimens, are inconsistent or overlap between the two subspecies.

The species *Aglaophamus neotenus*, transferred to *Nephtys* by Ohwada (1985), is synonymized with *N. cornuta*, even though the two species differ in the appearance of the ventral antennae (almost always bifid in *N. cornuta*, only occasionally bifid in *N. neotena*). Examination of about 30 specimens of *N. cornuta* and *N. neotena* from the type locality and an adjacent area showed that the two species may be viewed as representing two ends of a range of variability; in both species, ventral antennae were either basally inflated, or they had a lateral extension ranging from a boss to a true second branch. Four out of 28 specimens of *N. neotena* had clearly bifid ventral antennae (Noyes (1980) estimated 10% of all specimens), and 2 out of 30 specimens of *N. cornuta* showed basally inflated to bossed ventral antennae. The variability in the distribution of preacicular setae is similar in both species, although the setigers with crossbarred setae only tend to reach further back in *N. neotena*. About 40 specimens of *Nephtys* sp. A from southeast Alaska were examined for the same characters. About twice as many individuals possess bifid antennae with a shorter second branch than antennae with a lateral inflation or boss. In cases where both *N.* sp. A and *N. cornuta* were found, both forms occurred in about the same numbers, indicating that the variability of characters is intermediate between the Maine and Californian populations.

Type locality and type specimens. Washington, Friday Harbor (*N. cornuta*); San Francisco Bay (*N. cornuta franciscana*); holotype: USNM 26466. Maine, Damariscotta River (*N. neotena*); holotype: USNM 47165, paratypes: USNM 47166.

Biology. *N. cornuta* is a typical faunal element in shallow water with silty or muddy bottoms. The species has been used for pollution monitoring because of its tolerance to several pollutants. *N. cornuta* feeds on diatoms and copepods that are ingested with some sediment (Noyes, 1980). Gravid individuals are most frequently found in late winter and early spring, and spawning occurs in April and May; gametes are released through the anal pore, and early trochophores develop within 48 hours. After a lecitotrophic stage lasting about 30 days, the larvae become planktotrophic; metamorphosis takes place when the metatrochophores are 8 setigers long (Noyes, 1980).

Distribution. Eastern Canada to Maine; Alaska to southern California; subtidal to 440 m.

Nephtys ferruginea Hartman, 1940

Figure 13.9

Nephtys caecoides ferruginea Hartman, 1940:241, pl. 42, figs. 110-114, pl. 43, fig.115
Nephtys ferruginea: Berkeley and Berkeley, 1945:327-328.—Hartman, 1950:102-103; 1968:583.—Banse and Hobson, 1968:18.—Fauchald, 1972:91.—Lissner *et al*., 1986:D-10.—Hyland and Neff, 1988: A-2.—Hyland *et al*., 1990:F-1.

Material examined. California: Santa Maria Basin, off Point Sal, Sta. 31 (2); off Point Arguello, Sta. 58 (1); off Purisima Point, Sta. R-5 (3); Western Santa Barbara Channel, Sta. 80 (2).

Description. Length to 40 mm, width to 3 mm, segments to 70; body of adults with heavy rust-colored pigmentation consisting of a roughly triangular patch on anterior part of prostomium, a spread eagle pattern on posterior half of prostomium, transverse bars across middorsum of the first 15 to 20 setigers, and parallel oblique stripes dorsolaterally on those setigers when best developed (Fig. 13.9A, B); pigmentation fading in alcohol, less pronounced or completely absent in small individuals.

Prostomium about as long as wide, with 2 pairs of antennae of equal size, both directed laterally, posterior ones close to anterior ones. Proboscis proximally smooth, subdistally with 22 rows of about 5 papillae and long, slender middorsal papilla, and distally with 22 bifid papillae.

First parapodia small, directed forward, setae extending only to bases of antennae. Subsequent parapodia directed laterally, with rami becoming progressingly further apart toward posterior end; notopodia with low preacicular lamella, incised acicular lobe, and blunt, broad postacicular lamella projecting slightly beyond acicular lobe; dorsal cirri long, slender, sometimes basally inflated; interramal cirri first present on setiger 3, conspicuous throughout; in anterior setigers about half as long as interramal space, straight, slightly flattened, sometimes weakly curved; in posterior setigers as long as interramal space. Neuropodia with lobes similar to notopodia; ventral cirri slender, longer than dorsal ones, in posterior setigers becoming acuminate. Acicular lobes becoming less incised to conical along posterior part of body (Fig. 13.9C-E).

Preacicular setae short, thin, flexible, crossbarred along distal half (Fig. 13.9F); postacicular setae about twice as long and 2 to 3 times wider than preacicular setae, of 2 kinds: in upper notopodial and lower neuropodial position small fascicles of 5 to 6 finely serrated setae, tapering to pointed tip, stiff; in lower notopodial and upper neuropodial position larger fascicles of coarsely serrated setae with long, whiplike, flowing tips (Fig. 13.9G, H). Aciculae amber-colored, with curved tips.

Remarks. This species is easily recognized by the very characteristic pigmentation; however, there is some variability in the development of pigment among specimens of similar size, among specimens of different size, and the pigment tends to fade in alcohol. Young specimens are sometimes entirely unpigmented and may be confused with *N. californiensis* or *N. signifera*, but are distinguished from these

