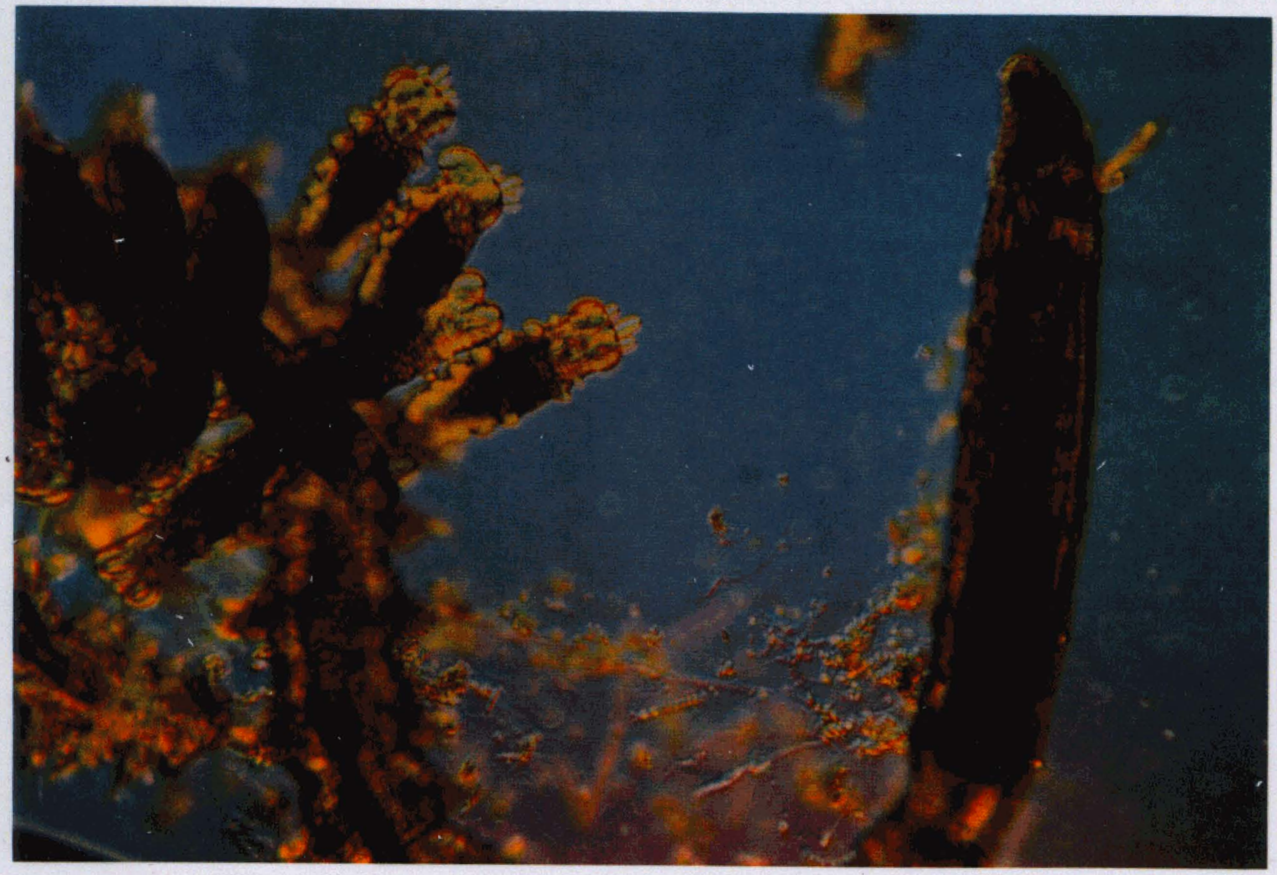
OCS Study
MMS 95-0016

Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and Western Santa Barbara Channel

FINAL REPORT
Volume 5 of 14

The Annelida Part 2 — Polychaeta: Phyllodocida (Syllidae and Scale-Bearing Families), Amphinomida, and Eunicida



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

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

FINAL REPORT
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The Annelida Part 2 — Polychaeta: Phyllodocida (Syllidae and Scale-Bearing Families), Amphinomida, and Eunicida

Edited by:

James A. Blake
Brigitte Hilbig
Paul H. Scott

Submitted by:

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

For:

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Minerals Management Service
Pacific OCS Region
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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.

PROJECT ORGANIZATION

PROGRAM MANAGER

DR. ANDREW L. LISSNER
Science Applications International Corporation
10260 Campus Point Drive
San Diego, California 92121

DEPUTY PROGRAM MANAGER

DR. JAMES A. BLAKE
ENSR Consulting and Engineering
89 Water Street
Woods Hole, Massachusetts 02543

PROJECT TECHNICAL OFFICER

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

CONTRIBUTING AUTHORS

DR. JAMES A. BLAKE
DR. BRIGITTE HILBIG
MS. LESLIE H. HARRIS
DR. JERRY D. KUDENOV
MR. R. EUGENE RUFF

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AFFILIATION: Science Applications International Corporation.

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

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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 5 are to continue coverage of the Polychaeta that was initiated in Volume 4. This volume concludes treatment of the so-called "errant" families. The following 13 families are treated in this volume: Syllidae, Aphroditidae, Polynoidae, Acoetidae, Pholoidae, Sigalionidae, Amphinomidae, Euphrosinidae, Onuphidae, Eunicidae, Lumbrineridae, Oenonidae, Dorvilleidae.

DESCRIPTION: Volume 5 concludes treatment of the so-called "errant" families and includes the Syllidae, 5 scale-bearing families (Aphroditidae, Polynoidae, Acoetidae, Pholoidae, and Sigalionidae), Amphinomidae, Euphrosinidae, and the Eunicida (Eunicidae, Onuphidae, Lumbrineridae, Oenonidae, and Dorvilleidae). The 13 chapters are organized into sections that include the morphology, taxonomic history, biology, keys to species, and descriptions of genera and species. Each species is fully illustrated with relevant characteristics labeled and identified.

SIGNIFICANT CONCLUSIONS: The keys, detailed descriptions, and illustrations to the 13 families treated in this volume represent a major contribution to polychaete systematics for the eastern Pacific. Many poorly known species are newly defined with new illustrations. The chapter on Syllidae defines a total of 34 species in the subfamilies Exogoninae (10, 6 new), Eusyllinae (12, 5 new), and Syllinae (12, 1 new, 3 provisional). Among the Polynoidae 22 species in 13 genera are included, with one new genus and species described. New species of *Pholoe, Onuphis, Parophryrotrocha, Ninoe*, and *Drilonereis* are described.

STUDY RESULTS: A total of 115 species in 57 genera are treated. One genus in the Polynoidae is new to science. Eighteen species are new to science as follows: Syllidae (12), Polynoidae (1), Pholoidae (1), Onuphidae (1), Lumbrineridae (1), Oenonidae (1), and Dorvilleidae (1). Three additional species are provisional new taxa, to be named in a later publication. The chapter on the Syllidae represents a major treatment of eastern Pacific genera and species of the subfamilies Exogoninae, Eusyllinae, and Syllinae. The species descriptions, especially of the new and provisional taxa are a major contribution. The 22 described species of Polynoidae include several poorly known taxa that are illustrated in detail for the first time. One new genus and species is described. Previous California records of *Lepidonotus squamatus* are referred to *L. spiculus*. Keys are provided to all species from the study area and in some cases, to species from adjacent areas. The treatment of other scale-bearing families is mostly limited to the material available from the MMS collections. For the Aphroditidae only juveniles are available from the MMS collections precluding any extensive review of California species. Sigalionidae and Acoetidae include previously known species, with updated descriptions and keys provided. For the Pholoidae, a new species of *Pholoe* is described. The amphinomid, *Chloeia pinnata* was found to have unusual bifurcate notosetae in posterior segments. These setae and other features of this common species are carefully illustrated; taxonomic implications of these findings are discussed. In the Euphrosinidae, 2 species were identified and described. Among the euniciform families, new species of *Onuphis, Ninoe, Drilonereis*, and *Parophryotrocha* are described. In the Oenonidae, *Arabella pectinata* and *A. protomutans* are newly reported for California. Keys are provided for all species treated.

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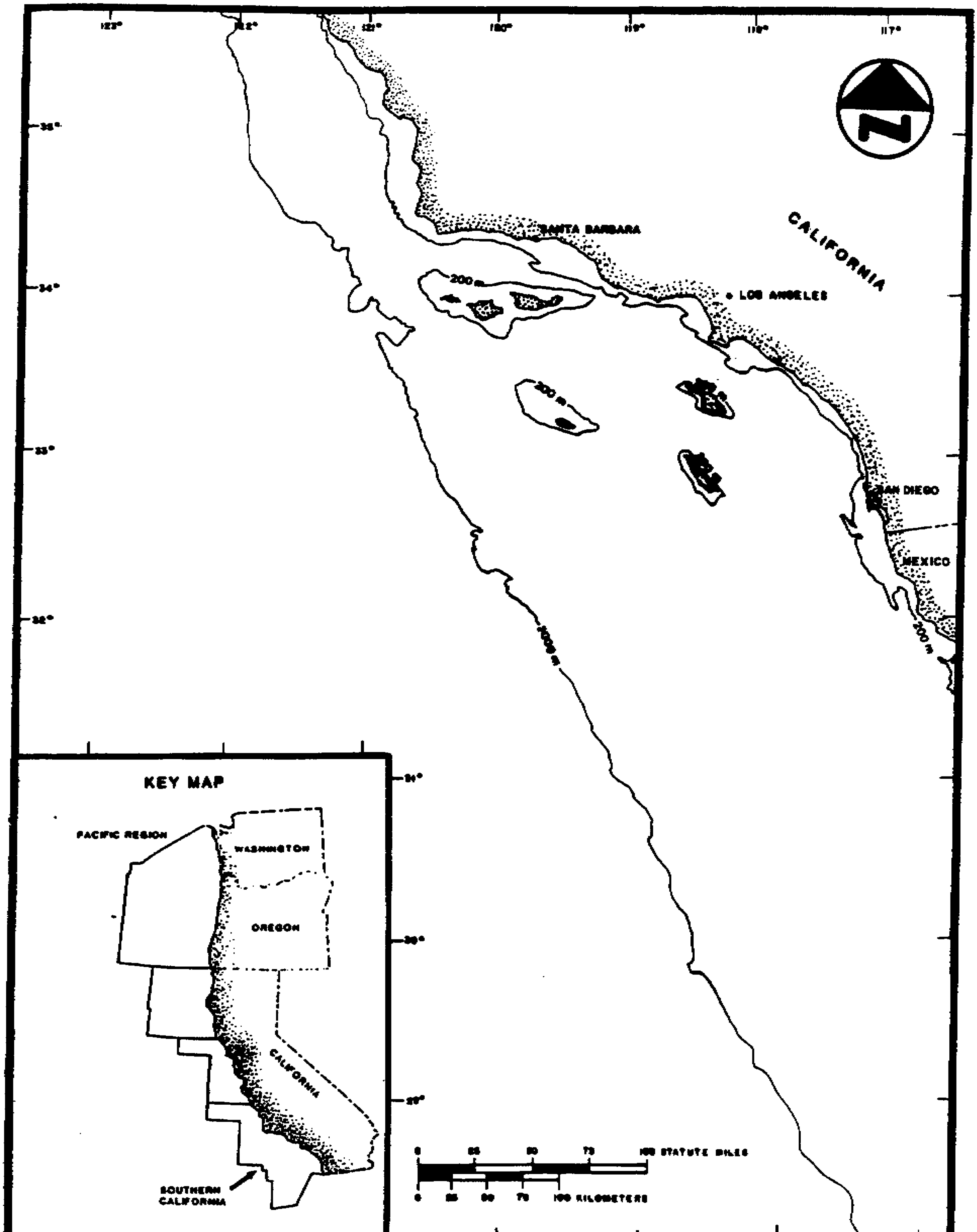

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15. Supplementary Notes

Contributing authors: James Blake, Brigitte Hilbig, Jerry Kudenov, Leslie Harris, R. Eugene Ruff

16. Abstract (Limit: 200 words)

Volume 5 is the second annelid volume, and continues coverage of the Polychaeta that began with Volume 4. This volume concludes treatment of the so-called "errant" families. The following 13 families are treated in this volume: Syllidae, Aphroditidae, Polynoidae, Acoetiodae, Pholoidae, Sigalionidae, Amphinomidae, Euphrosinidae, Onuphidae, Eunicidae, Lumbrineridae, Oenonidae, and Dorvilleidae. A total of 115 species in 57 genera are treated. One genus in the Polynoidae is new to science. Eighteen species are new to science as follows: Syllidae (12), Polynoidae (1), Pholoidae (1), Onuphidae (1), Lumbrineridae (1), Oenonidae (1), and Dorvilleidae (1). Three additional species of Syllidae are provisional new taxa, to be named later. The chapter on the Syllidae represents a major treatment of eastern Pacific genera and species of the subfamilies Exogoninae, Eusyllinae, and Syllinae. The species descriptions, especially of the new and provisional taxa are a major contribution. The 22 described species of Polynoidae include several poorly known taxa that are illustrated in detail for the first time. One new genus and species is described. Previous California records of *Lepidonotus squamatus* are referred to *L. spiculus*. Keys are provided to all species from the study area and in some cases, to species from adjacent areas. The treatment of other scale-bearing families is mostly limited to the material available from the MMS collections. For the Aphroditidae, only juveniles are available from the MMS collections precluding any extensive review of California species. Sigalionidae and Acoetidae include previously known species, with updated descriptions and keys. For the Pholoidae, a new species of *Pholoe* is described. The amphinomid, *Chloeia pinnata* was found to have unusual bifurcate notosetae in posterior segments. These setae and other features of this common species are carefully illustrated; taxonomic implications of these findings are discussed. In the Euphrosinidae, two species were identified and described. Among the euniciform families, new species of *Onuphis, Ninoe, Drilonereis,* and *Parophryotrocha* are described. In the Oenonidae, *Arabella pectinata* and *A. protomutans* are newly reported for California. Keys are provided for all species treated.

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List of Acronyms

AMNH	American Museum of Natural History, New York, New York, USA.
AMW	Australia Museum, Sydney, Australia.
ANSP	Academy of Natural Sciences, Philadelphia, Pennsylvania.
BLM	Bureau of Land Management.
BMNH	The Natural History Museum, London, United Kingdom
BRA	Refers to a station designation from the MMS Phase I Reconnaissance: Benthic Rocky, transect A/B.
BRC	Refers to a station designation from the MMS Phase I Reconnaissance: Benthic Rocky, transect C/D.
CASIZ	California Academy of Sciences, Department of Invertebrate Zoology, San Francisco, California, USA.
LACM	Natural History Museum of Los Angeles County, Los Angeles, California. Includes the type collections formerly lodged at Allan Hancock Foundation (AHF).
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA.
MMS	Minerals Management Service.
SCAMIT	Southern California Association of Invertebrate Taxonomists.
SBMNH	Santa Barbara Museum of Natural History, Santa Barbara, California, USA.
USNM	United States National Museum. A historical designation for the National Museum of Natural History (NMNH), Smithsonian Institution, Washington, D.C., USA.
ZMH	Zoologisches Museum, Hamburg, Germany

1. Family Syllidae Grube, 1850

by

Jerry D. Kudenov[1] and Leslie H. Harris[2]

Introduction

The Syllidae represent one of the most diverse and systematically challenging families of Polychaeta, with about 70 genera and over 600 species (Hartman, 1959, 1965; Fauchald, 1977; Pettibone, 1982). Syllids tend to be small, usually less than 10 mm long and 1 mm wide, and are especially well represented as epibiota on hard surfaces or on metazoans in intertidal, subtidal and shelf habitats. Other members of this family are also abundant or widely distributed in shallow soft-bottom environments. The Syllidae is represented by only a few genera in deeper waters, such as *Sphaerosyllis* and *Braniella* in slope and rise habitats.

Morphology

The body is usually small, short and slender or threadlike, nearly cylindrical to dorsoventrally flattened in cross section, and tapering anteriorly and posteriorly. The integument is generally smooth, but papillae of various shapes and distributions are sometimes present.

The prostomium tends to be wider than long. Eyes number two to three pairs; the posterior two pairs are arranged trapezoidally, and the anterior pair tends to be eyespots associated with the anteriormost region of prostomium. Antennae generally number three, including unpaired median and paired lateral antennae, which may be strongly articulated, wrinkled or smooth; they are absent in *Exogonella*. Nuchal organs may be present as epaulettes or lobes extending from the posterior prostomial margin, or as continuous transverse or paired postectal lobes. Palps are paired, usually large, roughly triangular in shape, range from being completely fused to free from one another, and project anteroventrally. However, the palps of *Autolytus* are greatly reduced, not visible dorsally, and project ventrally from the prostomium.

The pharynx is an eversible tube with a cuticular lining, and generally with a dorsomedian tooth that tends to be marginal or subdistal when the pharynx is everted, although it may be present in the middle or posterior half of the pharynx. Additionally, a distal circlet or arc of marginal pharyngeal teeth may accompany the dorsomedian tooth, all of which may become so well developed that together they appear to form a crown or trepan (as in *Trypanosyllis*). Sometimes the pharynx is described as being unarmed, i.e., pharyngeal teeth are absent, as in *Syllides*. A distal circlet of 10 soft papillae is usually also present, although these may be fewer in number or absent in some taxa. The proventriculus is conspicuous, with transversely striated muscles arranged in rows, and connects the anterior pharynx to the posterior intestine.

[1]Department of Biological Sciences, University of Alaska Anchorage, 3211 Providence Drive, Anchorage, Alaska 99508
[2]Invertebrate Zoology Section, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007

The tentacular segment is achaetous, and generally forms a complete ring, although sometimes it is dorsally reduced or variously developed into an occipital flap that extends anteriorly over the prostomium, covering one or both pairs of posterior eyes. Ventrally the tentacular segment forms the lips of the mouth. Tentacular cirri generally number two pairs, although only one pair may be present in *Exogone*; *Exogonella* lacks cirri altogether.

Parapodia are uniramous and similar all along the body in nonreproductive individuals; they may be biramous in reproductive individuals. Setae are generally compound falcigers (as in *Typosyllis*), or sometimes compound spinigers (as in some species of *Exogone* and *Pionosyllis*), or are entirely simple (as in *Haplosyllis*). In some taxa, the articulation between the blade and the shaft is fused. A dorsal and ventral simple seta may also be present in each fascicle for a varying number of segments. Aciculae are present in all parapodia, varying both in number and shape.

Dorsal cirri vary in shape and length, sometimes alternating between long and short, and generally present on all parapodia, although they may be absent from an anterior segment in some taxa. Dorsal cirri may be articulated or moniliform (as in *Syllis*, *Typosyllis* or *Trypanosyllis*); smooth (as in *Exogone*, *Odontosyllis* or *Pionosyllis*); or irregularly wrinkled (as in *Eusyllis* or *Streptosyllis*). Ventral cirri are mostly digitiform, and usually do not extend beyond the parapodial lobes; they are entirely absent from the subfamily Autolytinae.

The pygidium has a pair of anal cirri, and sometimes also a ventromedian cirrus. The cirri are usually slender, ranging from articulated to smooth.

Systematic History

Grube (1850) was the first to recognize syllids as a separate family, followed by Williams (1851) who also considered the Syllidae as a separate family. Other important early works on syllids include Quatrefages (1865), Malaquin (1893), Gravier (1900), Haswell (1920a, b; 1921), Fauvel (1923, 1934a, b) and Rioja (1925). Rioja (1925) divided the Syllidae into four subfamilies: Autolytinae, Exogoninae, Eusyllinae and Syllinae, each of which are defined and accompanied by a key below, and have been recognized by subsequent investigators (Fauchald, 1977; Pettibone, 1982).

Recent literature of importance includes the studies by Berkeley and Berkeley (1938, 1945), Rioja (1941, 1943), Uschakov (1955), Gidholm (1962, 1965, 1967a,b), Pettibone (1954, 1963, 1982), Imajima (1966a-e, 1967), Day (1967), Hartman (1961, 1968), Hartmann-Schröder (1971), Fauchald (1977), Uebelacker (1984), Russell (1987, 1989a-b, 1991) and San Martín (1990, 1991a,b). The excellent series of papers by Imajima (1966a-e, 1967) are undoubtedly the most important works that have consistently clarified important traits for the entire family. In this context, Imajima largely stabilized syllid systematics.

Principal Diagnostic Traits

The four subfamilies defined by Rioja (1925), and recognized by Imajima (1966a), Day (1967) and Uebelacker (1984) are characterized as follows:

Subfamily Autolytinae

Diagnosis. Body threadlike, 4-20 mm long, 0.5-1 mm wide. Palps partially to completely fused to one another, directed ventrally. Nuchal organs present either as conspicuous epaulettes or lobes. Tentacular cirri numbering 2 pairs. Antennae, tentacular cirri and dorsal cirri smooth. Ventral cirri absent. Pharynx long, coiled or sinuous, with a distal circlet of teeth (=trepan).

Subfamily Exogoninae

Diagnosis. Body rather compact, less than 8 mm long, 0.8 mm wide. Palps fused dorsally for at least one-half to all their length. Nuchal organs usually inconspicuous. Tentacular cirri usually numbering 1-2 pairs; may be absent. Antennae, tentacular cirri and dorsal cirri smooth. Ventral cirri present. Pharynx usually straight, with a middorsal tooth or unarmed.

Subfamily Eusyllinae

Diagnosis. Body usually at least 10 mm long. Palps only fused basally, free from one another distally. Nuchal organs large and conspicuous. Tentacular cirri numbering 1-2 pairs. Dorsal cirri smooth to wrinkled. Ventral cirri present. Pharynx usually straight, with a middorsal tooth with or without a marginal series of teeth, or unarmed.

Subfamily Syllinae

Diagnosis. Body usually at least 10 mm long, sometimes over 50 mm. Palps usually free basally. Nuchal organs usually small and inconspicuous. Tentacular cirri numbering 2 pairs. Dorsal cirri strongly articulated or moniliform. Ventral cirri present. Pharynx straight, with a middorsal tooth, with or without distal circlet of teeth (=trepan).

It is relatively easy to distinguish autolytins and exogonins from one another and from each of the other two subfamilies. Unfortunately, it is often difficult to identify both eusyllins and syllins to a subfamily because key characters sometimes overlap. For example, some eusyllins may have distinctly articulated dorsal cirri or basally fused palps and some syllins may have smooth dorsal cirri or basally separated palps (Day, 1967; Uebelacker, 1984). Fusion of palps in the Eusyllinae and Syllinae may be partly controlled by physical factors such as temperature (Piltz, 1980), suggesting that this particular character is not informative. Although distinctions between smooth to wrinkled versus articulated dorsal cirri of eusyllins and syllins are not always reliable, this trait is still the most practical one to use when placing these taxa into subfamilies.

A synopsis of the majority of syllid genera is presented by Fauchald (1977). Important generic traits include: body shape, epidermal papillae, prostomial antennae, occipital flap, tentacular cirri, nuchal organs, nature of dorsal and ventral cirri, nature and distribution of setae, aciculae, and nature and armature of the pharynx. Perhaps knowledge of the pharynx is the most critical of these traits. The pharynx may be unarmed, lacking any sort of dentition, or may have an internal valve. An armed pharynx can show a variety of dentition patterns: (a) a single middorsal tooth with a smooth or minutely dentate anterior rim or margin; (b) a continuous distal circlet of teeth (trepan) which may have an enlarged median tooth; (c) a discontinuous ventral arc or an incomplete circlet of teeth. The position of the middorsal tooth is also important because it can range from distal, subdistal, or proximal in the pharynx. Pharyngeal dentition is often the only way to separate such genera as *Eusyllis* and *Pionosyllis*.

Important species traits include: pigmentation patterns; shape and distribution of such structures as antennae and eyes, palps, nuchal organs, pharynx, proventriculus, peristomial cirri, occipital flap, parapodia, dorsal and ventral cirri, setae and aciculae. Among the more important traits noted above are the setae, aciculae, and pharynx. Both setae and aciculae must be examined and illustrated from superior and inferior regions of fascicles of anterior, middle and posterior parapodia using a compound microscope. It is also important to scan the entire specimen for the distribution and morphological changes in setae and aciculae along the body (Fauchald, 1977), especially in such genera as *Exogone*, *Syllides* and *Streptosyllis*. Typically, blades of compound falcigers tend to vary in length, decreasing both inferiorly within fascicles, and posteriorly along the body; aciculae generally decrease in both size and number per parapodium posteriorly along the body. Setae and aciculae must also be examined and illustrated using oil-immersion, particularly the ends of shafts and blade tips of compound setae, and the tips of both aciculae and simple setae. The pharynx is critical to species identifications, and it is usually not protracted in preserved specimens. Sometimes it can be readily observed through the body wall of small translucent specimens. Otherwise the pharynx must be removed if possible (Day, 1967; Fauchald, 1977; Uebelacker, 1984) and illustrated.

One must take care when identifying or describing syllids. Often, it is necessary to examine individual specimens one at a time. This does not mean that the taxon is so fraught with taxonomic difficulties that it should remain the purview of a few specialists. However, it is clear that much of the present confusion surrounding syllid systematics is due to at least three obvious factors. First, many workers have described new species, often in complicated genera, without having examined relevant type materials. Similarly, there is a tendency for some workers to apply names of species described from such areas as Europe (especially by Fauvel, 1923) to species that have similar suites of characters from the western coast of North America (Berkeley and Berkeley, 1948; Hartman, 1968). Such undue reliance on literature descriptions, instead of types, has cumulatively destabilized species concepts. For example, earlier records of *Exogone gemmifera* represent at least one undescribed species (Banse and Hobson, 1974; this study). Some of these species may truly be "cosmopolitan" in distribution, but until the types are critically examined, there is simply no way of knowing the number of "hidden" species involved. Secondly, well-known species that may have limited dispersal abilities have been identified far from their type localities. Again, many such identifications are seldom compared to types, which adds greater uncertainty to syllid systematics and further complicates efforts to identify species. A third factor is that a number of species are either too poorly known, original type specimens are no longer available, or lectotypes have not been redescribed.

Prospects for stabilizing syllid systematics will be attainable only in the long term. Systematic practice on and descriptions of syllids needs to be standardized. The best way to set this process in motion is for workers to compare their identifications to existing type material during revisionary studies of genera. Where type material is not available, one must obtain and describe specimens from type localities and not rely solely on published descriptions. Other systematic techniques should also be pursued in the study of syllids. For example, an intriguing karyological study (Curini-Galletti *et al*, 1991) summarized chromosomal data for syllids, and suggested that: (a) congeneric species usually have similar karyotypes; and (b) one likely mechanism of karyological evolution involves chromosomal fission or fusion, while polyploidy is speculated to be another mechanism that may have led to high numbers of chromosomes in both the Eusyllinae and Syllinae. Syllids are an ecologically important group of infauna and epibiota, and efforts to render them more understandable should be made by all interested polychaetologists.

Biology

Syllids are usually small, cryptic, highly motile polychaetes that dominate hard substrata. They are often associated with sponges, hydroids, corals, bryozoans, ascidians, algae and seagrasses. Syllids of the subfamily Exogoninae are well represented in soft sediments where they inhabit superficial layers, while others are common in algal mats and coral rubble. The entire family is best represented in shallow seas, being less diverse in deep water, although certain genera such as *Sphaerosyllis*, *Braniella* and *Syllis* are present.

Most syllids are considered to be carnivorous, piercing the body wall of prey with their armored pharynges, and ingesting body fluids through the pumping action of the highly muscular proventriculus. Other taxa, such as the Exogoninae may generally be selective deposit feeders or consume diatoms (Day, 1967; Fauchald and Jumars, 1979; Pettibone, 1982).

Syllid reproductive biology is both interesting and complex (Heacox, 1980; Heacox and Schroeder, 1981a,b). Sexes are separate, but species can generally reproduce both asexually and sexually. Asexual reproduction occurs through the formation of stolons which are posterior body segments of sexually derived adults (or parental atoke) that become transformed solely for the purpose of carrying gametes. Stolons are transient structures, with prostomia bearing appendages and 2 pairs of conspicuous eyes, long tentacular and dorsal cirri, and biramous parapodia with notopodial fascicles of long natatory or swimming capillary setae. Each stolon can either be produced singly, in long serial chains, or in dense clusters, detaching periodically to spawn (Dales, 1967; Schroeder and Hermans, 1975). Stolons of the Exogoninae, Eusyllinae and Syllinae tend to be morphologically similar: male and female stolons are called a chaetosyllis stage; those of *Trypanosyllis* and *Eurysyllis* are called a tetraglene stage. Stolons of the Autolytinae are dimorphic: male stolons are called polybostrichus stages and have long divergent palps; female stolons are called sacconereis stages with ventral pouches or marsupia containing large yolky ova (Gidholm, 1962).

Sexually reproducing syllids may spawn their gametes directly into seawater after they have become modified into swimming stages called epitokes. Epitokes generally have large eyes, and biramous parapodia with notopodial fascicles of long natatory setae in certain segments. Epitokes eventually swarm to surface waters in response to various environmental cues where gametes are released en masse, producing free-swimming larvae. Another mode of sexual reproduction is brooding by females in which developing embryos are attached directly in sacs to the dorsum, ventrum or parapodia. The embryos usually number two per segment, and develop directly into individuals with 4-6 segments that resemble small adults.

Key to the Subfamilies and Genera of the Syllidae (After Imajima, 1966a; Fauchald, 1977)

1A. Ventral cirri absent; dorsal cirri smooth .... **Autolytinae**[3]

1B. Ventral cirri present; dorsal cirri smooth to articulated 2

2A. Body small, usually less than 8 mm long; dorsal cirri smooth; palps fused for at least half their lengths (Figs. 1.1A, 1.7B, 1.10A) .... **Exogoninae** 4

2B. Body larger, usually more than 10 mm long; dorsal cirri smooth to articulated; palps not fused or fused only basally (Figs. 1.15A, 1.19A) 3

[3] No species of the Autolytinae were encountered in the collections examined as part of this study. The Autolytinae are, however, well represented in California waters (Hartman, 1968; L. Harris, personal observation, 1995).

3A. Palps fused basally (Figs. 1.19A, 1.20A); dorsal cirri smooth to wrinkled (Figs. 1.18A, 1.19A) .... **Eusyllinae** 7

3B. Palps not fused basally (Figs. 1.27A, 1.28A); dorsal cirri articulated (Figs. 1.26C, 1.28A) .... **Syllinae** 12

4A. Two pairs of tentacular cirri (Figs. 1.1A, 1.2A, 1.25B) 5

4B. One pair of tentacular cirri (Figs. 1.5A, 1.6A, 1.8A, 1.10A) 6

5A. Dorsal cirri long and filiform (Figs. 1.1A, 1.2A) .... *Brania*

5B. Dorsal cirri globular or spherical (Fig. 1.25E-G) .... *Eurysyllis*

6A. Dorsal cirri papilliform or ovoid (Figs. 1.4C, 1.7D-F) .... *Exogone*

6B. Dorsal cirri pyriform or flask-shaped (Figs, 1.8C-E, 1.9A, 1.10D-E) .... *Sphaerosyllis*

7A. Eversible pharynx unarmed (Figs. 1.21B, 1.22B-C) .... *Syllides*

7B. Eversible pharynx armed (Figs. 1.12A, 1.18A) 8

8A. Pharynx with a single middorsal tooth (Figs. 1.20B, 1.26B, 1.30C,D, 1.32A) 9

8B. Pharynx with a distal circlet of smaller curved teeth (Figs. 1.16B, 1.17E) .... *Odontosyllis*

9A. Middorsal tooth located in posterior region of eversible pharynx (Fig. 1.18A) .... *Opisthodonta*

9B. Middorsal tooth located in anterior region of eversible pharynx (Figs. 1.12A, 1.14B, 1.15B, 1.20B) 10

10A. Anterior margin or rim of eversible pharynx denticulated (Figs. 1.14B, 1.15B) .... *Eusyllis*

10B. Anterior margin or rim of eversible pharynx smooth 11

11A. Parapodia long; palps 2 times longer than prostomium (Figs. 1.11C, 1.12A) .... *Dioplosyllis*

11B. Parapodia short and conical; palps maximally same length as prostomium (Fig. 1.20B) .... *Pionosyllis*

12A. Pharynx with middorsal tooth (Figs. 1.23B, 1.25A, 1.26B, 1.32A) 13

12B. Pharynx with middorsal tooth and trepan (Fig. 1.30C-D) 15

13A. Setae include compound falcigers (Fig. 1.27C), dorsal and ventral simple setae, and pseudocompound setae (Fig. 1.27D-E) .... *Syllis*

13B. Setae include compound falcigers, some with extremely long spiniger-like blades, and dorsal and ventral simple setae 14

14A. Compound falcigers and spiniger-like falcigers with extremely long bidentate blades at least 4 times longer than inferiormost blades within fascicles of midbody segments (Figs. 1.23G, 1.24G,I) .... *Ehlersia*

14B. Only compound falcigers present (Figs. 1.32F-I, 1.33D-E, 1.34D-J) .... *Typosyllis*

15A. Palps same length as prostomium (Fig. 1.26A); body cylindrical; setae simple (Fig. 1.26D-E) .... *Geminosyllis*

15B. Palps shorter than prostomium (Figs. 1.29A, 1.30A-B); body flattened; setae compound (Figs. 29D-G, 30B-F) .... *Trypanosyllis*

List of Syllid Species

In all, 16 genera and 34 species of syllids have been identified in MMS samples from the Santa Maria Basin and western Santa Barbara Channel. One species is a new combination, and 14 other species in 11 genera are new to science. The following species list is organized by subfamily. Type specimens are deposited in the National Museum of Natural History, Smithsonian Institution (NMNH), Natural History Museum of Los Angeles County (LACM-AHF), Santa Barbara Museum of Natural History (SBMNH) and the Australian Museum, Sydney (AM W); all non-type specimens of new taxa listed below are deposited at the LACM-AHF. As noted above, the Autolytinae are not represented in voucher collections, and were infrequently encountered in MMS samples. Excellent papers on the Autolytinae by Gidholm (1962, 1965, 1967a,b) and Imajima (1966b) should be consulted.

Subfamily Exogoninae

Brania brevipharyngea Banse, 1972
Brania californiensis Kudenov and Harris, new species
Exogone (Exogone) lourei Berkeley and Berkeley, 1938
***Exogone (Exogone) dwisula* Kudenov and Harris, new species**
Exogone (Parexogone) molesta Banse, 1972
***Exogone (Parexogone) acutipalpa* Kudenov and Harris, new species**
***Exogone (Parexogone) breviseta* Kudenov and Harris, new species**
Sphaerosyllis californiensis Hartman, 1966
***Sphaerosyllis bilineata* Kudenov and Harris, new species**
***Sphaerosyllis ranunculus* Kudenov and Harris, new species**

Subfamily Eusyllinae

Dioplosyllis lagunae (Hartman, 1961), **new combination**
***Dioplosyllis tridentata* Kudenov and Harris, new species**
Eusyllis blomstrandi Malmgren, 1867
Eusyllis habei Imajima, 1966c
Eusyllis longocirrata Imajima, 1966c
Odontosyllis phosphorea Moore, 1909
***Odontosyllis fragilis* Kudenov and Harris, new species**
***Opisthodonta mitchelli* Kudenov and Harris, new species**
Pionosyllis magnifica Moore, 1906
***Pionosyllis articulata* Kudenov and Harris, new species**
Syllides reishi Dorsey, 1978
***Syllides mikeli* Kudenov and Harris, new species**

Subfamily Syllinae

Ehlersia heterochaeta (Moore, 1909)
Ehlersia hyperioni Dorsey and Phillips, 1987
***Eurysyllis spicum* Kudenov and Harris, new species**
Geminosyllis ohma Imajima, 1966d
Syllis spongiphila Verrill, 1885
Trypanosyllis (Trypanedenta) sp. A
Trypanosyllis (Trypanosyllis) coeliaca nipponica Imajima and Hartman, 1964
Trypanosyllis (Trypanosyllis) sp. A
Trypanosyllis (Trypanosyllis) sp. B
Typosyllis alternata (Moore, 1908)
Typosyllis bella (Chamberlin, 1919)
Typosyllis hyalina (Grube, 1863)

Description of Species

Subfamily Exogoninae

Genus *Brania* Quatrefages, 1866

Grubea Quatrefages, 1865:35 (in part).
Protogrubea Czerniavsky, 1881:414 (in part).
Pseudobrania San Martin in Sardá, 1984:7-13.
Pseudobrania: San Martín, 1984a:150-151.
Grubeosyllis Verrill, 1900, *sensu* San Martín, 1991b:716-717.

Type species: *Exogone pusilla* Dujardin, 1851

Diagnosis. Prostomium with 3 antennae. Palps well developed, fused at least basally, as long as prostomium. Two pairs of tentacular cirri. Small nuchal organs present between prostomium and tentacular segment. Pharynx with single middorsal anterior tooth. Dorsal cirri longer than setal lobes. Ventral cirri as long as setal lobes. Embryos carried on dorsum of females. Aciculae acuminate with sharp filiform tips, or distally notched or excavate, with blunt tip.

Remarks. San Martín (1984a) proposed the genus *Pseudobrania* to include previously described *Brania* species that have (a) prostomial antennae, tentacular and dorsal cirri long and fusiform; (b) acuminate acicula with distally sharp tips; and (c) palps completely united by a dorsal membrane, and not separated by a distal cleft or notch. This genus was prematurely described by Sardá (1984) but because it was based upon San Martín's unpublished dissertation, the authorship San Martín in Sarda must be applied. However, *Pseudobrania* is actually preoccupied in the Platyhelminthes, and San Martín (1991b:716-717) instead proposed using the previously named genus, *Grubeosyllis* Verrill, 1900. According to the scheme proposed by San Martín, *Brania sensu stricto* differs from *Grubeosyllis* in having, (a) prostomial antennae, tentacular and dorsal cirri clavate or truncate; (b) aciculae distally excavate with tooth or blunt tips; and (c) palps united basally by dorsal membrane, distally separated by a small notch or cleft. There are apparently other differences pertaining to morphology of the compound setae.

The necessity of San Martín's (1984a, 1991b) approach is highly questionable. *Brania sensu lato* includes 21 species (Fauchald, 1977), and is a relatively compact genus. The division of this genus tends to obscure similarities previously recognized among congeneric species. San Martín (1991b) also suggests a closer relationship between members of his newly redefined *Grubeosyllis* and *Parapionosyllis* Fauvel, 1923, than between *Grubeosyllis* and *Brania sensu stricto*. This statement is difficult to comprehend. For example, *Parapionosyllis* differs from *Grubeosyllis* in having one, instead of two pairs of tentacular cirri, and in having compound spinigers rather than compound falcigers. Finally, examinations of both *B. brevipharyngea* and a new *Brania* species described below from MMS materials suggests considerable overlap in the characters used by San Martín (1984a, 1991b) and Sardá (1984). For example, the palps of the new MMS *Brania* species are distally notched and separated from one another, the aciculae are distally blunt and excavate, and some of the dorsal cirri are filiform, while others may be clavate. Similarly, the aciculae of *B. brevipharyngea* are also excavate and distally blunt, although the palps appear to be fused by a dorsal membrane for their entire length. Perhaps the criteria used for these generic distinctions rely too heavily on soft anatomical features that not only change allometrically over life cycles, but also are easily influenced by collecting efforts and preservation. The above features for the two MMS *Brania* species significantly overlap the two separate sets of criteria defined by San Martín (1984a, 1991b) for both *Grubeosyllis* (=*Pseudobrania*) and *Brania*, call into serious question the usefulness of dividing such a relatively compact genus (*Brania sensu lato*) and shed considerable doubt on the validity of *Grubeosyllis*. Therefore, the traditional generic definition of *Brania* is followed here, and *Grubeosyllis* is considered to be a junior synonym of *Brania*.

Although Rioja (1941) described *Brania heterocirra* from Mexico, Westheide (1974) reported *B. heterocirra* from the Galapagos, Japan (where Imajima (1966a) recorded it as *B. clavata*), and Washington (where Banse (1972) in part identified it as *B. brevipharyngea*). *Brania heterocirra* is included in the key below since it seems likely to be encountered in the syllid fauna of southern California. There are several additional undescribed species of *Brania* in California (L. Harris, unpublished).

Key to Species of *Brania* From the Santa Maria Basin

1A. Dorsal cirri varying in length along body; pharynx and proventriculus in same number of segments; cutting surfaces of superior dorsal simple seta smooth to minutely serrated .... *Brania heterocirra*

1B. Dorsal cirri subequal in length along body; pharynx and proventriculus in different number of segments; cutting surfaces of superior dorsal simple seta strongly serrated 2

2A. Pharynx in 2 segments (Fig. 1.1A); proventriculus in 4 segments .... *Brania brevipharyngea*

2B. Pharynx in 4 segments (Fig. 1.2A); proventriculus in 2 segments (Fig. 1.2B) .... *Brania californiensis*

Brania brevipharyngea Banse, 1972

Figure 1.1

Brania brevipharyngea Banse, 1972:198-200, fig. 4.—Banse and Hobson, 1974:55.
Pseudobrania brevipharyngea: San Martín, 1984a:172, 174.—Sardá, 1984:12.
Grubeosyllis brevipharyngea: San Martín, 1991b:716-717.

Material Examined. California: Santa Maria Basin, off Purisima Point, Sta. BRA-20 (1, SBMNH 142697).—Washington: False Bay, San Juan Island, holotype (USNM 40711), paratypes (5, USNM 40712).

Description. Total body length about 3 mm, 0.4 mm wide without parapodia, 0.6 mm with parapodia, for 30-31 setigers (Banse, 1972); MMS specimen an anterior fragment 1.5 mm long, 0.4 mm wide, with about 20 setigers. Body of preserved specimens generally colorless except for slight pigmentation on tentacular segment. Setigers 7-15 ovigerous, each with 12 ova per segment in 1 specimen (Banse, 1972:199).

Prostomium wider than long (Fig. 1.1A); 2 pairs of eyes, anterior pair largest, lenticulate, in trapezoidal arrangement; additional pair of eyespots present on anterior prostomium medial to lateral antennae (Fig. 1.1A). Antennae longer than prostomium, bottle-shaped; median antenna arising between 2 pairs of large eyes; lateral antennae arising from anterior part of prostomium (Fig. 1.1A). Palps about as long as prostomium, fused completely (Fig. 1.1A). Pharynx extending through setiger 2 (2.5 setigers in MMS specimen); middorsal tooth subdistal, lacking distal circlet of soft papillae when everted. Proventriculus extending from setigers 3-6, with 20-25 rows of muscle cells (17-18 in MMS specimen). Tentacular segment distinct dorsally (Fig. 1.1A), with 2 pairs of bottle-shaped tentacular cirri; dorsal pair longest, each about as long as median prostomial antenna; ventral pair each about one-half length of dorsal ones (Fig. 1.1A).

Parapodia of median segments truncate, with small, distally rounded presetal lobes (Fig. 1.1B). Compound falcigers distally bidentate (Fig. 1.1C), 7 to 9 per parapodium. Blades decreasing in length inferiorly within fascicles, superior blades twice length of inferior blades; all with serrated cutting edges. Shafts of compound falcigers enlarged distally; superior distal surfaces serrated (Fig. 1.1C). Superior dorsal simple seta distally bidentate with serrated cutting surface (Fig. 1.1D), present in all setigers from setiger 1 or 4. Ventral inferior simple seta present from setigers 20-21 to end of body. One acicula per parapodium, distally blunt, beak-shaped (Fig. 1.1E). Dorsal cirri long, bottle-shaped, present on all segments (Fig. 1.1A,B). Ventral cirri digitiform, extending beyond parapodial lobes (Fig. 1.1B).