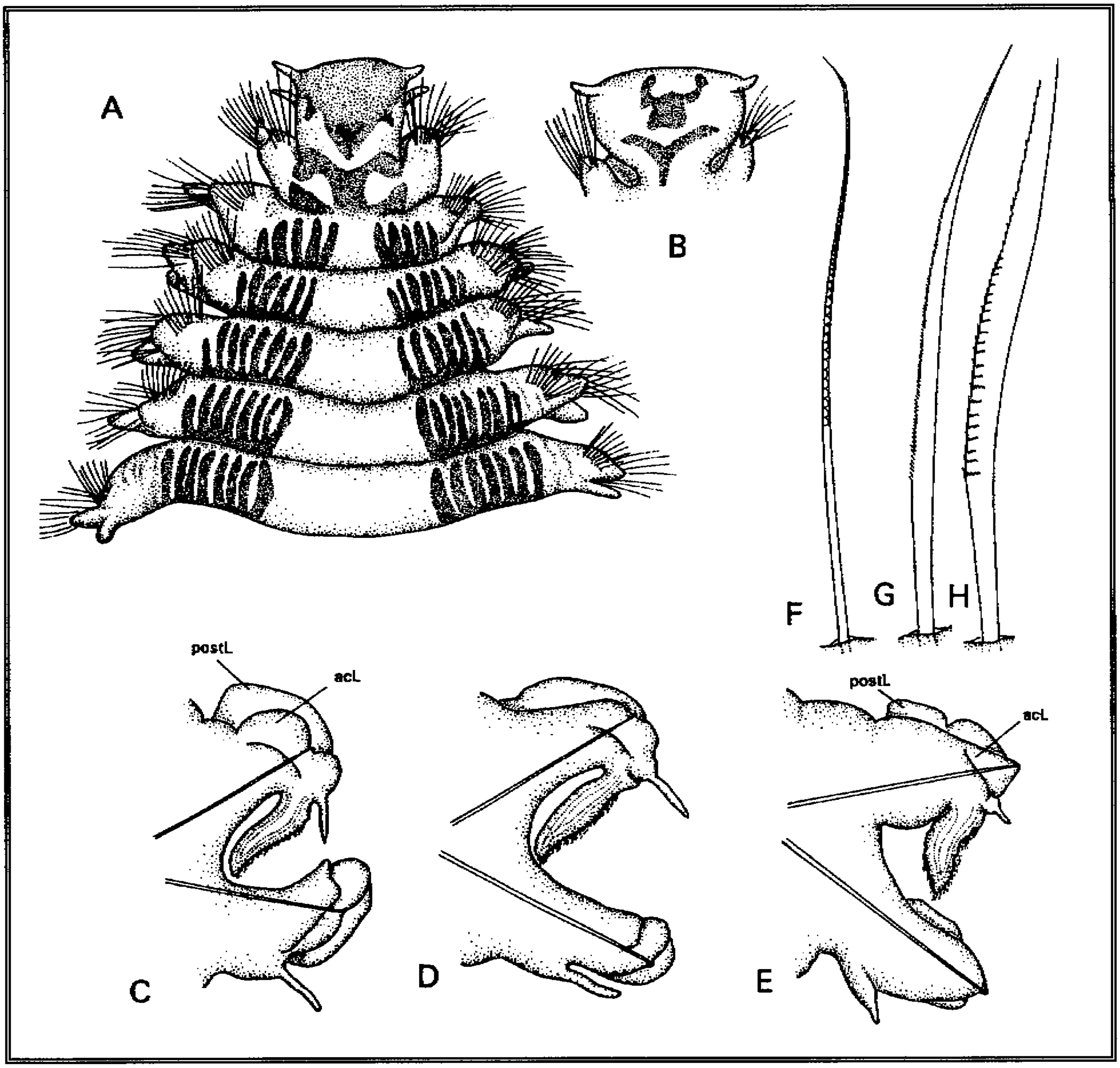

Figure 13.9. *Nephtys ferruginea*: A, anterior end, dorsal view; B, prostomium, variation in pigment pattern; C, anterior parapodium, anterior view; D, middle parapodium, anterior view; E, posterior parapodium, anterior view; F, preacicular seta, G, spinulose postacicular seta; H, spinose postacicular seta (A, C-D after Hartman, 1940).

two species by the presence of a middorsal proboscideal papilla and the distribution of setal types in the postacicular fascicles (see also remarks for *N. californiensis*).

Type locality and type specimens. Independencia Bay, Peru; holotype: LACM.

Habitat. The species is found in mud and clay.

Distribution. Peru to British Columbia, 20 to 450 m.

Nephtys punctata Hartman, 1938

Figure 13.10

Nephtys punctata Hartman, 1938:155-156, fig. 67; 1950:96-97; 1968:591.—Lissner *et al.*, 1986:D-10. —Imajima and Takeda, 1987:61-63.—Hyland and Neff, 1988:A-2.—Hyland *et al.*, 1990:F-1.

Material examined. California: Santa Maria Basin, off Point Arguello, Sta. 60 (2), Sta. 70 (4); off Point Sal, Sta. PJ-11 (1).

Description. Length to 100 mm, width to 6.5 mm, segments to 108. Body massive, muscular, with relatively small parapodia not exceeding body width in length except for few last segments. Color in alcohol uniformly tan, occasionally with brown pigment spots on notopodial bases and scattered pigment on postacicular lamellae of both rami, darkest on notopodia; setae dusky.

Prostomium relatively small in adult specimens; rectangular, slightly longer than wide, with small dorsal antennae and somewhat larger ventral ones (Fig. 13.10A). Nuchal organs located at postectal margins. Proboscis with 20 to 22 bifid terminal papillae, 22 rows of 4 to 5 subterminal papillae, and proximal minute wartlike papillae; middorsal papilla present, slender, much longer than other subterminal papillae (Fig. 13.10B).

First parapodia thick, directed forward, with rudimentary pre- and postacicular lamellae and few long, slender capillaries extending beyond prostomium; dorsal cirri small, ventral cirri somewhat enlarged with inflated base. Subsequent anterior parapodia with deeply incised acicular lobes and blunt, broad postacicular lamellae; neuropodial postacicular lamellae becoming more pointed and longer in middle parapodia; posterior parapodia with conical acicular lobes and short, blunt postacicular lamellae in both rami. Dorsal cirri very long and slender in segments with well-developed interramal cirri. Interramal cirri first present in setigers 8 to 11; only slightly larger than dorsal cirri at first, best developed from about setiger 20, then gradually decreasing in size in posterior segments, absent from last 10 or so segments (Fig. 13.10C-E). Preacicular setae short, stiff, crossbarred; postacicular setae much longer and flexible, of 2 kinds: finely serrated (spinulose) in small fascicles in upper notopodium and lower neuropodium, coarsely serrated (spinose) and tapering to long, whiplike tip in large fascicles in lower notopodium and upper neuropodium. Aciculae with blunt, straight tips.

Pygidium bearing very thin, filiform anal cirrus about as long as last 8 segments.

Remarks. *N. punctata* is easily recognized by the appearance of the interramal cirri on segment 8 and the presence of proximal wartlike papillae on the proboscis.

Type locality and type specimens. Alaska peninsula; holotype: USNM 20321.

Habitat. In the Santa Maria Basin, the species occurred in silt mixed with sand.

Distribution. Alaska to California; Kamchatka; Japan, 130 to 300 m.

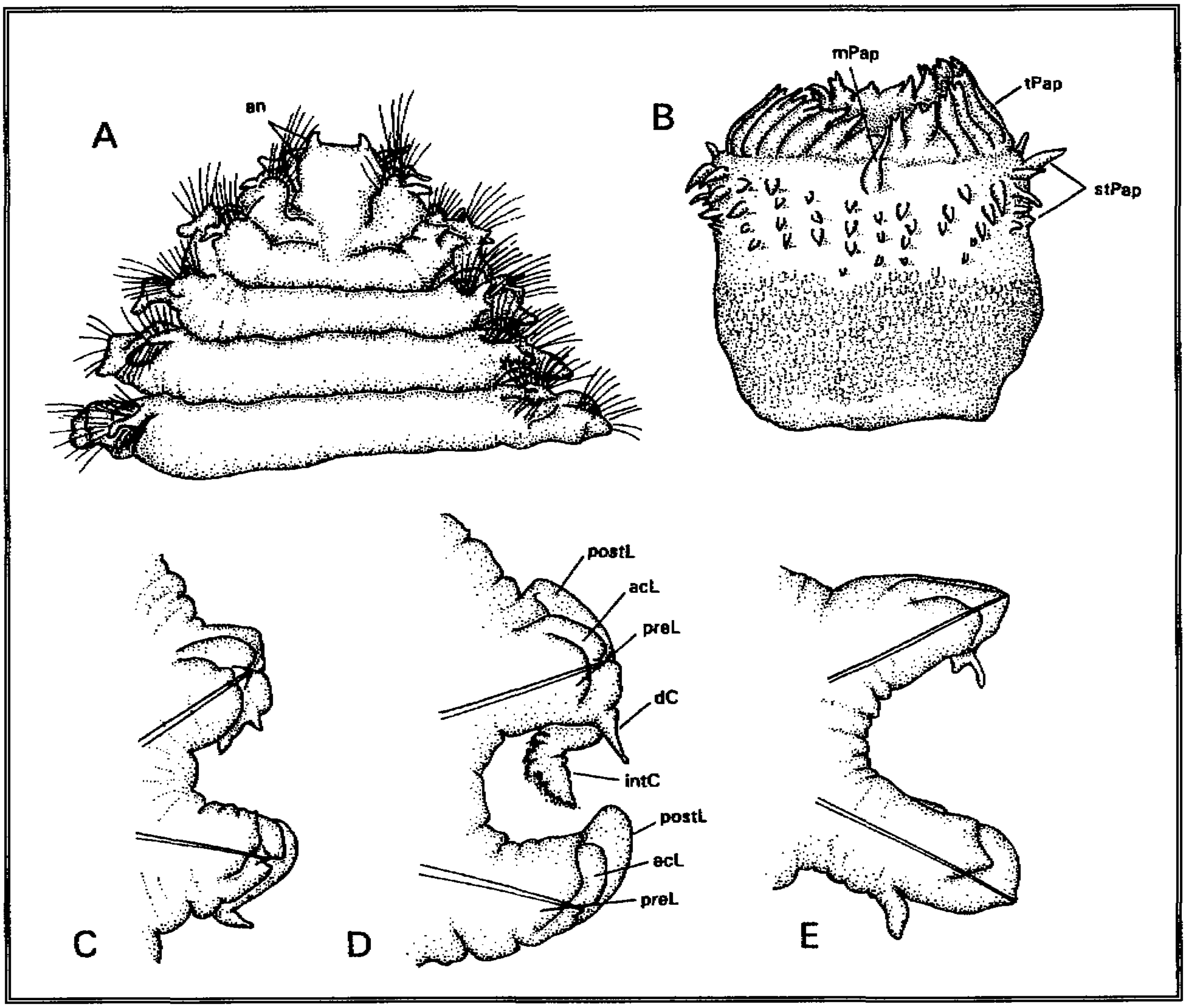

Figure 13.10. *Nephtys punctata*: A, anterior end, dorsal view; B, proboscis, dorsal view; C, 9th parapodium, anterior view; D, middle parapodium, anterior view; E, posterior parapodium, anterior view (all after Imajima and Takeda, 1987).

Nephtys schmitti Hartman, 1938

Figure 13.11

Nephtys schmitti Hartman, 1938:152-153, fig. 65; 1968:595.—Lissner *et al.*, 1986:D-10.—Hyland and Neff, 1988:A-2.—Hyland *et al.*, 1990:F-1.

Material examined. California: Santa Maria Basin, off Point Estero, Sta. 9 (2); off Point Buchon, Sta. 20 (2); off Point San Luis, Sta. R-3 (1).—Alaska: *Albatross* Sta. 3210 (holotype); Beaufort Sea (5) (*N. paradoxa*).

Description. Length to 90 mm, width to 8 mm, segments to about 100. Body wide and massive in pharyngeal region, gradually tapering toward pygidium and taking on ragged appearance due to

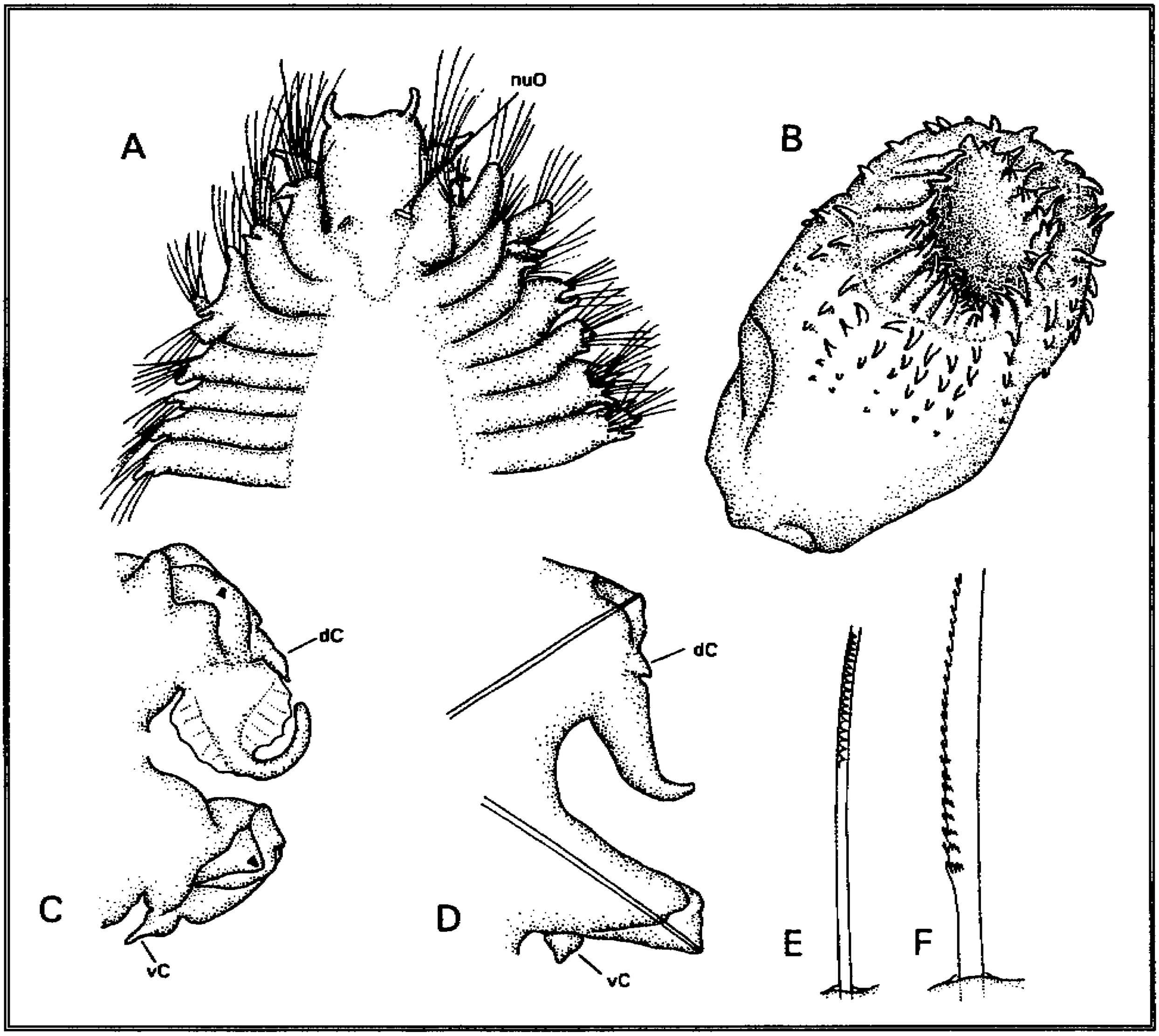

Figure 13.11. *Nephtys schmitti*: A, anterior end, dorsal view; B, proboscis, ventrolateral view; C, middle parapodium, anterior view; D, posterior parapodium, anterior view; E, preacicular seta; F, postacicular seta. (C after Hartman, 1938).

progressively longer parapodia, conspicuously exceeding body width from about mid-body. Color in alcohol uniformly tan, setae and tips of aciculae dark brown to almost black.