Pygidium with paired anal cirri, each bottle-shaped, 2-3 times length of anterior dorsal cirri.

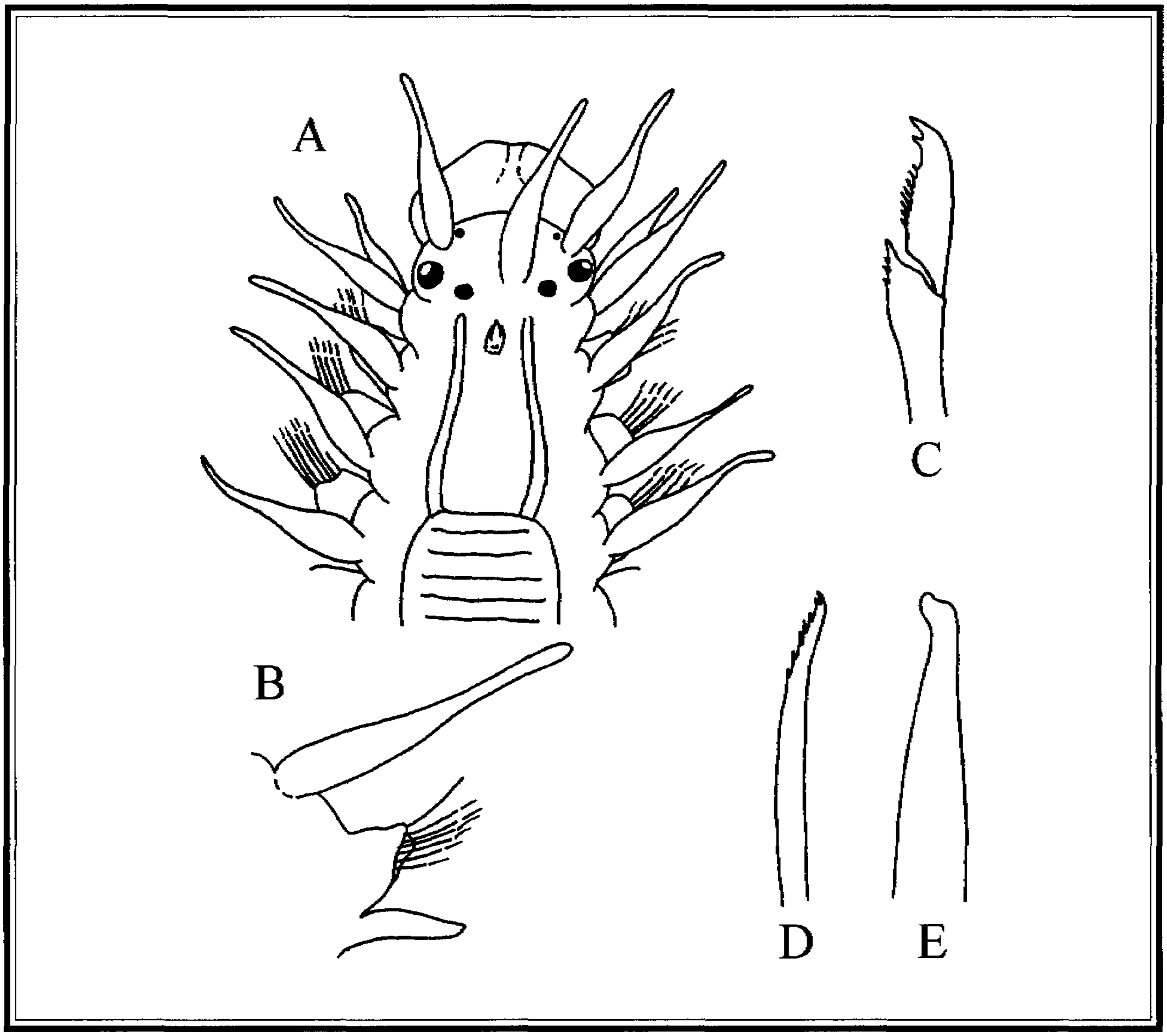

Figure 1.1. *Brania brevipharyngea*: A, anterior end, dorsal view, setae schematic; B, parapodium 16, posterior view; C, inferiormost compound falciger; D, superior dorsal simple seta; E, acicula. (A-E, redrawn from Banse, 1972)

Remarks. *Brania brevipharyngea* is characterized by the combination of a short pharynx about two segments long, and a relatively long proventricle about 4 segments in length (Banse, 1972:199-200). Westheide (1974) reassigned one paratype originally described by Banse as *B. brevipharyngea* to *B. heterocirra* Rioja, 1941.

Distribution. California; Washington; British Columbia.

Brania californiensis **Kudenov and Harris, new species**

Figure 1.2

Material Examined. California: off Point Arguello, Sta. BRA-6, holotype (USNM 170899).

Description. Holotype incomplete. Originally with 22 setigers; 16 setigers present at time of description. Length 1.4 mm, width 0.12 mm at setiger 6, without parapodia. Specimen colorless except for golden pigment just below constriction on antennae and tentacular cirri. Specimen originally carrying embryos dorsally on setiger 12 through 15 on the right side and setigers 12 and 13 on the left side; embryos 70 µm in length.

Prostomium wider than long; eyes numbering 2 pairs, located posteriorly on the prostomium; anterior pair largest, both sets lenticulate; additional pair of eyespots present on anterior prostomium medial to lateral antennae (Fig. 1.2A). Antennae longer than prostomium, bottle-shaped; median antenna located just anterior to posterior pair of eyes (Fig. 1.2A). Palps barely longer than prostomium, fused completely, pointed distally. Pharynx extending through setiger 4, bright reddish-brown; middorsal tooth subdistal; distal end appearing smooth (pharynx inverted in specimen) (Fig. 1.2A). Proventriculus extending from midpoint of setiger 4 to midpoint of setiger 6, with approximately 19 rows of muscle cells (Fig. 1.2A). Tentacular segment indistinct, with 2 pairs of bottle-shaped tentacular cirri; dorsal pair longest, each about two-thirds as long as median prostomial antenna; ventral pair each about two-thirds length of dorsal pair (Fig. 1.2A).

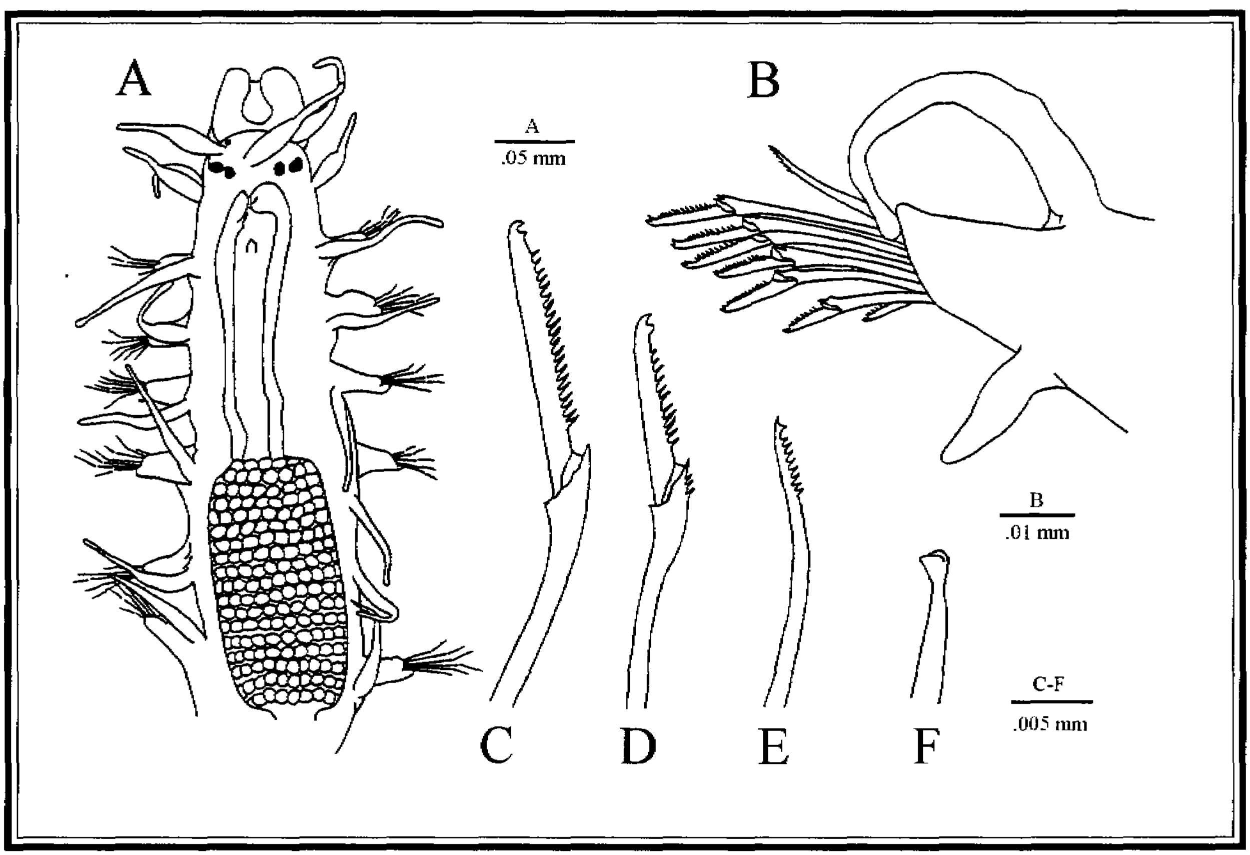

Figure 1.2. ***Brania californiensis*** **Kudenov and Harris, *new species*** : A, anterior end, dorsal view; B, parapodium 6; C, superior compound falciger, setiger 6; D, median compound falciger, setiger 6; E, dorsal simple seta, setiger 6; F, acicula, setiger 6. (A-F, originals by JDK)

Parapodia of median segments truncate, presetal and postsetal lobes equal in length; slight prolongation of superior lips around bases of superior simple setae (Fig. 1.2B). Compound falcigers distally bidentate (Fig. 1.2C,D), approximately 7 per parapodium. Blades decreasing in length inferiorly within fascicles (Fig. 1.2C,D), superior blades (Fig. 1.2C) twice length of inferior blades; all with serrated cutting edges (Fig. 1.2C,D). Superior blades decreasing gradually in length posteriorly. Shafts of compound falcigers enlarged distally; superior distal surfaces serrated (Fig. 1.2C,D). Superior dorsal simple seta distally bidentate with serrated cutting surface, present in all setigers beginning on setiger 1 (Fig. 1.2E). Ventral inferior simple seta present from setiger 18, continuing to at least setiger 22. One acicula per parapodium, distally blunt, beak-shaped (Fig. 1.2F).

Dorsal cirri long, weakly bottle-shaped, present on all segments. Ventral cirri digitiform, subequal to or shorter than parapodial lobes.

Pygidium unknown.

Remarks. *Brania californiensis* and *B. brevipharyngea* Banse 1972, are similar in setal morphology, setal distribution, and form of the dorsal cirri. *Brania californiensis* differs from *B. brevipharyngea* in having the pharynx present in four segments, instead of two, and the proventriculus in two segments instead of four. In addition, ventral cirri do not extend beyond the parapodial lobes of *B. californiensis*, in contrast to those of *B. brevipharyngea*.

Etymology. The species name, *californiensis*, refers to the state where the specimens were collected.

Distribution. Southern California.

Genus *Exogone* Örsted, 1845

Type species: *Exogone naidina* Örsted, 1845

Diagnosis. Prostomium with 3 antennae. Palps fused dorsally throughout most or all of length. One pair of tentacular cirri. Nuchal organs inconspicuous. Pharynx armed with single anterior middorsal tooth. Tentacular cirri, dorsal and ventral cirri ovoid to papilliform. Dorsal and ventral cirri shorter than setal lobes. Developing embryos attached ventrally to posterior margins of median segments of female (Imajima, 1966a; Fauchald, 1977; Uebelacker, 1984).

Remarks. San Martín (1991b) recognized three subgenera of the genus *Exogone*: (1) species of *Exogone (Parexogone)* Mesnil and Caullery, 1916, have unmodified compound "spinigers" and falcigers all with unmodified heterogomph hinges and shaft tips; (2) species of *Exogone (Exogone)* Örsted, 1845, all have modified compound "spinigers" and falcigers, all with modified heterogomph hinges and shaft tips; and (3) species of *Exogone (Sylline)* Claparède, 1864, all have compound setae strongly modified, with blades and shafts partially fused, or lacking blades. Unfortunately, San Martín (1991b) uses the term "spiniger" for any compound seta with a long blade. Many of the compound "spinigers" noted by San Martín are actually compound falcigers with long, tapering, distally bidentate blades, and explains the use of quotation marks in his definition of the above subgenera. The term spiniger is or should be used only to denote a "seta that tapers to a fine point" (Fauchald, 1977), and is used to describe the fine tapering blades of compound setae. San Martín (1991a) presents a useful key to the known species of each subgenus of *Exogone*, and a key to these subgenera is presented below.

Although the genus *Exogone* is well understood, several species from the Pacific coast of the United States and Canada have been erroneously identified as European species. For example, records of both *Exogone gemmifera* Pagenstecher, 1862, and *E. verugera* (Claparède, 1868) from southern and central California apparently cannot be verified, contrary to statements by Hartman (1968). Moreover, Westheide (1974) found that some materials previously identified as *E. gemmifera* both by Pettibone (1954) and Imajima

(1966a) represent a new species, *E. naidinoides*, later emended by Russell, 1991, which he also encountered in the Galapagos Islands and from Pt. Barrow, Alaska. Given these findings, the identity of two specimens reported as *E. gemmifera* by Lee and Rho (1992) from the Yellow Sea of Korea needs to be verified. Similarly, Westheide (1974) found that previous records of *E. verugera* from Japan (Imajima, 1966a) represent another species (*E. occidentalis*), also emended by Russell, 1991, that occurs in the Galapagos Islands; San Martín (1991b) considers *E. occidentalis* to be the junior synonym of *Exogone breviantennata* Hartmann-Schröder (1959); SCAMIT materials of *Exogone* sp. A from southern California may be identical to *E. breviantennata*. Finally, Westheide (1974) discovered some materials identified and described as *E. molesta* by Banse (1972) and *E. multisetosa* by Friedrich (1956) represented still another new species, *Exogone longicornis*. It is also likely that the specimens described by Banse and Hobson (1974) as *E. gemmifera* represent an undescribed species that is closely related, if not identical, to the MMS specimens identified as *Exogone dwisula*, new species, below. It seems likely that some of the species described by Hartmann-Schröder (1959) and Westheide (1974) will eventually be encountered in the syllid fauna of southern California: *Exogone breviantennata*, *E. longicornis* and *E. naidinoides* are included in the appropriate subfamily-level keys that follow.

Key to the Subgenera of *Exogone* (after San Martín, 1991b)

1A. Antennae closely set, often in middle of prostomium, between eyes (Fig. 1.3A); compound setae with highly modified blades, shafts and heterogomph joints (Figs. 1.3C-E, 1.4D-F); dorsal simple setae similar in all segments (Fig. 1.3B), or differing in form between anterior and posterior segments (Fig. 1.4G-I) 2

1B. Antennae widely spaced, with median antenna in middle of prostomium and lateral antennae in front of eyes; compound setae with unmodified blades, shafts and heterogomph joints (Fig. 1.6F-P); dorsal simple setae similar in all segments (Fig. 1.7S-U) .... *Exogone (Parexogone)*

2A. Compound setae with blades as long falcigers [=spinigers of San Martín] narrow, terminating in minutely bidentate tips (Fig. 1.3C), and blades of short falcigers with subdistal tooth larger than distal tooth (Fig. 1.3E); shaft tips and heterogomph hinges especially of anterior setae strongly modified (Fig. 1.3E); posterior dorsal simple setae thicker, differing in form to anterior simple setae (Fig. 4G-I) .... *Exogone (Exogone)*

2B. Compound setae all strongly modified, with blades partially fused to shafts and bayonet-shaped blades lacking; shaft tips distally truncate; dorsal simple setae generally similar throughout body, distally truncate with serrated cutting surfaces .... *Exogone (Sylline)*

Subgenus *Exogone (Exogone)* Örsted, 1845

Type species: *Exogone naidina* Örsted, 1845

Diagnosis. Antennae closely set together, usually arising between eyes; compound falcigers with modified blades, shaft tips and heterogomph joints; blades including long, narrow forms with minute, distally bidentate tips, and shorter forms with subdistal teeth larger than distal teeth; dorsal simple setae of 2 forms, differing between anterior and posterior body segments.

Key to Known Species of the Subgenus *Exogone (Exogone)* from the Northeast Pacific

1A. Dorsal cirri present on setiger 2 (Fig. 1.3A); shaft tips of compound spinigers of setiger 2 (sometimes also setiger 1) massively enlarged compared to those of adjacent setigers, distally falciform (Fig. 1.3C-D) 2

1B. Dorsal cirri absent on setiger 2 (Fig. 1.4A); shaft tips of compound spinigers and falcigers of setiger 2 enlarged compared to those of medial and posterior segments, not distally falciform (Fig. 1.4E) 3

2A. Antennae long, extending to or beyond anterior prostomial margin (Fig. 1.3A), median antenna 2-3 times longer than lateral antennae; proventriculus extending through 4-5 segments, with 18-24 rows of muscle cells; superior dorsal simple setae first present from setiger 1 .... *Exogone (Exogone) lourei*

2B. Antennae short, not extending to anterior prostomial margin, median antenna about as long as lateral antennae; proventriculus extending through 7-8 segments, with 25 or more rows of muscle cells; superior dorsal simple setae first present from setigers 10-14 .... *Exogone (Exogone) uniformis*

3A. Blades of compound setae in setigers 1-3 uniformly short, deeply bifid (Fig. 1.4D-E) .... *Exogone (Exogone) dwisula*

3B. Blades of compound setae in setigers 1-3 may include short and awl- or needle-like spinigers, or falcigers of various lengths 4

4A. Compound falcigers with blades long and tapering all along body; antennae short, subequal in length, much less than one-half length of prostomium; proventriculus extending through 2.5-3 segments with approximately 20 rows of muscle cells .... *Exogone (Exogone) breviantennata*

4B. Compound spinigers with awl-like blades; antennae long, with median at least 4 times longer than lateral antennae, and usually longer than combined length of prostomium and palps; proventriculus extending through 2 segments with 31 rows of muscle cells; 2 aciculae in anterior parapodia .... *Exogone (Exogone) longicornis*

Exogone (Exogone) lourei Berkeley and Berkeley, 1938

Figure 1.3

Exogone lourei Berkeley and Berkeley, 1938:44, figs. 6-12; 1948:79, fig. 117.—Rioja 1941: 703-4, pl. 3, fig. 10-13.—Berkeley, 1967:1055.—Pettibone, 1967:5. Hartman, 1968:425-426, figs. 1-5.—Banse 1972: 200-202, figs. 5a-d.—Banse and Hobson 1968:16, fig. 4d-e; 1974:58, figs. 14h-j.—Perkins 1981:1092.—Uebelacker, 1984:30-39 to 30-41, fig. 30-34 a-f.—Russell, 1991:55-57, fig. 2.
Exogone uniformis Hartman 1961:73-74 (in part, including pl. 6, fig. 1, pl. 7, fig. 1); Hartman 1968: 427-428 (in part, including figs. 1, 2).
Exogone dispar Pettibone, 1954:259 (in part).
Exogone (Exogone) lourei: San Martín, 1991a: 728, 735.
Sphaerosyllis californiensis Hartman, 1966: 196-197, pl. 3 (in part).

Material Examined. California: Santa Maria Basin, Stas. BRA-16 (3); 65 (1); off Point Sal, Sta. R-8 (33: USNM 170915); off Point Sal, Stas. PJ-1 (21); PJ-2 (75); PJ-3 (21); PJ-4 (2); PJ-5 (10); PJ-6 (50); PJ-7 (50); PJ-8 (10); PJ-9 (1); PJ-10 (65); PJ-11 (5); PH-F (?1, regenerating head); off Point Arguello, Stas. PH-I (3); PH-R (1); PH-U (2).—Western Santa Barbara Channel, BRC-1 (6, USNM 170914), (20, SBMNH 142698), (?1, regenerating head).—R/V *Velero IV* Sta. 5028-57, 1 paratype (removed from paratype lot of *Sphaerosyllis californiensis*, LACM-AHF Poly 1707).—R/V *Velero IV* Sta. 5102-57 (37: holotype and paratypes of *E. uniformis*, LACM-AHF Poly 170, 171, 521). British Columbia: False Narrows, holotype (USNM 32895).

Description. Up to 10 mm long, 0.2 mm wide, for 50 segments. Prostomium wider than long, pentagonal; eyes numbering 2 pairs; anterior pair largest, lenticulate, widest apart; posterior pair not lenticulate; all arranged trapezoidally (Fig. 1.3A). Antennae arising together from anterior part of prostomium; median antenna fusiform, about as long as palps, 2-3 times length of paired lateral antennae; latter small, digitiform (Fig. 1.3A). Palps long, completely fused (Fig. 1.3A). Nuchal organs small, paired, at postectal corners of prostomium. Pharynx usually extending to setiger 3 (Fig. 1.3A); anterior middorsal tooth subdistal, surrounded by distal circlet of 10 soft papillae when everted. Proventriculus usually extending through 4-5 segments, with 18-24 rows of muscle cells (Fig. 1.3A). Tentacular segment fused to prostomium; tentacular cirri numbering 1 pair, each small, papilliform (Fig. 1.3A).

Parapodia each with 5-9 setae per fascicle, including compound spinigers and falcigers plus simple setae (Fig. 1.3B-F). One or 2 compound spinigers occupying superior positions of fascicles; blades long, narrow; shafts of those in setiger 2, sometimes also setiger 1, greatly enlarged, thick, falciform (Fig. 1.3C,D). Compound falcigers with blades of similar lengths, all distally bidentate with primary tooth terminal, minute (Fig. 1.3E). Dorsal superior simple seta unidentate, slender, distally curved, minutely serrated from setiger 1; becoming thicker, sharply bent in posterior segments (Fig. 1.3B). Ventral seta curved, distally bidentate with bent tips in median and posterior segments (Fig. 1.3F). Dorsal and ventral cirri digitiform, present on all setigerous segments.

Pygidium with pair of long, cirriform anal cirri.

Remarks. *Exogone lourei* is characterized by long compound spinigers with greatly enlarged shafts on setiger 2, that may also occur on setiger 1; a long median and short paired lateral antennae; the proventriculus extending through 4 to 5 segments with around 16 to 30 (usually 18 to 24) rows of muscle cells. *E. lourei* was originally described from Vancouver, and has subsequently been reported from various localities along the Pacific coast of North America (Banse and Hobson, 1968; Hartman, 1968; Rioja, 1941), the Gulf of Mexico (Perkins, 1981; Uebelacker, 1984), Cuba and the Gulf of Mexico region (San Martín, 1991b), and Belize by Russell (1991) who confirmed both Perkins' and Uebelacker's records, and also emended the species description.

Various morphological characters were measured (by L. Harris) on 100 specimens of *Exogone lourei*; individuals ranging from 16 to 49 setigers. For example, the proventriculus extends through a range of 2-7 segments, is present in 4 to 5 segments in 70 specimens, and usually occurs from setigers 3-4 to 7-8 in individuals with non-everted pharynges. Rows of proventricular muscle cells range from 16-30, and usually number 18-24 in 94 specimens. Superior dorsal simple setae begin anywhere in setigers 1-19, and usually are found in setigers 1-9. Natatory setae are first present from setigers 13-15, and usually begin after setiger 15. Gametes are detectable in setigers 8-28, and usually seen in setigers 10-14. These and other data need to be further analyzed for size-related relationships. As one would anticipate, specimens with fewer than 27 setigers have smaller pharynges (2-3 segments) and proventricules (3-4 segments), dorsal simple setae from setiger 1, and proventricules with the same number of muscle rows as adults.

Exogone lourei is similar only to *E. uniformis* Hartman, 1961 in that both have compound spinigers with long blades and thick shafts in setiger 2. There tends to be considerable overlap in individual key characters between these species. *Exogone lourei* can be distinguished from *E. uniformis* by the combined presence of a median antenna much longer than the paired lateral antennae, 18-24 rows of proventricular muscle cells and a proventriculus in 4-5 segments, instead of short, subequal antennae, with 25 or more rows of proventricular muscle cells, and a proventriculus in 7-8 segments. Most of the paratypes of *E. uniformis* are actually specimens of *E. lourei*.

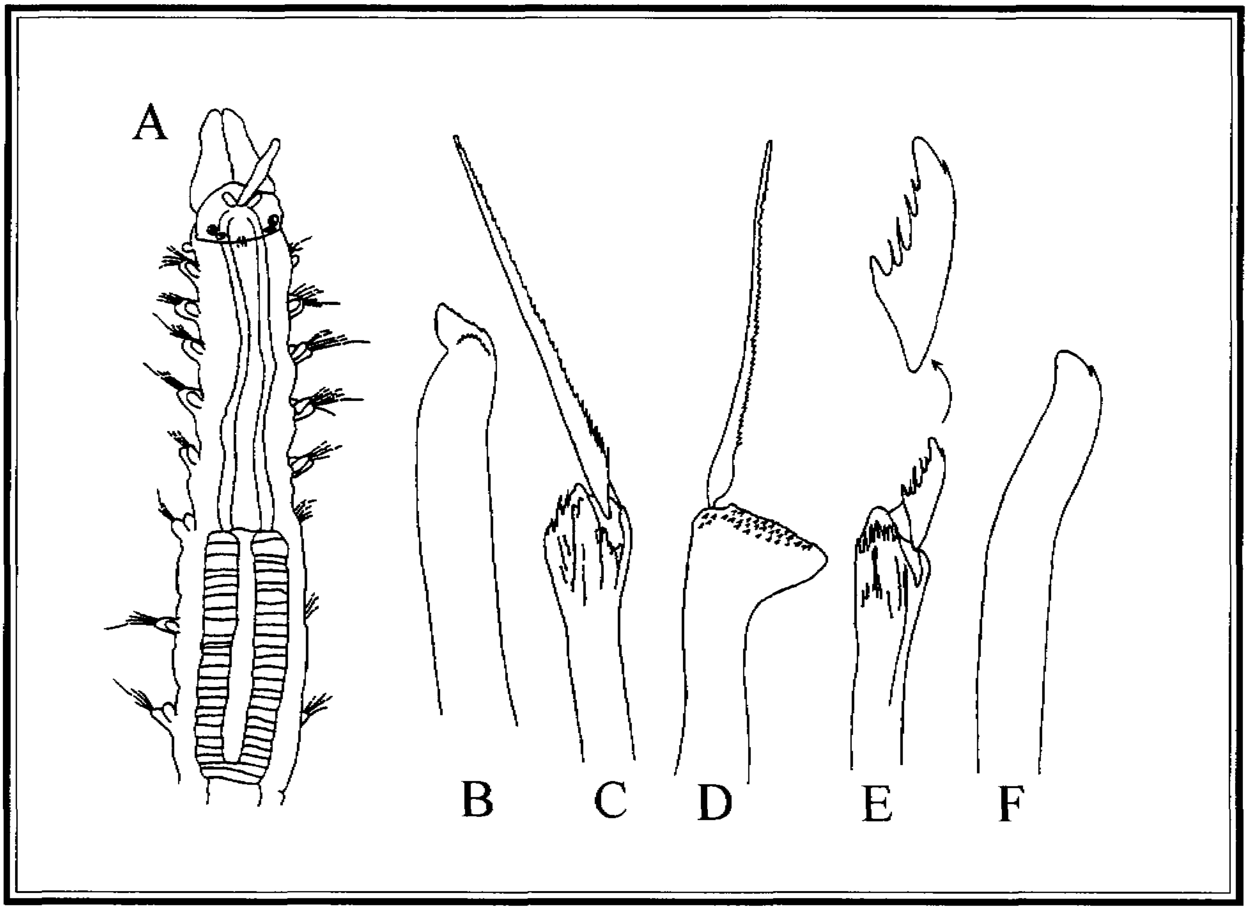

Figure 1.3. *Exogone (Exogone) lourei*: A, anterior end, dorsal view; B, dorsal simple seta from midbody region; C, superior spiniger from midbody region; D, compound spiniger, setiger 2; E, inferior compound falciger, with detail of blade, setiger 2; F, ventral simple seta. (A-F, after Uebelacker, 1984)

Distribution. British Columbia; Washington; Oregon; California; ?Mexico; Gulf of Mexico: Texas, Louisiana, Mississippi, Alabama, Florida; Cuba; Spain.

Exogone (Exogone) dwisula Kudenov and Harris, new species

Figure 1.4

Exogone uniformis Hartman 1961: 73-74 (in part); Hartman 1968: 427-428 (in part)
?*Exogone gemmifera*: Banse and Hobson 1974:56.
Sphaerosyllis californiensis Hartman, 1966:196-197, pl. 3 (in part).

Material Examined. California: Santa Maria Basin, BRA-6 rock (1); BRA-13 rock, 2 paratypes (AM W. 22190); BRC-13 rock, 1 paratype (SBMNH 142658), (1); BRC-14 rock (4); BRA-16 rock, 4 paratypes (LACM-AHF Poly 1662), (2); BRA-20 rock (3); BRA-25 rock, 3 paratypes (LACM-AHF Poly 1663) + (2).—Western Santa Barbara Channel, Stas. BRC-1 rock, 7 paratypes (USNM 170913); BRA-1 rock (3); BRA-2 rock (1).—La Jolla, off South Casas Reef, rocky intertidal (from *Phyllospadix* wash), 11

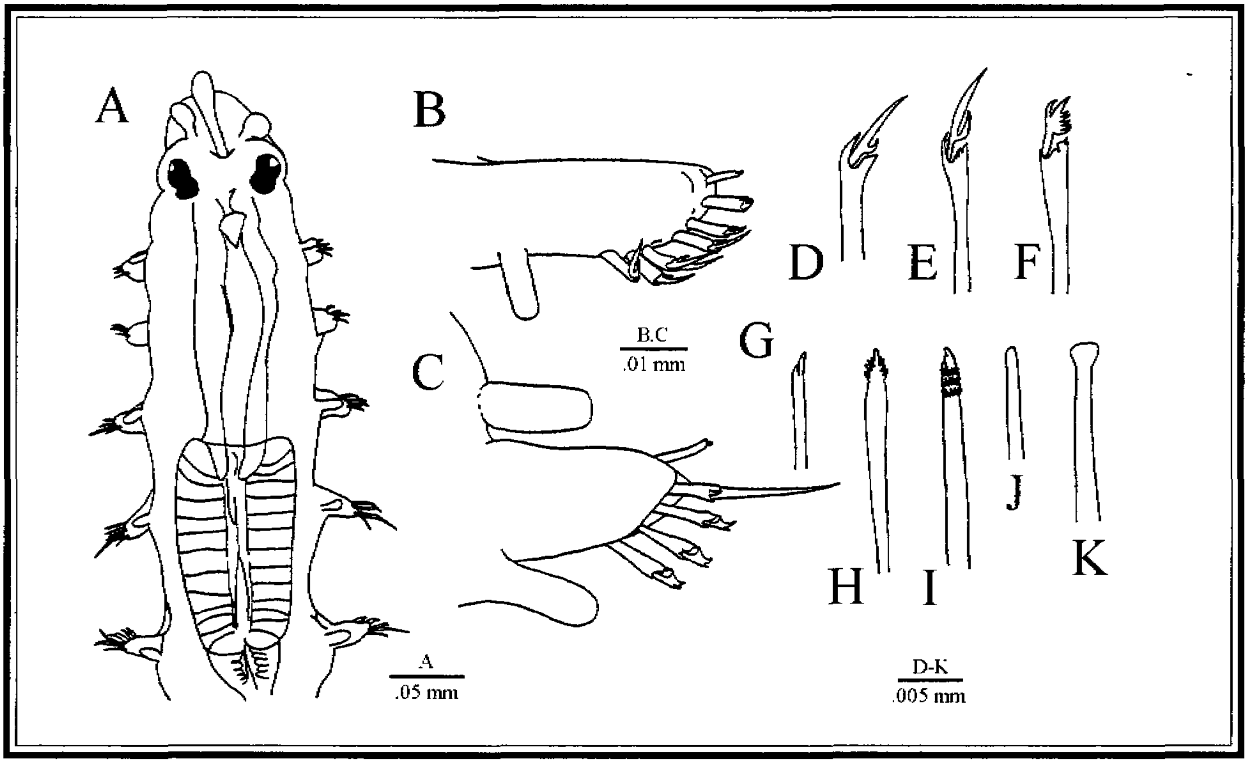

Figure 1.4. ***Exogone (Exogone) dwisula*** **Kudenov and Harris, new species**: A, anterior segments, dorsal view; B, right parapodium, setiger 2, ventral view; C, right parapodium, setiger 9, posterior view; D, compound falciger with can opener-like blades, setiger 1; E, superior compound falciger with can opener-like blades, setiger 2; F, compound falciger, setiger 5; G, dorsal simple seta, setiger 1; H-I, dorsal simple setae: H, setiger 6, ventral view; I, setiger 17, lateral view; J, acicula, setiger 1; K, acicula, setiger 17. (A-K, originals by JDK)

June 1979, coll. D.B. Cadien, holotype (LACM-AHF Poly 1661).—R/V *Velero IV* Sta. 5028-57, 3 paratypes (removed from paratype lot of *Sphaerosyllis californiensis*; LACM-AHF Poly 1659).—R/V *Velero IV* Sta. 5102-57, 2 paratypes (removed from paratype lot of *Exogone uniformis*; LACM-AHF Poly 171).

Description. Holotype 3.9 mm long, 0.2 mm wide without parapodia at setiger 6, for 34 setigers. Body fragile, semicircular in cross section, arched dorsally. Natatory setae and gametes first present from setigers 8-9. Brooding females with a single pair of embryos on ventrum of each segment from setigers 8-9.

Prostomium rectangular; 2 pairs of eyes, lenticulate, anterior and posterior eyes on each side connate, anterior pair largest; posterior pair sometimes covered by fold of tentacular segment (Fig. 1.4A). Antennae long, club-shaped to fusiform; median antenna about twice length of prostomium, arising from a point in front of anterior pair of eyes; lateral antennae one-half to three-fourths length of median antenna, arising slightly anterior to median antenna (Fig. 1.4A). All antennae arise at same level with median antenna when prostomium contracted. Palps wider than long, completely fused, usually arched, projecting ventrally (Fig. 1.4A). Nuchal organs inconspicuous, ciliated, arising from anterolateral margin of tentacular segment, continuing as bilobed nuchal glands internally. Pharynx usually extending through setiger 2(3), with large, anterior middorsal tooth, surrounded by distal circlet of 10 soft papillae when everted (Fig. 1.4A). Proventriculus present in 2.5 setigers, usually from setiger 3 through middle of setiger 5, with 14-16 rows of large muscle cells (Fig. 1.4A). Intestine with muscular valve-like structure at junction with proventriculus (Fig. 1.4A). Tentacular segment longer than prostomium and shorter than segments following, with 1 pair of small, ovoid tentacular cirri anterolaterally (not visible as illustrated).

Parapodial lobes stout, conical (Fig. 1.4B,C). Three types of compound setae present: (a) falcigers with long, deeply bifid blades (resembling a metal can opener in side view) numbering 7-10 per fascicle in setigers 1-3, all blades smooth, subequal within each of these first 3 fascicles, decreasing in length from setigers 1 to 3, with shafts terminating in strongly serrated edges, sometimes obscured by blades (Fig. 1.4D,E); (b) spinigers with long blades usually numbering 1, occasionally 2, as superiormost seta in fascicles from setiger 4 to end of body, increasing to maximal lengths in middle segments, decreasing posteriorly where blades are shortest (Fig. 1.4C); and (c) falcigers with short comblike bidentate blades numbering 3 in most fascicles from setiger 4, decreasing to 2 in far posterior fascicles, blades decreasing in length along body (Fig. 1.4F); cutting edges all coarsely dentate from setiger 4 becoming smooth in posterior segments, with shafts terminally serrated. Superior dorsal simple seta present from setiger 1 to end of body, terminating in abruptly tapered tips with close-set transverse rows of spines (Fig. 1.4G-I). Inferior ventral simple seta present from midbody setigers to end of body; bifid, with subdistal serrations. Aciculae usually 1 per parapodium in all setigers, occasionally 2 in anteriormost setigers; all terminating in distally enlarged blunt heads (Fig. 1.4J-K).

Dorsal cirri digitiform, present on all setigers except setiger 2, arising from body wall just above parapodial lobes (Fig. 1.4A-C). Ventral cirri digitiform, at least as large as dorsal cirri, not projecting beyond parapodial lobes (Fig. 1.4B,C).

Pygidium with 2 long, cirriform anal cirri, about as long as last 3 setigers.

Remarks. *Exogone dwisula* is characterized by the presence of two pairs of lenticulate eyes, pharynx in two segments, proventriculus in 2.5 segments with 14-16 well-defined rows of muscle cells, lacking dorsal cirri on setiger 2; with three kinds of compound setae including (a) compound falcigers with smooth deeply bifid blades distally in setigers 1-3, (b) usually a single compound spiniger with an awl-shaped blade next to the dorsal superior simple seta from setiger 4 to end of body, and (c) several compound falcigers with short distally bidentate blades with subdistal tooth much larger than distal tooth. The bifurcate nature of the awl-like blades is difficult to discern, even under oil immersion at the optimum viewing angle. *E. dwisula* inhabits snug, branching tubes composed of fine silt.

Exogone dwisula can easily be misidentified as *E. gemmifera* (Pagenstecher, 1862). Although we have not examined all of the materials identified by Hartman as *E. gemmifera*, a preliminary re-examination of some of her materials confirms the ease with which these two species can be confused. A primary point of confusion is the difference in proventricle length between European and eastern north Pacific specimens. Banse and Hobson (1974:56) suggest that the Pacific forms of *E. gemmifera* "...probably should be assigned to a new species."

Exogone dwisula and *E. gemmifera* are similar species having peculiar can opener-like blades on all falcigers of the first two or three setigers. *Exogone dwisula* always seems to have these setae in the first three setigers, whereas *E. gemmifera* specimens from Scandinavia have them in setigers 1-2 (L. Harris, pers. obs), while other European and Israeli specimens have them in setigers 1-3 (Ben-Eliahu, 1977). *Exogone dwisula* differs from *E. gemmifera* in having a proventriculus of 2.5 segments rather than 1.5-2 segments in length; 7-10 compound falcigers per fascicle in the first 2-3 setigers instead of 4 for specimens of similar sizes; and in having the cutting surfaces of dorsal superior simple setae heavily serrated rather than smooth. Indications are that San Martín (1991b) has identified another species (*Exogone* sp. A) that may also be a member of this species complex. Two specimens of *E. dwisula* were found in a paratype lot of *E. uniformis* Hartman.

Etymology. The term, *dwisula*, is the Indonesian name for a 2-pronged lance head, and here refers to the deeply bifid or can opener-like blades of compound falcigers.

Distribution. Southern California; possibly also Washington and British Columbia.

Subgenus *Exogone (Parexogone)* Mesnil and Caullery, 1916

Type species: *Paedophylax hebes* Webster and Benedict, 1884

Diagnosis. Prostomial antennae not all arising between eyes; compound setae all with similar unmodified blades of varying lengths, shaft tips and heterogomph joints; dorsal simple setae of one form, distally unidentate or bidentate.

Key to the Known Species of the Subgenus *Exogone (Parexogone)* from the Pacific Coast

1A. Transition between long and short blades of compound falcigers in all setigers gradual, with superior blades 1.5 to 3 times longer than inferior blades within fascicles (Fig. 1.5C-E, K) 2

1B. Transition between long and short blades of compound falcigers in setigers 1-4 abrupt, with superior blades 3 to 4 times longer than inferior blades within fascicles (Fig. 1.6E, H, 1.7K,P) .... *Exogone (Parexogone) molesta*

2A. Superior blades of compound falcigers 3 times longer than inferior blades (Fig. 1.6E, H); pharynx in 6-8 segments; all dorsal simple setae distally unidentate (Fig. 1.6Q, R)... .... *Exogone (Parexogone) acutipalpa*

2B. Superior blades of compound falcigers 1.5 times longer than inferior blades (Fig. 1.7K, P); pharynx in 4 segments; all dorsal simple setae distally bidentate (Fig. 1.7S-U) .... *Exogone (Parexogone) breviseta*

Exogone (Parexogone) molesta (Banse, 1972)

Figure 1.5

Exogone molesta Banse, 1972:203-205, fig. 6.—Banse and Hobson, 1968:15-16, fig. 4 a-c; 1974:58, fig. 14k,l.
Exogone (Parexogone) molesta: San Martín, 1991a:725.

Material Examined. California: Santa Maria Basin, off Point Estero, Sta. 3 (3); off Point Sal, Sta. 36 (1); off Purisima Point, Sta. 42(1); east of Point Conception, Sta. 85 (1); off Point Sal, Sta. R-8 (2, USNM 170917); off Point Sal, Stas. PJ-1 (22); PJ-2 (7); PJ-3 (4); PJ-4 (3); PJ-5 (2); PJ-6 (3); PJ-7 (64); PJ-8 (24); PJ-9 (2); PJ-10 (21); PJ-11 (24); off Point Arguello, Sta. PH-R (1).—Western Santa Barbara Channel, Sta. BRC-1 rock (2, USNM 170916).

Description. Specimens about 3 mm long, 0.2 mm wide excluding parapodia, 0.3 mm wide including parapodia, for up to 40 segments (Banse, 1972). Sexually mature individuals with both natatory setae and gametes first present from setiger 11.