Prostomium quadrangular, about as long as wide when proboscis retracted (pentagonal and wider than long as stated by Hartman (1938) when proboscis everted), with small antennae; ventral ones inserted closely behind the dorsal ones. Nuchal organs conspicuous, located at postectal margins (Fig. 13.11A). Proboscis proximally smooth, subdistally with 22 rows of 4 to 5 widely spaced, small papillae, none middorsal; distally surrounded by 20 bifid papillae (Fig. 13.11B).

First parapodia short, elongate, directed forward, with small dorsal and basally inflated, larger ventral cirri. Subsequent parapodia pointed anterolaterally to laterally, with low pre- and postacicular lamellae and prominent, conical acicular lobes on both rami; dorsal and ventral cirri broadly conical, tapering to pointed tip. Interramal cirri first present on setiger 7 or 8, only slightly larger than dorsal cirri at first; from about setiger 12 with lateral wings, broadly foliaceous on setigers 15 to 35, then long and digitiform, recurved; diminishing in size in posterior part of body, absent from few last setigers (Fig. 13.11C, D). Parapodial rami relatively close together in segments with foliaceous interramal cirri, widely separated in subsequent segments; pre- and postacicular lamellae rudimentary, acicular lobes rounded. Setae short and stiff throughout; preacicular setae crossbarred, postacicular setae 3 times as wide and about 3 times as long, spinose along short proximal part, distally smooth and tapering to fine, whiplike tip (Fig. 13.11E, F). Aciculae straight and blunt-tipped.

Pygidium small, bearing thin, filiform anal cirrus reaching back about 7 to 8 segments.

Remarks. *N. schmitti* is closely related to *N. paradoxa* Malm, 1874 and was believed to be a synonym by Imajima and Takeda (1987). However, examination of the holotype of *N. schmitti* and several specimens of *N. paradoxa* collected off Alaska (loan from Andrew Carey, Oregon State University) showed that those two species differ in the following characters: the number of terminal papillae is 20 in *N. schmitti* and 22 in *N. paradoxa*; the subterminal papillae are short in *N. schmitti* and long and slender in *N. paradoxa*; interramal cirri are foliaceous between segments 12 and 30 in *N. schmitti* and between segments 20 and 65 in *N. paradoxa*.

Type locality and type specimens. Alaskan peninsula; holotype: USNM 20323.

Habitat. In the Santa Maria Basin, the species was found in sediments with high silt content (77 to 87%) in 440 m depth.

Distribution. Alaska to central California, 400 to 1600 m.

Nephtys signifera Hilbig, 1992

Figure 13.12

Nephtys signifera Hilbig, 1992:719-721, fig. 5.
Nephtys sp. A Lissner *et al.*, 1986:D-10.
Nephtys sp. H Hyland and Neff, 1988:A-2.

Material examined. California: Santa Maria Basin, off Point San Luis, Sta. R-2: holotype (USNM 148706) and 1 paratype (USNM 148707); off Point Buchon, Sta. 13: 3 paratypes (SBMNH 35617); off Point Sal, Sta. 30: 6 paratypes (SBMNH 35618), Sta. PJ-1: 1 paratype (LACM-AHF POLY 1615), Sta. PJ- 6: 1 paratype (LACM-AHF Poly 1616).

Description. Length to 28 mm, width to 2 mm excluding parapodia, segments to 77. Body unpigmented except for central red eyespot on prostomium and dark brown to black subdermal eyes on setiger 3 in juveniles; setae dusky.

Prostomium quadrangular, about as long as wide when proboscis is retracted; oval and wider than long when proboscis is everted. Dorsal antennae smallest and well separated from ventral ones (Fig. 13.12A). Lateral edges below ventral antennae staining distinctly in methyl green; staining often including outer edges of brain and ventral edge of mouth (Fig. 13.12B). Proboscis proximally smooth, with 22 rows of about 5 papillae and a single middorsal one; distally surrounded with 20 bifid papillae (Fig. 13.12C).

First parapodia directed forward, reduced, with large ventral cirri and very long setae projecting well beyond prostomium. Subsequent parapodia in anterior part of body with low, rounded presetal lamellae, deeply incised acicular lobes, and bluntly rounded postacicular lamellae; notopodial postacicular lamellae pointed toward middorsum, neuropodial ones pointed slightly upward. Parapodia of middle and

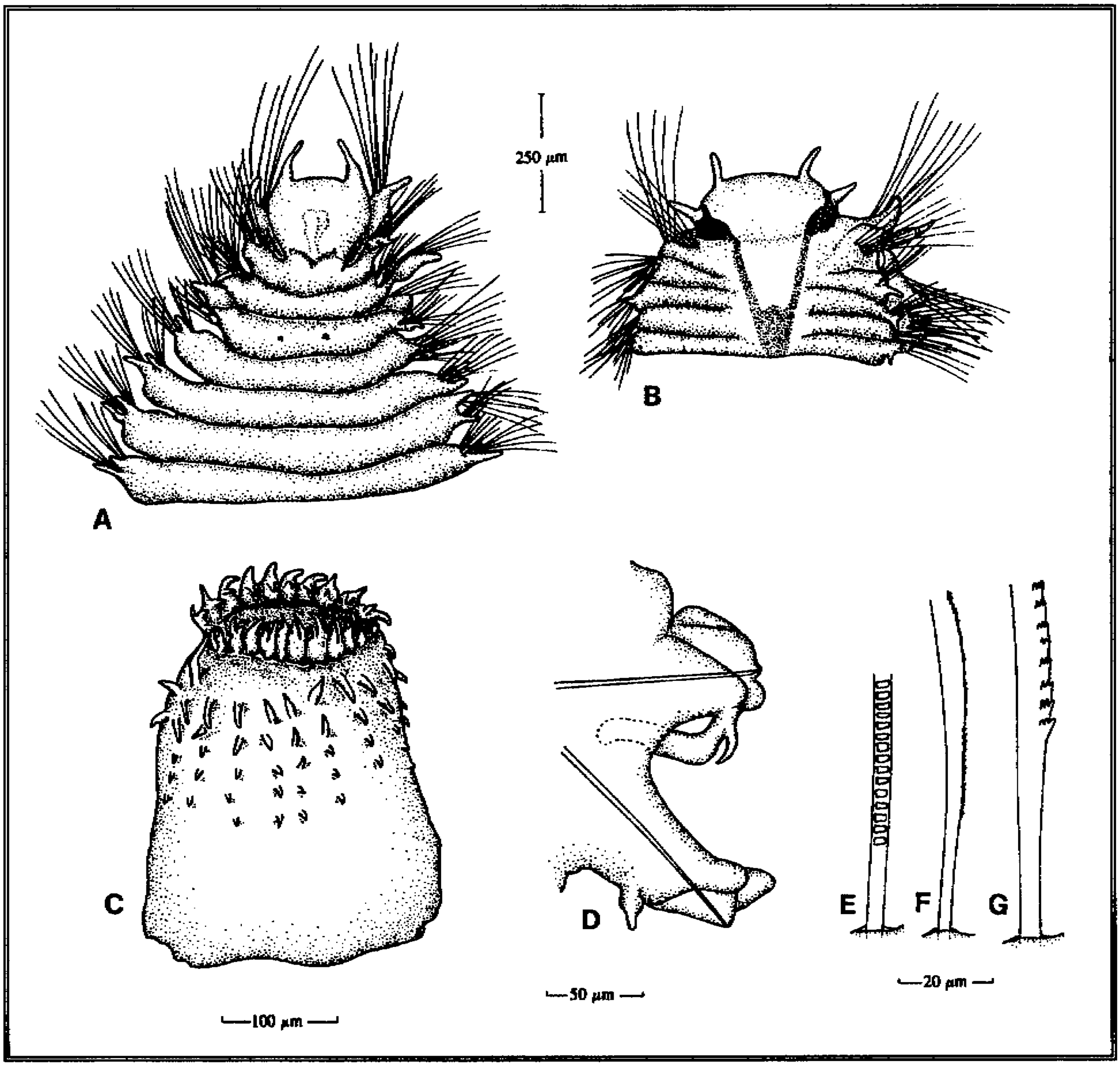

Figure 13.12. *Nephtys signifera*: A, anterior end, dorsal view; B, same, showing methyl green staining pattern; C, proboscis, lateral view; D, middle parapodium, anterior view; E, preacicular seta; F, spinulose postacicular seta; G, spinose postacicular seta (from Hilbig, 1992).

posterior segments similar to anterior parapodia except for slight changes in proportion (Fig. 13.12D); incision of acicular lobes becoming progressingly shallower and acicular lobes turning conical, postacicular lamellae diminishing in size and reduced in posterior segments. Interramal cirri first present on segment 3, small at first; wide, flattened, straight, in posterior segments more slender; heavily ciliated; occupying about one-third to one-half of interramal space, occasionally slightly curved. Dorsal cirri small and slender throughout; ventral cirri larger, conical.

Aciculae with curved, dusky tips. Preacicular setae crossbarred, short and stiff (Fig. 13.12E); postacicular setae on both rami smooth to spinulose and slender in small uppermost and lowermost fascicles, basally spinose in middle fascicles (Fig. 13.12F, G).

Pygidium with filiform anal cirrus.

Remarks. *Nephtys signifera* belongs to a small group of closely related, co-ocurring species characterized by interramal cirri that start in segment 3 and are in most cases straight and relatively short throughout. This group includes *N. californiensis, N. ferruginea, N. magellanica*, and *N. simoni*. *N. signifera* differs from these species most conspicuously by the presence of a glandular area along the lateral edges of the prostomium that stain with methyl green. Additionally, all the above mentioned species (with the exception of *N. magellanica*) have 22 rather than 20 distal papillae on the proboscis, and the distribution of spinose, spinulose, and smooth setae in the postacicular fascicle is distinctly different from that found in *N. signifera*. *N. magellanica* is the most closely related species; it differs from *N. signifera* in the number of subdistal rows of proboscideal papillae (20 rather than 22). It is possible that some of the specimens that Hartman (1950) assigned to *N. californiensis*, even though they had a middorsal proboscideal papilla, belong to *N. signifera* (see also remarks on *N. californiensis*).

Habitat. The species was found in sediments with high contents of sand or about equal amounts of sand and silt.

Distribution. Known only from central California, 110 to 220 m.

Nephtys simoni Perkins, 1980

Figure 13.13

Nephtys simoni Perkins, 1980:37-42, figs. 15, 16 (synonymy).—Lissner *et al.*, 1986:D-10.
?Nephtys simoni: Taylor, 1984:35-9, fig. 35-6.
Nephtys magellanica: Hartman, 1950:100-101. *Not* Hartman, 1938.

Material examined. California, Santa Maria Basin, off Point Arguello, Sta. 64 (1); San Diego Bay (1) (*N. magellanica*).—Florida: Hutchinson Island, 2 paratypes, LACM-AHF Poly 1291, 1292.

Description. Length to 110 mm (Atlantic specimens to 75 mm), width to 4 mm (Atlantic specimens to 3 mm), segments to 130. Body unpigmented, with colorless, flowing, silky setae.

Prostomium rounded, slightly longer than wide, with reddish central eyespot in juveniles; dorsal and ventral antennae well separated; dorsal antennae arising from anteroectal margin, directed anterolaterally; ventral antennae inserted at widest point of prostomium, pointing laterally, larger than dorsal ones (Fig. 13.13A). Proboscis long, proximally smooth, subdistally with 22 rows of about 4 to 8 papillae and a dorsomedian papilla as long as distal paired ones; distally surrounded by 22 bifid papillae (Fig. 13.13B).

First parapodia directed forward, small, extending as far as ventral antennae, with small digitiform dorsal cirri and large, flattened, basally inflated ventral cirri. Subsequent parapodia with low preacicular lamellae, pointed acicular lobes, and bluntly rounded postacicular lamellae distinctly longer than acicular lobes in anterior segments, diminishing in size toward posterior end and reduced in posterior segments (Fig. 13.13C-F). Interramal cirri first present on segment 3, short, wide, straight to weakly curved, heavily ciliated, occupying about one-third of interramal space. Preacicular setae crossbarred, short, stiff; postacicular setae much longer, flowing, of two kinds: (1) basally spinose capillaries in upper notopodial and lower neuropodial position (Fig. 13.13G, H), (2) finely spinulose capillaries in small fascicles of about 3 to 5 in lower notopodial and upper neuropodial positions (erroneously described as being entirely smooth by Perkins).

Pygidium with long, slender anal cirrus about as long as last 10 segments.

Remarks. Perkins (1980) tentatively transferred Californian and Alaskan specimens identified as *N. magellanica* by Hartman (1938, 1940, 1944, 1950, 1968) to *N. simoni*; one of the specimens referenced in her 1950 paper was reexamined, and the synonymy is confirmed. The specimens reported by Taylor