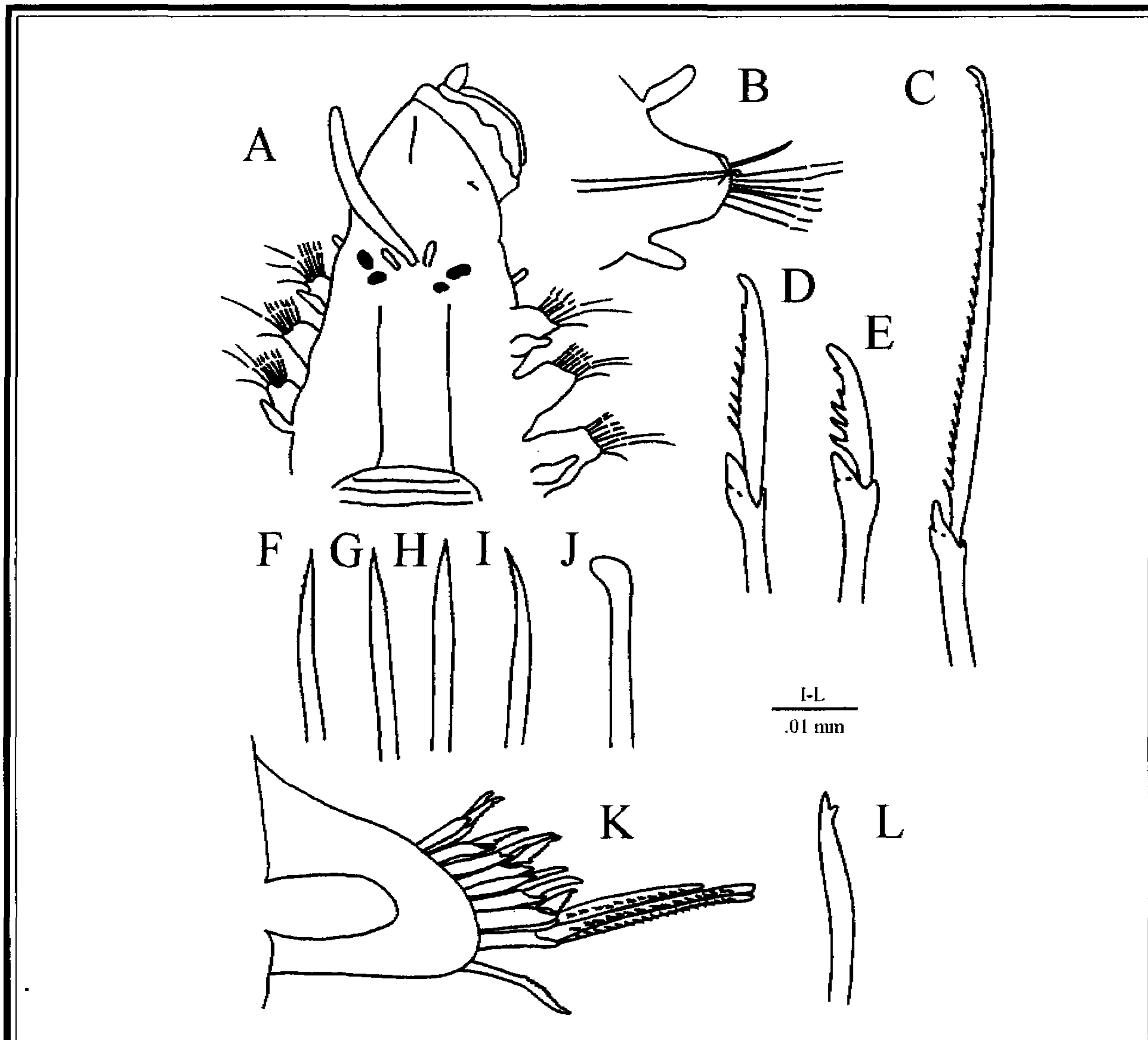

Figure 1.5. *Exogone (Parexogone) molesta*: A, anterior end, dorsal view slightly from the right side; B, parapodium 12; C, falciger with long blade from setiger 4; D, falciger with medium long blade from setiger 16; E, falciger with short blade from setiger 4; F-G, dorsal simple seta from two positions from setiger 8; H, same, far posterior segment; I, ventral simple seta from posterior setiger; J, acicula from setiger 16; K, parapodium 1, dorsal view; L, ventral simple seta, far posterior setiger. (A-H, redrawn from Banse, 1972; I-L, originals by JDK)

Prostomium wider than long; eyes oblong, numbering 2 pairs, anterior pair largest, arranged trapezoidally; eyespots absent (Fig. 1.5A). Antennae digitiform; median antenna longer than prostomium, 7-10 times length of lateral antennae; lateral antennae not extending beyond eyes; all arising between anterior pair of eyes (Fig. 1.5A). Palps long, distally pointed, fused completely, poorly defined from prostomium, depending on state of contraction (Fig. 1.5A). Pharynx extending to setigers 3-4, with distal anterior middorsal tooth (Fig. 1.5A). Proventriculus extending from setigers 4-5 through 4-4.5 segments, with about 20 rows of large muscle cells. Intestine with valve-like structure at junction with proventriculus. Tentacular segment fused with prostomium; 1 pair of tentacular cirri, each about size of lateral antennae.

Parapodia short, distally rounded, with small superior presetal lobe (Fig. 1.5B). Setae consisting of up to 4 superior compound falcigers with long unidentate blades each in setigers 1-15 (25) (Fig. 1.5C,K); and compound falcigers with blades short, distally bidentate, with secondary teeth strongly reduced (Fig. 1.5D,E); all together numbering about 12 per anterior parapodia, decreasing to 6 in median, and 4 in posterior parapodia. Blades all increasing in length from anterior to median body region, decreasing thereafter to end of body, and decreasing in length inferiorly within fascicles; long superior blades of anterior fascicles 3-4 times length of inferior blades, 4-5 times in median segments, and 1.25 times length in posterior segments. Long superior blades of median segments twice the length of anterior blades, 4 times length of blades in posterior segments with transition between long medial and short posterior blades sometimes abrupt; terminating in blunt, curved, unidentate tips in setiger 1 to around setiger 20, and either short and abruptly bidentate thereafter, or gradually decreasing in length and forming a slight subdistal tooth along setigers 20-25, and then becoming short and conspicuously bidentate at around setiger 25. Short blades in first few anterior setigers fairly uniform in length. Cutting edges of long superior falcigerous blades finely serrated; shorter falcigerous blades much more coarsely serrated, particularly inferior ones. Dorsal simple setae present in all setigers, distally pointed, unidentate, usually with slightly serrated cutting surface (Fig. 1.5F-H). Ventral inferior simple seta distally pointed, curved, usually unidentate, with slightly serrated cutting surface, from around setiger 25 to end of body (Fig. 1.5I), sometimes bidentate (Fig. 1.5L). One acicula per parapodium, distally blunt, knob-shaped (Fig. 1.5J).

Dorsal cirri digitiform, present on all setigers except setiger 2 (Fig. 1.5A). Ventral cirri digitiform, not extending beyond parapodial lobes (Fig. 1.5B).

Pygidium with paired, digitiform anal cirri, each about as long as last 1-3 setigers.

Remarks. Although Banse (1972) originally described the superior compound setae as being spinigerous, they lack tapering capillary tips so characteristic of spinigerous blades. In fact, the blade tips of these setae are all distally blunt and curved, and a secondary tooth is evident in posterior fascicles. Additionally, all other compound falcigers are more appropriately described as being distally bidentate rather than either unidentate or subbidentate.

Exogone molesta and *E. sexoculata* Hartmann-Schröder (1979) are similar in having a long median antenna and short lateral antennae, long pointed palps, superior compound falcigers with long blades three times the length of inferior blades within fascicles, two distinctly different populations of blades having abruptly different lengths within the same fascicle, and all blades coarsely serrated. *Exogone molesta* differs from *E. sexoculata* in having two pairs of eyes instead of eyes plus an additional pair of eyespots, all simple setae distally unidentate rather than bidentate, and apparently lacks a distal nipple-shaped parapodia lobe present in *E. sexoculata*.

Distribution. Southern California; Washington.

Exogone (Parexogone) acutipalpa Kudenov and Harris, new species

Figure 1.6

Materials examined. California: Santa Maria Basin, off Purisima Point, Sta. BRA-16 rock (1); Sta. R-5, 2 paratypes, (USNM 170910); off Point Sal, Stas. PJ-1, 1 paratype (SBMNH 142656) + (1); PJ-2, 1 paratype (AM W. 22188); PJ-6 (1); PJ-7, holotype (USNM 170908), 1 paratype (LACM-AHF Poly 1681) + (5); PJ-10, 2 paratypes (USNM 170909), 5 paratypes (LACM-AHF Poly 1682-1683).

Description. Holotype 2.6 mm long, 0.2 mm wide without parapodia at setiger 6; 0.25-0.3 mm wide with parapodia at setiger 6, for up to 40 setigers.

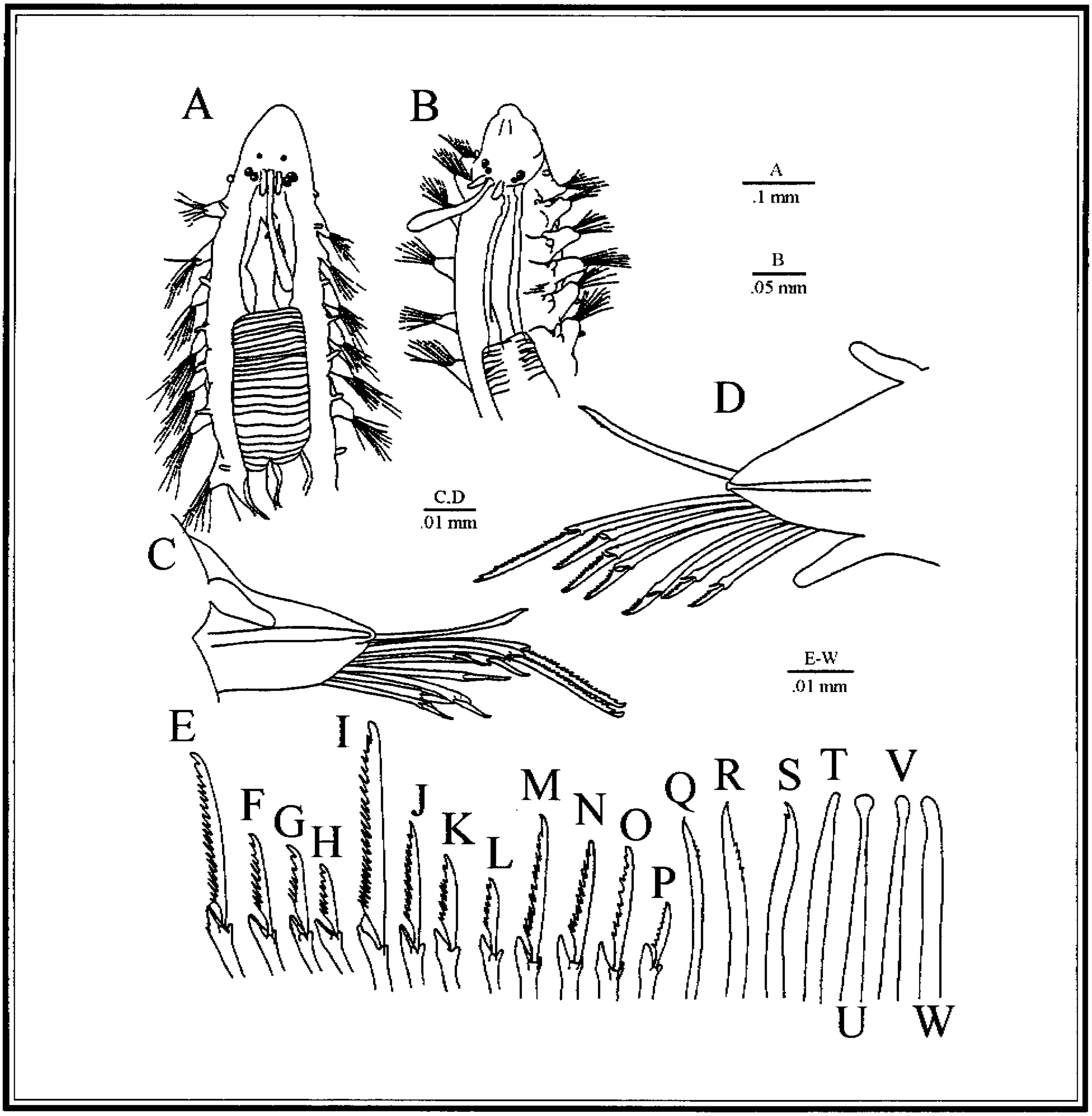

Figure 1.6. ***Exogone (Parexogone) acutipalpa*** **Kudenov and Harris, new species**: A, anterior end, dorsal view; B, same, dorsal view; C, right parapodium 1, dorsal view; D, left parapodium 16, posterior view; E-H, compound falcigers from setiger 2: E, superior seta with long blade; F, same, with shorter blade; G, lower intermediate seta; H, inferior seta; I-L, compound falcigers from setiger 12: I, superior seta with long blade; J, intermediate seta; K, low intermediate seta; L, inferior seta; M-P, compound falcigers from setiger 23: M, superior seta; N, upper intermediate seta; O, lower intermediate seta; P, inferior seta; Q-R, dorsal simple setae: Q, setiger 1; R, setiger 23; S, ventral simple seta from setiger 35; T-W, aciculae: T, setiger 1; U, setiger 12; V, setiger 9; W, setiger 30. (A-W, originals by JDK)

Prostomium wider than long; with 2 pairs of eyes, lenticulate, arranged in trapezoid, anterior pair larger; posterior pair often hidden by overlapping tentacular segment; eyes fragment easily, multiple eyes common; 1 pair of eyespots, situated just below junction of prostomium and palps (Fig. 1.6A,B). Three prostomial antennae, median one commonly 4 times longer than laterals but may be up to 10 times longer; all fusiform (Fig. 1.6A,B). Palps long and pointed, length greater than prostomial length (Fig. 1.6A,B). Pharynx in setigers 1-4, with distal anterior middorsal tooth (Fig. 1.6A). Proventricle in setigers 5-7, with about 20-23 rows of large muscle cells (Fig. 1.6A). One pair of tentacular cirri, smaller than lateral antennae, digitiform in shape (Fig. 1.6A,B).

Parapodia stout, conical, with small lobe where aciculae emerge through body wall (Fig. 1.6C,D). Setae are compound bidentate falcigers (Fig. 1.6E-P), 12-15 in anterior fascicles, 6-8 in median fascicles, and 4-6 in posterior fascicles. Blades with subdistal tooth reduced, forming a highly acute angle to long axis of blade; cutting edges with conspicuously variable teeth of different shape and size, usually slender, spine-like proximally, becoming saw toothlike distally (Fig. 1.6E-P); decreasing inferiorly within fascicles, with superior blades 3 times length of inferior blades (Fig. 1.6C-E,H,I,L); along body axis, blade lengths gradually increasing to medial segments, decreasing thereafter posteriorly. Dorsal superior simple seta first present from setiger 1, distally pointed, unidentate (Fig. 1.6Q,R), becoming slightly notched subdistally in posteriormost setigers (Fig. 1.6S); all with cutting surface slightly serrated. Ventral inferior simple seta present in posteriormost setigers, resembling dorsal simple setae, except for subdistal notch (Fig. 1.6T). Aciculae with curved tips, numbering 1 per parapodium (Fig. 1.6U-X). Dorsal cirri short, digitiform, present on all setigers except setiger 2, shorter than length of parapodial lobes (Fig. 1.6C,D). Ventral cirri short, digitiform, similar in size to dorsal cirri (Fig. 1.6C).

Pygidium with paired digitiform anal cirri of variable lengths, each about as long as last 1-3 setigers, plus smaller ventromedian cirrus.

Remarks. *Exogone acutipalpa* is most easily confused with *E. molesta* Banse in the northeastern Pacific since both species have a long median antenna, long pointed palps, and superior falcigers with conspicuously long blades. *Exogone acutipalpa* differs from *E. molesta* in having a pair of eyespots in addition to two pairs of eyes instead of lacking the paired eyespots, and in having blades of all compound falcigers gradually decreasing in length within all fascicles rather than having two groups of blades having abruptly different lengths in anterior and median fascicles.

Habitat. Soft, fine sediments in depths of 91.5-154 m.

Etymology. The specific epithet, *acutipalpa*, refers to the extremely pointed palps.

Distribution. Southern California.

Exogone (Parexogone) breviseta Kudenov and Harris, new species

Figure 1.7

Exogone sp. C SCAMIT Harris, 1987:1-8.

Material Examined. California: Santa Maria Basin, off Point Sal, Sta. PJ-7 (1).—Western Santa Barbara Channel, Goleta, 301(h) Sta. 2, 24-25 m, 14 April 1985, 1986, coll. MBC, 3 paratypes (LACM-AHF Poly 1678); Sta. 3, 25 m, 14 April 1986, coll. MBC, 2 paratypes (USNM 170911); Sta. 4, 29 m, 29 October 1985, coll. MBC, 1 paratype (USNM 170912); Sta. 6, 22-23.5 m, 14-15 April 1986, 1 paratype (SBNMH 142657), 4 paratypes (LACM-AHF Poly 1679-1680); Sta. 7, 23 m, 14 April 1986, coll. MBC, 1 paratype (AM W. 22189); Goleta, NPDES, Sta. 4, 29 m, 29 October 1985, coll. MBC (1).—Santa Catalina Island, Catalina Outfall, Sta. 1, 38 m, 2 November 1986, coll. B. Given (4); Sta. 3, 38 m, 2 November 1986, coll. B. Given, holotype (LACM-AHF Poly 1666).

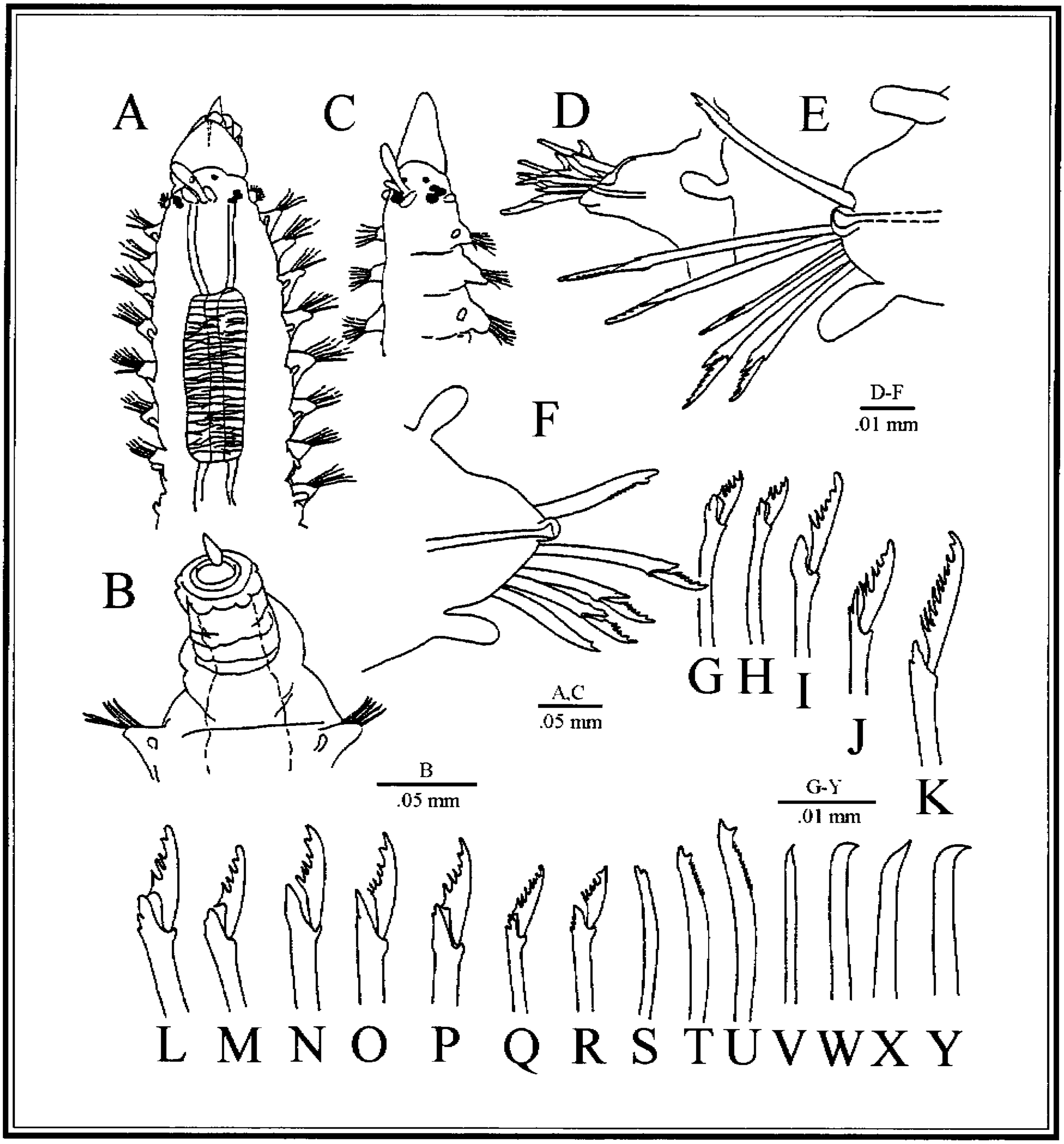

Figure 1.7. ***Exogone (Parexogone) breviseta* Kudenov and Harris, new species**: A, anterior end, dorsal view; B, pharynx and setiger 1, ventral view; C, anterior end, dorsolateral view; D, left parapodium 1, dorsal view; E, left parapodium 12, posterior view; F, right parapodium 25, anterior view; G-I, superior compound falcigers from setiger 2; J, same from setiger 3; K-M, compound falcigers from setiger 4: K, superior seta; L-M, upper intermediate setae; N-P, compound falcigers from setiger 25: N, superior seta; O, intermediate seta; P, inferior seta; Q, superior seta from midbody segment; R, same from far posterior segment; S-T, dorsal simple setae: S, from setiger 2; T, from midbody; U, from far posterior segment; V-Y, aciculae: V, from setiger 1; W, from midbody segment; X, from setiger 25; Y, from far posterior segment. (A-Y, originals by JDK)

Description. Holotype 1.8 mm long, 0.1 mm wide without parapodia at level of setiger 6, 0.2 mm wide with parapodia at level of setiger 6, for 33 setigers. Specimens up to 3.8 mm long. Surface pigmentation patterns absent; pharynx sometimes golden in color. Eggs first occur in setigers 9-10 and continue towards end of body; one complete mature specimen of 28 setigers with natatory setae in setigers 11-27.

Prostomium wider than long; eyes small, lenticulate, numbering at least 2 pairs, each pair frequently divided, forming separate multiple pairs, all arranged trapezoidally on posterior part of prostomium; with an additional pair of eyespots on anterior surface of prostomium (Fig. 1.7A,C). Antennae fusiform, close-set, as transverse group between posterior pair of eyes (Fig. 1.7A,C). Median antenna about twice length of prostomium; lateral antennae ranging from one-fifth to one-half length of median antenna (Fig. 1.7A,C). Palps pointed, longer than prostomium (Fig. 1.7A,C). Nuchal organs ciliated, located laterally at junction of prostomium and tentacular segment, continuing internally as bilobed glands. Pharynx extending through setiger 6, sometimes to setiger 8, with anterior middorsal tooth (Fig. 1.7A,B). Proventriculus present in setigers 7-8, sometimes setigers 8-9, with 20-23 rows of large muscle cells (Fig. 1.7A). One pair of tentacular cirri, similar in shape to lateral antennae, smaller (Fig. 1.7A,C).

Parapodia stout, conical, with small postsetal lobe (Fig. 1.7D-F). All setae compound falcigers with short, strongly serrated, distally bidentate blades (Fig. 1.7G-R). Blades decreasing in length within fascicles, superior blades less than twice length of inferior blades; all increasing in overall length from anterior to median setigers, decreasing thereafter posteriorly (Fig. 1.7C-E). Superior dorsal simple seta present in all setigers, inconspicuously bifid in anterior setigers (Fig. 1.7S), becoming thick and strongly bifid with serrated cutting surfaces in posterior setigers (Fig. 1.7T,U). Inferior ventral simple seta present in median and posterior setigers, distally bifid, particularly in posterior setigers. Acicula with distally bent tip, 1 per parapodium (Fig.. 1.7V-Y).

Dorsal cirri digitiform, shorter than parapodial lobes, present on all setigers except setiger 2 (Fig. 1.7A,E,F). Ventral cirri similar to dorsal cirri in shape, slightly smaller (Fig. 1.7E,F).

Pygidium with paired digitiform anal cirri of variable lengths, each about as long as last 1-3 setigers, plus smaller ventromedian cirrus.

Remarks. *Exogone breviseta* has been misidentified as *E. molesta* Banse by having long pointed palps, a long median antenna, and short lateral antennae. *Exogone breviseta* differs from *E. molesta* in lacking superior falcigers with long blades, and in having compound falcigers all subequal in length throughout the body, an anterior pair of prostomial eyespots, and a longer pharynx and a shorter proventriculus. *Exogone breviseta* has also been confused with *Exogone acutipalpa*, described above, in that both have a long median antenna, long distally pointed palps, two pairs of eyes plus anterior paired eyespots and blades of compound falcigers coarsely serrated. *Exogone breviseta* differs from *E. acutipalpa* in having the posterior two pairs of eyes small and divided into smaller separate structures, in having superior falcigers all with short rather than long blades, and in having a considerably shorter pharynx.

Exogone breviseta co-occurs with *E. lourei*, *E. molesta* and *E. uniformis*.

Habitat. Coarse, mixed and soft sediments in depths of 20-200 m.

Etymology. The species name, *breviseta*, refers to the short blades on all compound falcigers.

Distribution. Southern California.

Subgenus *Exogone (Sylline)* Claparède, 1864

Type species: *Sylline brevipes* Claparède, 1864

Diagnosis. Antennae closely set together, usually arising between eyes; compound falcigers with strongly modified bayonet-shaped blades partially fused to heterogomph joints; shaft tips usually truncate; dorsal simple setae of one form, generally distally truncate with serrated cutting surfaces.

Remarks. Both species in the key below lack dorsal cirri on setiger 2, and appear to have prostomia generally fused to the tentacular segment. *Exogone (Sylline) naidinoides* is not represented in MMS materials, although it is reported from the northeast Pacific; *E. (Sylline) fustifera* Haswell is reported from Australia.

Key to Selected Species of the Subgenus *Exogone (Sylline)* (after San Martín, 1991b)

1A. Bayonet-shaped compound falcigers from median segments including long and short blades .... *Exogone (Sylline) naidinoides*

1B. Bayonet-shaped compound falcigers from midbody segments thin with blades of uniform length .... *Exogone (Sylline) fustifera*

Genus *Sphaerosyllis* Claparède, 1863

Type species: *Sphaerosyllis hystrix* Claparède, 1863

Diagnosis. Prostomium with 3 antennae. Palps fused dorsally for most or entire length. One pair of tentacular cirri. Nuchal organs inconspicuous. Pharynx with single anterior middorsal tooth. Antennae, tentacular cirri and dorsal cirri usually flask-shaped (pyriform). Integument usually with glandular adhesive papillae.

Remarks. The majority of *Sphaerosyllis* species lack dorsal cirri on setiger 2 (San Martín, 1984a-b, 1991a; Riser, 1991). San Martín (1984b) relied on this and other features to define subgenera: *Prosphaerosyllis* San Martín, 1984b, for species with dorsal cirri on setiger 2; and *Sphaerosyllis* Claparède, 1863, for species lacking dorsal cirri on setiger 2. The subgenus *S. (Sphaerosyllis)* is further subdivided into the "*erinaceus*" and "*pirifera*" groups. The "*erinaceus*" group is partly characterized by having aciculae with tips flared and mucronate, the posterior eyes supposedly arranged in a straight transverse row, and have not been reported from the eastern Pacific; the "*pirifera*" group has aciculae with tips shaped like golf clubs, and eyes arranged polygonally. Riser (1991) suggests that the above subgenus concept may be inadequate in view of additional species described since San Martín first proposed this scheme. Russell (1989a) does not recognize San Martín's (1984b) subgenera since they are "...based more on artificial than on important phylogenetic characters." We concur with both Russell (1989a) and Riser (1991), and find the usefulness of San Martín's sphaerosyllid subgenera limited.

Riser (1991) also provides an important critique of systematic characters for *Sphaerosyllis*. Perhaps one of his most illuminating statements is that exogonine syllids (including *Sphaerosyllis* species that have dorsal cirri on setiger 2 as adults) usually lack dorsal cirri on setiger 2 prior to developmental differentiation of fore-gut elements. Identification of juvenile specimens will be difficult if one relies primarily on dorsal cirri. Care must therefore be taken to consider the age of one's specimens, especially since *Sphaerosyllis* that lack dorsal cirri on setiger 2 as adults have a pair of non-deciduous papillae that are larger than general body papillae.

Three species of *Sphaerosyllis* have been encountered in the MMS collection: *S. californiensis* Hartman, 1966; *S. bilineata*, new species; and *S. ranunculus*, new species. *Sphaerosyllis brandhorsti* Hartmann-Schröder, 1965, is included in the key below, although it was originally described from Chile, and later reported from Washington (Banse, 1972). Banse's record is based on an incomplete specimen which differs from Hartmann-Schröder's original account in potentially significant ways; it seems unlikely that *S. (S.) brandhorsti* occurs in the northeast Pacific. Unfortunately, we have not examined Banse's specimen. Records of *S. hystrix* from the northeast Pacific are probably based on Berkeley and Berkeley (1938), who distinguished this species by the presence of glandular pits containing bundles of minute rods in each segment. In contrast, *S. californiensis* was traditionally characterized by lacking these parapodial glands. However, subsequent examinations of *S. californiensis* type specimens confirms their presence (see below), and worms previously identified as *S. hystrix* from southern California are all *S. californiensis*. Moreover, Riser (1991) records *S. californiensis* from British Columbia, and it therefore seems likely that all records of *S. hystrix* in the northeast Pacific are either misidentified specimens of *S. californiensis,* or represent at least one undescribed species of *Sphaerosyllis*. In view of these findings, *S. hystrix* is excluded from the following key.

Key to Species of *Sphaerosyllis* from the Northeast Pacific

1A. Dorsal cirri similar to one another 2

1B. Dorsal cirri of two forms, not similar to one another 3

2A. Proventriculus usually present through 1.5-2 segments (Fig. 1.8A); dorsum with dense fields of filiform and elliptical papillae (Fig. 1.8C-D); ventrum lacking papillae; laterally with 2 pairs of conspicuous papillae per segment, each pair associated with basal anterior and posterior facies of parapodial lobes .... *Sphaerosyllis californiensis*

2B. Proventriculus present in 4 segments; dorsum with scattered, sparse fields of filiform papillae; ventrum with papillae; papillae inconspicuous on parapodia .... *Sphaerosyllis brandhorsti*

3A. Dorsum with 2 conspicuous dorsomedial longitudinal rows of distally knobbed macropapillae, 2 pairs per segment from setiger 4 or 5, alternating between a large anterior and smaller posterior pair per segment (Fig. 1.9A); ventrum with 12 digitiform papillae in 4 longitudinal rows of 3 papillae plus 2 additional longitudinal rows of 4 small, round papillae per segment, these altogether forming 6 longitudinal rows (Fig. 1.9C); dorsal cirri flask-shaped anteriorly, becoming cirriform posteriorly . ... *Sphaerosyllis bilineata*

3B. Dorsum without obvious dorsomedial longitudinal rows of papillae; ventrum with 2 pairs of papillae per segment, all arranged in 2 longitudinal rows; dorsal cirri mammiform in setigers 1-7 or 9 (Fig. 1.10D) and far posterior segments, digitiform in medial segments from setigers 8 to 10, or all digitiform from setigers 8-10 (Fig. 1.10E) .... *Sphaerosyllis ranunculus*

Sphaerosyllis californiensis Hartman, 1966

Figure 1.8

Sphaerosyllis californiensis Hartman, 1966:196-197, pl. 3; 1968:453-454, figs. 1-7.

Material Examined. California: R/V *Velero* Sta. 5028-57, holotype (LACM-AHF Poly 863) and 47 paratypes (LACM-AHF Poly 864).—Southeast of Point Conception, Sta. 86 (1, USNM 170926).—Santa Barbara, Camby's Reef, rock scraping, 16 m, 15 April 1983, coll. D. B. Cadien (2).—Gulf of the Farallones, Cordell Bank, Sta. 831033, coll. B. Schmieder (1).

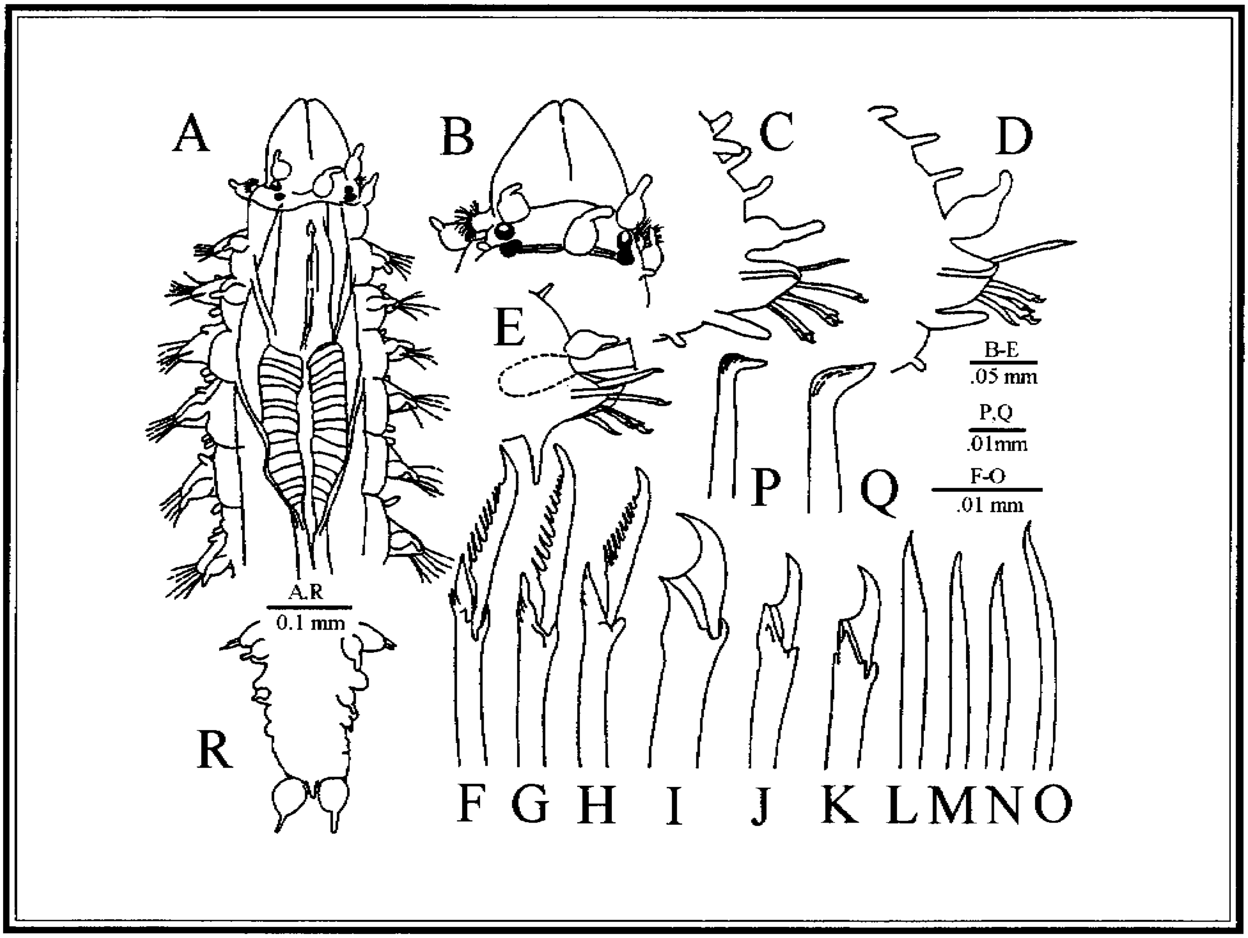

Figure 1.8. *Sphaerosyllis californiensis*: A, anterior segments, dorsal view (Goleta 6/III); B, prostomium, dorsal view; C, left parapodium, setiger 7, anterior view; D, left parapodium, setiger 30, anterior view; E, right parapodium, setiger 22, posterior view (LBGS B8/III); F-G, superior compound falcigers, setiger 2; H, inferior compound falciger, setiger 2; I-K, compound falcigers from setiger 31: I, superior seta; J, intermediate seta; K, inferior seta; L-N, dorsal simple setae: L, setiger 28; M, setiger 32; N, setiger 33; O, ventral simple seta, setiger 31; P-Q, aciculae: P, setiger 2; Q, setiger 31; R, Posterior end, dorsal view. (A-R, originals by JDK)

Description. Largest complete MMS specimen 3.7 mm long, 0.9 mm wide excluding parapodia and setae, for 40 setigers. Preserved specimens lack pigmentation. Integument covered with fine sediment (Hartman, 1966). Dorsum usually densely papillate, including conspicuous filiform papillae, up to 22 µm long, and short elliptical papillae (up to 8 µm long); all papillae gradually increasing in length posteriorly along body. Ventrum smooth, lacking papillae. Lateral margins of setigers with long papillae, 2 pairs per segment, each pair associated with anterior and posterior faces of basal parapodial lobes. Epitokous segments from setiger 10 to setiger 22 or sometimes almost to end of body.

Prostomium oval in outline, 3 times longer than wide, broadly fused dorsally with tentacular segment; eyes numbering 2 pairs, lenticulate, in trapezoidal to rectangular arrangement on posterior half of prostomium, anterior eyes largest; eyes connate (Fig. 1.8A,B). Median antenna slightly longer than lateral antennae, similar in shape, arising from anterior emargination of tentacular fold; lateral antennae arising anterolaterally from prostomium, with bulbous bases and cylindrical tips, extending to edge of palps (Fig. 1.8A,B). Palps short, dorsally fused; distal median notch as a wide furrow (Fig. 1.8B); palps covered dorsally with short papillae. Pharynx usually present in setiger 1 to middle of setigers 3-4 (in setigers 1-3.5 in holotype), with large anterior middorsal tooth (Fig. 1.8A). Everted pharynx surrounded by 10 widely spaced papillae. Proventriculus barrel-shaped, with 13-14 transverse rows of muscle cells, usually present in setigers 5-6 (in setigers 3.5-5 in holotype) (Fig. 1.8A), sometimes in setigers 3-5 or 4-6, or in setigers 4-8 in highly contracted specimens.

Tentacular segment visible dorsally as fold covering posterior half of prostomium, including posterior pair of eyes and sometimes anterior pair of eyes. Tentacular cirri similar to lateral antennae, arising ventrolaterally in relation to anterior pair of eyes (Fig. 1.8A,B). Small papillae present on anterior margin of tentacular fold.

Parapodial lobes conical, distally blunt (Fig. 1.8C-E), each with 3 conspicuous distal papillae as follows: longest papilla on posterior basal surface of parapodium; shortest papilla on anterior distal surface; intermediate papilla on posterior distal surface. Parapodial glands present from setiger 5, conspicuous from setigers 7-8, medial to dorsal cirri, containing spherical yellow granules which can fade and be undetectable in some preserved specimens.

Compound setae numbering 5-7 per fascicle in anterior segments, 3-5 in posterior segments; blades unidentate, longer in anterior segments, becoming stouter, more triangular posteriorly. Superior blades of anterior segments coarsely (sometimes finely) serrated, 2-3 times longer than smooth inferior blades (Fig. 1.8F-H); those of posterior segments subequal, superior blades finely serrated to smooth, inferior ones smooth (Fig. 1.8I-K). Ends of shafts with 2-3 denticles on cutting surface plus additional hair like processes (Fig. 1.8F,G). Dorsal simple seta present in all setigers, slightly curved subdistally; anterior simple setae smooth, appearing finely hirsute when highly worn; posterior setae shorter with serrated cutting surfaces (Fig. 1.8L,M). Inferior simple seta small, smooth, present in last 2-19 setigers (Fig. 1.8N,O). Aciculae normally numbering one per parapodium, thick, tapering abruptly to tip bent distally at a right angle (Fig. 1.8P), gradually becoming more stout posteriorly (Fig. 1.8Q). Additional acicula sometimes present in setigers 1-7, slender, distally pointed. Natatory capillary setae long, smooth, in setal sac located between neuropodia and dorsal cirri (Fig. 1.8E). Notoaciculae absent.

Dorsal cirri similar to antennae in shape, slightly thinner basally, absent from setiger 2 (Fig. 1.8A); longer than anterior parapodial lobes, equal to or somewhat shorter than median and posterior parapodial lobes. Ventral cirri short, cylindrical, sometimes extending beyond parapodial lobes (Fig. 1.8C-E).

Pygidium hemispherical, subdistally encircled by about 10 long papillae, with 2 long clavate anal cirri, these slightly larger than nearest dorsal cirri, plus an additional cluster of smaller papillae surrounding anal opening, sometimes obscured by circlet of longer papillae or anal cirri.

Remarks. Re-examination of type materials revealed the presence of 2 specimens of an undescribed *Sphaerosyllis* species (described below), a specimen of *Exogone lourei*, and 3 specimens of *E. dwisula*, as noted above. While this finding does not alter the species concept of *S. californiensis*, Hartman's original description appears to be based on one or two type specimens; new illustrations are here provided for additional information.

Riser (1991) examined west coast specimens of *Sphaerosyllis pirifera* Claparède, 1868, and found that nearly all were *S. californiensis*. *Sphaerosyllis pirifera* appears not to be represented along the western coast of North America (Riser, 1991:216) as first reported by Berkeley and Berkeley (1948). In addition, examination (by LHH) of specimens identified and archived by O. Hartman both as *S. hystrix* Claparède, 1863 and *S. pirifera* were also found to be *S. californiensis*. It is likely that *S. hystrix* is not represented in the polychaete fauna of southern California. Additional specimens previously identified as *S. hystrix* from other localities along the western coast of North America need to be re-examined to determine whether it is represented in our fauna as also indicated by Berkeley and Berkeley (1948).

Habitat. Silt, mixed soft sediments and rocky subtidal habitats.

Distribution. Southern California.

Sphaerosyllis bilineata Kudenov and Harris, new species

Figure 1.9

Sphaerosyllis californiensis Hartman, 1966:196-197, pl. 3; 1968:453-454, figs. 1-7 (in part).

Material Examined. California: Santa Maria Basin, off Purisima Point, Stas. BRA-13 rock, paratype (USNM 170924); BRC-13 rock (1); BRC-14 rock, paratype (AM W. 22193); BRA-16 rock, 11 paratypes (LACM-AHF Poly 1664, 1665); BRA-27 (SBMNH 142699)..—Western Santa Barbara Channel, south of Point Conception, Sta. 84, paratype (USNM 170925); off Point Conception, Sta. BRC-2 rock (1); San Francisco Bay, off Hunters Point, ESA Homeporting, Sta. HP1B, 37°43'30.8"N, 122°21'25.8"W, 9 m, 8 September 1986, coll. Kinnetic Laboratories, Inc., holotype (LACM-AHF Poly 1673).—R/V *Velero IV* Sta 5028-57, 2 paratypes (removed from paratype lot of *Sphaerosyllis californiensis*; LACM-AHF Poly 1675).

Description. Holotype complete with 31 setigers, 3 mm long, 0.3 mm wide without parapodia, 0.4 mm wide with parapodia. Body slender, dorsum convex, lacking pigmentation patterns; dorsum appears light yellow due to encrusted silt. One female with dorsally attached embryos on setigers 11-17. Two sexually mature males with sperm in setigers 8-24 or 26.

Prostomium wider than long, with small conical papillae dorsally and laterally; 2 pairs of eyes, large, lenticulate, 2 eyes on each side set close together; posterior pair usually covered by dorsal fold of tentacular segment (Fig. 1.9A); additional pair of anterior eyespots present adjacent to lateral antennae (not illustrated). Median antenna arising from posterior margin of prostomium, on border of dorsal fold; lateral antennae smaller than median, cylindrical with bulbous bases (Fig. 1.9B). Palps longer than wide, anterior margins blunt, directed ventrally. Small, conical papillae present on dorsal and lateral margins of palps, and anterior margin of tentacular fold. Ciliated nuchal organs present between prostomium and tentacular segment (Fig. 1.9A). Pharynx long, narrow, thick-walled, extending to setiger 3-4, or setigers 2-6 in contracted specimens, often appearing sinuous in preserved specimens; middorsal tooth large, positioned one-quarter length of pharynx behind anterior pharyngeal margin when everted (Fig. 1.9A). Proventriculus normally extending through 3-4 segments, barrel-shaped with 20-23 rows of muscle cells (Fig. 1.9A). Tentacular segment and prostomium fused dorsally. Tentacular cirri similar to prostomial antennae, but smaller (Fig. 1.9B).