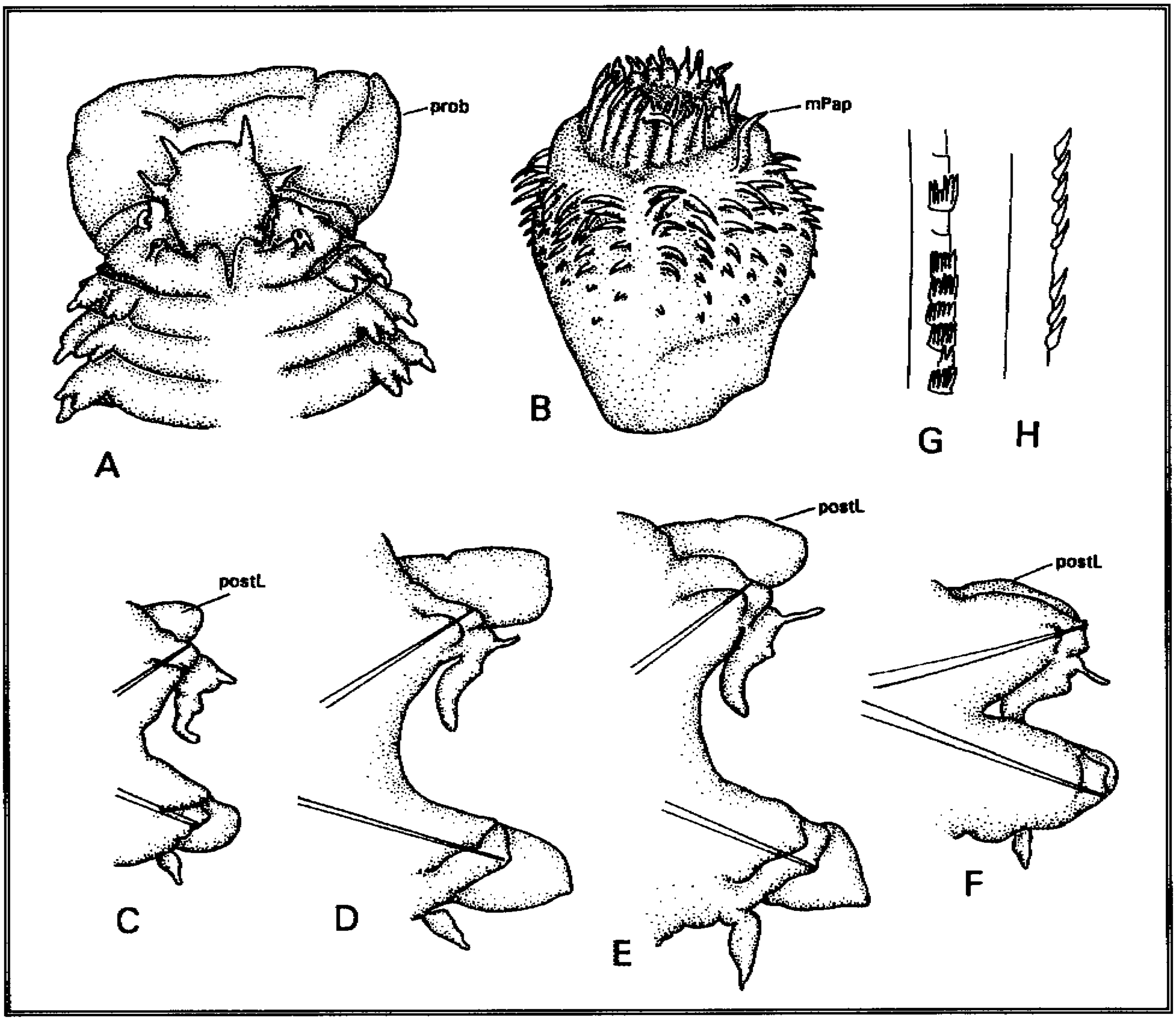

Figure 13.13. *Nephtys simoni*: A, anterior end, dorsal view; B, proboscis, dorsolateral view; C, 3rd parapodium, anterior view; D, 10th parapodium, anterior view; E, 23rd parapodium, anterior view; F, posterior parapodium, anterior view; G, H, details of basal part of postacicular seta. (all after Perkins, 1980).

from the Gulf of Mexico may belong to *N. magellanica*; the illustration of a middle parapodium shows a strongly recurved interramal cirrus that is distinctly longer than one-third of the interramal length.

Type locality and type specimens. Hutchinson Island, Florida; holotype: USNM 58725; paratypes: USNM 58726, LACM-AHF Poly 1291-1292, FSBC I 22641-22656.

Distribution. North Carolina to Florida; ?Gulf of Mexico; California to Venezuela; 10 to 189 m.

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14. FAMILY PARALACYDONIIDAE PETTIBONE, 1963

by

James A. Blake[1]

Introduction

The Paralacydoniidae is a small, and poorly known family of burrowing polychaetes that includes only a single genus, *Paralacydonia*, and one to three species, depending upon opinion. These worms are all small, and closely related to nephtyids. *Paralacydonia* was formerly included in the Lacydoniidae, but was referred to a separate family by Pettibone (1963). A single species, *P. paradoxa* Fauvel occurs in shelf and slope sediments off California and elsewhere in North America.

Morphology

The body of *Paralacydonia* is elongate, and subrectangular in cross section. The prostomium is conical in shape and bears two pair of small frontal antennae (Fig. 1A,B). Palps, eyes and medial antenna are lacking. The first segment is achaetous and lacks cirri. The pharynx bears a terminal circlet of papillae; jaws are lacking. Parapodia of setiger 1 are uniramous; following segments are biramous. Both rami are well developed and supported by internal acicula; long, flattened pre- and postsetal lobes are present and the widely separated rami resemble the form seen in nephtyids (Fig. 1C); a long lateral ciliated channel runs the length of the body between these rami. Notosetae are simple; neurosetae are mostly compound spinigers. Dorsal and ventral cirri are short and tapered. The pygidium is bulbous, with a pair of long cirri.

Taxonomic History

Paralacydonia was described by Fauvel (1913). The genus was referred to the phyllodocid subfamily Lacydoniinae by Fauvel (1914, 1923). Subsequent authors have either referred the genus to this subfamily, or to the Lacydoniidae at full family rank (Hartman, 1959, 1968; Day, 1967; Uschakov, 1972; Fauchald, 1977; Gathof, 1984). A separate family, the Paralacydoniidae was established by Pettibone (1963) because she considered that, while *Lacydonia* had affiliations with the Phyllodocidae, *Paralacydonia* was more closely related to the Nephtyidae. Based upon a consideration of the morphology of both *Lacydonia* and *Paralacydonia*, I support Pettibone's position that a separate family should be maintained for *Paralacydonia*. In my opinion, *Lacydonia* species more closely resemble phyllodocids and hesionids, while *Paralacydonia* species resemble nephtyids.

Three species of *Paralacydonia* have been described: (1) *P. paradoxa* Fauvel (1913, 1914), the type species, from the Mediterranean; (2) *P. weberi* Horst (1923) from the Dutch East Indies; and (3) *P. mortensensi* Augener (1924) from New Zealand. Augener (1927) later synonymised *P. mortensensi* with *P. weberi* and Uschakov (1958, 1972) considered all three to represent the same species. To my knowledge, no one has ever examined the type specimens of the three species to confirm the various synonymies proposed. The type species, *P. paradoxa*, has been widely reported from the worlds oceans since its original description. The species was reported by Uschakov (1958, 1972) and Uschakov and Wu (1965) from off China and other western Pacific locations; off California by Hartman (1960, 1968),

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Hartman and Barnard (1958), and Blake *et al.*, 1992; the eastern United States by Pettibone (1963); the Gulf of Mexico by Gathof (1984); and off South Africa by Day (1967). The species is strictly subtidal, having been recorded by these authors from about 25 to 3000 m.

Description of Species

Paralacydonia Fauvel, 1913

Diagnosis. Prostomium elongate, somewhat conical, with 4 short frontal antennae. Tentacular segment achaetous, without cirri. Proboscis muscular, unarmed. First setigerous segment uniramous, all subsequent segments biramous. Parapodia well developed, with elongate rami bearing flattened pre- and postsetal lamellae; ventral border of notopodia and dorsal border of neuropodia ciliated and joined at body wall forming continuous notch, adjacent segments forming a ciliated channel extending along length of body. Notosetae all simple capillaries; neurosetae compound spinigers.