Parapodial lobes triangular, each with 2 digitiform papillae, on anterior face and distally on posterior face (Fig. 1.9C). Setae generally compound falcigers, numbering 6-7 per fascicle anteriorly, decreasing to 5 posteriorly. Blades unidentate, longest anteriorly, gradually decreasing in length posteriorly (Fig. 1.9D); superiormost blade (sometimes 2 superiormost blades) in each fascicle with finely serrated cutting margins, others smooth. Superior dorsal simple seta distally unidentate, with smooth cutting surface, in all setigers. Inferior simple seta unidentate, slightly serrated to smooth, in last 2-8 setigers. One acicula per parapodium, slender, subdistally enlarged, bent.

Dorsal cirri flask-shaped on setiger 1, about equal to or slightly larger than prostomial antennae; larger, longer from setiger 2, becoming cirriform posteriorly, extending beyond parapodial lobes (Fig. 1.9A-B). Ventral cirri digitiform, not extending beyond parapodial lobes (Fig. 1.9C).

Each segment with 1 or 2 transverse rows of papillae, with 4 papillae per row (Fig. 1.9A). Dorsum of setigers 1-3 or 4 each with 4 filiform papillae in single transverse row per segment; setigers 4-5 to end of body each with 8 filiform papillae in an anterior-posterior transverse row. Middle 2 papillae of all segments distally knobbed, together forming two dorsomedian longitudinal rows along body; those of anterior segmental rows from setiger 4 largest, alternating with shorter papillae in posterior rows to end of body. Smaller outer papillae of anterior segmental rows arising from body wall superior to parapodial lobes and anterior to dorsal cirri; those of posterior segmental rows located just anterior to intersegmental annuli. All papillae gradually increasing in length posteriorly.

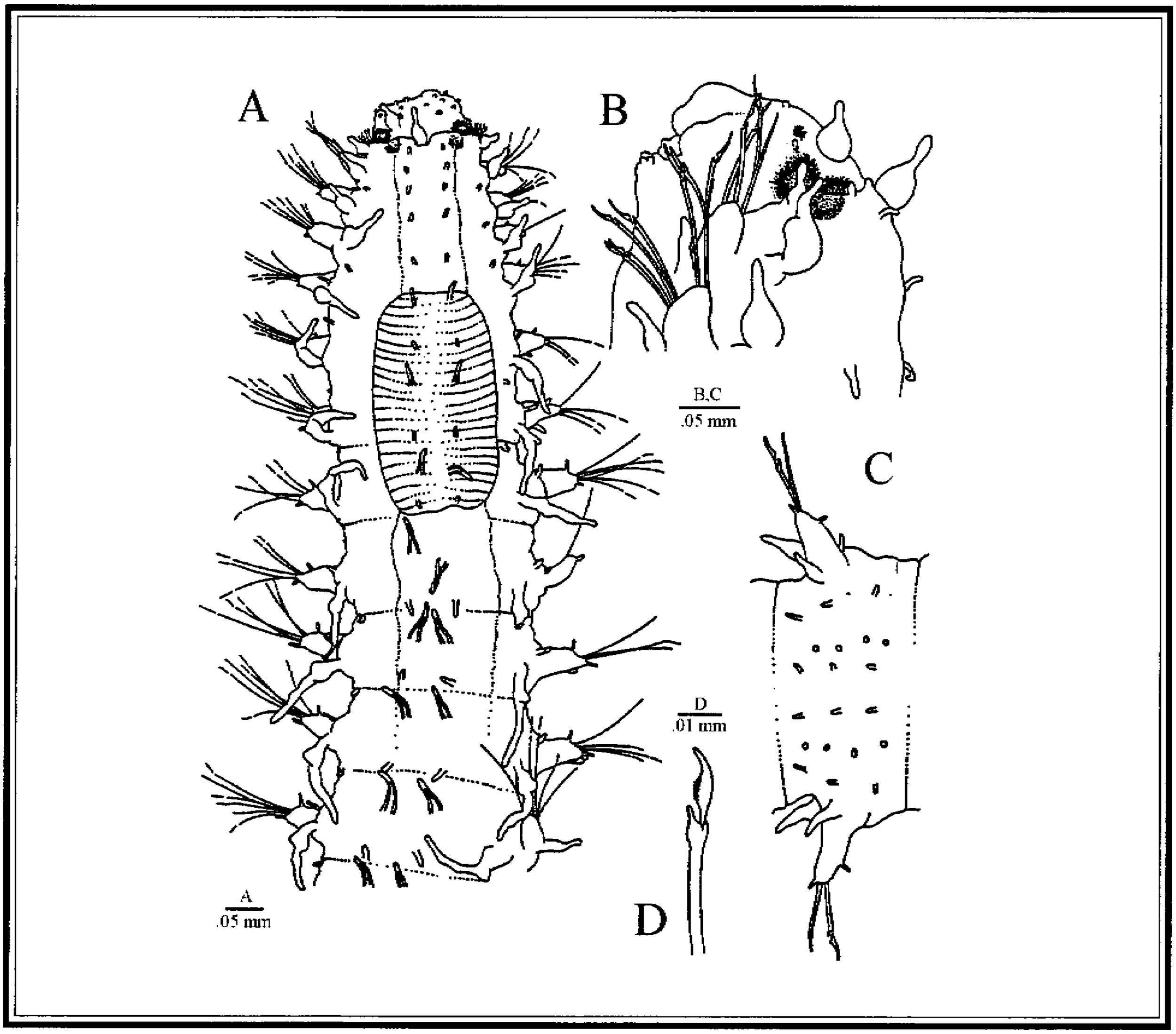

Figure 1.9. ***Sphaerosyllis bilineata* Kudenov and Harris, new species**: A, anterior segments, dorsal view; B, prostomium and setigers 1-2, lateral view; C, ventrum, median setiger; D, superior compound falciger, setiger 8. (A-D, originals by J. Dorsey)

Ventrum with 20 papillae per segment in 6 longitudinal rows, including 12 digitiform papillae in 4 longitudinal rows of 3 papillae, and 2 longitudinal rows of 4 short round papillae (Fig. 1.9C).

Pygidium with paired anal cirri, these 2-3 times longer, and 3-4 times wider than dorsal cirri of last setiger; circlet of 8-10 small, digitiform papillae present above anal cirri.

Remarks. *Sphaerosyllis bilineata*, *S. longipapillata* Hartmann-Schröder, 1979, *S. riseri* Perkins 1981, and *S. tetalix* Eliason, 1920 are similar in having four papillae per segment, all arranged in two longitudinal rows along the dorsum. All species also have an additional pair of papillae per segment, each in front of the dorsal cirri on the body wall superior to the parapodia. *Sphaerosyllis bilineata* differs from the other listed taxa in having one pair of small papillae per segment in setigers 1-3 or 4, and two pairs of different sized papillae that alternate regularly from setigers 4-5 to the end of the body; papillae are the same size in all segments for the other three species except *S. longipapillata* which lacks papillae from the two dorsal rows in setigers 1-6. *Sphaerosyllis bilineata* further differs from the above listed species in having an additional pair of small papillae dorsolaterally along the posterior margin of each segment. The alternating rows of long and short papillae are the most conspicuous feature of *S. bilineata*.

The compound falcigers of both *S. bilineata* and *S. riseri* differ from those of *S. longipapillata* and *S. tetralix* in having superior blades all serrated instead of all smooth. *Sphaerosyllis bilineata* differs from *S. riseri* in having slightly longer blades, and 20-23 rows of proventricular muscle cells rather than 17-18.

Habitat. Rocky substrates in depths of 89-126 m.

Etymology. The species name, *bilineata*, refers to the paired dorsomedial rows of conspicuous papillae.

Distribution. California.

Sphaerosyllis ranunculus Kudenov and Harris, new species

Figure 1.10

Material Examined. California: off Point San Luis, Sta. R-2 (14, USNM 170930); off Point Sal, Stas. PJ 1 (46); PJ-2 (27, including 1 brooding 2 setiger larvae); PJ-3, 3 paratypes (AM W. 22194) + (11); PJ-4, 5 paratypes (SBMNH 142661) + (3); PJ-5 (9); PJ-6 (42); PJ-7 (47); PJ-8, 15 paratypes (USNM 170929) + (36); PJ-9 (31); PJ-10 (67); PJ-11, 35 paratypes (LACM-AHF Poly 1668) + (21).—U.S. Army Corps of Engineers, dump site LA-5, Sta. BD 5-4(3), 32°32'20"N, 117°20'35"W, 188 m, 12 Dec. 1983, coll. MBC Applied Environmental Sciences, holotype (USNM 170927).—Between Point San Pedro and Pescadero Point, FTSP-Corps of Engineers, Stas. B5-W(3), 37°29'21"N, 122°55'32"W, 128 m, 10 October 1986, coll. Kinnetic Laboratories, Inc. (KLI), (1); B5-W(4), 5 paratypes (USNM 170928); B2-W(5), 37°22'10"N, 122°49'27"W, 128 m, 11 October 1986, coll. KLI (1); B2-N(1) 37°23'09"N, 122°49'34"W, 126 m, 2-3 April 1986, coll. KLI, 5 paratypes, (LACM-AHF Poly 1667).—Mexico: Tijuana, Tijuana Oceanographic Engineering Study, Sta. B10(3), 32°35.74'N, 117°10.34'W, 18 m, 18 July 1986, coll. MBC Applied Environmental Sciences, (1).

Description. Holotype incomplete, 1.3 mm long, 0.15 mm wide including parapodia, for 23 setigers. Body slender, circular in cross section in atokous specimens; oval to dorsoventrally flattened in epitokous specimen. Dorsum with micropapillae (best observed in lateral view). Ventrum with 2 longitudinal rows of papillae, usually two pairs per segment; each lower papilla on ventrolateral margin loosely associated with parapodia (Fig. 1.10D). Color in alcohol light yellow; pigmentation absent.

Prostomium small, micropapillate; 3 pairs of eyes, all lenticulate; posterior 2 pairs largest, nearly equal in size, arranged trapezoidally; anterior pair in front of lateral antennae (Fig. 1.10A-C). Antennae small, inconspicuous, mammiform (basally spherical, abruptly becoming distally papilliform); median antenna arising between or slightly behind posterior eyes; lateral antennae arising between anterior and middle pair of eyes; each about one-half size of median antenna (Fig. 1.10A-C). Palps small, fused completely (Fig. 1.10A-C), directed ventrally, micropapillate. Pharynx extending to middle of setiger 3, with middorsal tooth in anterior quarter when inverted (Fig. 1.10A). Proventriculus in 3.5 segments, extending from middle of setiger 3 to end of setiger 6 when pharynx inverted; in 4 segments when pharynx everted; with about 20 (19-22) rows of muscle cells (Fig. 1.10A). Retractor muscle visible through body wall, especially along right side of body in PJ1/3; running from body wall around level of setiger 2 to intestinal region posterior to proventriculus (Fig. 1.10A).

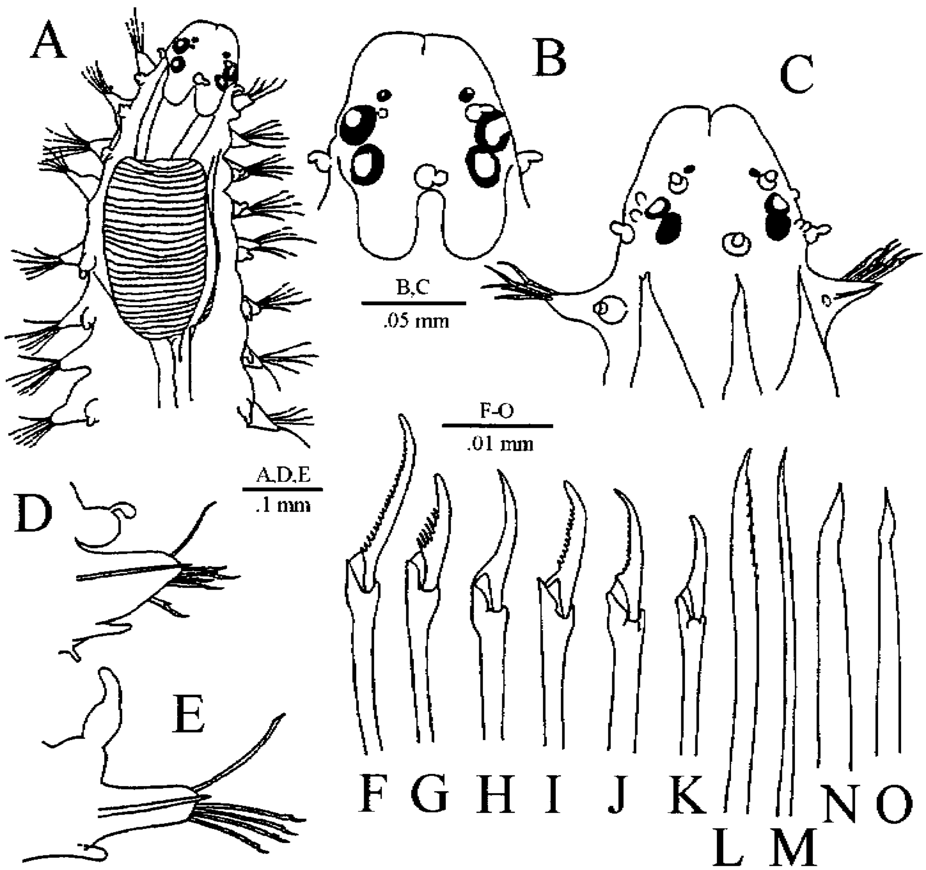

Figure 1.10. ***Sphaerosyllis ranunculus* Kudenov and Harris, new species:** A, anterior end, dorsal view; B, prostomium, dorsal view; C, prostomium, ovigerous female, dorsal view; D, right parapodium, setiger 7, anterior view; E, right parapodium. setiger 16, anterior view; F-G, compound falcigers from setiger 4: F, superior seta; G, inferior seta; H-I, compound falcigers from setiger 5: H, inferior seta; I, superior seta; J, compound falciger, setiger 20; K, compound falciger, setiger 22; L, dorsal simple seta, setiger 18; M, ventral simple seta, setiger 23; N, acicula, setiger 15; O, acicula, setiger 19. (A-O, originals by JDK)

Tentacular segment fused to prostomium, not visible dorsally (Fig. 1.10A,C); 1 pair of tentacular cirri, similar in form and size to antennae (Fig. 1.10B,C). Parapodia uniramous, triangular, distally pointed in atokous specimens; stout, thick in anterior segments (Fig. 1.10D), becoming longer, narrower in middle and posterior segments (Fig. 1.10E). Compound falcigers present in all setigers, all unidentate (Fig. 1.10F-K); numbering around 7-8 per anterior fascicle, around 3-5 in posterior fascicles. Blades of setigers 1-3 decreasing in length inferiorly within fascicles, cutting edges all finely serrated; blade lengths of following setigers more variable, with tendency for superiormost to have somewhat more coarsely serrated cutting margins, and inferiormost blades to be smooth (Fig. 1.10F-I). Blades of posterior setigers usually smooth, slightly shorter than those in anterior segments (Fig. 1.10J,K). Superior dorsal simple seta first present from setiger 1 to end of body, distally unidentate, with serrated cutting surfaces (Fig. 1.10L). Ventral inferior simple seta first present in last 8 or fewer posterior segments, distally unidentate, smaller than dorsal simple seta, generally smooth (Fig. 1.10M). One acicula per parapodium, distally pointed, projecting through parapodium, although tip tightly covered and readily visible through cuticle; distally flexed, with "flat" surface representing dorsal surface (Fig. 1.10N,O).

Dorsal cirri on all setigers, small, apparently contractile; those of setigers 1-7 or 9 mammiform (Fig. 1.10D), commonly becoming digitiform from setiger 8-10 to end of body (Fig. 1.10E); sometimes remaining mammiform on all setigers or having mammiform cirri on anterior and posterior segments, digitiform cirri medially. Ventral cirri small, digitiform, arising basally from and not extending beyond parapodial lobes (Fig. 1.10D,E).

Pygidium micropapillate, with paired anal cirri, surrounded by circlet of small digitiform papillae.

Length of other specimens at least 2.5 mm, 0.15 mm wide excluding setae, for 24 setigers (PJ-2(3)); all incomplete. Epitokous specimen (PJ-1(3)) with biramous parapodia beginning in setiger 8 and continuing through last setiger, each with a dense fascicle of long, fine capillary setae emerging from notosetal sacs located between dorsal cirri and parapodia. Gametes first visible from setiger 8; 4 external eggs carried dorsally per segment, with dorsomedial rows easily detached, rarely present on preserved specimens.

Remarks. Most Phase II MMS specimens here identified as *Sphaerosyllis ranunculus* were originally identified as *S. brandhorsti* Hartmann-Schröder, 1965. Based on the present samples, *S. brandhorsti* is probably not present along southern California. *Sphaerosyllis ranunculus* differs from *S. brandhorsti* in having minute prostomial antennae and tentacular cirri compared to relatively large, conspicuous appendages, in having clavate dorsal cirri of similar size through setiger 7 generally becoming digitiform thereafter instead of being clavate in all body segments, and in having blades of inferior compound falcigers smooth rather than serrated. *Sphaerosyllis brandhorsti* was originally described from Chile, and was subsequently reported from Orcas Island, Washington, on the basis of a single specimen by Banse (1972:209). Although Riser (1991) suggests that the degree of fusion between the prostomium and tentacular segment is an unreliable character in the systematics of *Sphaerosyllis*, Banse notes that his specimen differs from the types of *S. brandhorsti* by the fusion of these two areas. Banse further notes the absence of epidermal papillae in his specimen. These same differences exist in the present materials compared to the original description of *S. brandhorsti*, and lead us to doubt Banse's identification.

Habitat. Soft sediments, including isolated rocks in soft sediments, in depths of 18-128 m.

Etymology. The term, *ranunculus*, is *Latin* for tadpole, and refers to the body shape of these specimens.

Distribution. Southern California, San Diego to San Francisco; central Oregon; Puget Sound Washington.

Subfamily Eusyllinae

Genus *Dioplosyllis* Gidholm, 1962

Type Species: *Dioplosyllis cirrosa* Gidholm, 1962

Diagnosis. Prostomium with 3 antennae. Palps large, lingulate, fused basally. Nuchal organs as transverse ridges when present. Two pairs of tentacular cirri. Parapodia long. Pharynx with a middorsal anterior tooth and additional smaller teeth, with a smooth rim, or with a few teeth.

Remarks. Although *Dioplosyllis octodentata* Perkins, 1981 is included in the key below, it was originally described from the east coast of Florida, and may occur at other localities in the Gulf of Mexico (Uebelacker, 1984).

Key to the Species of *Dioplosyllis* from California

1A. Compound falcigers with distally bidentate blades with minutely serrated cutting edges (Fig. 1.11E); pharynx in 2 segments; proventriculus in 3-4 segments, with about 90 rows of muscle cells .... *Dioplosyllis lagunae*

1B. Compound falcigers include distally tridentate blades with conspicuously serrated cutting edges (Fig. 1.12D); pharynx in 7-8 segments (Fig. 1.12A); proventriculus in 5-7 segments with 30-33 rows of muscle cells (Fig. 1.12A) 2

2A. Compound falcigers tridentate blades enshrouded by distal hoods (Fig. 1.12D); distal teeth of blades aligned parallel to long axis of blade; shaft tips of compound falcigers distally pointed, entire .... *Dioplosyllis tridentata*

2B. Compound falcigers include bi-, tri- and multidentate blades, distal hoods absent; distal teeth of blades paired to unpaired, depending on state of wear; shaft tips of compound falcigers deeply notched and distally bifid .... *Dioplosyllis octodentata*

Dioplosyllis lagunae (Hartman, 1961), new combination

Figure 1.11

Orseis lagunae Hartman, 1961:64-65; 1968:371-372, figs. 1-2.
Dioplosyllis broadi Mueller and Fauchald, 1976:19-22, figs. 1-6.

Material Examined. California: Santa Catalina Island, Big Fishermans Cove Pier, holotype of *Dioplosyllis broadi* (LACM-AHF Poly 1141).—Laguna Beach, intertidal, holotype of *Orseis lagunae* (LACM-AFH Poly 135).

Description of Atokous Form. Length at least 15 mm, 2.5 mm wide excluding parapodia, 5.2 mm wide including parapodia; an anterior fragment with 10 segments. Body short, inflated (Hartman, 1961).

Prostomium wider than long; 2 pairs of eyes, large, conspicuous; anterior pair set farthest apart, posterior pair near postectal margins, all trapezoidally arranged. Antennae long, slender, cirriform. Median antenna arising just anterior to anterior eyes. Lateral antennae anterior to anterior eyes. Palps long, distally inflated, projecting ventrally.

Parapodia thick, triangular. Setae compound falcigers with distally bidentate blades. Blades decreasing in length inferiorly in fascicles, superior blades twice the length of inferior blades; angle between two distal teeth large, with subdistal tooth projecting outward obliquely.

Dorsal cirri long, slender, cirriform. Ventral cirri similar in form to dorsal cirri, extending beyond parapodial lobes.

Description of Epitoke Form. Length up to 24 mm, 2.1 mm wide excluding parapodia, 6.1 mm wide with parapodia, for 13 setigers (Mueller and Fauchald, 1976). Body widest medially, tapering anteriorly and posteriorly; dorsum strongly arched; ventrum flat. In live specimens, pigmentation on dorsum generally brownish purple, ventrum lighter; segments with paired series of transverse ridges, each purple ridge separated from neighboring ridges by cream colored grooves, 2 per tentacular segment, increasing to 12 on setiger 4, 17-18 on setiger 8 (Fig. 1.11A). Parapodia with ridges running parallel to body axis, each ridge purple with white spots (Fig. 1.11A). Dorsal and ventral cirri each with 10 longitudinal stripes, consisting of series of small purple spots.

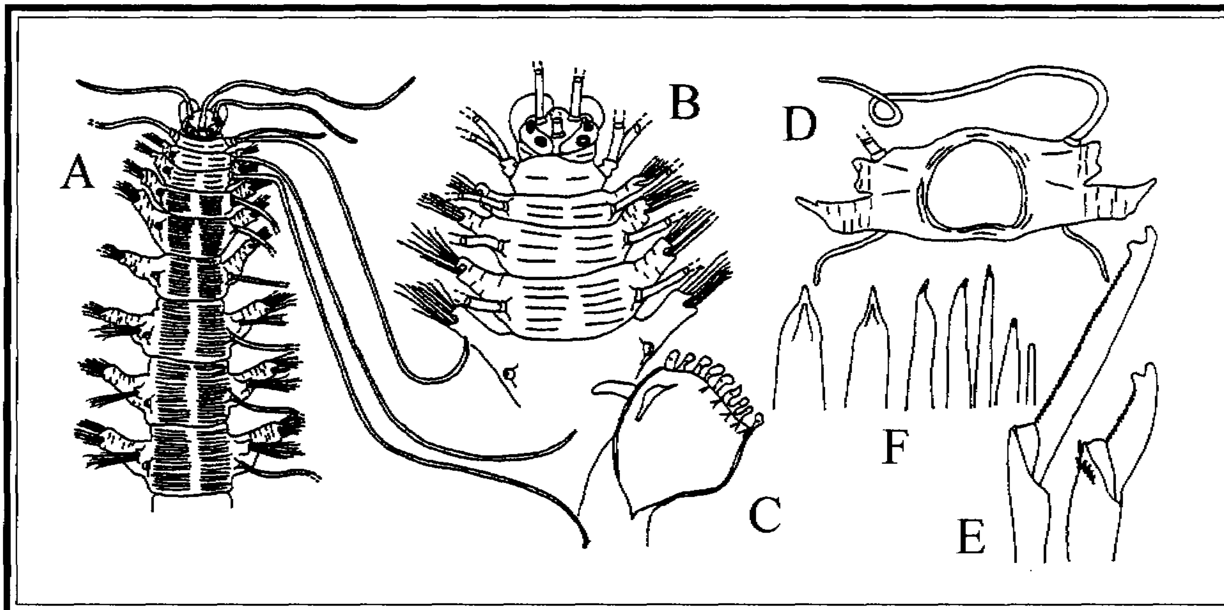

Figure 1.11. *Dioplosyllis lagunae*: A, anterior end, dorsal view; B, prostomium and anterior segments, dorsal view; C, pharynx; D, setiger 7, anterior view; E, compound falcigers, setiger 7; F, neuroaciculae, setiger 7. (A-F, redrawn from Mueller and Fauchald, 1976)

Prostomium wider than long; 2 pairs of eyes, subequal, posterior pair lenticulate, anterior pair set farthest apart, all arranged trapezoidally (Fig. 1.11A,B). Antennae long, wrinkled to smooth with short ceratophores; median antenna arising between anterior and posterior eyes, extending posteriorly to setiger 6; lateral antennae arising from anterior margin of prostomium, extending posteriorly to setiger 5 (Fig. 1.11A). Paired nuchal organs at postectal corners of prostomium (Fig. 1.11A,B). Palps thick, rounded, more than twice length of prostomium, fused basally (Fig. 1.11A,B); palpostyles present. Pharynx to setiger 2, with subdistal anterior tooth plus 5 evenly spaced curved teeth, surrounded by distal circlet of 10 soft papillae when everted (Fig. 1.11C). Proventriculus present in setigers 3-6, with about 90 rows of muscle cells.

Tentacular segment conspicuous dorsally (Fig. 1.11A,B). Two pairs of tentacular cirri, wrinkled to smooth, similar in form to prostomial antennae; dorsal pair longest, each extending posteriorly to setiger 8; ventral pair about half as long as dorsal ones; all with cirriphores.

Parapodia long, triangular (Fig. 1.11D). Compound setae bidentate falcigers numbering 25-30 per fascicle (Fig. 1.11E). Blades longest superiorly, decreasing in length inferiorly within fascicles, with minutely serrated cutting edges (Fig. 1.11E). Shaft tips distally bifid, with denticles on subdistal superior surfaces (Fig. 1.11E). Neuroacicula varying in thickness, tapering abruptly, 6-7 per parapodium from setiger 6 (Fig. 1.11F). Capillary setae long, from setiger 6. Notoacicular lobe inferior to fascicles of capillary setae, numbering 6-7 per fascicle from setiger 6.

Dorsal cirri long, cirriform, smooth to wrinkled, those of setigers 1-2 extending to setiger 11-12; all with short, conspicuous ceratophores (Fig. 1.11A). Ventral cirri long, cirriform, extending to middle of adjacent setigers (Fig. 1.11D).

Pygidium with paired anal cirri, long and cirriform.

Remarks. The single type specimen described as *Orseis lagunae* Hartman, 1961 from Laguna Beach is not a hesionid and is here referred to *Dioplosyllis*. Hartman's (1961) original description lacks illustrations; Hartman (1968) depicted two compound falcigers that looked similar to those of *D. broadi* presented by Mueller and Fauchald (1976). Comparisons of the types of both *O. lagunae* and *D. broadi* by one of us (L. Harris) confirms their synonymy.

Habitat. Intertidal and shallow subtidal rocky substrata.

Distribution. Southern California.

Dioplosyllis tridentata Kudenov and Harris, new species

Figure 1.12

Material Examined. California: off Purisima Point, Sta. BRC-13 rock, holotype (USNM 170900).

Description. Holotype 5 mm, 0.5 mm wide without parapodia, 1 mm wide with parapodia. Body broken into anterior piece with 21 setigers; posterior piece with 12 setigers of which latter 4 or 5 regenerating. Pigmentation patterns absent.

Prostomium wider than long, pentagonal, with deep median cleft (Fig. 1.12A); 2 pairs of eyes, lenticulate, anterior pair largest, in trapezoidal arrangement (Fig. 1.12A); a minute pair of eyespots present on anterior prostomium margin, medial to lateral antennae. Antennae smooth, cirriform, longer than prostomium; median antenna about 5 times longer than prostomium, arising between anterior and posterior pairs of eyes; lateral antennae about twice length of prostomium, arising medial to each anterior eye. Palps long, flat, thick, about 1.5 times longer than prostomium, basally fused, projecting ventrally, lacking palpostyles (Fig. 1.12A). Nuchal organs paired transverse ridges along postectal border of prostomium (Fig. 1.12A). Pharynx tubular, extending through setiger 8 when inverted, middorsal tooth subdistal (dissected) (Fig. 1.12A); distal circlet of soft papillae not observed. Proventriculus extending through setigers 9-15, with about 30 rows of large muscle cells.

Tentacular segment narrow, with 2 pairs of long, cirriform tentacular cirri, each with short cirrophores; dorsal pair probably longest, each at least as long as median antenna (remaining right tentacular cirrus distally broken); paired ventral cirri broken off.

Parapodia long, slender, distally conical to triangular, gradually increasing in length to middle segments, decreasing in length thereafter (Fig. 1.12C). About 15-18 compound setae per anterior fascicle (ca. setiger 5), increasing to 20-25 per medial fascicle (ca. setiger 15), decreasing to around 17-19 per posterior fascicle (ca. setiger 29). Blades distally bidentate, largest denticle strongly curved, enshrouded by distal hood; blades longest superiorly, just over twice length of inferior blades within same fascicle, all decreasing in length inferiorly within fascicles; all with minutely serrated cutting edges. Shaft tips distally entire, with denticles scattered on subdistal superior surfaces. Neuroaciculae taper to knobbed tips, not projecting through parapodial lobes, numbering 1 per parapodium.

Dorsal cirri long, smooth, cirriform (mostly broken), all with short cirrophores, arising from body wall; right dorsal cirrus of setiger 1 present, extending posteriorly to around setigers 13-14. Ventral cirri glandular, basally inflated, tapering distally; not extending beyond parapodial lobes, short in anterior segments, becoming longer, better developed in middle segments, decreasing in length posteriorly.

Pygidium with paired anal cirri, all regenerating.

Remarks. *Dioplosyllis tridentata* and *D. octodentata* Perkins, 1981, are similar in having tridentate compound falcigers, in contrast to the four other described *Dioplosyllis* species summarized by Mueller and Fauchald (1976), which have bidentate compound falcigers. *Dioplosyllis tridentata* differs from *D. octodentata* in having distal hoods on blade tips; in having minute rather than coarse serratia on the cutting edges of

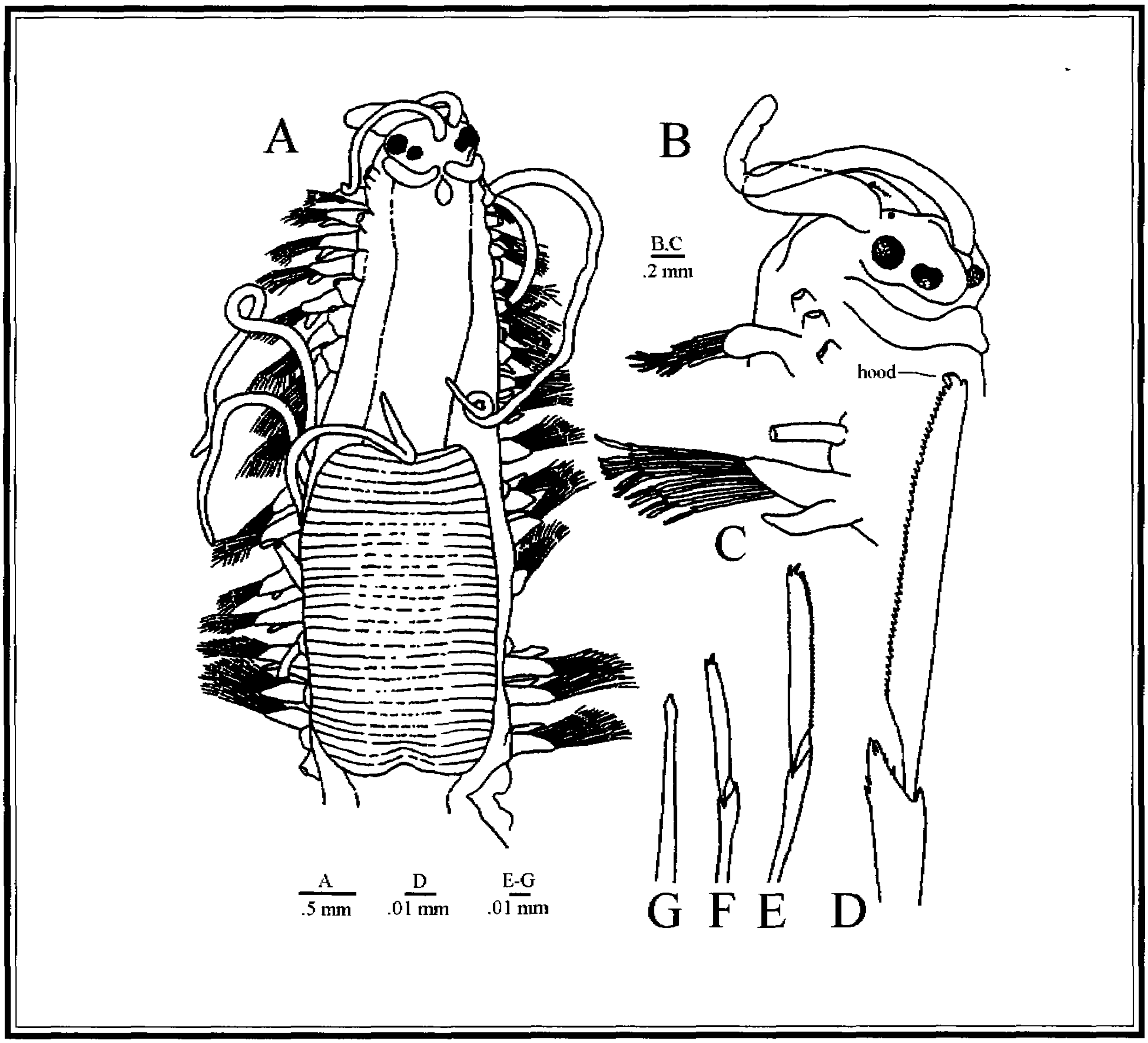

Figure 1.12. ***Dioplosyllis tridentata*** **Kudenov and Harris, new species**: A, anterior segments, dorsal view; B, prostomium and setiger 1, lateral view; C, left parapodium, median segment, posterior view; D-E, superior compound falcigers; F, inferior compound falciger; G, acicula. (A-C, E, F, redrawn from originals by J. Dorsey; D, original by JDK)

blades; in having shaft tips of compound falcigers distally entire instead of bifid and deeply notched; in having the pharynx extend through eight rather than seven segments; in having the proventriculus extend through seven segments with around 30 rows of muscle segments, instead of five or seven segments with about 33 rows. The pharyngeal armature of these two species may also differ, although it is difficult to clearly examine the pharynx of *D. tridentata* without damaging the single specimen. For example, *D. tridentata* seems to have a single large subdistal tooth while *D. octodentata* has a single large tooth plus seven smaller ones. The margin of the pharynx in *D. tridentata* appears to be smooth.

Dioplosyllis tridentata is readily distinguished from *D. lagunae* from southern California, besides the differences in compound falcigers noted above, in lacking palpostyles; the pharynx extending through 8 instead of 3-4 segments and the proventriculus through 6-7 rather than 3 segments; with around 30 instead of around 90 rows of muscle cells in the proventriculus; and in having shaft ends of compound falcigers distally entire instead of deeply notched or bifid.

Habitat. Rocky substrata.

Etymology. The name, *tridentata*, refers to the presence of 3 teeth on blades of compound falcigers.

Distribution. Southern California.

Genus *Eusyllis* Malmgren, 1867

Type species: *Eusyllis blomstrandi* Malmgren, 1867

Diagnosis. Prostomium with 3 antennae. Palps fused basally. Nuchal organs usually as ciliated ridges between prostomium and tentacular segment. Occipital flap sometimes present. Antennae, tentacular and dorsal cirri smooth to indistinctly articulate. Pharynx with middorsal tooth and denticulate rim. Setae compound falcigers.

Remarks. The presence of a denticulate pharyngeal margin or rim is critical to the systematics of *Eusyllis*, and must be determined before specimens can be correctly identified to this genus. Specimens with retracted pharynges must therefore be dissected to avoid confusion with the closely similar *Pionosyllis.*

Key to Species of *Eusyllis* from California (after Imajima, 1966c)

1A. Ventral cirri of setiger 1 foliaceous, much larger than those following (Fig. 1.14K); marginal rim of pharynx smooth dorsally, denticulate ventrally (Fig. 1.14B) .... *Eusyllis habei*

1B. Ventral cirri of setiger 1 similar in form and size to those following; marginal rim of pharynx uniformly denticulate 2

2A. Dorsal cirri of middle body segments 2-3 times longer than body width (Fig. 1.15C); blades of compound falcigers long and narrow (Fig. 1.15E,F) .... *Eusyllis longicirrata*

2B. Dorsal cirri of middle body segments two-thirds length of body width (Fig. 1.13A,B); blades of compound falcigers short and stout (Fig. 1.13E-G) .... *Eusyllis blomstrandi*

Eusyllis blomstrandi Malmgren, 1867

Figure 1.13

Eusyllis blomstrandi Malmgren, 1867:159.—Augener, 1928: 721.—Annenkova, 1938: 153, fig. 6.—Fauvel, 1923:293-294, fig 112 h-m.—Wesenberg-Lund, 1947:11-13, fig. 3; 1950a:16; 1950b:48; 1951: 37.—Berkeley and Berkeley, 1948:84-85, fig. 126.—Pettibone, 1954:260-261, fig. 28 g-i.—1963:119-120, fig. 31 n-p; Imajima, 1966c:92-94, text-fig. 29, a-h.—Banse and Hobson, 1968:15-16, figs. 4 a-c; 1974:56, figs. 14 b-c.—Hartmann-Schröder, 1971:158, fig. 52.
Eusyllis bloemstrandi Friedrich 1938:122 (misspelling of *E. blomstrandi*).
Typosyllis collaris Hartman 1948:23, fig. 6 a-c.

Materials examined. California: Santa Maria Basin, Sta. R-1 (1, USNM 170903).

Description. Specimens 10-12 mm long, 0.8-1.2 mm wide, with 50 segments; single MMS specimen an anterior fragment 3.5 mm long, 0.5 mm wide excluding parapodia, with 28 setigers. Body slender, pale brown in alcohol; each segment with single, dorsal transverse ciliary band (Imajima, 1966c; Banse and Hobson, 1968).

Prostomium wider than long, anterior margin somewhat rounded; 2 pairs of eyes, red, in trapezoidal arrangement, anterior pair largest; additional pair of red eyespots usually present on anterior prostomium margin (Fig. 1.13A). Antennae smooth to wrinkled proximally, distinctly articulated distally; median antenna arising between largest pair of eyes, around 5 times longer than prostomium; lateral antennae, arising from anterior edge of prostomium, each about one-half length of median antenna (Fig. 1.13A). Palps broad, flat, triangular, slightly fused basally (Fig. 1.13A). Pharynx thick, about as wide as proventriculus; anterior rim finely denticulate, with anterior middorsal tooth, surrounded by distal circlet of 10 soft papillae when everted. Proventriculus extending from setigers 7-8 to 13-16.

Tentacular segment reduced dorsally, forming low occipital flap covering posterior prostomium margin. Two pairs of tentacular cirri, proximally smooth, weakly articulated distally; dorsal pair longest, each about as long as median antenna; ventral pair about half as long as dorsal ones (Fig. 1.13A).

Parapodia bluntly conical (Fig. 1.13B-D). Setae generally compound falcigers (Fig. 1.13E-G); blades short, distally bidentate with cutting edges serrated. Blades decreasing in length inferiorly within fascicles; those of anterior segments slender (Fig. 1.13E), becoming more stout posteriorly (Fig. 1.13F,G), especially in inferior part of fascicles. Superior distal ends of shafts minutely serrated (Fig. 1.13E-G). Dorsal superior and ventral inferior seta present in fascicles of posterior segments. Two to 3 aciculae per anterior parapodium, decreasing to 1 per posterior parapodium; distally curved, pointed, mallet-shaped (Fig. 1.13H).

Dorsal cirri basally smooth to wrinkled, weakly to distinctly articulated distally (Fig. 1.13A-D). Dorsal cirri of setiger 1 longest, longer than median antenna, with 40-50 articles (Fig. 1.13B); setiger 2 dorsal cirri short, about one-half length of first pair; cirri on setigers 3 and 4 long; on setiger 5 short; on setiger 6 long; on setiger 7 to end of body about two-thirds body width. Ventral cirri thick, foliaceous, extending beyond parapodial lobes (Fig. 1.13B-D).

Remarks. The present record of *Eusyllis blomstrandi* is based on a single anterior fragment from Phase II. Although this species is widely reported from the west coast of North America (Berkeley and Berkeley, 1945; Banse and Hobson, 1968, 1974; Hartman, 1968), Banse and Hobson (1968) noted different pharyngeal morphology compared to that described by both Malmgren (1867) and Imajima (1966c). We suspect that specimens identified as *E. blomstrandi* at least from southern California represent an undescribed species. Efforts to address this issue must await additional, well-preserved specimens and re-examination of Malmgren's specimens.

Distribution. California to Alaska; Japan; Labrador Sea to Massachusetts; Spitsbergen; Iceland; Ireland; Mediterranean Sea.

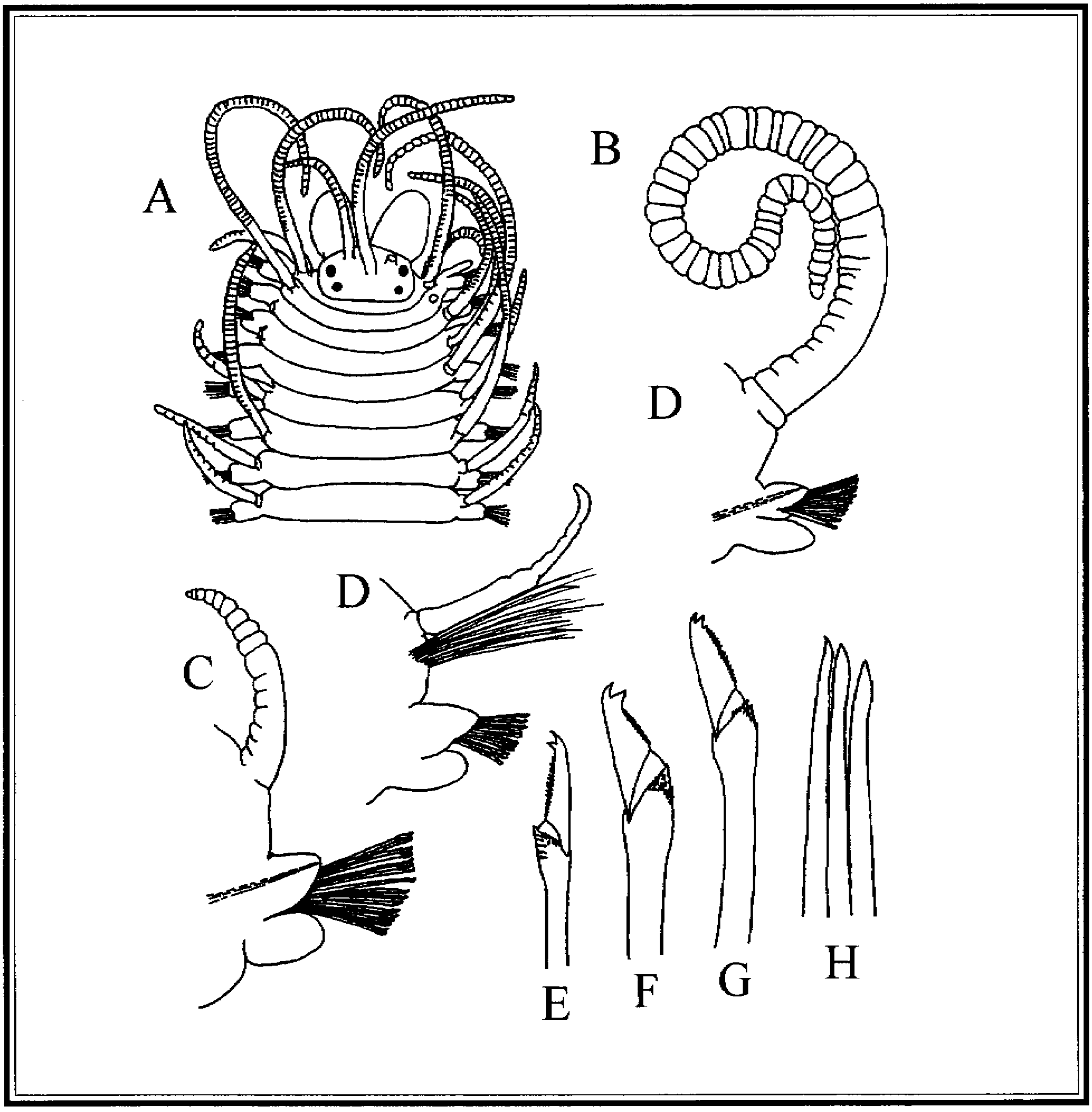

Figure 1.13. *Eusyllis bloomstrandi*: A, anterior end, dorsal view; B, parapodium 1; C, parapodium 15; D, parapodium 17 from epitokous specimen; E, inferior compound falciger, parapodium 1; F, inferior compound falciger, middle body segment; G, superior compound falciger, middle body segment; H, aciculae, parapodium 1. (A-H, modified and redrawn from Hartmann-Schröder, 1971)

Eusyllis habei Imajima, 1966

Figure 1.14

Eusyllis habei Imajima, 1966c:97-99, text-fig. 31, a-k.

Material Examined. California: between Point San Luis and Point Sal, Sta. BRA-25 rock (5, USNM 170904) + (2); off El Morro, Sta. BRA-27 (5, SBMNH 142700); east of Point Conception, Sta. BRC-01 rock (1); off Point Conception, Sta. BRA-02 rock (2); off point San Luis, Stas. R-1 (2, USNM 170905); R-8 (2, USNM 170906); off Point Arguello, Stas. PH-F (5); PH-I (1); PH-U (1); PH-W (4).

Description. Length up to 5 mm, 0.9 mm wide, for 43 setigers (Imajima, 1966c); MMS specimens all incomplete, 2.1 mm long, 0.2 mm wide excluding setae, for 24 setigers. Body pale yellow white in alcohol. Some Japanese specimens with 2 dorsal transverse color bands per segment (Imajima, 1966c); most MMS specimens with 1 black transverse band on anterior edge of each segment, bands sometimes incomplete middorsally. Body fragile.

Prostomium wider than long; 2 pairs of eyes, each circular in outline, arranged trapezoidally, anterior pair set farthest apart (Imajima, 1966c); MMS specimens with conspicuous reddish-brown eyes (Fig. 1.14A). Antennae weakly annulated; median antenna arising between anterior pair of eyes, 4-5 times longer than prostomium; lateral antennae arising from anterior prostomium margin, each about one-half length of median antenna (Fig. 1.14A). Nuchal ridges paired, extending broadly along posterior prostomial border. Palps about as long as prostomium, distally rounded, basally fused (Fig. 1.14A,K). Pharynx extending through setiger 6 when inverted, setiger 3 when everted; ventral rim of everted pharynx with 20-26 denticles, dorsal rim smooth with large, distal, spindle-shaped middorsal tooth, all surrounded by distal circlet of 10 soft papillae (Fig. 1.14B). Proventriculus present in setigers 6 to 9-10, with 23-24 rows of muscle cells, anterior 20 of these large, conspicuous.

Tentacular segment reduced dorsally. Two pairs of tentacular cirri; dorsal pair each about as long as median antenna; ventral pair each about one-third length of dorsal pair (Fig. 1.14A).

Parapodia short, thick, conical (Fig. 1.14C). Compound setae bidentate falcigers with minutely serrated cutting edges (Fig. 1.14D-G). Blades decreasing in length inferiorly within fascicles, posteriorly along body axis. Superior blades of anterior, middle segments oar-shaped, 2-2.5 times longer than inferior blades (Figs. D,E); those of posterior segments shorter, just slightly longer than inferior blades (Figs. F,G). Anterior setigers each with 10-15 superior falcigers with long blades and 20-30 inferior falcigers with short blades; median setigers each with 10 falcigers. Dorsal superior and ventral inferior simple seta present in posterior setigers; dorsal seta capillariform with cutting surface minutely serrated (Fig. H), ventral seta stout, distally bidentate (Fig. I). One to 2 aciculae in anterior parapodia and 1 acicula in median parapodia; distally blunt (Fig. J).

Dorsal cirri of setiger 1 longest, 2 times longer than median antenna, alternating long and short thereafter; long cirri equal to and short ones one-half body width (including parapodia). Ventral cirri of setiger 1 foliaceous, flattened; digitiform from setiger 2 to end of body; all shorter than parapodial lobes.

Remarks. This is the first record of *Eusyllis habei* from the western coast of North America. The MMS specimens generally conform to features previously described, although they are smaller.

Distribution. Southern California; Japan.

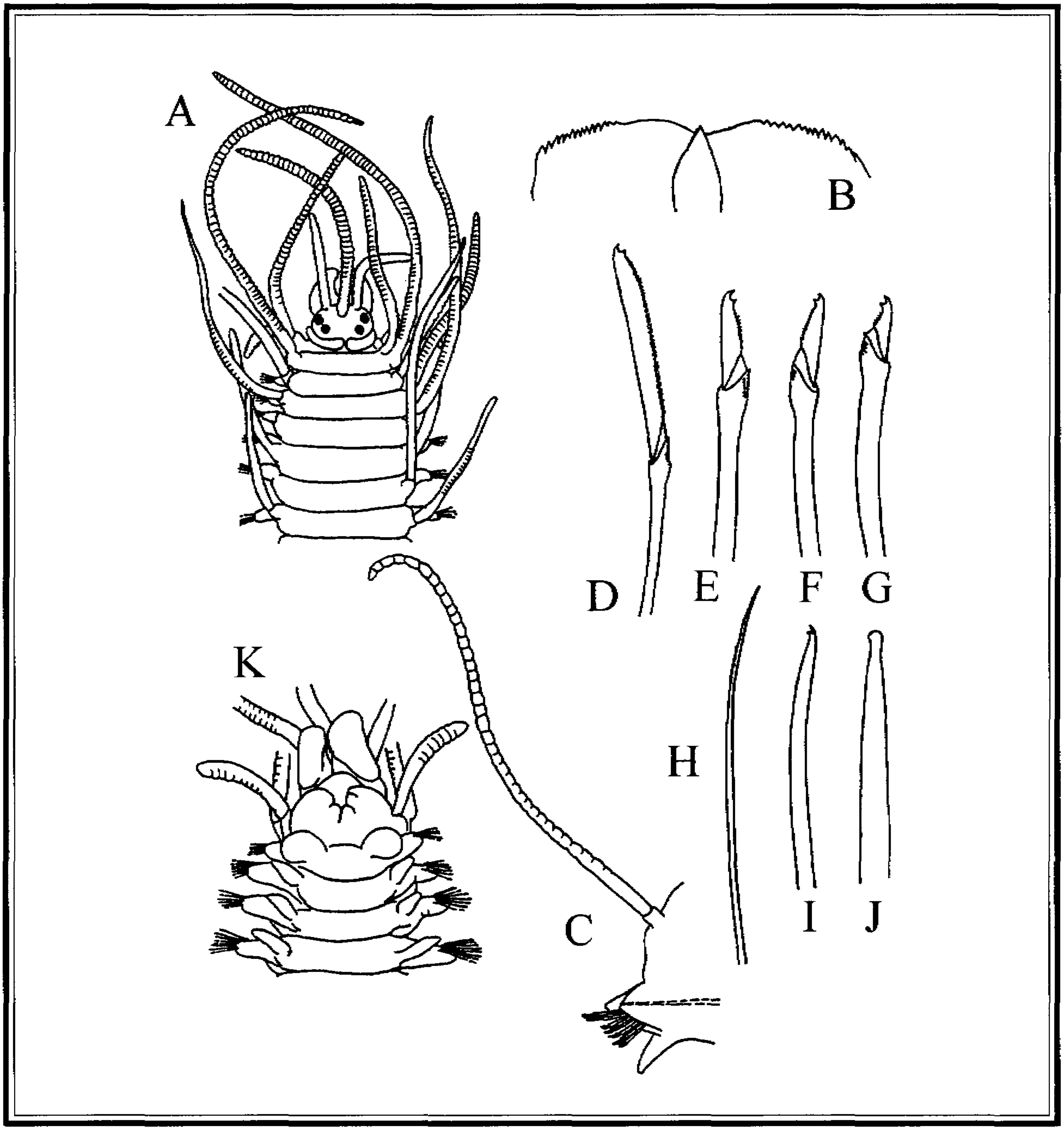

Figure 1.14. *Eusyllis habei*: A, anterior end, dorsal view; B, pharynx, dissected; C, parapodium 18; D, superior compound falciger, middle segment; E, inferior compound falciger, middle segment; F, superior compound falciger, posterior segment; G, inferior compound falciger, posterior segment; H, dorsal simple seta, posterior segment; I, ventral simple seta, same posterior segment as H; J, acicula, median parapodium; K, anterior end, ventral view. (A-K, redrawn from Imajima, 1966c)

Eusyllis longicirrata Imajima, 1966

Figure 1.15

Eusyllis longicirrata Imajima, 1966c:94-97, text-fig. 30, a-f.

Material Examined. California: between Point San Luis and Point Sal, Sta. BRA-25 rock (3, USNM 170907).

Description. Length up to 18 mm, 1.2 mm wide for 87 setigers (Imajima, 1966c); all MMS specimens anterior fragments up to 2 mm long, 0.5 mm wide excluding parapodia for 21 setigers.

Prostomium wider than long, anterior margin slightly rounded, posterior middorsal cleft deep, extending to center of prostomium (Fig. 1.15A); 2 pairs of eyes, red, anterior pair largest, farthest apart. Antennae long, smooth, slender. Median antenna arising from middle of prostomium, 4 times longer than prostomium; lateral antennae arising from anterior prostomial margin, each one-half length of median antenna. Nuchal organs paired, extending along posterior margin of prostomium (Fig. 1.15A). Palps longer than prostomium, narrow, distally rounded, not fused basally (Fig. 1.15A). Everted pharynx extending through 5 or 8 segments in two MMS specimens, with anterior rim minutely denticulate, with middorsal subdistal tooth, surrounded by distal circlet of 10 soft papillae. Proventriculus in setigers 13-21 (Imajima, 1966c; Fig. 1.15B); MMS specimens with proventriculus in setigers 9-17 or 6-14 (8 segments) with 32-34 rows of muscle cells.

Tentacular segment reduced dorsally. Two pairs of tentacular cirri; dorsal pair as long as median antenna; ventral pair each one-half length of dorsal tentacular cirri.

Parapodia elliptical in outline, distally rounded (Fig. 1.15C). Setae compound falcigers (Figs. D,E). Blades distally bidentate with cutting edges minutely serrated; decreasing in length inferiorly within fascicles, superior blades two times longer than inferior blades. Two to 3 aciculae per parapodium, distally pointed, slightly curved (Fig. 1.15F).

Dorsal cirri with long cirriphore, smooth, considerably more slender, longer than both antennae, tentacular cirri (Fig. 1.15A,C); alternating long and short along body. Long dorsal cirri of anterior segments up to 4 times longer than body width, decreasing to 3 times in middle body segments; short dorsal cirri 2 times body width throughout, gradually decreasing in overall length posteriorly. Ventral cirri digitiform, extending beyond parapodial lobes.

Remarks. This is the first record of *Eusyllis longicirrata* from the eastern Pacific. The MMS specimens generally conform to features previously described, although they are smaller.

Distribution. Southern California; Japan.

Genus *Odontosyllis* Claparède, 1863

Type species: *Syllis fulgurans* Audouin and Milne-Edwards, 1833

Diagnosis. Prostomium with 3 antennae. Palps either fused basally or separate. Nuchal organs large, curved ciliated ridges along posterior margin of prostomium. Two pairs of tentacular cirri. Occipital flap usually present. Antennae, tentacular cirri and dorsal cirri smooth. Pharynx with fewer than 20 curved teeth.

Remarks. The key presented below includes all known species, and one new species, from the Pacific coast of North America from California to Alaska. Only *Odontosyllis phosphorea* and *O. fragilis* were encountered in MMS materials.

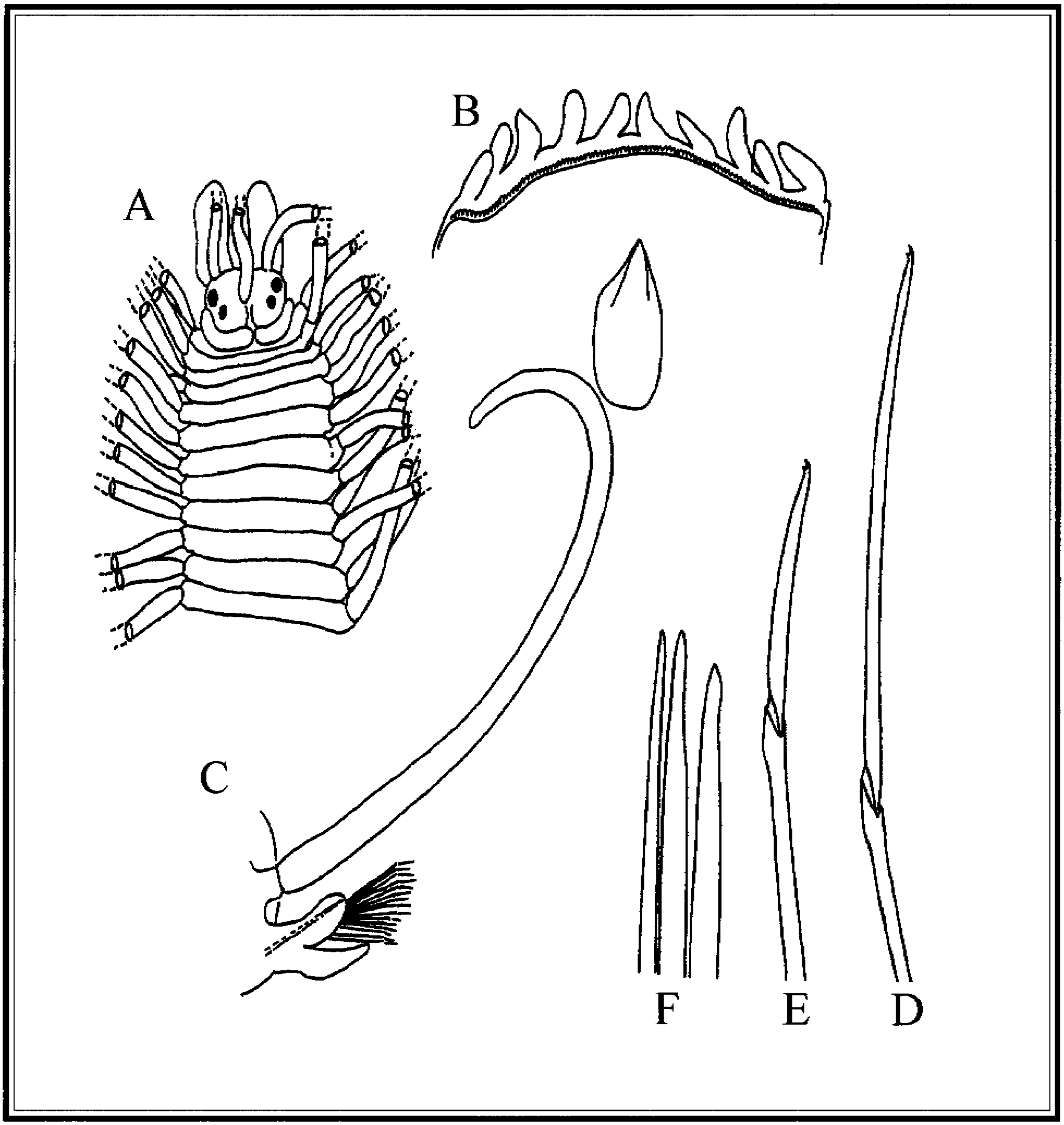

Figure 1.15. *Eusyllis longicirrata*: A, anterior end, dorsal view, distal parts of antennae, tentacular and dorsal cirri omitted; B, pharynx dissected; C, parapodium 11; D, superior compound falciger, parapodium 11; E, inferior compound falciger, parapodium 11; F, aciculae, parapodium 11. (A-F, redrawn from Imajima, 1966c)

Key to Known Species of *Odontosyllis* from the Northeast Pacific (after Banse and Hobson, 1974)

1A. Median antenna arising from anterior prostomium margin; palps small, projecting ventrally, not visible in dorsal view .... *Odontosyllis parva*

1B. Median antenna arising from dorsal surface of prostomium near anterior pair of eyes (Figs. 1.16A, 1.17A); palps large, projecting anteroventrally, visible in dorsal view (Figs. 1.16A, 1.17A) 2

2A. Proventriculus extending through about 20 segments; blades of bidentate compound falcigers short, cutting edges minutely serrated in anterior fascicles and smooth in posterior fascicles; preserved specimens lack color patterns .... *Odontosyllis fulgurans japonica*

2B. Proventriculus extending through 10 or fewer segments; blades of bidentate compound falcigers long and short, with cutting edges all serrated or all smooth; preserved specimens usually with dorsal pigmentation 3

3A. Proventriculus extending through 9-10 segments with 60-67 rows of muscle cells; blades of compound falcigers with serrated cutting edges (Fig. 1.16E,G); dorsum with dark pigment spot every third to fourth intersegmental groove or with black transverse line on each of the first 20 segments (Fig. 1.16A); occipital flap with or without black pigment; pharynx with 6 distal teeth (Fig. 1.16B) .... *Odontosyllis phosphorea*

3B. Proventriculus extending through 12 segments with approximately 300 rows of small, dense muscle cells; blades of compound falcigers with smooth cutting edges (Fig. 1.17F,G); middorsum with a dark pigment spot in middle of every segment including tentacular segment (Fig. 1.17A); occipital flap without black pigment (Fig. 1.17A); pharynx with 5 distal teeth (Fig. 1.17E) .... *Odontosyllis fragilis*

Odontosyllis phosphorea Moore, 1909

Figure 1.16

Odontosyllis phosphorea Moore, 1909:327.—Berkeley and Berkeley, 1948:82.—Hartman, 1961:76-7; 1968:441-442, figs. 1-3.—Banse, 1972:207-209, fig. 7G-N.—Banse and Hobson, 1974:58, fig. 15c-d.—Blake, 1975:189, pl. 35, fig. 133.

Odontosyllis phosphorea nanaimoensis E. Berkeley, 1923:207; 1961:1321.—Berkeley and Berkeley, 1948:82.—Pettibone, 1967:5.

Hesperalia nans Chamberlin, 1919:9.

Not *Hesperalia californiensis* Chamberlin, 1919:9. *Fide* Hartman, 1961:9.

Not *Odontosyllis phosphorea* Berkeley and Berkeley, 1938:42. *Fide* Banse, 1972:207.

Material Examined. California: Santa Maria Basin, Sta. BRA-16 rock (1); between Point Estero and Point Buchon, Sta. 6, rock (4, SBMNH 142701).—Laguna Beach, holotype of *Hesperalia californiensis* Chamberline, 1919, ovigerous (MCZ 2149); holotype of *Hesperalia nans* Chamberlin, 1919, ovigerous, dried (MCZ 2150).—Santa Catalina Island, type of *Odontosyllis phosphorea* (USNM 17214).—British Columbia: Nanaimo, syntypes of *O. phosphorea nanaimoensis* (15, USNM 32858).

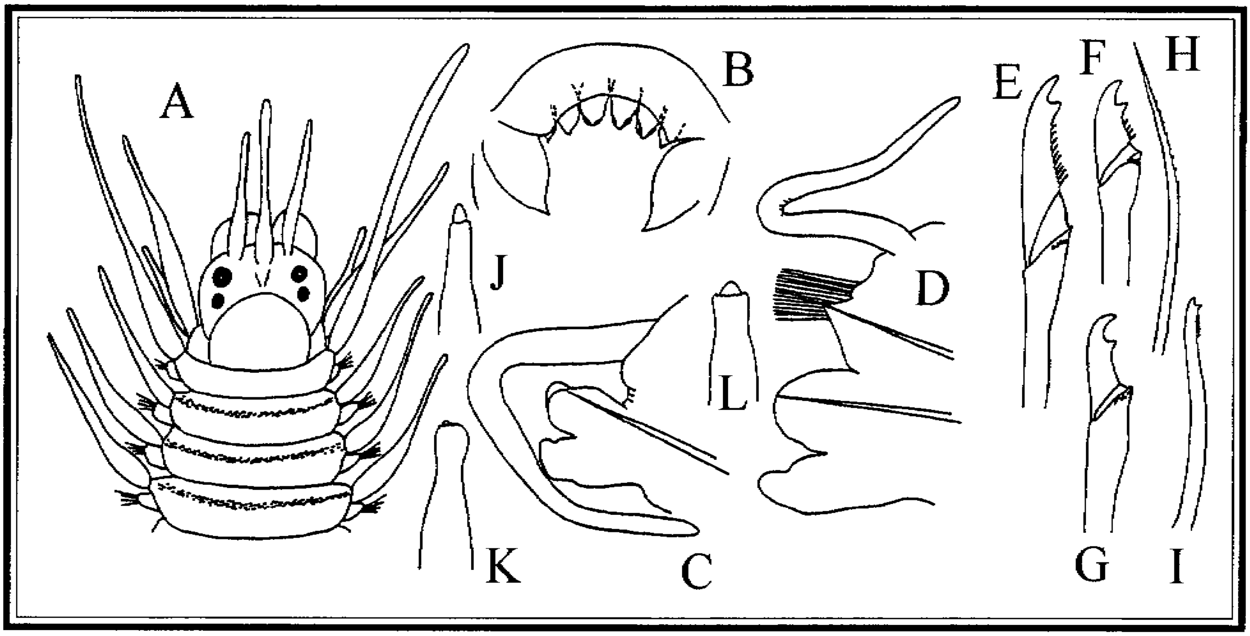

Figure 1.16. *Odontosyllis phosphorea*: A, anterior end, dorsal view; B, teeth and lateral chitinized regions of pharynx, frontal view; C, anterior parapodium; D, medial biramous parapodium from epitokous specimen; E, compound falciger, setiger 10; F, same, setiger 70; G, same, from inferior fascicle; H, dorsal simple seta, posterior segment; I, ventral simple seta, posterior segment; J, acicula, setiger 1; K, same, posterior segment; L, same, setiger 70. (A, modified from Blake, 1975; B, E-F, H-L, redrawn from Banse, 1972; C-D, G, redrawn from Moore, 1909)

Description of Epitokous Form. Length 20 to 30 mm, 2.5 mm wide, for about 90 segments (Moore, 1909; Hartman, 1968); MMS specimens up to 9.5 mm long, 0.7 mm wide excluding parapodia, for 69 setigers. Dorsum arched, ventrum flattened. Color in life variable: pale yellow to ivory with dark or black middorsal spot every third or fourth intersegmental groove or as a black transverse line on each of first 20 setigers followed by faint middorsal pigment spot in each successive medial segment; occipital flap darkly pigmented.

Prostomium small, wider than long; 2 pairs of eyes, black; anterior pair widest apart; posterior pair lying in crescent-shaped patch of dark pigment; all arranged trapezoidally (Fig. 1.16A). Median antenna small, smooth, arising between anterior pair of eyes; lateral antennae smooth, subequal in length and arising slightly anterior to median antenna (Fig. 1.16A). Palps thick, fleshy, projecting ventrally, fused basally. Everted pharynx extending to setiger 6-8, with circlet of 6 distal teeth (Fig. 1.16B). Proventriculus from setigers 7-9 to 17-19; muscle rows ranging from 60-67, depending on body size.

Tentacular segment reduced dorsally, obscured by prostomium, with semicircular occipital flap extending forward to cover anterior pair of eyes (Fig. 1.16A). Two pairs of tentacular cirri, smooth to wrinkled; dorsal pair longest, about 3 times longer than prostomium; ventral pair about one-half length of dorsal pair (Fig. 1.16A).

Parapodia short; uniramous, distally rounded in anterior segments (Fig. 1.16C); biramous in median segments with notopodial lobes triangular, neuropodial lobes rounded (Fig. 1.16D) Setae including compound falcigers with distally bidentate blades with serrated cutting margins, about 30 per anterior fascicle at setiger 10 (Fig. 1.16E), decreasing thereafter to about 24 per median fascicle, and 18 per posterior fascicle (Fig. 1.16F,G). Blade lengths subequal within anterior medial and posterior fascicles; decreasing slightly in overall length from anterior to posterior setigers. Dorsal simple seta distally unidentate, wide, present in last 2-4 setigers of complete specimens (Fig. 1.16H). Ventral simple seta distally bidentate, present in last few posterior setigers (Fig. 1.16I). Capillary swimming setae long, from setigers 21-22. Neuroaciculae 4 per anterior parapodia (Fig. 1.16J), decreasing to 2 in median and posterior parapodia (Fig. 1.16K,L). Notoacicula thin, tapering distally, deeply embedded, 1 per notopodium of median segments.

Dorsal cirri smooth with short cirriphores; alternating long and short. Ventral cirri thick, distally blunt, projecting slightly beyond parapodial lobes in median segments.

Remarks. *Odontosyllis phosphorea* is a well-defined species commonly associated with rocky habitats from western Canada to southern California that is readily collected using night lights. Banse (1972) reported the cutting edges of compound falcigers in specimens he examined to be serrated, in contrast to Moore's (1909) originally observations and illustration, which is included in this study (Fig. 1.16G); Banse's data are used in the above key.

Hartman (1961) proposed that *Hesperalia californiensis* Chamberlin, 1919, is a junior synonym of *O. phosphorea*. Re-examination of the types of both species by one of us (L. Harris) revealed that *H. californiensis* is a species of *Odontosyllis*, but not *O. phosphorea*. *Odontosyllis phosphorea* differs from *O. californiensis* in having blades of compound setae with secondary teeth located subdistally, rather than at the midpoint of the cutting edge. However, *H. nans* Chamberlin, 1919, has the identical pigmentation pattern and setae that are characteristic of *O. phosphorea*. We suggest that the latter two species are synonyms, although the type of *H. nans* has dried out, and precise comparisons are not presently feasible.

Distribution. Pacific coast, Mexico to British Columbia.

Odontosyllis fragilis Kudenov and Harris, new species

Figure 1.17

Material Examined. California: Western Santa Barbara Channel, east of Point Conception, Sta. BRA-1 rock, holotype (USNM 170918).

Description. Holotype complete specimen 5.4 mm long, 0.3 mm wide excluding setae, with 65 segments in 3 parts: anterior part with 19 setigers; middle part with 15; posterior with 30. Color in alcohol generally white, except for middorsal pigment patch on each segment, including patch under occipital flap on tentacular segment.

Prostomium wider than long, with deep medial cleft along posterior margin; 2 pairs of eyes, lenticulate, connate, arranged trapezoidally; anterior pair largest (Fig. 1.17A). Antennae smooth; median antenna inserted on anterior prostomium margin, longer than prostomium, just anterior to anterior pair of eyes; lateral antennae inserted near anterior edge of prostomium, slightly shorter than median antenna (Fig. 1.17A). Palps large, globular, directed ventrally, basally free, visible in dorsal view (Fig. 1.17A). Pharynx extending to setiger 4 when inverted; with at least 5 curved, subequal chitinous teeth (dissected), 1 middorsal, 2 dorsolateral and 2 ventrolateral in position (Fig. 1.17E). Proventriculus in setigers 5-16, with approximately 300 rows of minute, densely packed muscle cells (dissected) barely visible using 250× magnification.

Tentacular segment dorsally distinct from prostomium and setiger 1, with tongue-shaped occipital flap extending over prostomium, not covering eyes (Fig. 1.17A). Two pairs of tentacular cirri, subequal, smooth and longer than prostomial antennae; dorsal pair longest, each nearly 2 times longer than median antenna (Fig. 1.17A).

Parapodia tapering, with distally truncate presetal lobe extending beyond parapodial lobe in anterior segments (Fig. 1.17B); gradually becoming smaller, distally incised into 2 unequal lobes, superior lobe smallest, associated with acicula in medial and posterior segments (Fig. 1.17C,D,I). All setae compound falcigers (Fig. 1.17F,G), around 10-15 anteriorly, decreasing to about 7-12 posteriorly. Blades similar in size, distally bidentate, increasing slightly in length inferiorly within fascicles (Fig. 1.17F,G). Superior blades with distal tooth smaller than subdistal tooth, becoming larger in inferior blades; smooth cutting edges, although 2 additional,

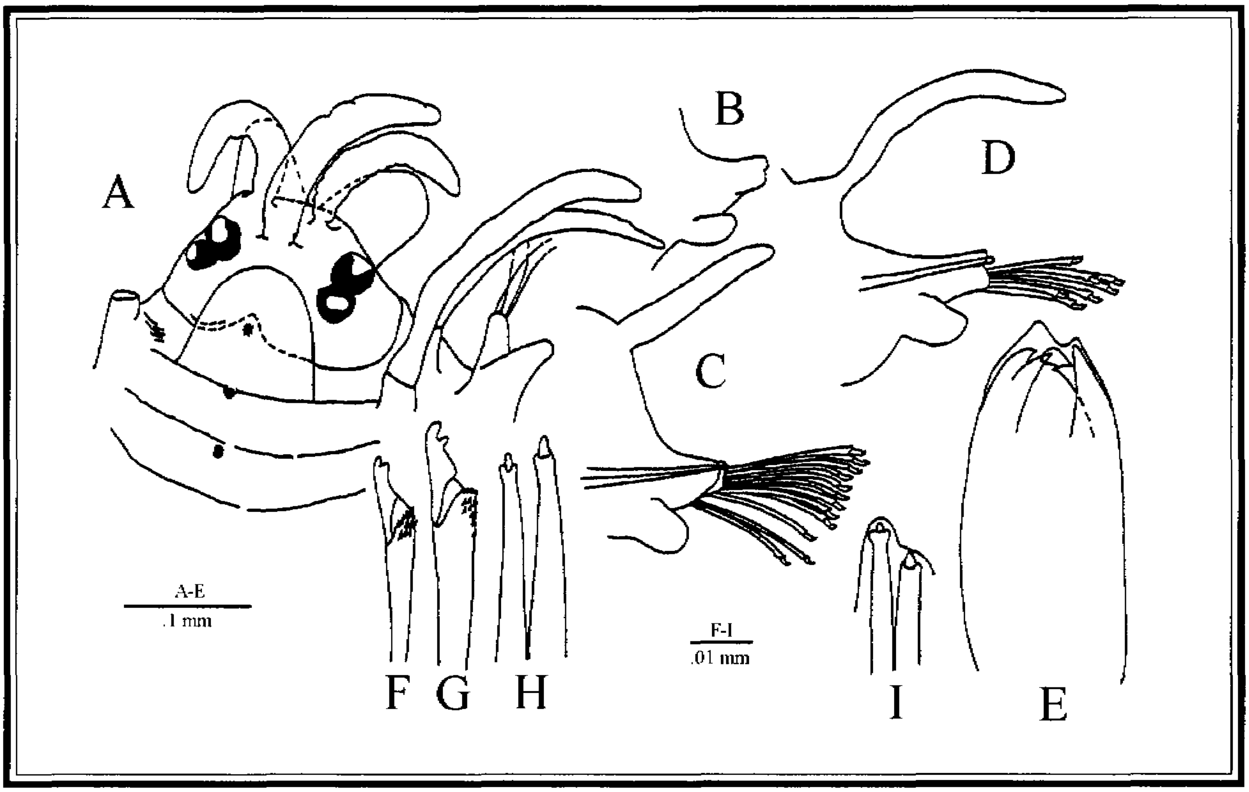

Figure 1.17. ***Odontosyllis fragilis* Kudenov and Harris, new species:** A, anterior segments, dorsal view; B, left parapodium, setiger 11, setae omitted, anterior view; C, left parapodium, setiger 11, including dorsal cirrus and setae, anterior view; D, left parapodium, setiger 36, anterior view; E, pharynx, dissected, dorsolateral view; F, superior compound falciger, setiger 11; G, inferior compound falciger, setiger 11; H, paired aciculae, setiger 11; I, paired aciculae embedded in acicular lobe, setiger 11. (A-I, originals by JDK)

small denticles sometimes present on largest inferior blades. Shafts distally inflated, with subdistal spines on superior surfaces, these best developed on superior setae (Fig. 1.17F,G). Two aciculae per parapodium, not projecting through parapodial lobes or cuticle; distally pointed, tip circumscribed by flange or collar (Fig. 1.17H,I).

Dorsal cirri smooth, cirriform, arising from body wall. Ventral cirri thickly digitiform, inflated, not extending beyond parapodium.

Pygidium unknown.

Remarks. *Odontosyllis fragilis* is characterized by the presence of a dorsomedian row of pigment spots from the tentacular segment to the end of the body, 5 subequal chitinous teeth in the pharynx of which one is middorsal, pharynx in setigers 1-4, proventriculus in setigers 5-16 with perhaps 300 rows of small, tightly packed muscle cells that are poorly discernable using 250 x magnification; blades of compound falcigers all distally bidentate with smooth cutting edges, and two acicula per parapodium. The proventriculus is particularly unusual, and is not like those described for known *Odontosyllis* species.

Etymology. The name, *fragilis*, alludes to the fact that specimens are extremely delicate, and seldom remain intact.

Distribution. Southern California.

Genus *Opisthodonta* Langerhans, 1879

Type species: *Opisthodonta morena* Langerhans, 1879

Diagnosis. Prostomium with 3 antennae. Palps fused basally. Nuchal organs large, ciliated ridges between prostomium and tentacular segment. Two pairs of tentacular cirri. Antennae, tentacular cirri and dorsal cirri smooth, slender. Pharynx armed with a large middorsal posterior tooth. Some anterior parapodia with thick aciculae.

Remarks. Hartmann-Schröder (1971) reviewed the genus *Opisthodonta* which includes the type species *O. morena* (Langerhans, 1879) and *O. pterochaeta* (Southern, 1914). *Opisthodonta* is polytypic as presently defined: *O. pterochaeta* is more closely allied to the *Streptosyllis*-complex in having huge aciculae terminating in flat, enlarged ends plus thick compound falcigers with short blades confined to anterior segments, and will be assigned to a new genus elsewhere (Dorsey and Kudenov, in preparation); it will not be included in this analysis.

Opisthodonta mitchelli Kudenov and Harris, new species

Figure 1.18

Material Examined. California: Santa Maria Basin, off Point Arguello, Sta. BRA-6, rock, holotype (USNM 170919) + 2 paratypes (LACM-AHF Poly 1674); Stas. BRA-13, rock, paratype (AM W. 22191); BRC-13, rock (1); BRC-14, rock (1); BRA-16 rock, paratype (USNM 170920); BRA-21 rock (1); between Point San Luis and Point Sal, Sta. BRA-25 (2); off El Morro, Sta. BRA-27 (1); off Point Estero, Sta. 1, 2 paratypes (LACM-AHF Poly 1669); off El Morro, Sta. 6, 6 paratypes (LACM-AHF Poly 1670); off Point Arguello, Sta. PH-N (1).—Western Santa Barbara Channel, east of Point Conception, Stas. BRA-1 rock (1); BRC-1 rock, paratype (SBMNH 142659); south of Point Conception, Stas. BRA-2, rock (1); BRC-2, rock (1).

Description. Holotype 9.5 mm long, 0.5 mm wide without parapodia at setiger 7, with 60 setigers. Body coiled, strongly arched dorsally, flattened ventrally; fragile. Body wall pigmentation absent in preserved specimens; pharynx dark reddish brown.

Prostomium subrectangular to pentagonal; 2 pairs of eyes, anterior pair largest, lenticulate, widely separated, in trapezoidal arrangement; additional pair generally present medial to and near bases of lateral antennae, minute, lenticulate, absent in holotype (Fig. 1.18A). Antennae long, smooth; median antenna arising from posterior margin of prostomium, just anterior to nuchal organs, extending posteriorly to setiger 10-11, 2.5-3 times longer than lateral antennae; lateral antennae arising from anterior margin of prostomium, anterior to largest pair of eyes; each 2.5 times longer than prostomium (Fig. 1.18A). Nuchal ridge continuous, conspicuously ciliated, present on posterior prostomial margin (Fig. 1.18A). Palps square, extremely well developed, fused basally; shorter, wider than prostomium (Fig. 1.18A). Pharynx wide, thick-walled, with middorsal tooth in posterior half; extending to setiger 12 when retracted (Fig. 1.18A); when everted, extending to setigers 10-11 with distal circlet of 10 soft papillae (Fig. 1.18B). Proventriculus long, barrel-shaped, in setigers 13-20 (extending to setigers 16-20), with approximately 23-27 rows of muscle cells.

Tentacular segment dorsally distinct from prostomium, not as wide as following segments (Fig. 1.18A). Dorsal tentacular cirri three-fourths length of median antenna; ventral tentacular cirri one-third length of dorsal cirri (Fig. 1.18A).

Parapodia with single anteriorly placed node, usually located over tips of aciculae (not illustrated). Parapodial lobes of setigers 1-12 thick, fleshy, broadly truncate with pronounced ventral lip, appearing crowded and together conveying impression of a modified anterior region (Fig. 1.18A,B); parapodia of median and posterior setigers longer, thinner. Setae generally compound falcigers (Fig. 1.18D,E); blades all bifid, each

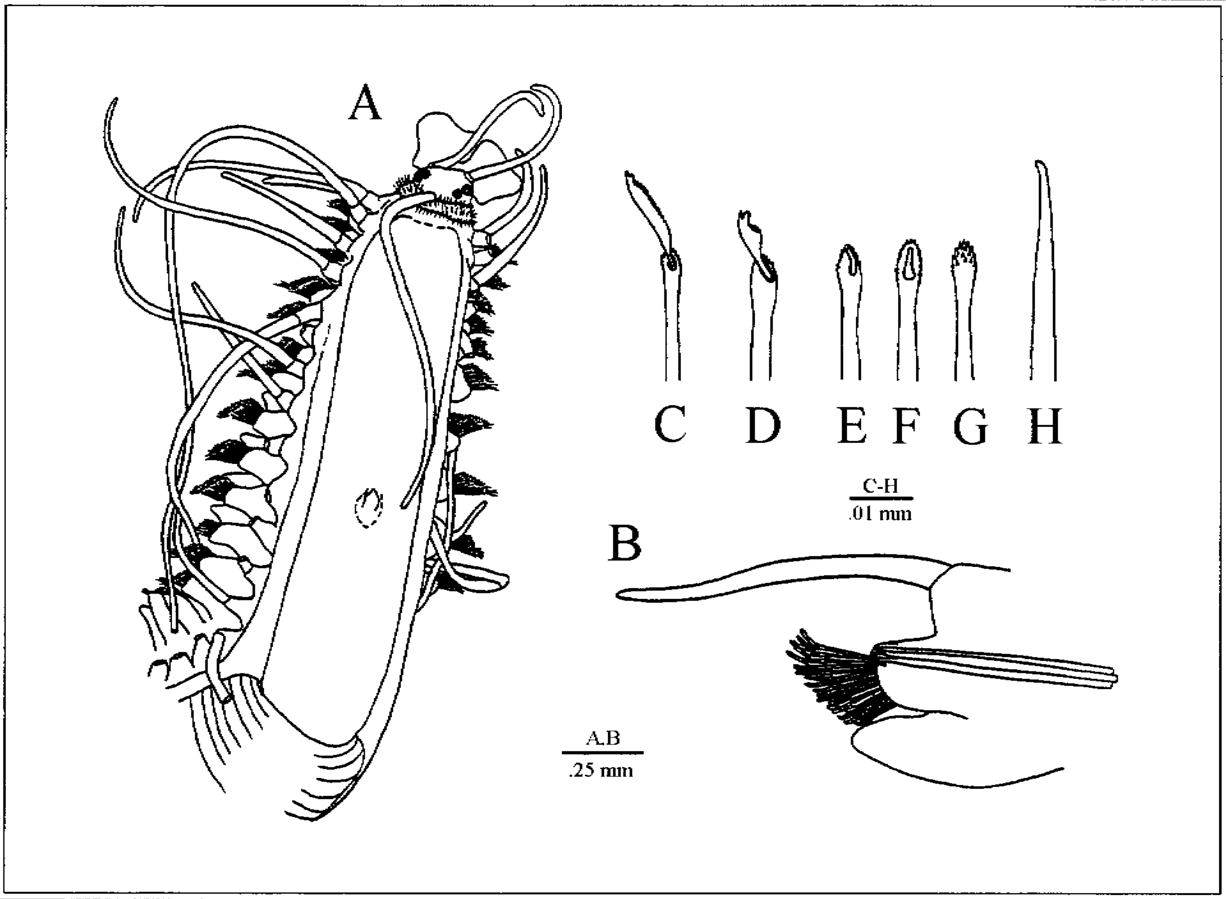

Figure 1.18. ***Opisthodonta mitchelli*** **Kudenov and Harris, new species:** A, Anterior end, dorsal view; B, right parapodium, setiger 4, anterior view; C, superior compound falciger, setiger 4; D, inferior compound falciger, setiger 4; E, shaft tip of compound falciger, posteroventral view; F, shaft tip of compound falciger, ventral view; G, shaft tip of compound falciger, dorsal view; H, Acicula. (A-G, redrawn from originals by J. Dorsey)

with fine, long serrations on cutting edges, suggesting presence of sheath at low magnification. Setigers 1-12 with 3-5 superior falcigers with blades (Fig. 1.18C) 2 times longer than middle and inferior blades (Fig. 1.18D) within fascicles, latter short and numerous, arranged in close-set dorso-ventral rows. Setae of median, posterior setigers consisting of 1-2 superior falcigers with blades slightly longer than others within fascicles, all gradually decreasing inferiorly; median setigers with 7-9 compound setae per fascicle, decreasing to 4-5 posteriorly. Shaft endings all strongly serrated, distally excavate (Fig. 1.18E-F). Dorsal simple seta present in median setigers to end of body, long, slender, tips appearing flattened, distally bifid, gently curved; cutting surface serrated. Ventral inferior seta present in last 10-13 setigers, stout, distally bifid with small superior tooth; cutting surface serrated. Three aciculae per anterior parapodia, of these 2 slightly enlarged, all with bent tips, decreasing to 1 per parapodium in posterior segments (Fig. 1.18H).

Dorsal cirri inserted on small elevations above parapodia, cirrophores conspicuous; alternating in length along body, longest anteriorly, decreasing in overall length posteriorly (Fig. 1.18A). Cirri of setiger 1 largest, extending posteriorly over 17 segments, those of setiger 2 over 6-7 segments (Fig. 1.18A). Longer dorsal cirri of median and posterior setigers extending over 2-3 segments; shorter cirri over 1-2 segments. Ventral cirri large, foliaceous in anterior segments, extending beyond tip of parapodial lobes (Fig. 1.18B), gradually become smaller, digitiform, not extending beyond parapodia in median and posterior segments.

Pygidium semicircular, with 2 long, smooth anal cirri.