***Paralacydonia paradoxa* Fauvel, 1913**

Figure 14.1

Paralacydonia paradoxa Fauvel, 1913:54, fig. 10; 1914:118, pl. 7, figs. 1-9; 1923:198, fig. 74 a-i.—Uschakov, 1958:416, fig. 1; 1972:216-217, pl. 39, figs. 4-9.—Uschakov and Wu, 1965:8, figs. 2E-H.—Hartman, 1960:86, pl. 6; 1968:329, 3 figs.—Pettibone, 1963:184-186, fig. 46.—Gathof, 1984:34-5, fig. 34-3, 4a-i.—Day, 1967:350, fig. 15.3.e-h.—Blake *et al.*, 1992:Appendix A.—SAIC, 1992:Appendices A and B.

Material examined. California, off San Francisco, continental slope depths, R/V *Point Sur*, Sta. 3-8, 37°27.13'N, 123°23.02'W, 2005 m, 13 Sept. 1991 (1).

Description. A moderate sized species, up to 20 mm long and 1.5 mm wide for about 70 segments. Color in alcohol: light tan with scattered brown pigment granules.

Prostomium somewhat conical, dorsoventrally flattened; eyes lacking; with 4 short, indistinct frontal antennae (Fig. 14.1A). Peristomial segment large, but achaetous, dorsally forming complete ring and ventrally forming lateral lips of mouth; tentacular cirri lacking.

First setiger uniramous, subsequent parapodia biramous. Parapodia well developed, with long rami bearing elaborate pre- and postsetal lamellae and short, digitiform dorsal and ventral cirri (Fig. 14.1B). Parapodia with ciliated interramal border, forming ciliated channel or groove along body. Notosetae simple, slender, with finely serrated edge; neurosetae including few simple setae in inferior position in fascicles; rest of setae compound spinigers, with tip of shaft spinous, blades finely serrate (Fig. 14.1C).

Distribution. Off California, in mud, 50-2100 m; Massachusetts to North Carolina; also other areas in the North Atlantic; Mediterranean; Yellow Sea; South Africa.

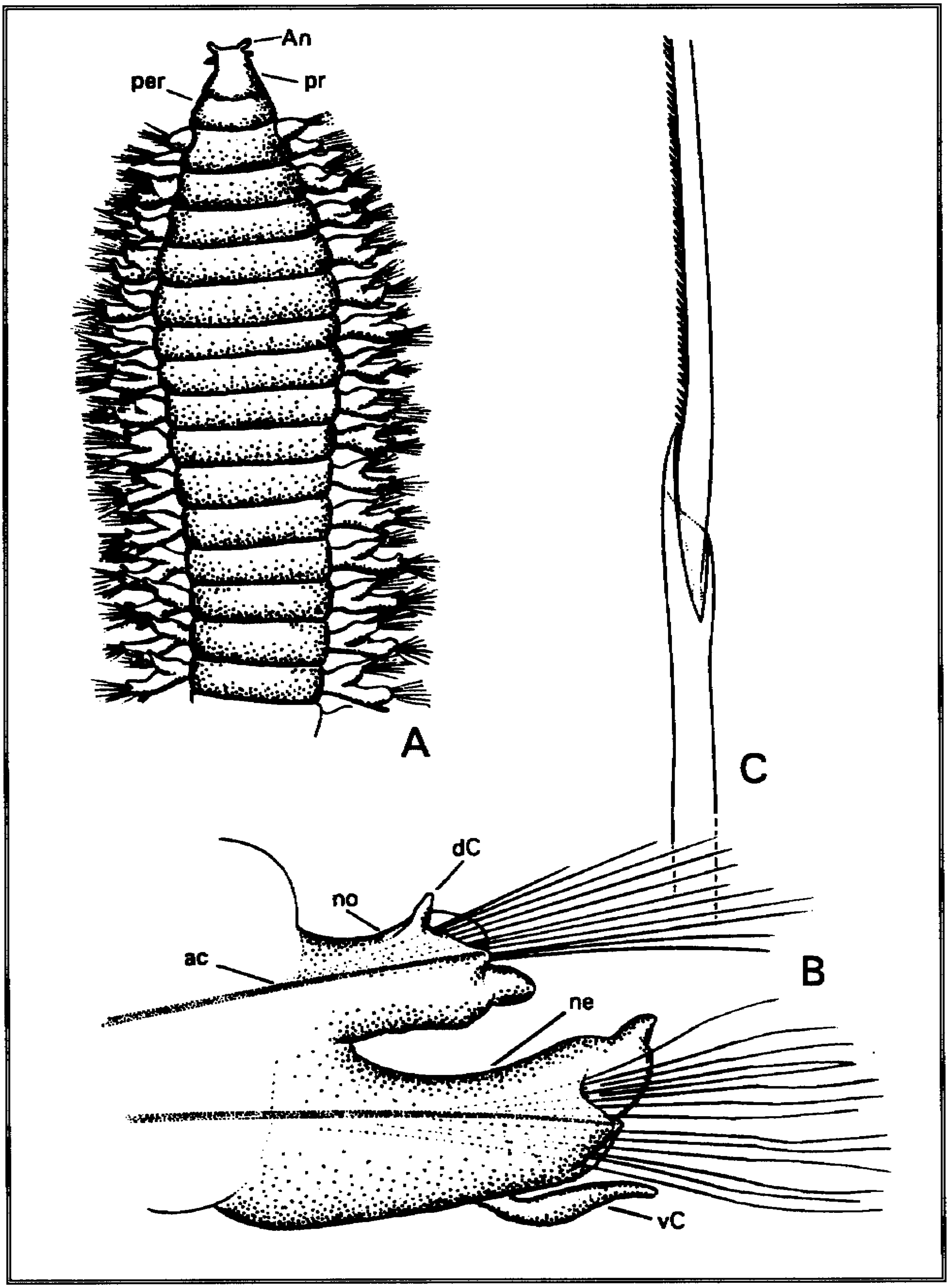

Figure 14.1. *Paralacydonia paradoxa*: A, anterior end, dorsal view; B, middle parapodium, anterior view; C, neuroseta. (after Hartman, 1960).

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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.