Additional details are here provided for small specimens measuring 1.8 mm long, with 22 setigers: pharynx extending to setiger 6; proventriculus present in setigers 12-19; broadly truncate parapodia confined to setigers 1-6. A complete juvenile measures 1 mm long, 12.5 μm wide excluding parapodia, with 13 setigers. Six eyes present. Pharynx inverted, extending to setiger 4. Proventriculus in setigers 5 to anterior setiger 7, with around 25 rows of muscle cells. Truncate parapodia in setigers 1-4 enlarged. Compound falcigers numbering 10 per fascicle in setigers 1-4, blades longest in superiormost 2 to 3 setae; numbering 6-7 per fascicle in median parapodia; and 3 in posterior parapodia. Dorsal superior simple seta beginning in setigers 9-13. Ventral inferior simple seta beginning in setigers 11-13. Dorsal cirri proportionately smaller compared to adults; anterior ones as long as body width; posterior ones 2 times length of the body. Ventral cirri foliaceous in setigers 1-6, transitional in form in setigers 7-8, becoming digitiform in setigers 9-13.

Remarks. *Opisthodonta mitchelli* differs from *Opisthodonta* sp. B (Uebelacker, 1984) in lacking long spiniger-like falcigers, and instead having short-bladed falcigers enclosed by a sheath; continuous instead of paired nuchal organs; aciculae tapering and slightly bent distally instead of being straight and terminating in a distal knob and subdistal flange that is marginally dentate; and foliaceous and digitiform ventral cirri rather than auricular ventral cirri.

Opisthodonta mitchelli also differs from *Opisthodonta* sp. A (Uebelacker, 1984) in lacking aciculae with distally rounded ends and characteristic subdistal clefts, in having the proventriculus longer, extending through 6-7 segments with 23-27 rows of muscle cells, instead of 2-4 segments with 19-23 rows; and in having ventral cirri both foliaceous and digitiform rather than auricular.

Opisthodonta mitchelli differs from *O. morena* in lacking enlarged aciculae in anterior segments; superior compound blades of anterior setigers two times instead of four times longer than middle and inferior blades within fascicles; 23-27 instead of 18-24 rows proventricular muscle cells; and simple setae in median and posterior segments.

One female specimen of *O. mitchelli* (Sta. PH-N) has gametes beginning in setiger 20; all others non-reproductive.

Habitat. Soft bottoms and rocky substrata, in depths of 72-111 m.

Etymology. This species is named in fond memory and honor of Charles "Mitch" Mitchell, Sr., who was a special person to both L. Harris and John H. Dorsey, and whose absence is deeply regretted.

Distribution. Southern California.

Genus *Pionosyllis* Malmgren, 1867

Type species: *Pionosyllis compacta* Malmgren, 1867

Diagnosis. Prostomium with 3 antennae. Palps fused basally or separate. Nuchal organs usually as ciliated ridges along postectal margins of prostomium. Two pairs of tentacular cirri. Antennae, tentacular cirri and dorsal cirri smooth to weakly articulated. Pharynx with a single middorsal tooth; rim smooth.

Remarks. The presence of a smooth, edentate pharyngeal margin or rim is critical to the systematics of *Pionosyllis* species. This character must be determined before specimens can be correctly assigned to this genus. Specimens with retracted pharynges must therefore be dissected to avoid confusion with *Eusyllis*.

Although *Pionosyllis gigantea* Moore, 1908, was not encountered in MMS materials examined, it is widely distributed both latitudinally and bathymetrically from Alaska to southern California (Hartman, 1968), and is included in the key below. *Pionosyllis uraga* Imajima, 1966, has also been found in southern California (L. Harris, personal observation).

Key to the Species of *Pionosyllis* from California

1A. Blades of compound setae at least 3 times longer than basal width (Fig. 1.120C-E) 2

1B. Blades of compound setae short, less than 3 times longer than wide (Fig. 1.19C); antennae arise from anterior prostomium margin (Fig. 1.19A) .... *Pionosyllis magnifica*

2A. Superior compound falcigers with extremely long, spiniger-like bidentate blades in all segments, 6-10 times longer than inferior blades in fascicles (Fig. 1.20C-E); antennae distally articulated (Fig. 1.20A,B); dorsal cirri irregularly alternating in length along body (Fig. 1.20A) .... *Pionosyllis articulata*

2B. Superior compound falcigers with blades of uniform length within fascicles; antennae distally smooth; dorsal cirri usually long, not alternating in length along body ....*Pionosyllis gigantea*

Pionosyllis magnifica Moore, 1906

Figure 1.19

Pionosyllis magnifica Moore, 1906:223-225, pl. 10, figs. 9-11; 1908:325.—Annenkova, 1938:152.—Hartman, 1968:447-448, figs. 1-3.
Eusyllis magnifica Pettibone, 1954:261-262.—Banse and Hobson, 1974:56, fig. 14f.

Material Examined. California: Santa Maria Basin, between Point Estero and Point Buchon, Sta. 6 rock (1, USNM 170923).—Washington: Puget Sound, holotype (USNM 5533).

Description. Length 48 mm, 2 mm wide excluding dorsal cirri and setae, 150 segments (Moore, 1906; Hartman, 1968); MMS specimen 2.5 mm long, 0.3 mm wide for 17 setigers. Body widest in middle body segments, flattened, tapering markedly both anteriorly and posteriorly. Pigmentation absent in preserved specimens.

Prostomium small, depressed, wider than long, subrectangular; 2 pairs of black eyes, anterior pair largest, arranged trapezoidally (Fig 1.19A). Antennae slender, long, arising near anterior prostomium margin; median antenna 3-3.5 times longer than prostomium (lost in MMS specimen); paired lateral antennae each 2-3 times longer than prostomium (Fig. 1.19A). Palps large, projecting anteroventrally, basally fused (Fig. 1.19A). Everted pharynx with subdistal, middorsal tooth plus distal circlet of 10 soft papillae. Proventriculus of MMS specimen present in 4.5 segments.

Tentacular segment distinct, reduced dorsally (Fig. 1.19A), well-developed ventrally as lips. Two pairs of tentacular cirri, long, slender, smooth; dorsal pair 4 times and ventral pair 2.5 times longer than prostomium (Fig. 1.19A).

Parapodia stout, fleshy, distally rounded (Fig. 1.19B), becoming more elongate, conspicuous posteriorly. Setae compound falcigers with bidentate blades (Fig. 1.19C), about 40 per fascicle in median segments where best developed. Blade lengths decreasing inferiorly within fascicles; all with serrated cutting edges. Notoaciculae slender, curved, acutely pointed, 1 per parapodium in median segments, ventral to dorsal cirriphores (Fig. 1.19B); neuroaciculae stout, distally knobbed, 3-4 per parapodium.

Dorsal cirri cirriform, smooth to wrinkled (not annulated), resembling one another throughout; longest in anterior segments, decreasing to about one-half body width in median segments; all with long, pronounced dorsal cirrophores. Ventral cirri short, stout and enlarged, distally blunt, not extending beyond parapodial.

Pygidium small, with paired anal cirri, each the length of the last 12 segments.

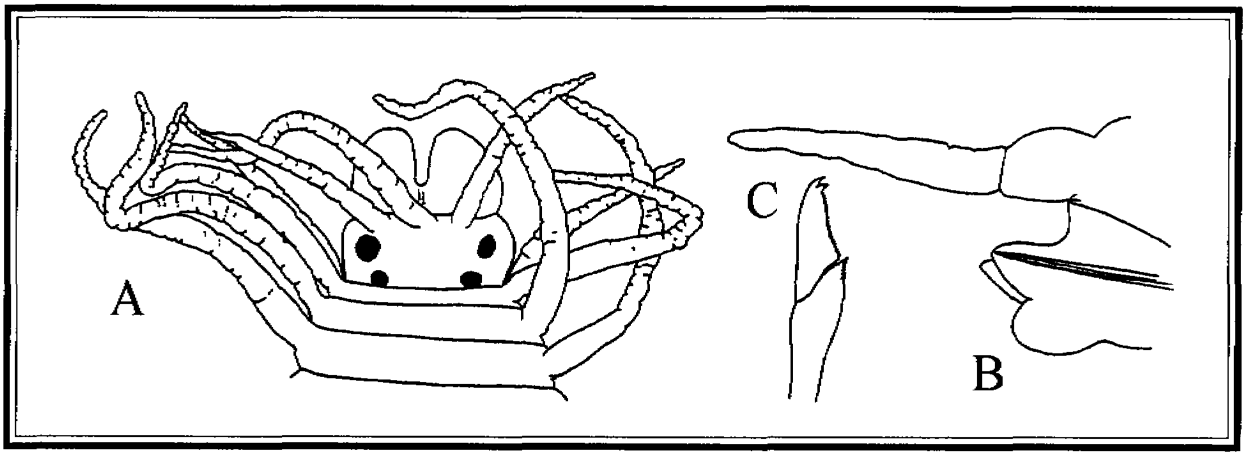

Figure 1.19. *Pionosyllis magnifica*: A, anterior end, dorsal view; B, parapodium; C, compound falciger. (A-C, redrawn from Moore, 1906)

Remarks. *Pionosyllis magnifica* is a long established species normally associated with muddy, sandy and shelly sediments in shallow habitats of Alaska, British Columbia and Washington (Pettibone, 1954; Hartman, 1968; Banse and Hobson, 1974). The single MMS specimen is poorly preserved. Pettibone (1954) referred Moore's species to *Eusyllis* on the basis of its denticulate pharyngeal margin. Examination of Moore's type by one of us (L. Harris) confirmed the presence of a smooth pharyngeal margin, and supports the original placement of this species in *Pionosyllis*.

Habitat. Mud, sand and shelly bottoms, to a depth of 109 m.

Distribution. California; Washington; Alaska.

Pionosyllis articulata Kudenov and Harris, new species

Figure 1.20

Material Examined. California: Santa Maria Basin, off Point Estero, Sta. 2, 3 paratypes (SBMNH 142660) + (4); off Purisima Point, Sta. 42, 1 paratype (USNM 170922) + (9); off Point Buchon, Sta. 12 (6); off Point San Luis, Sta. 22 (1); off Point Sal, Sta. 30, 4 paratypes (AM W. 22192); Sta. 43 (1); off Point Arguello, Sta. 64 (2); off Point Buchon, Sta. BRC-26 Extra, rock, holotype (USNM 170921); off El Morro, Sta. BRA-28 Extra, rock, 6 paratypes (LACM-AHF Poly 1671); off Point Sal, Stas. PJ-1 (3); PJ-2 (4); PJ-5 (1); PJ 6 (5); PJ-7, 13 paratypes (LACM-AHF Poly 1672) + (24); PJ-8 (2); PJ-10 (22); PJ-16 (1).—Western Santa Barbara Channel, off Point Conception, Sta. BRA-2 (1).—Point Loma, head of Coronado Canyon, Army Corp of Engineers, Stas. BD5-2 (3).

Description. Holotype measures 6 mm long, 0.3 mm wide excluding parapodia, 0.5 mm wide with parapodia (at setiger 7); 68 setigers. Body coiled, threadlike; setigers 1-9 each short, usually contracted, parapodia closely spaced, setigers becoming longer from setiger 10 (Fig. 1.20A); dorsum with paired transverse bands of cilia on each segment, conspicuous in reproductive individuals. Pigment absent in preserved specimens; pharynx reddish-brown. Sexually mature specimens with swimming setae beginning on setiger 21, continuing to near end of body; with 2-4 eggs per segment in setigers to far posterior.

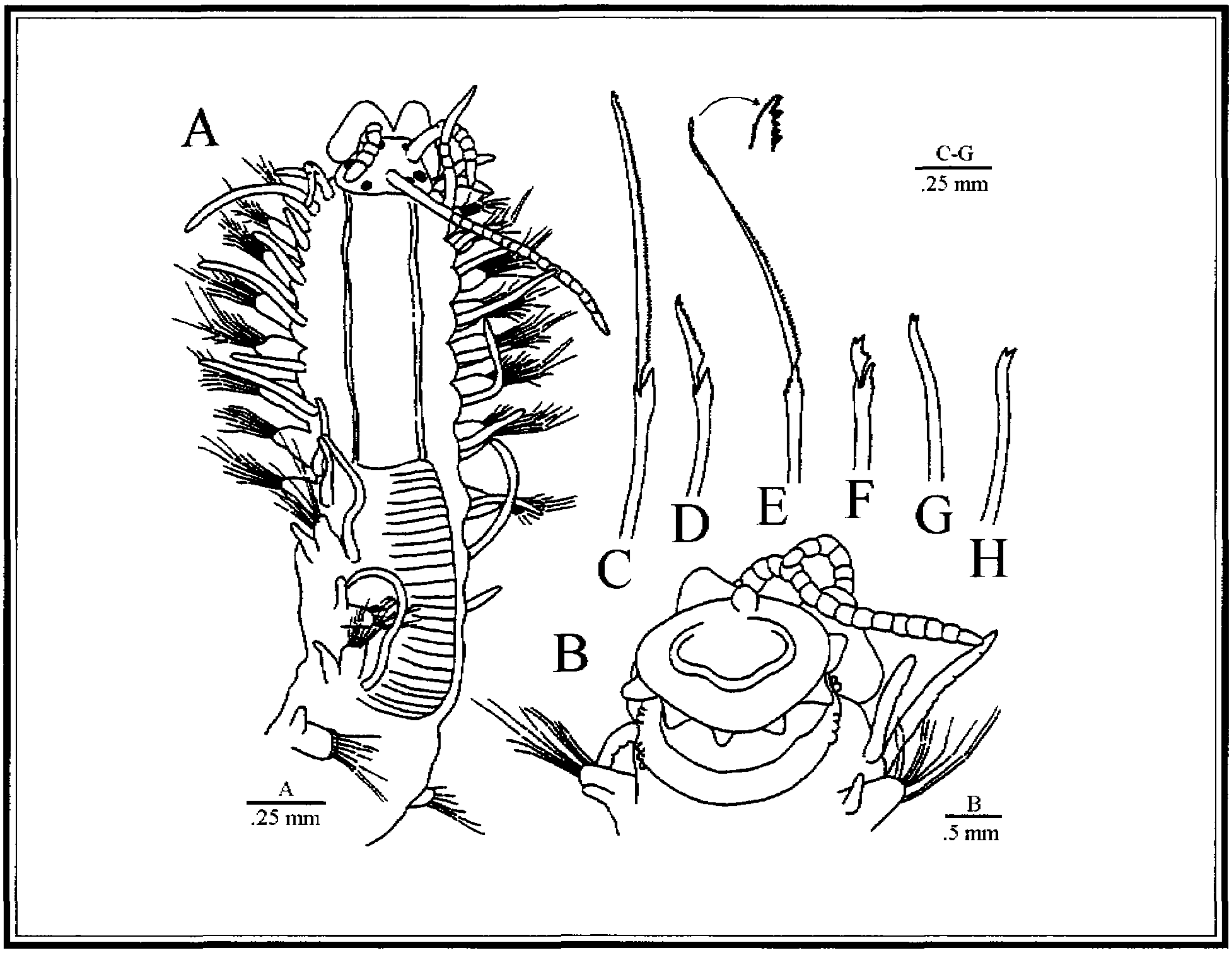

Figure 1.20. ***Pionosyllis articulata* Kudenov and Harris, new species**: A, anterior end, dorsal view; B, pharynx and setiger 1, ventral view; C, superior compound falciger, setiger 6; D, inferior compound falciger, setiger 6; E, superior compound falciger, with detail of tip, setiger 40; F, inferior compound falciger, setiger 40; G, dorsal simple seta, setiger 40; H, ventral simple seta, setiger 40. (A-H, redrawn from originals by J. Dorsey)

Prostomium wider than long (Fig. 1.20A); 2 pairs of eyes, in trapezoidal arrangement, anterior pair largest, lenticulate; additional pair of eyespots sometimes present, usually on anterior prostomium margin, anterior and medial to lateral antennae (Fig. 1.20A). Antennae slender, basally smooth (Fig. 1.20A); median antenna long, about 5 times width of prostomium, with about 16 distal articles; arising just posterior to midpoint of prostomium; lateral antennae about one-half length of median antenna, each with 6 distal articles, arising near anterior border of prostomium. Palps large, flattened, rounded anteriorly, slightly fused basally (Fig. 1.20A); distal one-third to one-half usually projecting ventrally. Nuchal organs not observed. Pharynx extending to setigers 6-7, with anterior middorsal tooth; chitinized margin smooth, surrounded by circlet of 10 soft distal papillae, with small papillae-like thickenings on proximal circumoral ring (Fig. 1.20B). Proventriculus extending from setigers 7-8 to 10-12, usually 5 segments in length, with 22-24 rows of muscle cells (Fig. 1.20A).

Tentacular segment as long as setiger 1, usually contracted, with 2 pairs of tentacular cirri, similar in form to prostomial antennae, distal articles sometimes present; dorsal pair longest, each about same length as lateral antennae; ventral pair each about one-third to one-half length of dorsal pair (Fig. 1.20A,B).

Parapodia conical, distally rounded, with small round pre-, and post-setal lobes. Compound setae bidentate falcigers. Blades decreasing in length posteriorly along body and inferiorly within fascicles; blades in setigers 1-19 thin, becoming more stout from setiger 20 to end of body. Distal denticle of short blades in setigers 1-19 somewhat larger than subdistal denticle (Fig. 1.20E); from setiger 20 becoming smaller than subdistal denticle, sharply bidentate (Fig. 1.20F). Cutting edges finely serrated in blades of anterior fascicles, becoming coarser, less numerous in blades of posterior fascicles. Superiormost falcigers with extremely long blades in all setigers, numbering 4-5 in anterior segments, decreasing to 1 posteriorly (Figs. C,D); blades of superior 4-5 compound falcigers within fascicles of setigers 1-19 six times length of those inferiormost (Figs. C,E), increasing after setiger 20 up to 10 times length (Figs. D,F). Dorsal simple seta from setigers 21-22 to end of body, initially unidentate, becoming bidentate posteriorly, with smooth cutting surfaces (Fig. 1.20G). Ventral simple seta from about setiger 36 to end of body, bifid, with smooth cutting surfaces (Fig. 1.20H). Aciculae numbering 2 per anterior parapodia, increasing to 3-4 in posterior segments; anterior ones terminating in diamond-shaped tips, generally becoming distally blunt posteriorly except for one enlarged geniculate form.

Dorsal cirri present on all segments, smooth except for those of setiger 1, which are slightly articulate distally (Fig. 1.20A); irregularly alternating in length all along body (short-long, two short-one long). Those of setiger 1 1.3-1.5 times longer than dorsal tentacular cirri; all generally increasing in length to middle body where longest up to 2.5 times the width of median segments, shortest one-half this width (both estimates excluding parapodia). Ventral cirri of anterior segments digitiform (Fig. 1.20B), not extending beyond parapodial lobes, decreasing to about one-half the length of median, posterior parapodia.

Pygidium with 1 pair of anal cirri, each long, smooth; median digitiform cirrus short.

Remarks. *Pionosyllis articulata* is characterized by the presence of superior compound falcigers with extremely long spiniger-like blades in all setigers; change in shape of falcigers after setiger 19; prostomial antennae distally articulated; dorsal cirri that alternate long and short; acicula increasing in numbers in posterior parapodia; presence of simple superior and inferior setae; and setigers 1-9 apparently shorter than those following. Although the small paired eyespots are usually present on the anterior prostomium, they apparently can occur nearly anywhere on the prostomium or be absent. For example, they may either be located next to the median antenna, or along the posterior prostomium, in addition to the usual location noted above.

Superior compound falcigers with extremely long blades are present in fascicles of *P. articulata*, *P. ehlersiaeformis* Augener, 1913, *P. weismannioides* Augener, 1913, *P. augeneri* Hartmann-Schröder, 1979, *P. longisetosa* Hartmann-Schröder, 1965, and *P. uraga* Imajima, 1966c. *Pionosyllis articulata* differs from these species in having antennae distinctly articulated distally rather than smooth or indistinctly wrinkled. *Pionosyllis articulata*, *P. longisetosa* and *P. uraga* differ from species listed above in having compound setae with long blades in all setigers; these setae are first present in median setigers of *P. ehlersiaeformis*, *P. weismannioides*, *P. augeneri*. Both *P. articulata* and *P. longisetosa* differ from *P. uraga* in that the long blades of compound setae are falcigerous and distally bidentate rather than spinigerous and distally tapered to fine points. *Pionosyllis articulata* differs from *P. longisetosa* in having long, thin, whip-like blades each 6-10 times longer than inferior setae in the same fascicles, rather than wide blades each around 3 times longer than inferior setae; spiniger-like blades with finely serrated cutting edges in contrast to ones with coarsely serrated cutting edges; blades with subdistal tooth well defined instead of being weakly defined; falcigers becoming stout in medial segments rather that being of uniform throughout; simple setae distally bidentate with serrated cutting surfaces instead of distally rounded and unidentate with smooth cutting surfaces; and having dorsal cirri alternating irregularly in length, rather than regularly. *Pionosyllis articulata* further differs from *P. uraga* in having blades of compound falcigers from median segments short, sharply bidentate, rather than butter knife-like and weakly bidentate; and having digitiform ventral cirri instead of foliaceous ones that are broadly attached to parapodial lobes.

The tips of long spiniger-like blades from compound falcigers must be examined using oil immersion. It may be possible to subdivide *Pionosyllis* into a subgenus of species all having long spiniger-like compound setae similar to the way *Ehlersia* has functionally been separated from *Typosyllis* (Uschakov, 1955; Day, 1967; Banse and Hobson, 1974; Uebelacker, 1984; Dorsey and Phillips, 1987). Although such an investigation falls well outside the scope of the present study, it is likely to be both interesting and productive.

Habitat. Soft bottoms and rocky substrata, in depths of 60-205 m.

Etymology. The species name, *articulata*, refers to the characteristic distal articulations of the prostomial antennae, and dorsal cirri of setiger 1.

Distribution. Southern to central California.

Genus *Syllides* Örsted, 1845

Type species: *Syllides longocirrata* Örsted, 1845

Diagnosis. Prostomium with 3 antennae. Tentacular segment frequently collar like and ciliated. Two pairs of tentacular cirri. Some dorsal cirri usually articulated. Setae and aciculae of anterior segments not enlarged. Pharynx usually unarmed, with smooth anterior marginal rim.

Remarks. Banse (1971) reviewed the genus, and provided descriptions, illustrations and a key. The key below includes both *Syllides japonica* Imajima, 1966c, and *S. longocirrata*, which have been reported from Washington and British Columbia (Banse and Hobson, 1974).

Key to Known Species of *Syllides* from the Northeast Pacific

1A. Two kinds of dorsal simple setae present: thick with bent tips in setigers 1-5; thin and distally tapering from setiger 6 to end of body .... *Syllides longocirrata*

1B. One kind of dorsal simple seta present in all segments (Figs. 1.21D, 1.22R,S) 2

2A. Dorsal cirri with bright, reflective golden yellow pigment in most articles; 20 or fewer articles per dorsal cirrus (Figs. 1.21C, 1.22D-G) 3

2B. Dorsal cirri lack reflective pigment; 20-30 articles per dorsal cirrus .... *Syllides japonica*

3A. Dorsal cirri with 15-20 spherical articles (Fig. 1.21A,C); median antenna shorter than lateral antennae (Fig. 1.21A); integument with epidermal papillae (Fig. 1.21A); compound and dorsal simple setae lack distal hoods; dorsal simple setae capillary tipped (Fig. 1.21D) .... *Syllides reishi*

3B. Dorsal cirri with 5-8 tear drop-shaped articles (Fig. 1.22D-G); median antenna longer than lateral antennae (Fig. 1.22A); integument lacking papillae; compound and dorsal simple setae enshrouded by distal hoods (Fig. 1.22R-T); dorsal simple setae distally blunt (Fig. 1.22R-T) .... *Syllides mikeli*

Syllides reishi Dorsey, 1978

Figure 1.21

Syllides reishi Dorsey, 1978:24-26, figs. 1d, 2 a-f.

Material Examined. California: Santa Maria Basin, Sta. BRA-13 rock (1, USNM 170934); off El Morro, Sta. 6 rocks (1).—San Clemente Island, holotype (LACM-AHF Poly 1255) and paratypes (9, LACM-AHF Poly 1256).

Description. Length 2 mm, 0.4 mm wide excluding parapodia, for 30 setigers (Dorsey, 1978). Body golden brown in life, epidermal papillae dark brown. Epidermal papillae small, irregularly shaped, multilobate, abundant on dorsum, becoming numerous on ventrum, infrequent on prostomium, palps, parapodia; absent from intersegmental regions. Articles of dorsal cirri contain golden yellow pigment (Fig. 1.21C).

Prostomium wider than long with pharynx inverted (Fig. 1.21A), pentagonal when everted (Fig. 1.21B); 2 pairs of eyes, lenticulate, subequal in size, anterior pair set farthest apart, all arranged trapezoidally; additional pair of eyespots present on anterior prostomium margin (Fig. 1.21A,B). Antennae smooth to wrinkled; median antenna arising between posterior pair of eyes, up to 1.5 times longer than prostomium; lateral antennae arising in front of and medial to anterior pair of eyes, each 3 times longer than prostomium, two times longer than median antenna (Fig. 1.21A,B). Pharynx extending to setiger 3, unarmed; lacking distal circlet of soft terminal papillae when everted. Proventriculus extending through setigers 4-7 when pharynx inverted.

Tentacular segment distinct dorsally (Fig. 1.21A). Tentacular cirri cirriform, wrinkled, 2 pairs; dorsal pair 1.2 times longer than lateral antennae, nearly 3 times longer than prostomium; ventral pair about as long as dorsal pair.

Parapodia short, conical (Fig. 1.21C). Compound setae bidentate falcigers (Fig. 1.21D,E), 8-9 in anterior fascicles, decreasing to 2-5 in posterior fascicles. Blades longest superiorly, 2 times longer than inferior blades within fascicles, gradually decreasing posteriorly along body; all with minutely serrated cutting edges (Fig. 1.21D). Dorsal simple seta with capillary tip, present from setiger 1, with serrated cutting surface (Fig. 1.21F). Aciculae with distally enlarged tips, 1 per parapodium (Fig. 1.21G).

Dorsal cirri of setiger 1 inflated, wrinkled; strongly articulated from setiger 2 to end of body, with 15-20 articles anteriorly, decreasing to about 10 articles posteriorly. Articles each with 1-2 vesicles, variably present, containing golden-yellow granules (Fig. 1.21C). Ventral cirri digitiform, as long as or longer than parapodial lobes, also containing golden-yellow granules.

Pygidium with paired anal cirri plus median unpaired ventral cirrus; all spherical, equal in size.

Remarks. *Syllides reishi* is a well defined species originally described from San Clemente Island, that seems to be present only in rocky habitats along southern California. Refer to the discussion of *S. mikeli* below for additional comments concerning *S. reishi.*

Distribution. Southern and central California.

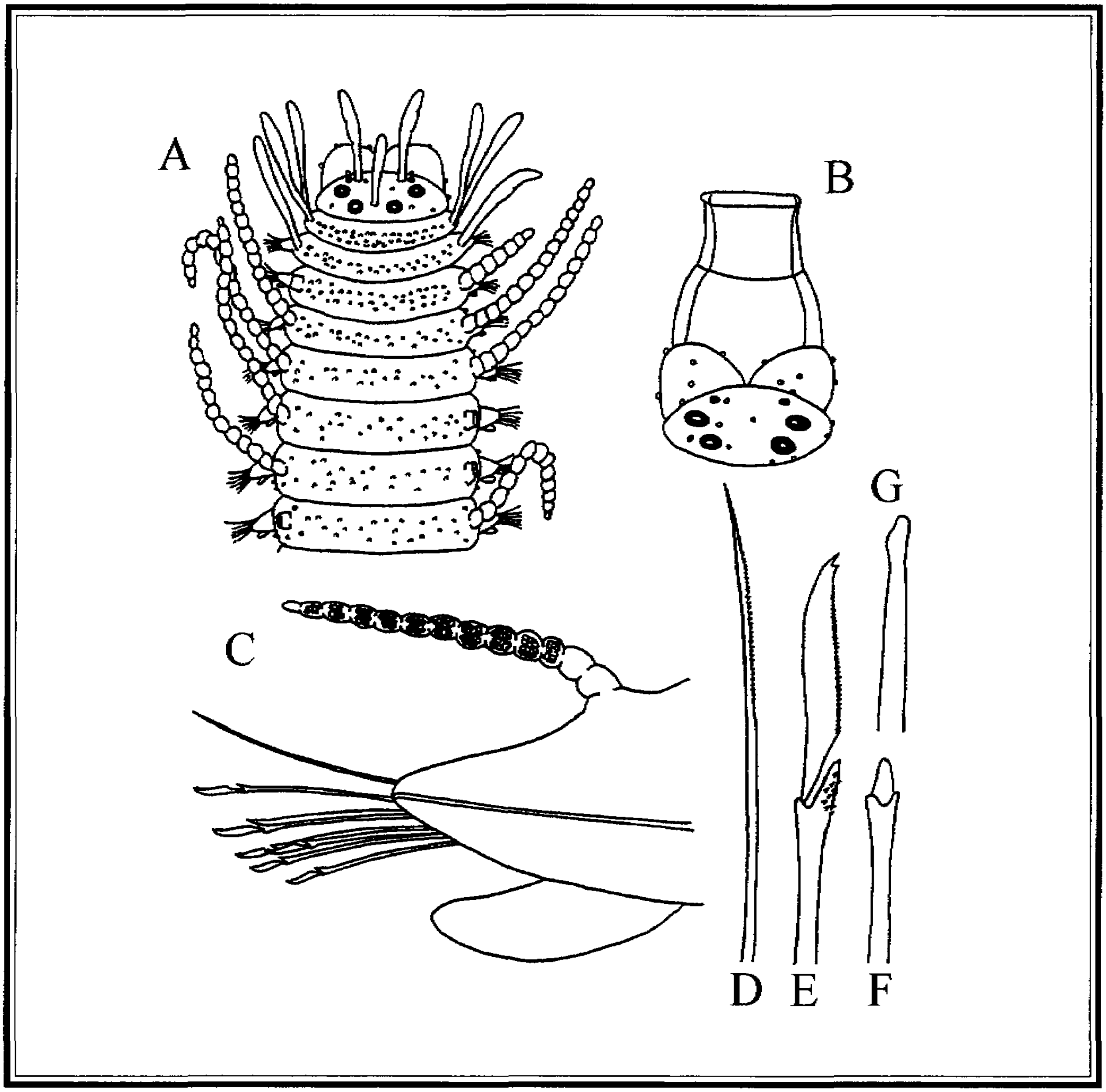

Figure 1.21. *Syllides reishi*: A, anterior end, dorsal view; B, prostomium and everted pharynx, dorsal view; C, parapodium 16, posterior view; D, dorsal simple seta, parapodium 10; E, compound falciger, parapodium 10; F, shaft end of compound falciger, ventral view; G, acicula, parapodium 10. (A-G, redrawn from J. Dorsey, 1978)

Syllides mikeli Kudenov and Harris, new species

Figure 1.22

Material Examined. California: Santa Maria Basin, off Point Sal, Stas. PJ-1, 1 paratype (SBMNH 142662) + (1); PJ-2 (1); PJ-3 (1); PJ-7, holotype (USNM 170931), 1 paratype (USNM 170932), 4 paratypes (LACM-AHF Poly 1676); PJ-8, 1 paratype (LACM-AHF Poly 1677); PJ-10, 1 paratype (AM W. 22195) + (2); PJ-16, 3 paratypes (USNM 170933).

Description. Holotype complete, 1.4 mm long, 0.2 mm wide excluding parapodia, 0.3 mm wide with parapodia, for 26 setigers. Body excluding dorsal cirri white in preserved specimens; articles of dorsal cirri with golden-brown pigment granules in transmitted light, yellow-brown in reflected light. Epidermal papillae absent. Each segment with a dorsal transverse row of cilia.

Prostomium wider than long with pharynx inverted; pentagonal when everted; 3 pairs of eyes, lenticulate, middle pair largest and set farthest apart, posterior 2 pairs arranged trapezoidally; anterior pair associated with lateral antennae (Fig. 1.22A,B). Antennae smooth to wrinkled; median antenna arising between posterior pair of eyes, up to 2 times longer than prostomium; lateral antennae arising in front of and medial to anteriormost pair of lenticulate eyes, each 1.5 times longer than prostomium, two-thirds length of median antenna (Fig. 1.22A). Pharynx extending to junction of setigers 3-4 or through setiger 4, unarmed (Fig. 1.22A); subdistal circlet of 10 soft terminal papillae (Fig. 1.22C), uni- to trilobed when pharynx everted, shape apparently associated with extent of pharyngeal eversion. Proventriculus extending through setigers 4 to 7-8 when pharynx inverted (Fig. 1.22A), from junction of setigers 1-2 through setiger 6 when pharynx everted, with about 46 rows of small muscle cells.

Tentacular segment distinct dorsally, glandular, with anterior margin conspicuously ciliated (Fig. 1.22A,B). Tentacular cirri cirriform, wrinkled to smooth, 2 pairs; dorsal pair about as long as lateral antennae; ventral pair about one-half length of dorsal cirri (Fig. 1.22A,B).

Parapodia narrow, conical (Fig. 1.22D-G). Compound setae bidentate falcigers with minutely serrated cutting edges and hoods covering both cutting edges and distal tips (Fig. 1.22H-Q); hoods well-developed in setae of anterior fascicles. Setae number 10 per fascicle each in setigers 1-2, increasing to 12-14 each in setigers 5-6, decreasing to 8-9 to end of body. Superior blades of anterior setigers narrow, longest, distally twisted (Fig. 1.22H,I,K), 2 times longer than inferior blades within anterior fascicles (Fig. 1.22J,L), gradually decreasing posteriorly along body (Fig. 1.22P,Q); 1-2 per fascicle in setiger 1; 2-3 in setiger 2; 3 in setigers 5-6; 2 from setiger 7 to end of body. Dorsal superior simple seta slender, capillary, present from setiger 1 with minute denticles of long serrated cutting surface covered by long hood (Fig. 1.22R,S), terminating in bubble-shaped capsule around unidentate tip posteriorly (Fig. 1.22T). Ventral inferior simple seta long, capillary, lacking distal hood, present in last few posterior parapodia (Fig. 1.22U). Aciculae distally blunt anteriorly (Fig. 1.22V), with distal knobs posteriorly (Fig. 1.22W), 1 per parapodium.

Dorsal cirri of setigers 1-2 cirriform (Fig. 1.22A), wrinkled to smooth, strongly articulated thereafter to end of body, articles tear drop-shaped, increasing in length to setigers 3-6 (Fig. 1.22D), decreasing gradually thereafter to end of body. Dorsal articles of setiger 3 (= 5); setiger 4 (= 5-6); setiger 5 (= 5-8); setiger 7 (= 4-6); setiger 9 (= 5-6); setiger 19 (= 4-5); each with 1-2 vesicles containing reflective golden-yellow pigment. Ventral cirri digitiform, extending almost to but not beyond end of parapodial lobes (Fig. 1.22D-G).

Pygidium with paired anal cirri plus median unpaired ventral cirrus.

Remarks. *Syllides mikeli*, *S. reishi*, *S. japonica* Imajima, 1966c, and *S. longocirrata* Örsted, 1845 *sensu* Banse (1971) are reported from the western coast of North America. *Syllides mikeli* is superficially similar to *S. reishi* in that both have golden-yellow pigment granules in the articles of the dorsal cirri. *Syllides mikeli* differs from *S. reishi* in having a long median and short lateral antennae rather than a short median antenna and longer laterals; lacking epidermal papillae; having both compound falcigers and dorsal simple

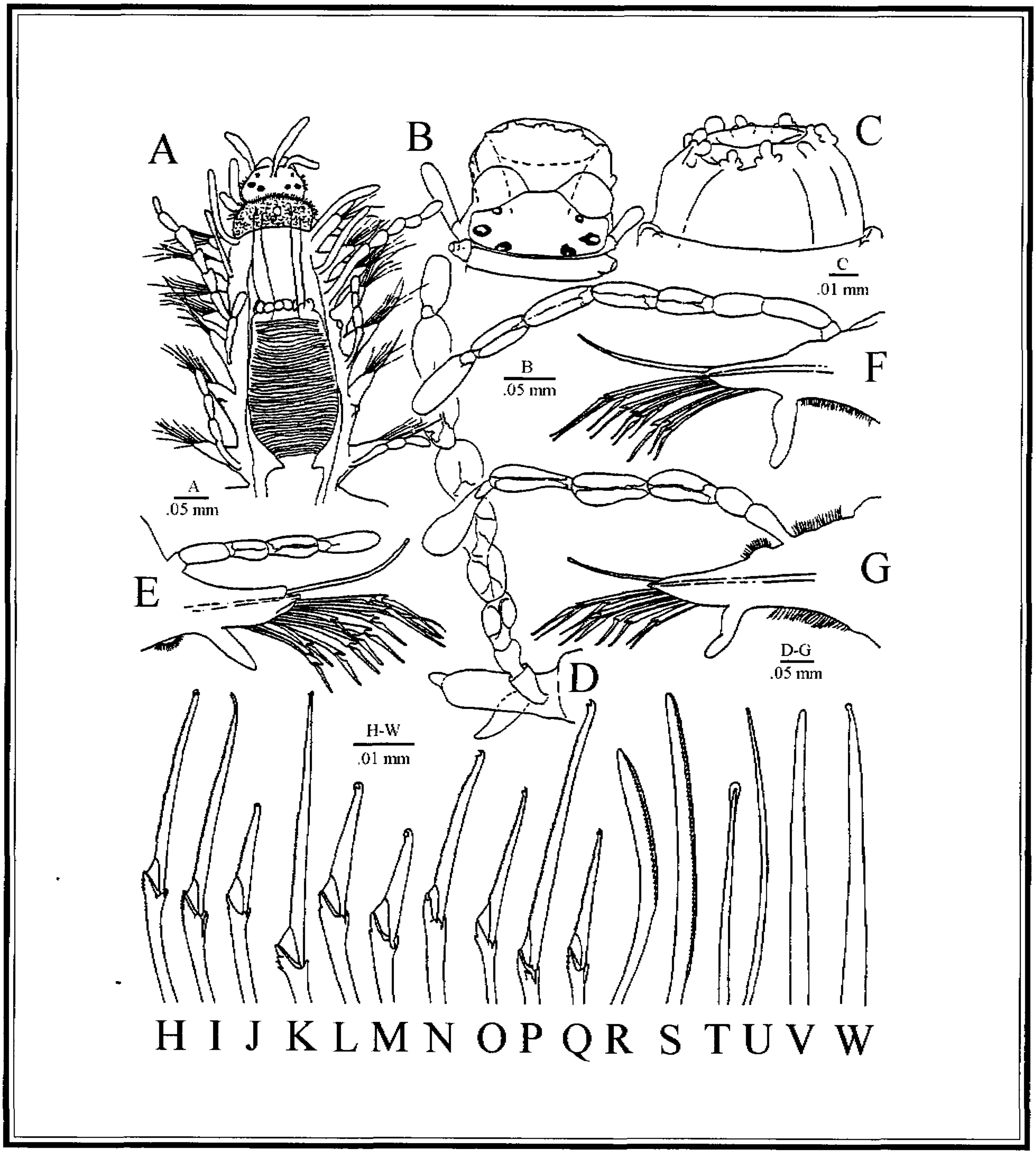

Figure 1.22. ***Syllides mikeli*** **Kudenov and Harris, new species**: A, anterior end, dorsal view; B, prostomium and pharynx everted, dorsal view; C, pharynx, dorsal view; D, left parapodium, setiger 5, dorsal view; E, left parapodium, setiger 7, anterior view; F, right parapodium, setiger 9, anterior view; G, right parapodium, setiger 19, anterior view; H-J, compound falcigers from setiger 1; H-I, superior setae; J, inferior seta; K-M, compound falcigers from setiger 3: K, superior seta; L, intermediate seta; M, inferior seta; N-O, inferior compound falcigers, setiger 6; P-Q, compound falciger from setiger 20; P, superior seta; Q, inferior seta; R-T, dorsal simple setae: R, setiger 1; S, setiger 16; T, setiger 20 with distal hood, dorsal view; U, ventral simple seta, setiger, far posterior segment; V-W, aciculae: V, setiger 2; W, setiger 19. (A-W, originals by JDK)

setae with distal hoods; and in having dorsal cirri with tear drop-shaped rather than spherical articles, and these numbering 5-8 per dorsal cirrus instead of 15-20. *Syllides mikeli* is characteristically associated with soft bottom habitats, in contrast to *S. reishi* which is associated with rocky substrata. *Syllides mikeli* differs from *S. japonica* in lacking 3-4 coarse basal serratia on the blades of superior compound falcigers; in having 5-8 tear drop-shaped instead of 20-30 spherical articles per dorsal cirrus; and in having digitiform rather than ellipsoidal ventral cirri. *Syllides mikeli* differs from *S. longocirrata* as described by Banse (1971) in having a single kind of dorsal superior simple seta instead of two kinds including a thick, stout and distally blunt form in setigers 1-5; in having bidentate rather than unidentate compound setae; and in lacking basal spurs on the blades of superior compound falcigers.

We suspect the five specimens described by Banse (1971) as *S. japonica* represent an undescribed species. For example, the blades of superior compound falcigers of Banse's specimens are five times the length of inferior blades within fascicles rather than two times as reported by Imajima (1966c); the number of setae per fascicle number 10-20 rather than 5-12; the proventriculus extends through 6 segments and not 4-5; and that number of articles in dorsal cirri number 10-20 instead of 20-30. Banse's materials need to be re-examined with these differences in mind.

Etymology. This species is named for Tim Mikel, ABC Laboratories, Ventura, California, in appreciation of his friendship to the first author.

Distribution. Central California.

Subfamily Syllinae

Genus *Ehlersia* Quatrefages, 1865

Type species: *Syllis sexoculata* Ehlers, 1864

Diagnosis. Prostomium with 3 antennae. Two pairs of tentacular cirri. Antennae, tentacular cirri and dorsal cirri of anterior segments articulated. Pharynx with subdistal middorsal tooth and smooth anterior marginal rim. Compound setae falcigerous, with superior blades spiniger-like in appearance, at least 4 times longer than inferior blades within fascicles of median and posterior parapodia. Two simple setae per median and posterior setal fascicles.

Remarks. Compound setae with extremely long blades invariably have blunt unidentate, knobbed or minutely bidentate tips, are present in the superiormost region of fascicles, and are most appropriately described as compound falcigers. Previous reports of compound spinigers tend to refer to these setae (Uebelacker, 1984; Dorsey and Phillips, 1987).

Dorsey and Phillips (1987) note that *Ehlersia* and *Typosyllis* differ primarily in the respective presence or absence of falcigers with long blades, and this trait has been used by other workers (Imajima, 1966e; Gardiner, 1976; Ben-Eliahu, 1977; Fauchald, 1977). Banse and Hobson (1974) first used blade ratios (4.0) within fascicles to separate species of these genera, as do Dorsey and Phillips (1987); Uebelacker (1984) uses a higher ratio (5.0). Preliminary morphometric data provided by Dorsey and Phillips (1987:155, 159) seem to support the use of setal ratios, although it is not possible to assess their data with regard to body size. A more rigorous multivariate analysis of setal variation in both of these taxa may substantiate the validity of this approach (see Vogt and Kudenov, 1994).