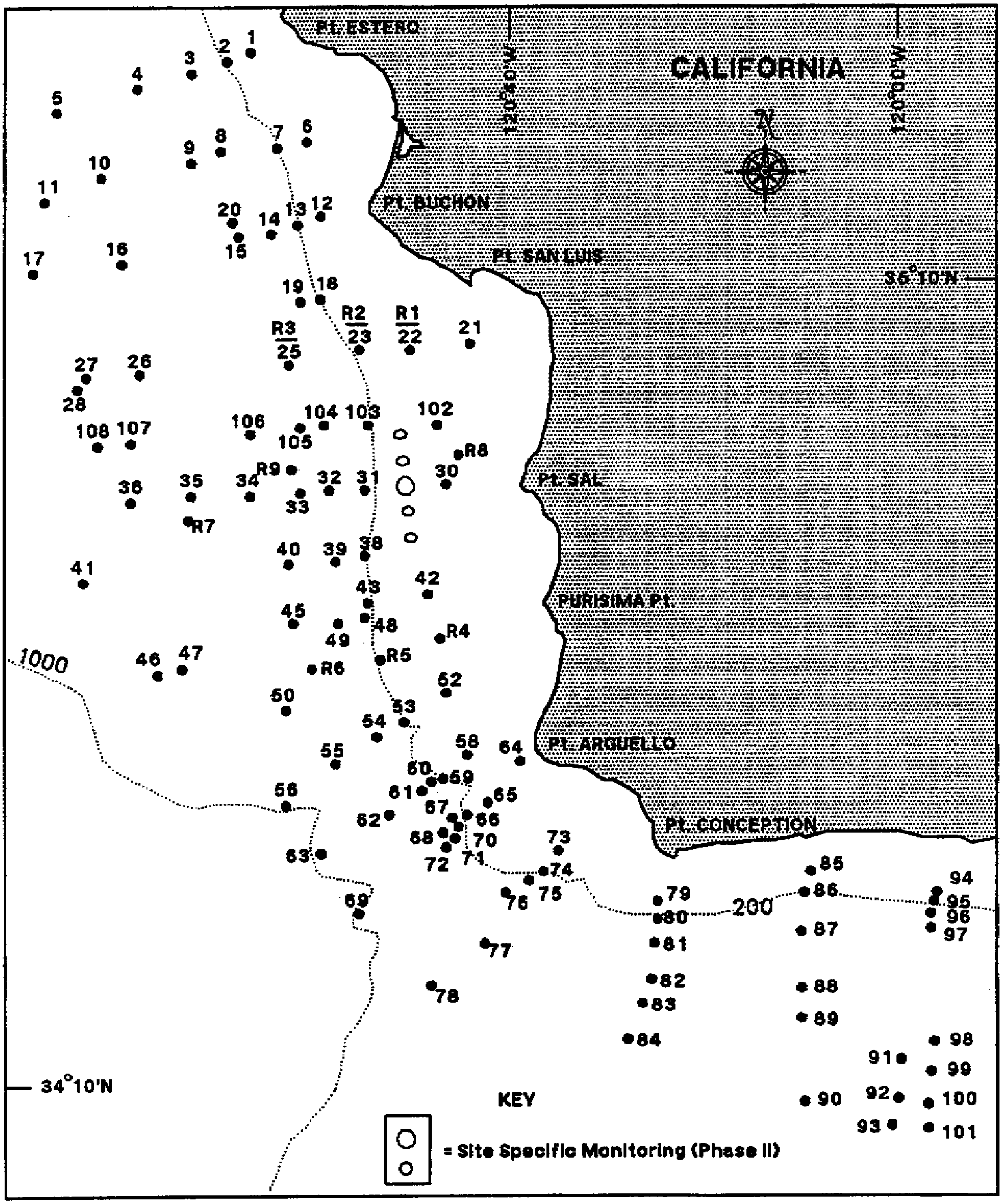

Figure A.1. Map showing location of soft substrate stations from Phase I and Phase II MMS Reconnaissance and Monitoring Programs.

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. 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.4. 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

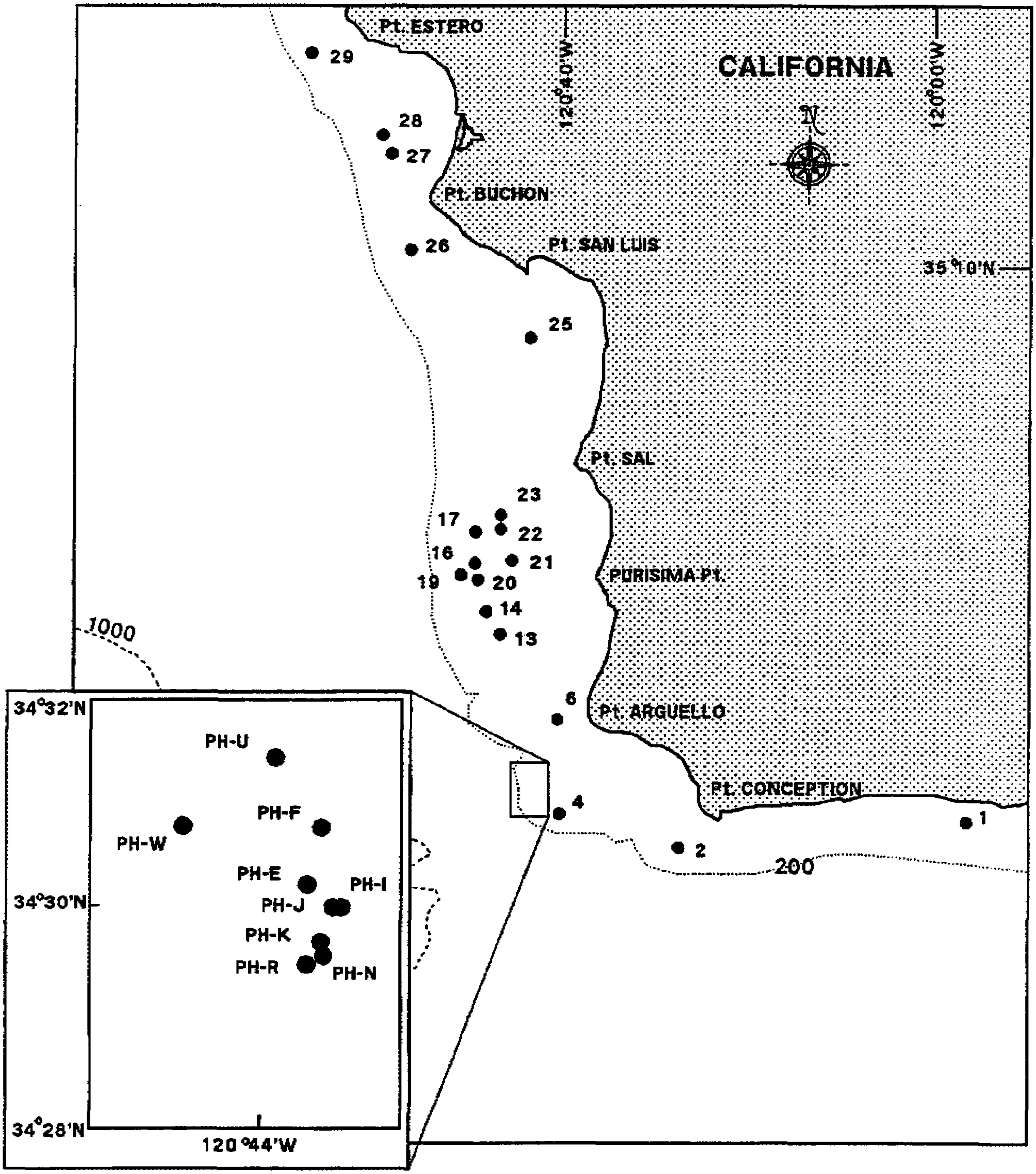

Figure A.2 Map showing locations of hard substrate stations from Phase I and Phase II MMS Reconnaissance and Monitoring Programs.

TAXONOMIC INDEX

Numbers in bold type indicate figures

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 assure that their development is in the best interest of all our people. The Department also has a major responsibility for American Indian reservation communities and for people who live in Island territories under U.S. Administration.