Key to the MMS Species of *Ehlersia* from the Northeast Pacific

1A. Prostomium with 3 pairs of eyes (Fig. 1.23A); blades of superior compound falcigers from midbody segments 4 times longer than inferior blades within fascicles (Fig. 1.23G,E); proventriculus in 6-9 segments with 30-36 rows of muscle cells .... *Ehlersia heterochaeta*

1B. Prostomium without eyes (Fig. 1.24A,C); blades of superior compound falcigers from midbody segments 10 times longer than inferior blades within fascicles (Fig. 1.24G,H); proventriculus in 4-7 segments with 40-43 rows of muscle cells .... *Ehlersia hyperioni*

Ehlersia heterochaeta (Moore, 1909)

Figure 1.23

Syllis (Ehlersia) heterochaeta Moore, 1909:322-325, pl. 15, figs. 1-5.—Treadwell, 1914:176.—Rioja, 1941:694-695.—Berkeley and Berkeley, 1948:76, fig. 113.—Banse and Hobson, 1974:62, fig. 16 k-l.—Dorsey and Phillips, 1987:153-156, fig. 1 a-h.
Syllis heterochaeta Moore, 1923:256.
Ehlersia heterochaeta: Hartman and Barnard, 1958:21, 55.
Langerhansia heterochaeta: Hartman and Barnard, 1960:90, 276.—Hartman, 1963:17; 1968:435-434, figs. 1-7.
Syllis (Ehlersia) cornuta: Pettibone, 1954:253, fig. 28f (in part). *Not* Rathke, 1843.
Syllis cornuta: Pettibone, 1963:118, figs. 31i,j (in part). *Not* Rathke, 1843.

Material Examined. California: Santa Maria Basin, Sta. BRA-16 rock (1, USNM 170935); off Point Buchon, Sta. 12 (1, SBMNH 142702); off Point Sal, Sta. 30 (2); off Purisima Point, Sta. 42 (1; USNM 98785); Santa Maria Basin, Sta. 52 (1); off Point Arguello, Stas. 64 (1); Sta. 72 (1; USNM 98784); off Point Sal, Stas. R-8 (4, USNM 170936); PJ-1 (1); PJ-2 (2); PJ-3 (2); PJ-6 (7); PJ-7 (5); PJ-8 (5); PJ-10 (2); J-11 (2).—San Nicolas Island, holotype (USNM 17400).

Description of Atoke. Length about 30 mm, 2 mm wide, for 80 segments (Moore, 1909; Dorsey and Phillips, 1987); MMS specimens 12 mm long, 0.6 mm wide without setae, for 110 segments. Large black pigment patch on posterior prostomium sometimes absent.

Prostomium pentagonal, wider than long; 3 pairs of eyes, middle pair largest, posterior pair lenticulate, all in trapezoidal arrangement; additional pair of eyes present as pigment specks on anterior margin (Fig. 1.23B,C). Antennae strongly articulated; median antenna long, with 13-26 articles, arising between 2 posterior pairs of eyes; lateral antennae arising from anterior prostomium margin, in front of, slightly medial to largest pair of eyes, each with 10-17 articles (Fig. 1.23B,C). Palps large, triangular, distally round, not fused basally. Everted pharynx with anterior unpaired tooth, surrounded by distal circlet of 10 soft papillae when everted. Proventriculus present in 6-9 setigers, with 30-36 rows of muscle cells.

Tentacular segment dorsally distinct from prostomium and setiger 1; 2 pairs of tentacular cirri with numerous articles, resembling antennae; dorsal pair each with 17-21 articles; ventral pair each with 9-12 articles (Fig. 1.23B,C).

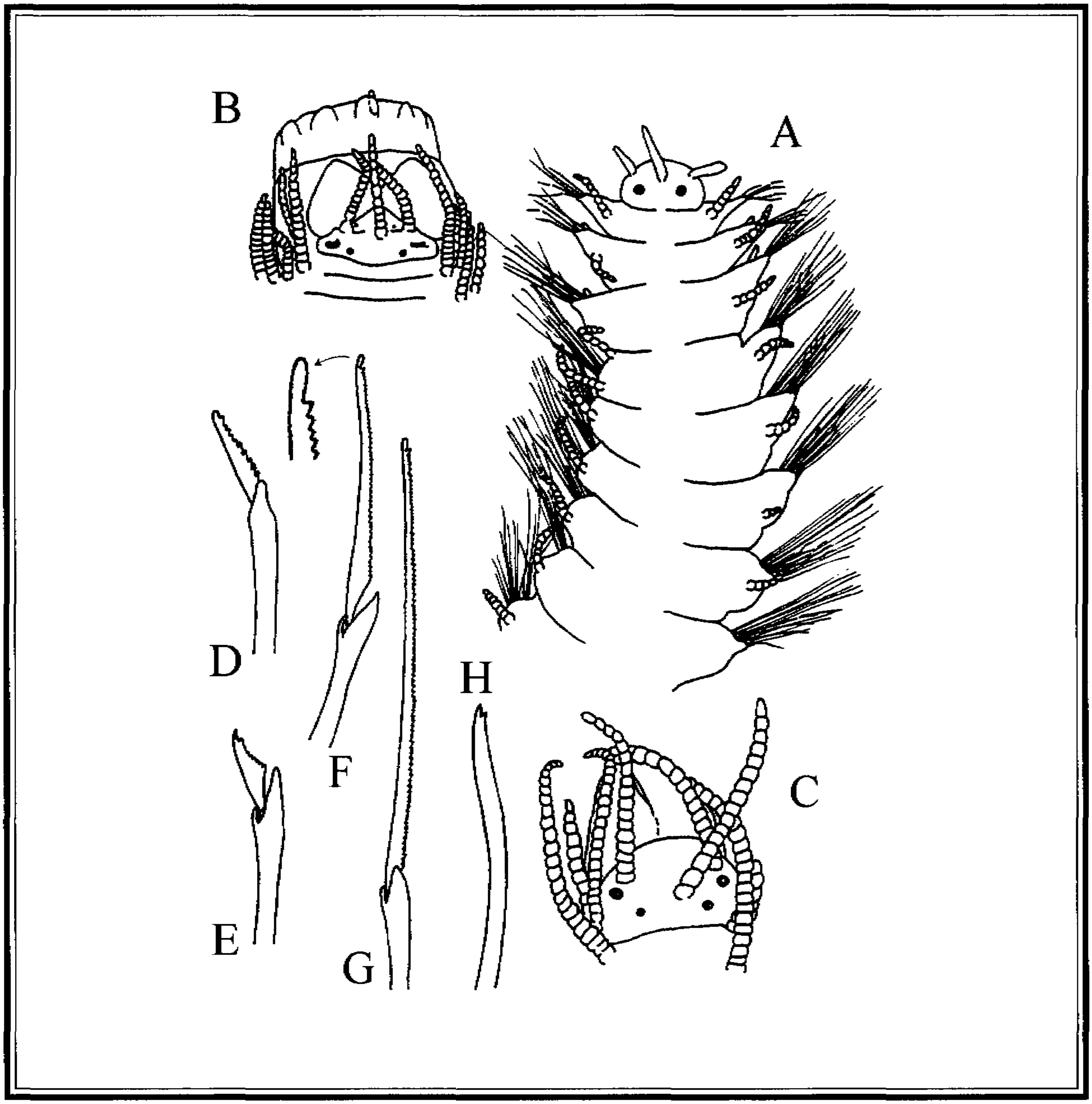

Figure 1.23. *Ehlersia heterochaeta*: A, anterior end, male epitoke, dorsal view; B, anterior end, atoke, dorsal view; C, anterior end, atoke, dorsal view; D, inferior compound falciger, anterior segment; E, inferior compound falciger, posterior segment; F, superior compound falciger, anterior segment, with detail of tip; G, superior compound falciger, posterior setiger; H, ventral simple seta, posterior setiger. (A-H, after Dorsey and Phillips, 1987).

Parapodia distally rounded. Compound setae bidentate falcigers (Fig. 1.23D-G), with 10-16 to 21-28 setae per anterior fascicle, decreasing to 6-7 per posterior fascicle. Blades decreasing in length inferiorly within fascicles. Superiormost falcigers with longest blades 3-4 times length of inferiormost blades within fascicles, numbering 3-4 per anterior fascicle decreasing to 2 per posterior fascicle, each with subterminal tooth round, poorly defined and finely denticulate cutting edges (Fig. 1.23F,G); middle, inferior blades short, sharply bidentate, with cutting edges coarsely serrated (Fig. 1.23D,E). Dorsal simple seta distally unidentate, present in median segments to end of body. Ventral simple seta distally bidentate, present in last few posterior segments (Fig. 1.23H). Five to 7 aciculae per anterior parapodium, decreasing to 1-2 per posterior parapodium.

Description of Epitoke. Male epitoke 8.7 mm long, 0.8 mm wide including parapodia (Dorsey and Phillips, 1987). Prostomium oval; 1 pair of eyes, lenticulate; antennae smooth with median antenna arising anterior to eyes, about two times longer than lateral antennae, which arise anterolaterally from prostomial border (Fig. 1.23A). Parapodial lobes conical. Compound falcigers distally bidentate, resembling those described for atokous form; 4-7 per fascicle including 1-2 superior setae with long blades 3-4 times length of inferior ones, latter with short blades strongly bidentate. Cutting edges of superior blades finely serrated; inferior blades coarsely serrated. One acicula per parapodium, thick, distally pointed, yellow. Long capillary swimming setae from setiger 3. Dorsal cirri articulated, long cirri with up to 11 articles alternating with short cirri with up to 8 articles. Ventral cirri digitiform, not extending to ends of parapodial lobes. Pygidium with paired anal cirri, each with 21 articles; ventromedian cirrus digitiform.

Remarks. *Ehlersia heterochaeta* is widely distributed along the Pacific coast of North America where it commonly inhabits mixed sediments. Dorsey and Phillips (1987:153) state that the holotype of *E. heterochaeta* is missing and established a neotype (ANSP 3328). In actuality, the holotype is at the National Museum of Natural History, Smithsonian Institution (USNM 17400; Loi, 1980). *Ehlersia heterochaeta* is also discussed below in the remarks for *E. hyperioni* (Dorsey and Phillips).

Habitat. Mixed sediments in shelf and canyon depths, 15-409 m.

Distribution. Western Mexico to Western Canada.

Ehlersia hyperioni (Dorsey and Phillips, 1987)

Figure 1.24

Syllis (Ehlersia) hyperioni Dorsey and Phillips, 1987:156-159, fig. 2 a-c, fig. 3 a-k.

Material Examined. California: western Santa Barbara Channel, Sta. 46 (1, USNM 000000); east of Point Conception, Sta. 94 (1, SBMNH 142904).—Santa Monica Bay, holotype (LACM-AHF Poly 1436); 3 paratypes (LACM-AHF Poly 1437-1439).

Description. Length up to 21.6 mm, 0.4 mm wide including parapodia at level of proventriculus, for 122 setigers (Dorsey and Phillips, 1987); MMS specimens anterior fragments, up to 3 mm long, 0.3 mm wide excluding parapodia and setae, for up to 22 setigers. Body long, threadlike; tan in color, occasionally with specks of dark pigment in dorsal cirri of anterior and median segments, parapodia, ventral cirri; pharynx orange-brown.

Prostomium wider than long, anterior margin with palps indistinct; eyes absent (Fig. 1.24A-C). Antennae with short ceratophores; median antenna arising from middle of prostomium, with up to 26 articles; lateral antennae two-thirds length of median, with 11-13 articles (Fig. 1.24A-C). Palps long, twice length of prostomium, fused basally (Fig. 1.24A,B). Retracted pharynx extending to setiger 13, with anterior middorsal tooth; surrounded by distal circlet of 10 soft papillae when everted (Fig. 1.24C). Proventriculus extending

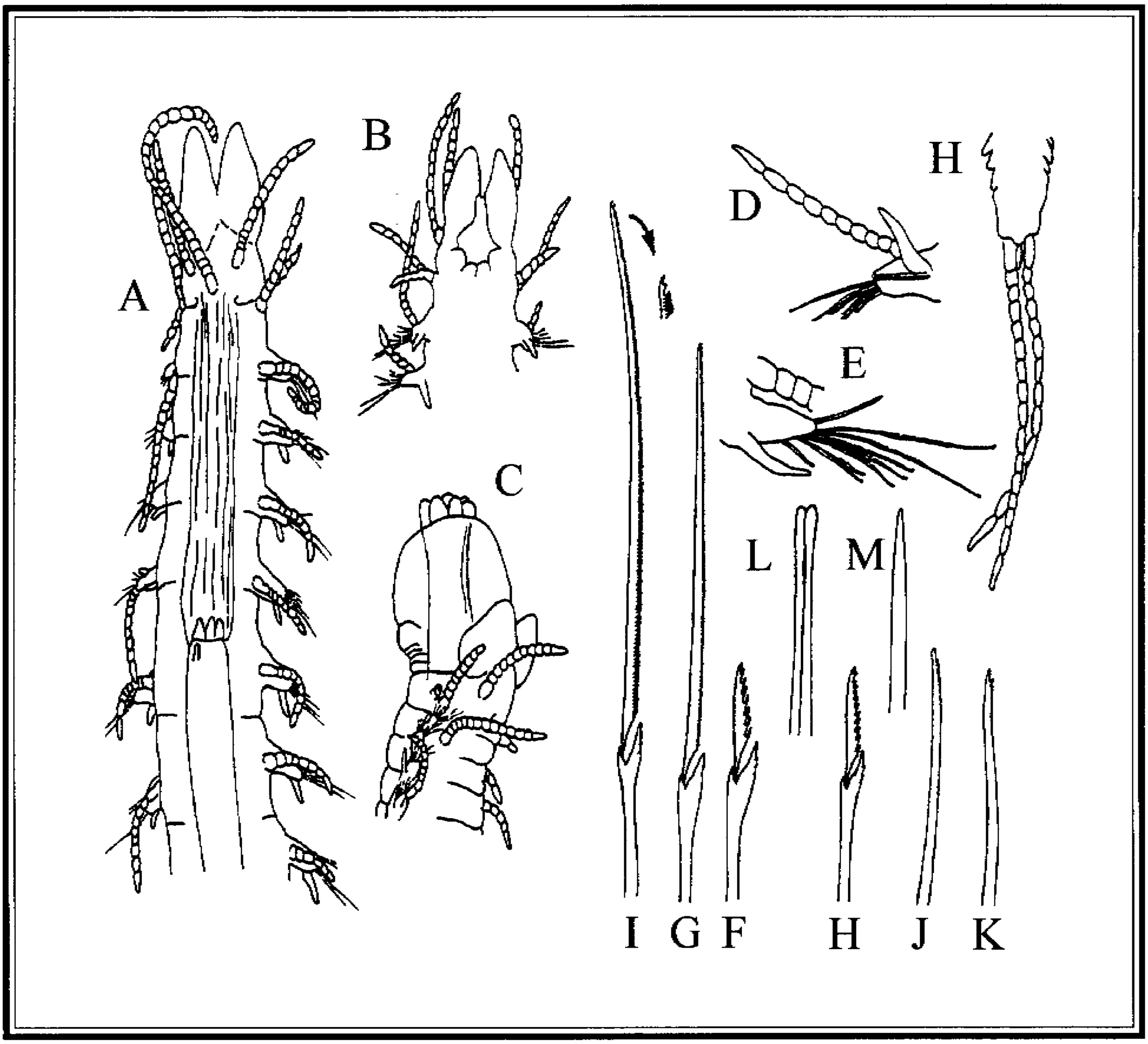

Figure 1.24. *Ehlersia hyperioni*: A, anterior end, holotype, dorsal view; B, anterior end, holotype, ventral view; C, anterior end, lateral view; D, left parapodium, setiger 9, posterior view; E, right parapodium, setiger 78, posterior view; F, inferior compound falciger, anterior setiger; G, superior compound falciger, posterior setiger; H, inferior compound falciger, posterior setiger; I, superior compound falciger, posterior setiger, with detail of tip not to scale; J, dorsal simple seta, posterior setiger; K, ventral simple seta, posterior setiger; L, paired aciculae, anterior setiger; M, acicula, posterior setiger; N, pygidium, holotype, dorsal view. (A-N, modified from Dorsey and Phillips, 1987)

through setigers 10-16 when pharynx inverted, 13 segments long when everted; 40-43 rows of muscle cells.

Tentacular segment distinct from prostomium, not fused to setiger 1; 2 pairs of cirri, with short cirrophores, dorsal pair longest, each with 7-15 articles; ventral pair each with 4-9 articles (Fig. 1.24A-C).

Anterior setigers 1.5 times wider than long (Fig. 1.24A). Anterior parapodial lobes conical, distally blunt, with small pre- and postsetal lobes, gradually becoming longer posteriorly (Fig. 1.24D,E). Compound falcigers distally bidentate (Fig. 1.24F-I), 8-11 per anterior fascicle, decreasing to 5-7 per posterior fascicle. Blades decreasing markedly in length inferiorly within fascicles. Superiormost blades 2-3 per fascicle, increasing in length posteriorly along body, each 6-8.5 times longer than inferior blades, with finely denticulate cutting edges (Fig. 1.24G,I); inferior blades with cutting edges more coarsely serrated (Fig. 1.24F,H). Dorsal simple seta from middle setigers to end of body, unidentate, with coarsely serrated cutting surfaces (Fig. 1.24J). Ventral simple seta in posterior setigers, sigmoid, distally bidentate, with finely serrated cutting surface (Fig. 1.24K). Two aciculae per anterior parapodium, each distally blunt, sometimes dark (Fig. 1.24L), decreasing to 1 per posterior parapodium, stouter with pointed tips (Fig. 1.24M).

Dorsal cirri longest anteriorly, gradually decreasing posteriorly, not alternating in length, with short cirriphores; anterior cirri with 7-13 articles, middle and posterior cirri with 7-9 articles. Ventral cirri digitiform, short anteriorly, becoming longer posteriorly, extending just to end of parapodial lobes.

Pygidium with paired anal cirri, each with basal cirrophores and up to 18 articles; midventral unpaired papilla digitiform (Fig. 1.24N).

Remarks. *Ehlersia hyperioni* and *E. heterochaeta* are sympatric. *Ehlersia hyperioni* differs from *E. heterochaeta* in lacking eyes, and in having superior blades of compound falcigers from middle body segments up to 10 times longer than inferiormost blades of the same fascicle in contrast to four times longer in the same body region. Dorsey and Phillips (1987) provide morphometric data describing blades of compound setae for both of these species.

Habitat. In mixed to fine sediments on the continental shelf, 12-146 m.

Distribution. Southern California to Washington.

Genus *Eurysyllis* Ehlers, 1864

Type species: *Eurysyllis tuberculata* Ehlers, 1864

Diagnosis. Body short, flattened. Prostomium with 3 globular antennae. Palps globular, not fused basally. Two pairs of globular tentacular cirri. Pharynx with a trepan of 10 teeth and a middorsal tooth. Dorsal cirri globular. Dorsum covered with longitudinal rows of globular papillae.

Remarks. Hartman (1965:28) assigned *Eurysyllis,* without comment or subsequent discussion, to her new subfamily Eurysyllinae, from the Syllinae. The genus has also been associated with the Exogoninae. Hartmann-Schröder (1971) noted Hartman's subfamily and that *Eurysyllis* differs from Exogoninae species in palp morphology and pharyngeal armature, although its reproduction is more characteristic of the Syllinae. Garwood (1991) synonymized the Eurysyllinae with the Syllinae, formally transferring *Eurysyllis* to the Syllinae primarily on the basis of reproductive similarities. Garwood's revision is followed here.

Eurysyllis spicum Kudenov and Harris, new species

Figure 1.25

Material Examined. California: Santa Maria Basin, off Purisima Point, Stas. BRA-20, paratype (SBMNH 142655); BRC-13, holotype (USNM 170901); between Point San Luis and Point Sal, Sta. BRA-25, paratype (USNM 170902).—Western Santa Barbara Channel, off Point Conception, Sta. BRA-2, paratype (LACM-AHF Poly 1660).

Description. Holotype 2.2 mm long, 0.4 mm wide, without parapodia, 0.6 mm wide with parapodia, for 49 setigers; paratypes with 56-66 setigers. Body ribbon-like, dorsum slightly arched in cross section, ventrum flat; pigmentation absent in preserved specimens. Integument encrusted with fine sediment; thin, delicate, transparent, internal septa visible. Golden-brown granules in antennae, cirri and papillae of freshly preserved specimens (Fig. 1.25A). Sexual reproduction by stolons, beginning on setiger 40; sperm fill all but last 2-3 segments in males.

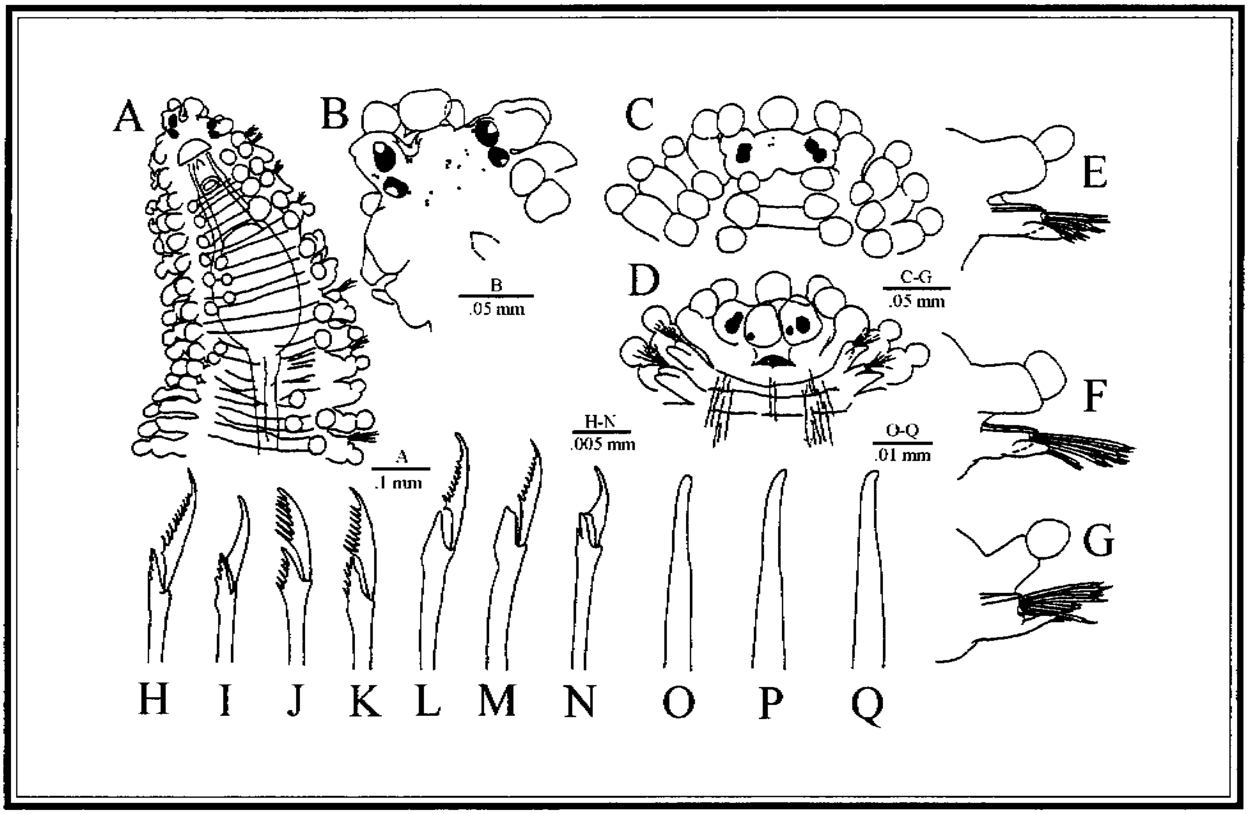

Figure 1.25. ***Eurysyllis spicum* Kudenov and Harris, new species:** A, anterior segments, dorsal view (SBMNH); B, prostomium, dorsal view (SBMNH); C, anterior segments, dorsal view (Sta. BRC-13); D, anterior segments, ventral view (Sta. BRC-13); E, right parapodium, setiger 11, posterior view; F, right parapodium, setiger 25, posterior view; G, right parapodium, setiger 50, posterior view; H, superior compound falciger, setiger 11; I, inferior compound falciger, setiger 11; J-K, superior compound falcigers, setiger 25; L-M, superior compound falcigers, setiger 50; N, inferior compound falciger, setiger 50; O, acicula, setiger 11; P, acicula, setiger 25; Q, acicula, setiger 50. (A-Q, originals by JDK)

Prostomium subrectangular, with large round lateral lobes, anterior middorsal region elevated; 3 pairs of eyes; 2 pairs large, lenticulate, in trapezoidal arrangement, plus additional ventral pair posterior to palps; numerous additional eye spots dispersed over prostomium (Fig. 1.25A-D). Antennae spherical, papilliform; median antenna arising from anterofrontal swelling; lateral antennae arising from anterolateral prostomial lobes (Fig. 1.25A-D). Palps spherical, papilliform, larger than antennae; basally free, projecting ventrally (Fig. 1.25D). Prostomium, antennae and tentacular cirri covered by thick cuticle; latter otherwise thin. Pharynx from setigers 2-3, extending to middle of setiger 7; middorsal tooth at anterior pharyngeal border (Fig. 1.25A); encompassed by distal circlet of 10 large, soft lobes when everted. Trepan of 10 small, sharply pointed, light-colored teeth. Proventriculus cylindrical, from middle of setiger 7 to 11, approximately 23 rows of muscle cells (Fig. 1.25A); attenuated extension lacking muscle cells in setiger 12.

Tentacular segment narrower than following segments; dorsal tentacular cirri spherical, slightly larger than either lateral antennae or following dorsal cirri; ventral pair one-half length of dorsal pair, attached ventrally, not visible from above (Fig. 1.25A-D).

Setigers 6-7 times wider than long (Fig. 1.25A). Parapodia small, distally rounded to conical anteriorly (Fig. 1.25E), becoming squared-off posteriorly (Fig. 1.25F,G). Setae generally compound falcigers with short unidentate blades (Fig. 1.25H-N); 18-20 per fascicle in anterior segments, decreasing to 13-15 posteriorly. Number of setae per fascicle increase with body size. Blades longest in anterior fascicles (Fig. 1.25H,I), decreasing in length both inferiorly within fascicles (Fig. 1.25H,I) and posteriorly along body, becoming more strongly curved posteriorly (Fig. 1.25J-N). Cutting edges of superiormost 5-8 blades of fascicles with long, fine teeth (Fig. 1.25J,K); remaining setae smooth (Fig. 1.25I,N). Shaft tips of superiormost 5-8 setae within fascicles finely denticulate (Fig. 1.25H-I); remainder normally smooth (Fig. 1.25L-N). One acicula per parapodium, stout with bent, blunt tip (Fig. 1.25O-Q). Ventral simple seta present in 8 or fewer posteriormost setigers.

Dorsal cirri with single distal papilliform article attached to stout cirrophores, extending beyond parapodial lobes (Fig. 1.25E-G). Ventral cirri conical anteriorly (Fig. 1.25E,F) to digitiform posteriorly (Fig. 1.25G), extending beyond parapodial lobes, especially in posterior segments.

Dorsum with 4, occasionally 5, large globular papillae per segment, forming 4 longitudinal rows; fifth papilla located next to cirrophore (Fig. 1.25A).

Pygidium with 2 anal cirri similar in form to dorsal cirri, larger, distally pointed; cirrophores conspicuously developed.

Remarks. Four species of *Eurysyllis* are presently recognized: *E. spicum*, *E. tuberculata* (Ehlers, 1864), *E. ehlersi* Benham, 1927, and *E. pacificus* (Hartman, 1954). *Eurysyllis spicum*, *E. tuberculata* and *E. pacificus* all have longitudinal rows of conspicuous dorsal papillae, and are here considered members of this genus. In contrast, *E. ehlersi* clearly lacks dorsal papillae based on Benham's description, and most likely should be transferred to *Plakosyllis* Hartmann-Schröder, 1956. This decision, however, will be deferred pending examination of Benham's type, and *E. ehlersi* will continue to be considered a congener of the other three species treated here.

Eurysyllis spicum differs from *E. tuberculata* in having aciculae distally blunt rather than mucronate, the pharynx present in four to five segments instead of two to three segments, the proventriculus with 23 rows of muscle cells present in four segments in contrast to 13-20 rows in three segments, ventral cirri conical to digitiform instead of auricular, and unidentate blades of compound falcigers within the same fascicles both serrated and smooth instead of all serrated. In this latter feature, *E. spicum* also differs from *E. pacificus* in which the unidentate blades are smooth, and more noticeably curved distally. Additional published information providing detailed descriptions of *E. pacificus* are apparently nonexistent, and efforts to locate Hartman's paratype (originally described as *Sphaerodorum pacificum*) in the LACM-AHF collections were unsuccessful. Lützen (1961) first recognized the aberrant nature of Hartman's species, and Laubier (1968) strongly suspected it was a species of *Eurysyllis*. More detailed comparisons between *E. spicum* and *E. pacificus* must await examination of the latter's holotype. *Eurysyllis spicum* differs from *E. ehlersi* in having the pharynx in four to five rather than six segments, the proventriculus in four instead of eight segments, blades of compound falcigers unidentate and not bidentate, and ventral cirri conical to digitiform rather than ovoid and projecting beyond parapodial lobes.

Finally, Hartman (unpublished) seems to have suspected that *Plakosyllis americana* Hartman, 1961, had longitudinal rows of papillae on the dorsum, and should be assigned to *Eurysyllis*. Re-examination of the *Plakosyllis americana* types (LACM-AHF Poly 0865, 0866) did not confirm this suspicion, although the dorsal papillae are rather easily detached during the examination of preserved specimens of *E. spicum*.

Etymology. The term, *spicum*, is *Latin* for "ear of grain," and refers to the kernel-like arrangement of large dorsal papillae.

Distribution. Southern and central California.

Genus *Geminosyllis* Imajima, 1966d

Type species: *Trypanosyllis (Trypanedenta) ohma* Imajima and Hartman, 1964

Diagnosis. Body subcylindrical. Prostomium with 3 antennae. Two pairs of tentacular cirri. Antennae, tentacular cirri and dorsal cirri slender, articulated. Pharynx with a trepan of 10 teeth with or without a single large middorsal tooth. All setae simple.

Geminosyllis ohma (Imajima and Hartman, 1964)

Figure 1.26

Trypanosyllis (Trypanedenta) ohma Imajima and Hartman, 1964:129-130, pl. 31, figs. a-d.
Syllis (Haplosyllis) spongicola: Uschakov, 1955:179, fig. 50, A.
Geminosyllis ohma: Imajima, 1966d:233-235, text-fig. 43, a-g.

Material Examined. California: Santa Maria Basin, between Point San Luis and Point Sal, Sta. BRA-25 (1); off Point Arguello, Sta. BRA-6 (1, SBMNH 142704).—Western Santa Barbara Channel, east of Point Conception, Sta. BRC-1 (6).—Japan: Shirikishinai, 20 July 1959, holotype (LACM-AHF Poly 0857).

Description. Length up to 32 mm, 2 mm wide including parapodia, with 82 setigers (Imajima and Hartman, 1964); MMS specimen (SBMNH) complete, 3.5 mm long, 0.2 mm wide excluding parapodia and setae, for 31 setigers. Body subcylindrical; preserved specimens lacking color patterns.

Prostomium pentagonal in outline, posterior margin entire, lacking median cleft; 2 pairs of eyes, anterior pair reniform, largest, farthest apart; posterior pair round (Fig. 1.26A,B). Median antenna inserted between posterior pair of eyes, with 30 annulations (18 in MMS specimen); lateral antennae arising from anterior prostomium margin, each with about 25 annulations (11-13 in MMS specimen) (Fig. 1.26A,B). Palps thick, large, conspicuous, broadly triangular (Fig. 1.26A). Everted pharynx long, cylindrical, with distal circlet of 10 soft papillae, chitinized lining dark brown (inverted pharynx in setigers 1-8 in MMS specimen); trepan with 10 triangular teeth plus a sharp subterminal middorsal tooth (Fig. 1.26B). Proventriculus present in setigers 12-21 (in setigers 9-12 in MMS specimen), with 40-50 rows of muscle cells (holotype with 44 cells; MMS specimen with 50).

Dorsal tentacular cirri about as long as lateral antennae; ventral tentacular cirri one-half length of dorsal tentacular cirri (Fig. 1.26A,B).

Parapodia short, distally blunt, with presetal lobe (Fig. 1.26C). Setae simple, numbering 6-7 per fascicle; distally bifid, subdistally enlarged or spoon-shaped, with smooth to finely serrated cutting surfaces (Fig. 1.26D,E). Ventral simple seta present in far posterior segments (in last 10 setigers in MMS specimen), distally bifid (Fig. 1.26F). Aciculae distally rounded, 4 per median parapodia, decreasing to 1 in posterior segments (Fig. 1.26G).

Dorsal cirri of anterior segments alternating between long ones with 35 articles and short ones with about 30 articles (Fig. 1.26A,C); in MMS specimens, dorsal cirri of setiger 1 with 16 articles, short dorsal cirri of setiger 2 with 8-9, long alternating with 2 short of midbody segments with 8 and 4, respectively. Ventral cirri digitiform, extending just beyond parapodium (Fig. 1.26C).

Pygidium with long anal cirri (with 11 articles in MMS specimen).

Remarks. This is the first formal record of this species from the northeastern Pacific. The MMS specimens are generally consistent with the features previously described for *Geminosyllis ohma*, although they are significantly smaller in body size and sexually immature.

Distribution. Japan; Russia (Kurile Islands); southern California.

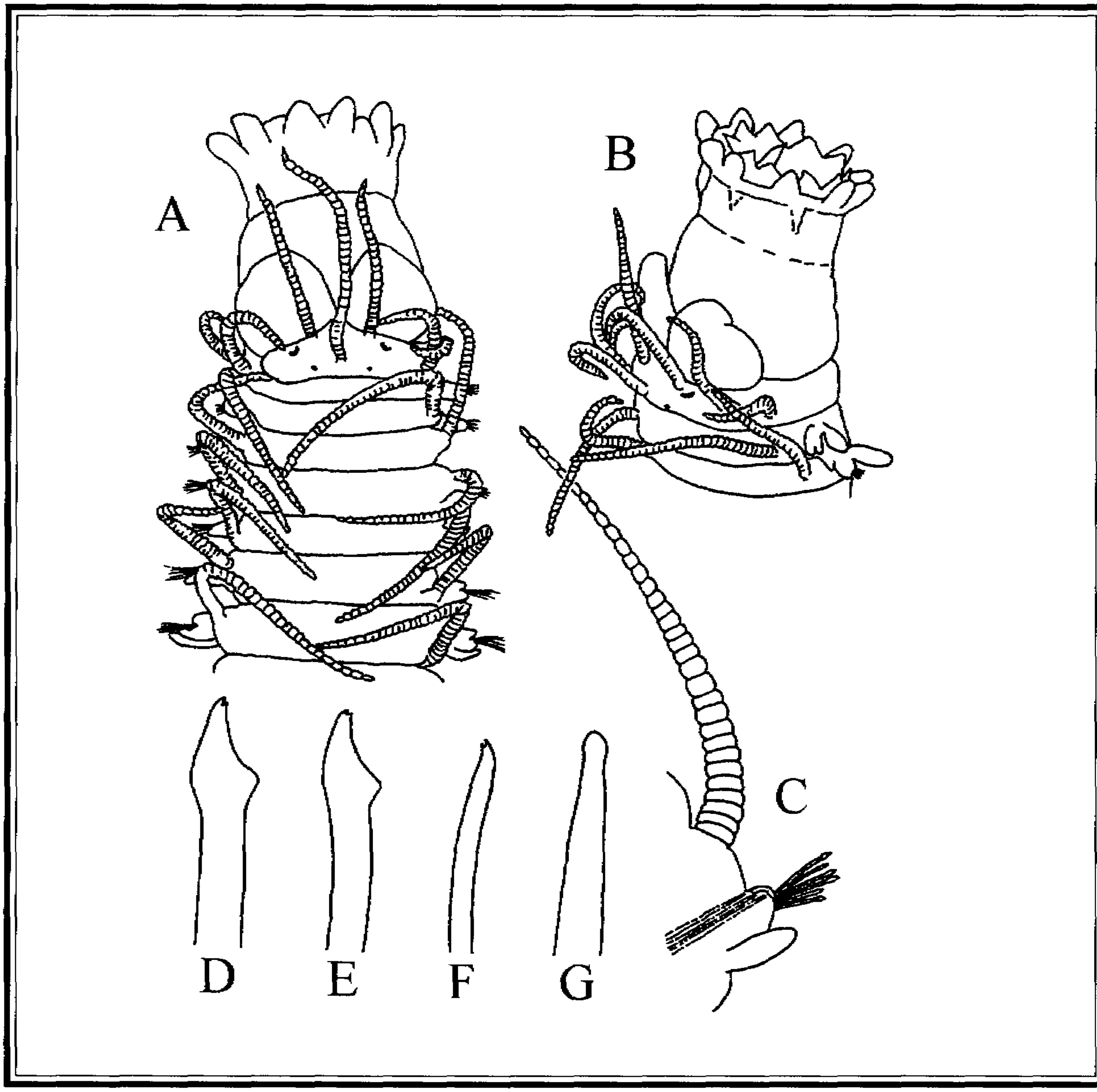

Figure 1.26. *Geminosyllis ohma*: A, anterior end with pharynx everted, dorsal view; B, anterior end, detail of pharyngeal armature, dorsolateral view; C, parapodium 18; D, bifid simple seta with smooth cutting edge from anterior parapodium; E, bifid simple seta with minute serrations along cutting edge from same anterior parapodium as D; F, ventral simple seta, posterior parapodium; G, acicula, posterior parapodium. (A-G, redrawn from Imajima, 1966d)

Genus *Syllis* Lamarck, 1818

Type species: *Syllis monilaris* Lamarck, 1818

Diagnosis. Prostomium with 3 antennae. Two pairs of tentacular cirri. Antennae, tentacular cirri and dorsal cirri all strongly articulated. Pharynx with a single middorsal anterior tooth, smooth marginal rim and distal circlet of 10 soft terminal papillae. Compound falcigers present in all setigers and pseudocompound setae and a superior and/or inferior simple seta variably present from median segments.

Remarks. Species of *Syllis* are readily distinguished from those of *Typosyllis* by the presence of pseudocompound setae. Refer to the Remarks section following the diagnosis of *Typosyllis* for further comments.

Syllis spongiphila Verrill, 1885

Figure 1.27

Syllis spongiphila Verrill, 1885: 435.—Hartman, 1944: 339, pl. 24, fig. 10.—Pettibone, 1963: 114-115, fig. 30 g, h.—Banse and Hobson, 1974: 61, fig. 16p.—Imajima, 1966d:250-251, text-fig. 491-s.
Syllis sclerolaema Ehlers, 1901: 86, pl. 10, figs. 1, 2.—Monro, 1930: 102, fig. 35.—Berkeley and Berkeley, 1938: 40, fig. 5.—Hartman, 1953: 20, fig. 2; 1964: 92.—Uschakov, 1955: 179, fig. 50, d.—Imajima and Hartman, 1964: 122-124, pl. 28, figs. i, j, pl. 29, figs. a-i. *Fide* Imajima, 1966d.
Syllis (Typosyllis) sclerolaema Wesenberg-Lund, 1962:54, fig. 15. *Fide* Imajima, 1966d.

Material Examined. California: Santa Maria Basin, Stas. BRA-20 rock (3, SBMNH 142705); BRA-13 (1); BRC-13 (1); BRA-16 (3); between Point San Luis and Point Sal, Sta. BRA-25 rock (1, USNM 170938).—Western Santa Barbara Channel, east of Point Conception, Sta. BRC-1 rock (4); south of Point Conception, Sta. BRC-2 (1).

Description. Length about 27 mm, 1.5 mm wide with parapodia, excluding setae, with about 90 segments (Hartman, 1944; Imajima, 1966d); complete MMS specimens (Sta. BRC-1) up to 13.5 mm long, 0.4 mm wide excluding parapodia and setae, for 68 segments. Body pigmentation patterns absent in preserved specimens. Mature specimen with a few oocytes in setigers 17-42 (Sta. BRC-1).

Prostomium slightly wider than long, subglobular; posterior margin entire; 2 pairs of eyes, set in trapezoidal arrangement, anterior pair largest; additional pair of eyespots absent (Fig. 1.27A). Median antenna with 25-30 articles (MMS specimens with 18-22), arising from center of prostomium; lateral antennae with slightly fewer articles (MMS specimens with 15), each arising anterior to anterior eyes (Fig. 1.27A). Palps large, subtriangular, basally free, about as long as prostomium (Fig. 1.27A). Everted pharynx in setigers 1-13 with middorsal anterior tooth; with distal circlet of 10 soft papillae and smooth anterior margin. Proventriculus extending from setiger 14 through setigers 22-24, with 47 rows of muscle cells.

Twp pairs of tentacular cirri, resembling antennae; dorsal pair about as long as median antenna (MMS specimens with 17-22 articles); ventral pair about two-thirds length of dorsal pair (MMS specimens with 9-14 articles) (Fig. 1.27A).

Parapodia conical (Fig. 1.27B). Setae generally pseudocompound (Fig. 1.27C-E), although 3-5 obviously compound falcigers with bidentate blades and serrated cutting edges usually present in anterior fascicles (Fig. 1.27C). Pseudocompound setae with distally bidentate tips numbering 6-8 per fascicle in median (Fig. 1.27E) and posterior fascicles, sometimes present also in anterior fascicles (Fig. 1.27D). Ventral simple seta slender, distally bidentate with subtly serrated cutting surfaces present in posterior parapodia (Fig. 1.27F). Aciculae distally curved, numbering 3-4 per parapodium in median segments (Fig. 1.27G).

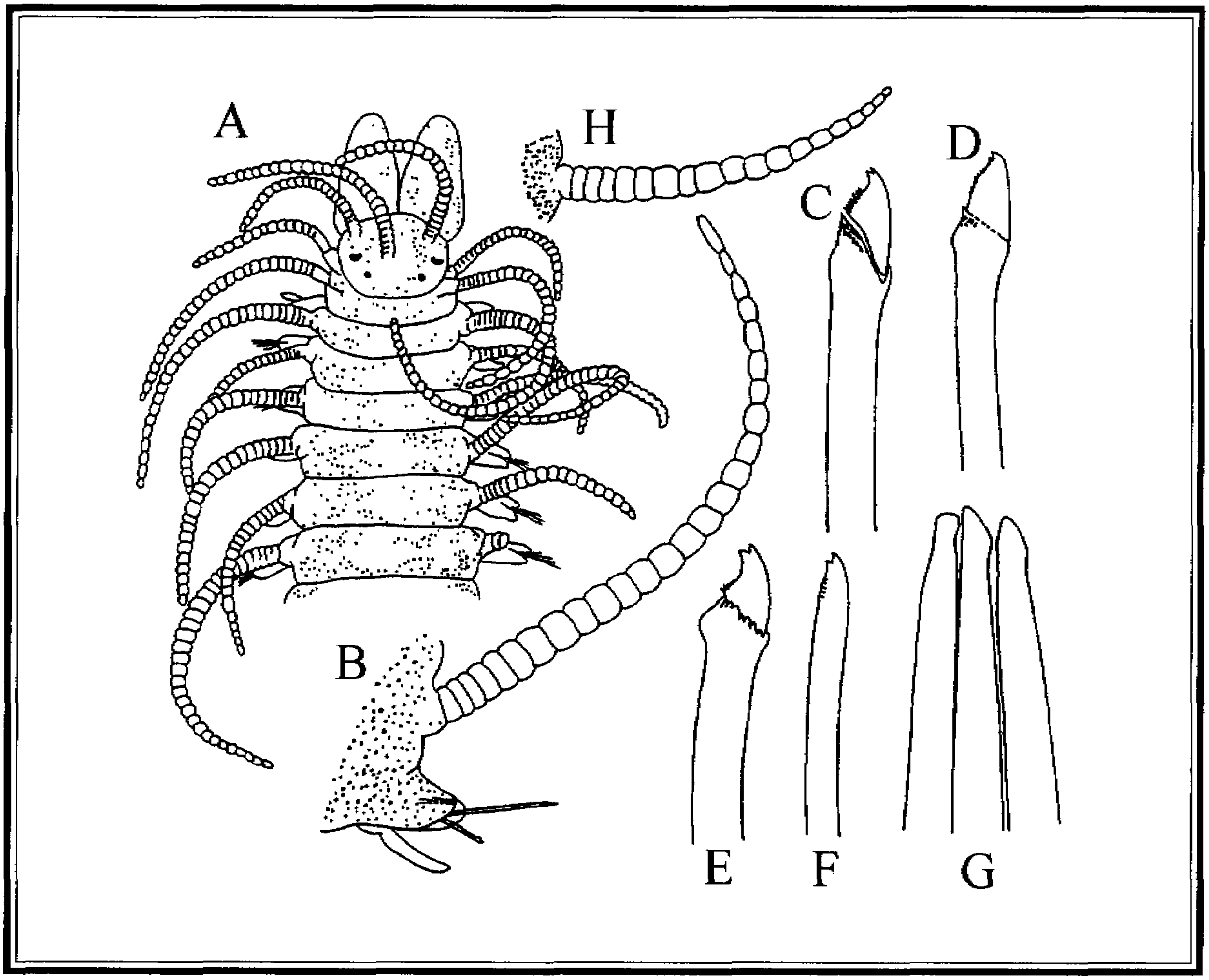

Figure 1.27. *Syllis spongiphila*: A, anterior end, dorsal view; B, parapodium 21 with long dorsal cirrus; C, composite falciger, setiger 1; D, pseudocomposite falciger, setiger 1; E, same, median parapodium; F, ventral simple seta, posterior parapodium; G, aciculae; H, short dorsal cirrus, parapodium 22. (A-H, redrawn from Imajima, 1966d)

Dorsal cirri articulated, alternating in length on median and posterior segments, and occasionally also on anterior segments (Fig. 1.27B,H); long cirri on setiger 1 each with 30-36 annulations (MMS specimens with 15-20); short cirri on setiger 2 each with 20 (MMS specimens with 9-10) (Fig. 1.27A); thereafter alternating with long cirri having 20-40 articles (MMS specimens with 8), and short ones with 16-30 (MMS specimens with 5). Ventral cirri slender, digitiform, extending to ends of parapodial lobes (Fig. 1.27B).

Pygidium with long paired anal cirri.

Remarks. As presently recognized, *Syllis spongiphila* is a widespread species associated with poriferans, mussels, mud, sand, gravel, and hard surfaces such as shells and rocks.

Distribution. Southern California; Washington; British Columbia; Japan; Sea of Okhotsk; Chile; Falkland Islands; Massachusetts.

Genus *Trypanosyllis* Claparède, 1864

Type species: *Syllis zebra* Grube, 1860.

Diagnosis. Body long, usually dorsoventrally flattened, with numerous short, wide segments. Prostomium with 3 antennae. Palps separate basally. Nuchal organs conspicuous ridges along postectal margin of prostomium. Two pairs of tentacular cirri. Antennae, tentacular cirri and dorsal cirri strongly articulated. Pharynx with terminal trepan of 10 teeth, with or without an additional middorsal anterior tooth. Setae simple or compound falcigers.

Remarks. Imajima and Hartman (1964) distinguish two major groups representing three subgenera of *Trypanosyllis* on the basis of the pharyngeal middorsal tooth and setae. For example, the first major group, represented by the stem genus *Trypanosyllis (Trypanosyllis)* is defined by the presence of a pharyngeal trepan with a middorsal tooth. The other major group has a trepan and lacks a middorsal tooth, and is characterized by two subgenera: *Trypanosyllis (Trypanedenta)* has compound setae only; and *Trypanosyllis (Trypanobia)* has simple setae only. This scheme is followed below.

Subgenus *Trypanosyllis (Trypanosyllis)* Imajima and Hartman, 1964

Type species: *Trypanosyllis (Trypanosyllis) zebra* (Grube, 1860)

Diagnosis. Trepan usually surrounded by fleshy distal circlet of 10 soft terminal papillae. Dorsal cirri long or short, closely articulated. Setae usually compound falcigers with uni- or bidentate blades; simple setae may be present in posterior segments. Tetraglene individuals produced asexually by budding of posterior segments.

Key to the Species of *Trypanosyllis (Trypanosyllis)* from California

1A. Blades of superior compound falcigers distally bidentate with serrated cutting edges, becoming unidentate and smooth inferiorly within fascicles (Figs. 1.28B-D, 1.29D-G) 2

1B. Blades of all compound falcigers distally bidentate, cutting edges of superior blades smooth, becoming serrated inferiorly within fascicles (Fig. 1.30F-H); proventriculus extending through 4-5 segments .... *Trypanosyllis (Trypanosyllis)* sp. B

2A. Proventriculus in 7 segments; parapodia distally conical (Fig. 1.28A); aciculae not projecting through parapodia; ventral cirri not projecting beyond parapodial lobes; occipital flap absent .... *Trypanosyllis (Trypanosyllis) coeliaca nipponica*

2B. Proventriculus in 3.5 segments; parapodia distally rounded (Fig. 1.29B,C); aciculae projecting through parapodia (Fig. 1.29B,C); ventral cirri projecting beyond parapodial lobes; occipital flap may be present (Fig. 1.29A) .... *Trypanosyllis (Trypanosyllis)* sp. A

Trypanosyllis (Trypanosyllis) coeliaca nipponica Imajima and Hartman, 1964

Figure 1.28

Trypanosyllis (Trypanosyllis) coeliaca nipponica Imajima and Hartman, 1964:124-125, pl. 29, fig. j; pl. 30, figs. a-e.—Imajima, 1966d:236-237.

Material Examined. California: Santa Maria Basin, Sta. BRA-16 (1, USNM 170940).—Japan: Shirikishinae, holotype (LACM-AHF Poly 858) and paratypes (LACM-AHF Poly 859).

Description. Length up to 17 mm, 2.2 mm wide; with 140 setigers (Imajima and Hartman, 1964); MMS specimens about 4.5 mm long, 0.5 mm wide without parapodia, 0.7 mm wide with parapodia, for 63 setigers. Body strongly flattened, lacking color patterns in alcohol. Prostomium rectangular, 2 times wider than long, lacking obvious median cleft; 2 pairs of eyes, anterior pair largest (Fig. 1.28A). Palps conical, not fused (Fig. 1.28A). Median and lateral antennae stout, short, each with 10-12 distinct articulations; all arising from anterior margin of prostomium (Fig. 1.28A). Everted pharynx with distal circlet of 10 soft papillae; trepan with 11 teeth including middorsal one. Proventriculus short, extending through setigers 13 to junction of setigers 18-19. Parapodia short, conical (Fig. 1.28B). Setae generally compound falcigers (Fig. 1.28C-E). Blades with finely serrated cutting margins; superior blades within fascicles distally bidentate (Fig. 1.28C); middle and inferior blades distally unidentate with single accessory tooth (Fig. 1.28D); inferior blades unidentate (Fig. 1.28E); (uncommon in MMS specimens). Shafts with subdistal serratia on superior surfaces (Fig. 1.28C-E). Posteriormost parapodia each with a ventral simple seta with subdistal tooth. Dorsal cirri thick, short, with 8-14 annulations (MMS specimen with 10-13). Ventral cirri digitiform, not extending beyond parapodial lobes (Fig. 1.28B). Aciculae numbering 1-2 per parapodium, tapering to pointed tips (Fig. 1.28F). Pygidium with pair of short anal cirri.

Remarks. This is the first formal record of *Trypanosyllis (Trypanosyllis) coeliaca nipponica* from the northeastern Pacific. The MMS specimens are generally consistent with the features previously described for the subspecies, although they are significantly smaller in body size.

Distribution. Northern Japan; southern California.

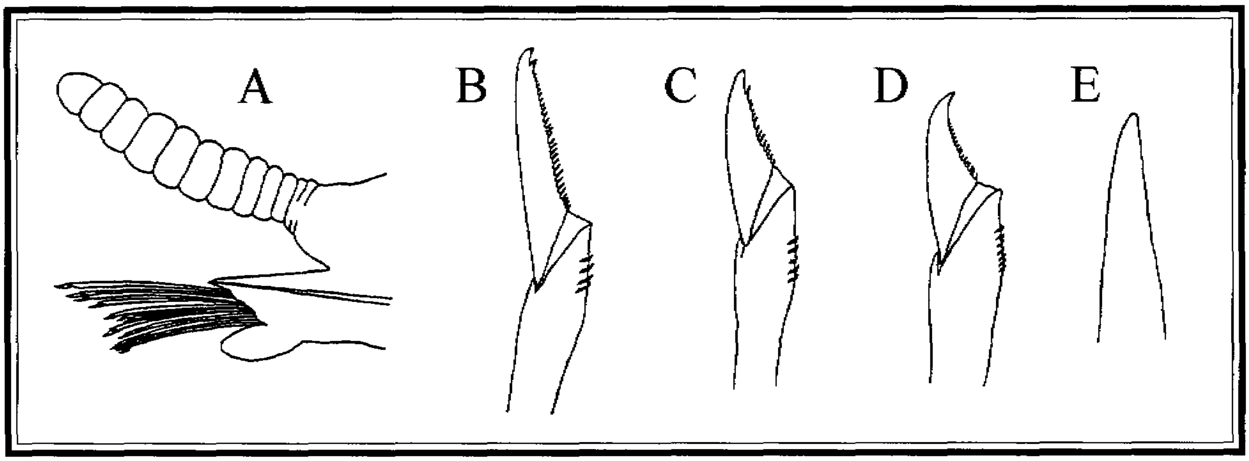

Figure 1.28. *Trypanosyllis (Trypanosyllis) coeliaca nipponica*: A, anterior end, dorsal view; B, median parapodium; C, superior compound bidentate falciger, setiger 6; D, median compound falciger, setiger 6; E, inferior compound unidentate falciger; F, acicula, distal end. (A-F, redrawn Imajima and Hartman, 1964)

Trypanosyllis (Trypanosyllis) sp. A

Figure 1.29

Material Examined. California: Santa Maria Basin, Stas. BRA-13 (1, USNM 170941), (1); BRA-16 (3); BRA-20 (4)—Western Santa Barbara Channel, south of Point Conception, Sta. BRC-2 (2).

Description. Complete specimens 4 mm long, 0.7 mm wide excluding setae, for 61 setigers. Body strongly flattened dorsoventrally; lacking pigmentation patterns, pale yellow in alcohol.

Prostomium subrectangular, shaped somewhat like a bowtie; 2 pairs of eyes, connate, lenticulate, anterior pair largest, all arranged trapezoidally (Fig. 1.29A). Antennae arise from anterior frontal margin of prostomium; median antenna slightly longer than prostomium, with about 8 articles; lateral antennae smaller, with 5-6 articles (Fig. 1.29A). Palps small, globular, shorter than prostomium, separate (Fig. 1.29A). Pharynx extending to setiger 10. Proventriculus present in setigers 11-14 or 15. Trepan partly visible through body wall, with obvious middorsal tooth plus 10 irregular denticles, all sharply pointed (not dissected).

Tentacular segment reduced dorsally; occipital flap small, marginally ciliated (Fig. 1.29A). Two pairs of tentacular cirri; dorsal pair largest, each with 3 distal articles and long cirrophore together nearly as long as prostomium; ventral pair smaller, each with 1-2 articles, about one-half length of dorsal pair (Fig. 1.29A).

Parapodia well developed, broadly rounded distally (Fig. 1.29B,C). Setae compound falcigers (Fig. 1.29D-G), numbering 7-8 per anterior fascicles, decreasing gradually to 3-5 in far posterior fascicles. Blades decreasing in length inferiorly within fascicles: superior ones longest, distally bidentate with serratia of cutting edge each long, coarse (Fig. 1.29D); intermediate blades also bidentate, cutting edges with a few poorly defined beadlike enlargements or smooth (Fig. 1.29E,F); inferior blades unidentate, smooth (Fig. 1.29G). One to 3 aciculae per parapodium, thick, sigmoid, projecting through parapodial lobes (Fig. 1.29H).

Dorsal cirri of setiger 1 with 8 distinct articles (Fig. 1.29A), those following each generally with 7, decreasing to 6 posteriorly (Fig. 1.29B,C), last few segments each with 4 articles (Fig. 1.29I); all with cirrophores, each around 2 times longer than wide. Ventral cirri bluntly conical, extending just beyond parapodial lobes, present on posterior face of parapodia (Fig. 1.29B,C).

Pygidium with paired anal cirri, tapered distally, each with 2 large articles (Fig. 1.29I).

Remarks. The MMS specimens have both bidentate and unidentate compound falcigers within the same fascicle, a feature characteristic of *Trypanosyllis (Trypanosyllis) coeliaca nipponica*. In addition, the median and lateral antennae of both species also arise from the frontal margin of the prostomium. *Trypanosyllis (Trypanosyllis)* sp. A differs from *T. (Trypanosyllis) coeliaca nipponica* in having an occipital flap and generally having compound falcigers with different blade morphology, although the superior compound falcigers of the two taxa are quite similar. It is probable that present materials of *T. (Trypanosyllis)* sp. A are all juvenile specimens and that the above differences are transient juvenile features: the specimens all are rather small and sexually immature. It therefore seems appropriate to note the apparent similarities between the present materials and *T. (Trypanosyllis) coeliaca nipponica*, and to tentatively identify these specimens as *T. Trypanosyllis* sp. A, pending acquisition of additional specimens.

Habitat. Rocky substrata, in depths of 75-237 m.

Distribution. Southern and central California.

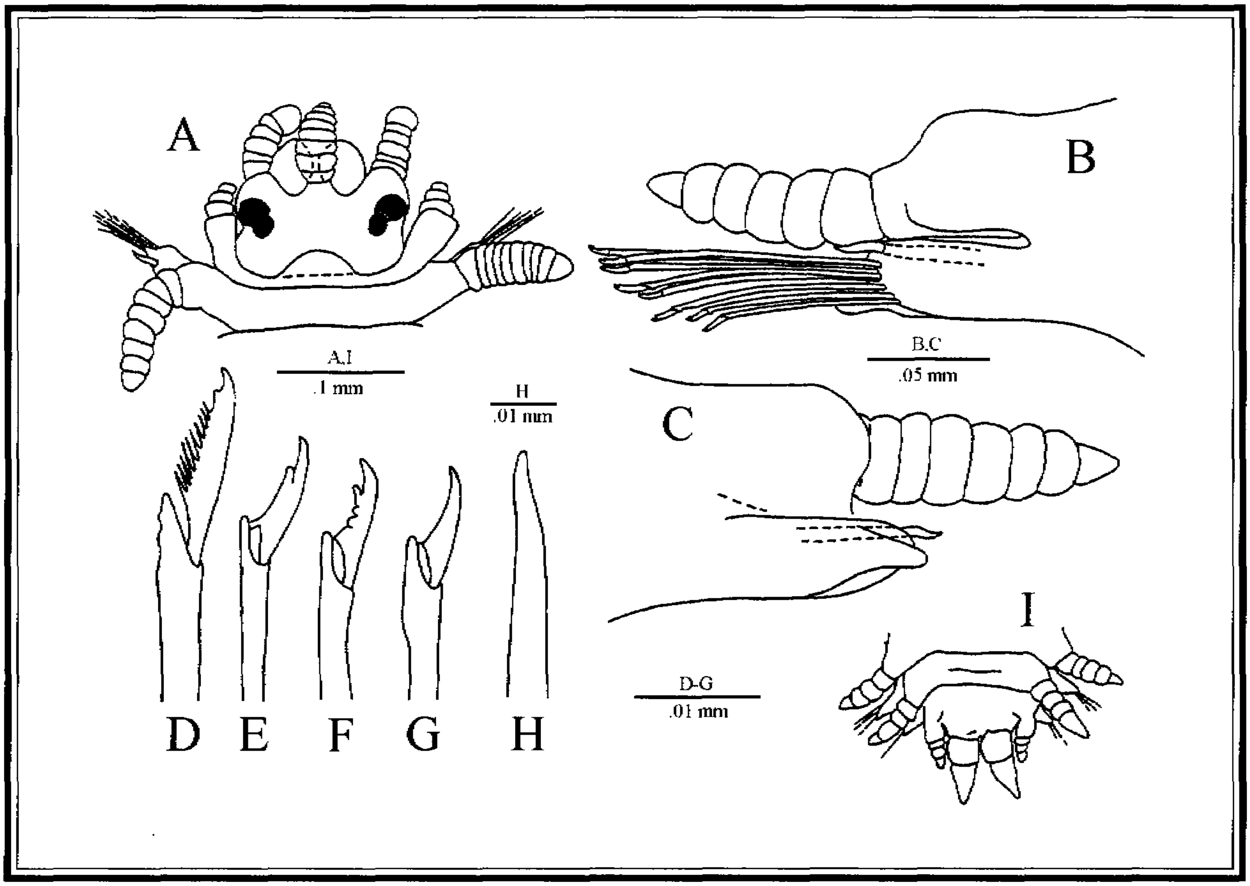

Figure 1.29. *Trypanosyllis (Trypanosyllis)* sp. A: A, prostomium and setiger 1, dorsal view, (USNM); B, right parapodium, setiger 13, anterior view; C, same, posterior view; D, superior compound falciger, setiger 13; E, intermediate compound falciger, setiger 13; F, low intermediate compound falciger, setiger 13; G, inferior compound falciger, setiger 13; H, acicula, setiger 13; I, Posterior end, dorsal view. (A-I, originals by JDK)

Trypanosyllis (Trypanosyllis) sp. B

Figure 1.30

Material Examined. California: Santa Maria Basin, Stas. BRA-16 rock (1, SBMNH 142707); BRA-20 rock (1, USNM 170942); west of Point Conception, Sta. BRA-4 (1, SBMNH 142708); between Point Estero and Point Buchon, Sta. 6, rocks (1).

Description. Length up to 2 mm, 1 mm wide excluding setae, for 29 segments including 10 regenerating posterior setigers (SBMNH voucher); USNM voucher an anterior macerated fragment, poorly preserved, 1.5 mm long, 0.8 mm wide excluding setae, for 18 setigers; all other specimens smaller. Body dorsoventrally flattened; pigmentation patterns absent in alcohol.

Prostomium wider than long, with posteromedian cleft; 2 pairs of eyes, lenticulate, anterior pair largest, all trapezoidally arranged (Fig. 1.30A,B). Antennae usually arising from anterofrontal margin of prostomium, all slightly longer than prostomium; median antenna with 9-12 distinct articles; lateral antennae each with 7-9 articles (Fig. 1.30A,B). Palps small, globular, one-half length of prostomium, separate (Fig.

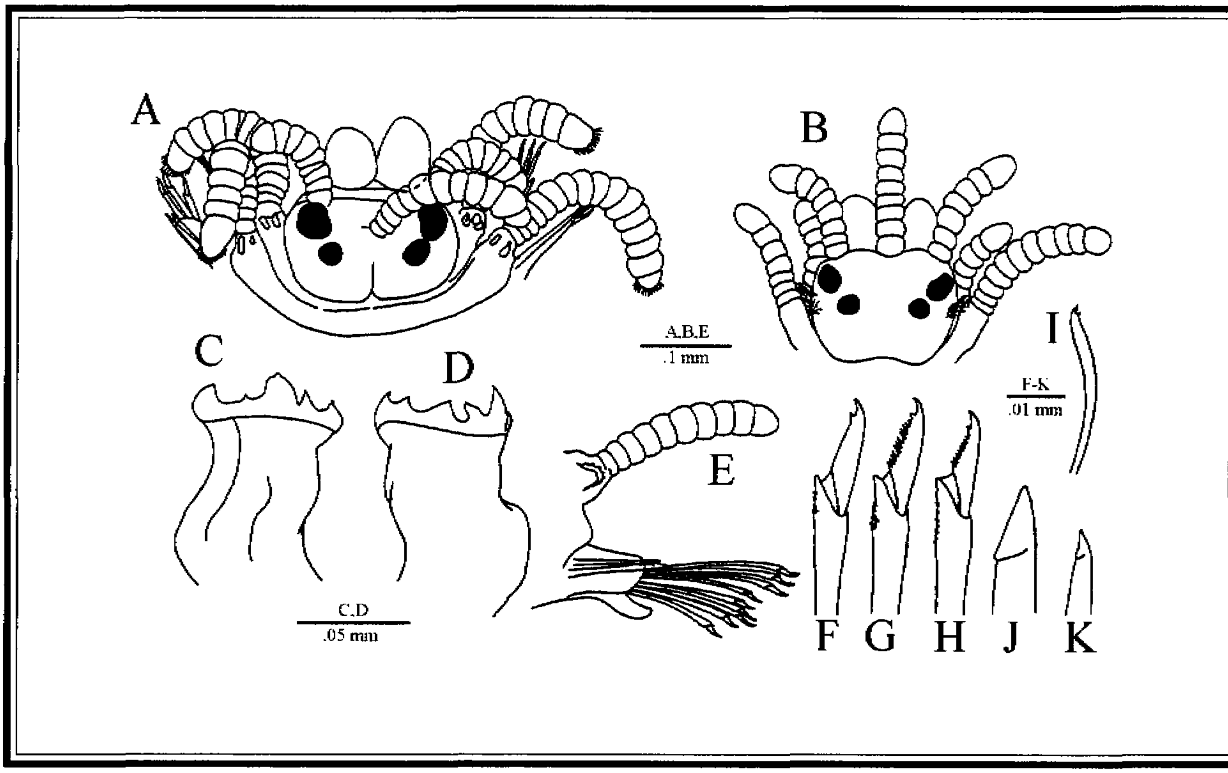

Figure 1.30. *Trypanosyllis (Trypanosyllis)* sp. B: A, prostomium and setigers 1-2, dorsal view (USNM); B, prostomium, dorsal view (SBMNH); C, everted pharynx showing trepan, dorsal view (SBMNH); D, everted pharynx showing trepan, ventral view; E, median segment, anterior view; F, superior compound falciger, median setiger; G, intermediate compound falciger, median setiger; H, inferior compound falciger, median setiger; I, ventral simple seta, setiger 25; J, inferior acicula, median setiger; K, superior acicula, median setiger. (A-K, originals by JDK)

1.30A,B). Pharynx extending to setigers 7-8. Trepan with middorsal tooth plus 10 distal teeth (Fig. 1.30C,D). Proventriculus extending through 4-5 segments, present in setigers 8-12 or 9-14.

Tentacular segment distinct, reduced dorsally (Fig. 1.30A,B). Two pairs of tentacular cirri, all with short cirrophores characteristically vesiculate; dorsal pair longest, longer than median antenna, with 12-14 articles; ventral pair one-half length of dorsal pair, each with about 5-7 articles (Fig. 1.30A,B).

Parapodia tapering slightly, distally truncate (Fig. 1.30E). Compound setae distally bidentate (Fig. 1.30F-H), numbering around 8-10 per anterior fascicles, decreasing in median and posterior fascicles. Blades subequally long within fascicles (Fig. 1.30F-H), length decreasing gradually posteriorly. Cutting edges of superior blades smooth (Fig. 1.30F), becoming conspicuously serrated inferiorly (Fig. 1.30G,H). Distal superior ends of shafts dentate (Fig. 1.30F-H). Ventral simple seta distally bidentate, sigmoid, sometimes present in far posterior segments (Fig. 1.30I; illustrated for specimen from Sta 6). Aciculae numbering 2-3 per parapodium, projecting through distal lobe; each with a characteristic ventrally thickened, hook-like subdistal collar (Fig. 1.30J,K).

Dorsal cirri short, each with 10-12 articles, not looping back on themselves; cirrophores short, each characteristically vesiculate (Fig. 1.30A,E). Ventral cirri digitiform, extending beyond parapodial lobes (Fig. 1.30E).

Pygidium (SBMNH secondary voucher) with paired anal cirri, regenerating, each with 5-6 articles.

Remarks. MMS materials of *Trypanosyllis (Trypanosyllis)* sp. B were originally identified in part as *T. (Trypanosyllis) brevicirrata* Uschakov, 1950, based on the presence of short dorsal cirri and the apparently unidentate falcigers in all setigers. All present MMS materials have bidentate compound falcigers, have a small body size, and lack gametes. It seems likely that specimens here identified as *T. (Trypanosyllis)* sp. B are unidentifiable juveniles. All are substantially smaller than mature forms of described Pacific west coast species which normally have large body sizes and numerous segments. For example, *T. (Trypanedenta) ingens* Johnson, 1901, is 130 mm long for 476 segments; *T. (Trypanedenta) gemmipara* Johnson, 1901, is 40-68 mm for 385 segments; and *T. (Trypanedenta) intermedia* Moore, 1909, is 60 mm for 230 segments. However, Perkins (1981) described sexually mature specimens of *T. (Trypanosyllis) savagei* from Florida less than 5 mm for 80 segments. All MMS specimens here referred to *T. (Trypanosyllis)* sp. B are less than 2 mm long, and are sexually immature. Two of these specimens are regenerating body parts: one a head plus anterior segments, the other posterior segments; none represent stolons.

Habitat. Rocky substrata, in depths of 91.5-237 m.

Distribution. Southern and central California.

Subgenus *Trypanosyllis (Trypanedenta)* Imajima and Hartman, 1964

Type species: *Trypanosyllis (Trypanedenta) gemmipara* Johnson, 1901

Diagnosis. Trepan with 10 teeth, middorsal subdistal tooth absent. Dorsal cirri thick, heavily articulated. Setae compound falcigers with uni- or bidentate blades. Tetraglene individuals produced asexually by budding of posterior segments.

Trypanosyllis (Trypanedenta) sp. A

Figure 1.31

Material Examined. California: Santa Maria Basin, Sta. BRA-21 (1, USNM 170939).—*Trypanosyllis (Trepanedenta) gemmipara*: Tomales Bay, 9 June 1941, from bryozoan-sponge masses, coll. O. Hartman (LACM-AHF, Hartman lot N47).—La Jolla, Bird Rock, 30 May 1938, coll. O. Hartman (1, LACM-AHF, Hartman lot N1031); north of Scripps Pier, 13 Feb 1938, coll. O. Hartman (1, LACM-AHF, Hartman lot N1032).—Japan, Shirikishinai, October 1955, coll. M. Imajima (1, LACM-AHF, Hartman lot N11086).

Description. Length approximately 22 mm, 2 mm wide excluding parapodia, for around 120 segments. Body twisted into spiral, poorly preserved anteriorly, lacking antennae, tentacular and dorsal cirri; dorsal cirri present posteriorly; dorsum flesh colored, lacking color patterns; sexually mature.

Prostomium wider than long, with conspicuous posteromedian cleft, trapezoidal in shape, anterior margin widest. Two pairs of eyes, all lenticulate, anterior pair largest and farthest apart, all in subrectangular arrangement. Antennae lost. Palps about as long as prostomium, free basally, projecting ventrally. Pharynx long, extending to midsetiger 16; distally with 5 ventral and 7 dorsal terminal papillae, each group separated from the other by lateral gaps (dissected). Trepan with 10 pale brown teeth, largest appearing midventral; middorsal tooth absent. Proventriculus present from setiger 16 to 28; 39 muscle rows, each with conspicuous muscle cells.

Tentacular segment incomplete dorsally. Tentacular cirri lost.

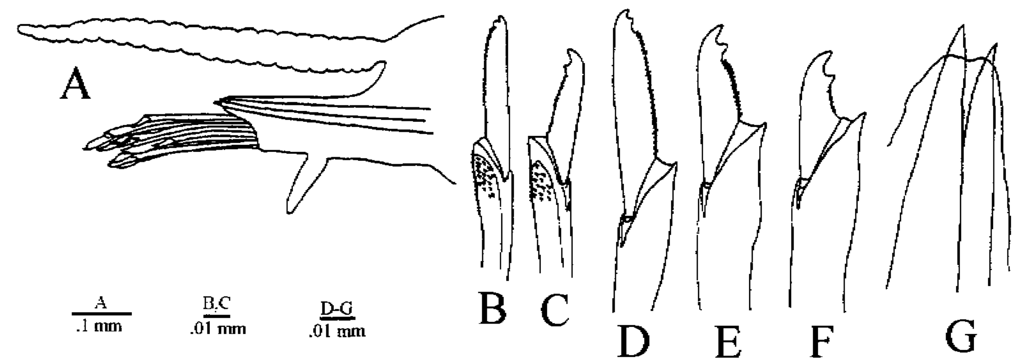

Figure 1.31. *Trypanosyllis (Trypanedenta)* sp. A: left parapodium from far posterior segment, posterior view; B-C, compound falcigers from setiger 15; D-F, compound falcigers from far posterior segment: D, superior seta; E, intermediate seta; F, inferior seta; G, aciculae from far posterior segment. (A-G, originals by JDK)

Parapodia long, distally pointed (Fig. 1.31A). Setae generally delicate, bidentate compound falcigers (Fig. 1.31B,C). Blades long, narrow with secondary tooth subdistal to primary tooth in most all falcigers (Fig. 1.31B,C), becoming more widely spaced in far posterior segments (Fig. 1.31D-F). Blades with cutting edges minutely serrated (Fig. 1.31B-F). Aciculae straight, projecting through parapodial lobes, up to 5 per anterior parapodium, decreasing to 1-2 posteriorly (Fig. 1.31G).

Dorsal cirri thick, alternating long and short along the body; in midposterior segments long cirri each with around 45 articles, short cirri each with 27. Ventral cirri short, smooth, digitiform, may extend to and sometimes beyond parapodial lobes in anterior and midbody segments.

Remarks. *Trypanosyllis (Tranpanedenta)* sp. A was collected from one location in Santa Maria Basin. Although poorly preserved, the species is partly characterized by having a pharynx that extends to midsetiger 16, with 2 distal groups of terminal papillae (5 ventral and 7 dorsal ones, observed by dissecting the inverted pharynx), which are separated from one another by lateral gaps, and a trepan with 10 teeth, the largest tooth appears to be midventral; a proventriculus in 13 segments (setiger 16 to 28) with 39 rows of conspicuously large muscle cells; delicate bidentate compound falcigers with blades long and narrow, secondary teeth all subdistal, and cutting edges minutely serrated in all fascicles; and ventral cirri extending to or slightly beyond parapodial lobes.

Trypanosyllis (Trypanedenta) sp. A is similar to specimens of *T. (T.) gemmipara* Johnson, 1901, noted above (see Materials Examined) in having bidentate compound falcigers in all setigers; it differs from *T. (T.) gemmipara* in having all secondary teeth subdistal rather than in the middle of the blade; blades all long and narrow with cutting edges minutely serrated, instead of short, stout triangular blades, with cutting edges smooth or serrated; 12 terminal pharyngeal papillae arranged in a ventral and dorsal group, in contrast to 8 or 11; a trepan of 10 teeth, the largest one of which appears to be midventral, instead of 8 or 11; and a proventriculus present in 13 segments rather than 4 or 8 segments.

The compound falcigers of the above MMS specimen are similar to those described by Imajima (1966d) from inferior and posterior fascicles of *T. (T.) gemmipara* from Japan. However, the MMS specimen is sexually mature, and is not a juvenile *T. (T.) gemmipara*. In addition, an examination of *T. (T.) gemmipara* specimens from California and Japan revealed that all had well-developed compound falcigers with stout, smooth triangular blades with the secondary tooth located about midway along the cutting edge; none had long, narrow, distally bidentate blades with serrated cutting margins characterized by Imajima (1966d). Although the poorly preserved MMS specimen precludes a more detailed analysis, these findings suggest that the taxon it represents is not conspecific with *T. (T.) gemmipara*. Resolution of this question must await the acquisition of additional materials.

Finally, Imajima and Hartman (1964) do not describe the presence of a large midventral pharyngeal tooth in the genus *Trypanosyllis*. Such a character may be important at the level of subgenus. If this is true, then the species represented by the MMS specimen described above may represent a new subgenus if the pharynges of all known *T. (Trypanedenta)* species are found to lack a midventral tooth.

Habitat. Associated with rocky substrates in depths of 75-90 m.

Distribution. Southern and central California.

Genus *Typosyllis* Langerhans, 1879

Type species: *Syllis krohnii* Ehlers, 1864

Diagnosis. Prostomium with 3 antennae. Two pairs of tentacular cirri. Palps broadly triangular, fused basally. Antennae, tentacular cirri and dorsal cirri strongly articulated. Pharynx with single middorsal anterior tooth, with smooth marginal rim, and distal circlet of 10 soft terminal papillae. Setae usually compound falcigers with uni- or bidentate blades, with a superior and/or inferior simple seta variably present in posterior setigers.

Remarks. Fauchald (1977) notes 89 described species of *Typosyllis*, which is one of the most complex and systematically challenging of syllid genera. Some workers include *Typosyllis* (and *Ehlersia, Haplosyllis*) as subgenera of *Syllis* (Fauvel, 1923; Day, 1967; Uebelacker, 1984; Dorsey and Phillips, 1987). *Haplosyllis* has simple setae, and is readily separable from the other three taxa. Note that the separation of *Syllis sensu lato* into three separate groups is based on setal traits not normally used to separate other syllid genera, and fails to reduce the nearly incomprehensible complexity of *Typosyllis* (Uebelacker, 1984). This strongly suggests that traditional means of identifying and separating *Typosyllis* species are inadequate, and that additional characters are needed before many of the systematic issues concerning *Typosyllis* can be resolved. Such an undertaking is well beyond the scope of this chapter. However, we prefer to recognize four separate but closely related genera for matters of practicality. Besides the approximate number of *Typosyllis* species noted above, at least 45 *Syllis* species, 16 *Ehlersia* species, and 10 *Haplosyllis* species have also been reported (Fauchald, 1977; Pettibone, 1982; Dorsey and Phillips, 1987). A single large genus (*Syllis*) with over 150 species tends to obscure the critical and urgent need to revise this taxon based on combinations of both traditional and new characters. To this end, Piltz (1980) provides an example of the kinds of characters that can be used to further resolve the complexity surrounding *Typosyllis* and *Syllis*.

Key to Species of *Typosyllis* from California

1A. Dorsum with 2 reddish brown transverse lines per anterior segment in life (instead of faded brown in preserved material) (Fig. 1.33B); palps not fused basally (Fig. 1.33A); dorsal cirri thick, alternating in length, long cirri of median segments each with 25 and short cirri with 14 articles (Fig. 1.33C) .. .. *Typosyllis bella*

1B. Dorsum with transverse bands of dark pigment on every 1-3 segments (Fig. 1.34A), or lacking any pigment pattern; palps fused basally (Figs. 1.32B, 1.34A); dorsal cirri usually slender, alternating in length, each with fewer articles in midbody segments 2

2A Dorsum usually with broad transverse bands of broken brown pigment on every 1-3 segments (Fig. 1.34A), or lacking pigment pattern; long dorsal cirri of median segments each with 14 (Fig. 1.34C) and short cirri with 11 articles (Fig. 1.34B); compound falcigers with short, stout blades (Fig. 1.34D-G) .... *Typosyllis hyalina*

2B. Dorsum without pigmentation patterns; long dorsal cirri of median segments each with 25 (Fig. 1.32C) and short cirri with 18 articles; compound falcigers with longer, more narrow blades (Fig. 1.32F-I) .... *Typosyllis alternata*

Typosyllis alternata (Moore, 1908)

Figure 1.32

Syllis alternata Moore, 1908:323-325, figs. a-f; 1909:321.—Annenkova, 1938:148.—Berkeley and Berkeley, 1938:37-38; 1948:77-78, fig 115.—Rioja, 1941:691-692, pl.3, figs. 1-9.
Typosyllis alternata: Hartman, 1948:21; 1968:479-480, figs. 1-5.—Imajima, 1966e:273-275, text-fig. 58a-l.
Syllis (Typosyllis) alternata: Uschakov, 1955:180, fig. 50, z-l.—Banse and Hobson, 1974:64, fig. 16 a.—Day, 1973:30.—Gardiner, 1976:141, fig. 13 b-c.
Syllis cornuta Pettibone, 1954:253 (in part).

Material Examined. California: off Point Arguello, Sta. BRA-6 rock (3, USNM 170944) + (3, SBMNH 142709); off El Morro, Sta. BRA-27 rock (1, USNM 170945); between Point Estero and Point Buchon, Sta. 6, rocks (5, USNM 170943).—Alaska: Behm Canal, holotype (USNM 5542).

Description. Length up to 44 mm, with 125-160 segments (Moore, 1908; Imajima, 1966e); MMS specimens 10 mm long, 0.4 mm wide excluding parapodia, for 88 segments. Glandular tissue on body wall present on every segment just posterior to dorsal cirri.

Prostomium wider than long, somewhat pentagonal; 3 pairs of eyes, all lenticulate, middle pair largest, farthest apart; posterior 2 pairs set in trapezoidal arrangement; anterior pair as eyespots, each present on anterior margin of prostomium, just medial to paired lateral antennae (Fig. 1.32A,B). Median antenna inserted between 2 posterior pairs of eyes, with up to 30 articles (14-19 in MMS specimens); lateral antennae inserted far forward on anterior margin of prostomium, each with 15-18 articles (9-12 in MMS specimens) (Fig. 1.32A,B). Palps broad, distally rounded, fused basally (Fig. 1.32A,B). Nuchal organs in juvenile specimen with 27 setigers small, paired, at postectal corners of prostomium (Fig. 1.32B). Pharynx usually present in setigers 1-8 or to setigers 10-12, anterior middorsal tooth large, conspicuously visible through body wall in setiger 3; with distal circlet of 10 soft papillae when everted. Proventriculus beginning from setigers 9-19 (9-16 in MMS materials), depending on extension of pharynx, extending through 12 segments, with an average of 39 rows muscle cells (34-40 in MMS specimens).

Tentacular segment forming complete, distinct ring (Fig. 1.32A). Two pairs of tentacular cirri, resembling prostomial antennae in form, shorter; dorsal pair longest, each about three-quarters length of median antenna, with 15-23 articles; ventral pair each about one-half length of dorsal pair, with 8-17 articles (Fig. 1.32A,B).

Parapodia thick, fleshy lobes (Fig. 1.32C-E). Setae generally compound falcigers with bidentate blades (Fig. 1.32F-J), around 8-12 per fascicle, thickest in medial segments. Blades longest superiorly (Fig. 1.32G), about 2 times longer than inferior blades in anterior segments decreasing to 1.5 in medial segments (Fig. 1.32F); all decreasing in length inferiorly within fascicles (Fig. 1.32I,J); all with coarsely serrated cutting edges. Dorsal and ventral simple setae present in posterior segments, each distally bidentate with serrated cutting surfaces (Fig. 1.32K-M). Up to 5 aciculae per anterior parapodium, decreasing to 1 in posterior parapodia; distally pointed, slightly curved distally, thickest emerging through parapodial lobes (Fig. 1.32N,O).

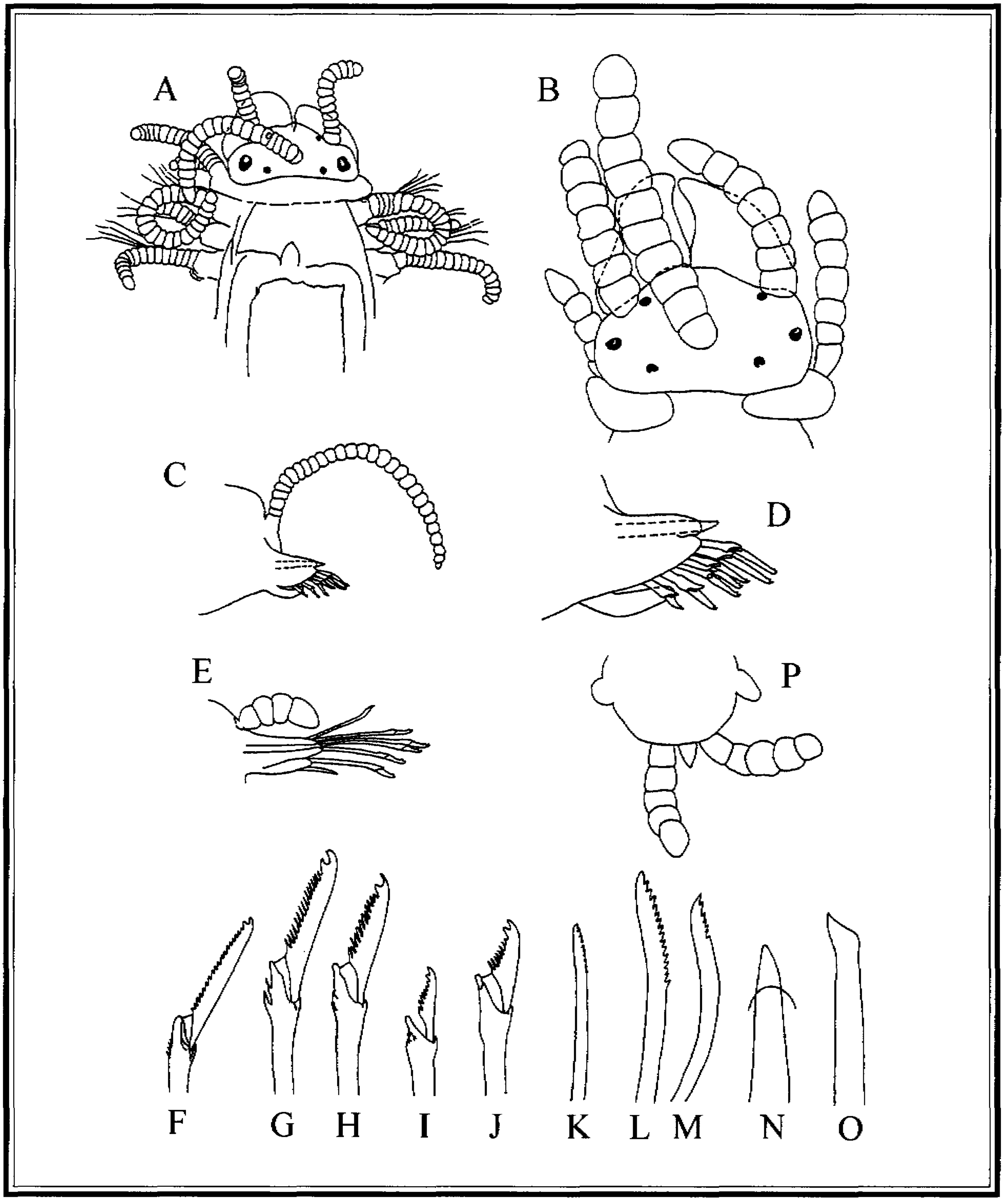

Figure 1.32. *Typosyllis alternata*: A, anterior segments, dorsal view; B, prostomium, dorsal view; C, left parapodium, median segment, anterior view; D, left parapodium, median segment, dorsal cirri omitted, anterior view; E, right parapodium, setiger 14, anterior view; F, superior compound falciger, median segment; G-H, J, compound falcigers from setiger 14: G, superior seta; H, intermediate seta; J, inferior seta; I, inferior compound falciger, median segment; K-L, dorsal simple setae: K, median segment; L, setiger 14; M, ventral simple seta, setiger 14; N-O, aciculae: N, median segment; O, setiger 14; P, pygidium, dorsal view. (A-P, originals by JDK)

Dorsal cirri strongly articulated, alternating long and short, although longest overall in anterior 15 segments, decreasing gradually in medial and posterior segments. Dorsal cirri of setiger 1 longest, with 35 articles; setiger 2 with 25 articles; long ones in medial segments with 25, short ones with 18 articles. In specimens with about 60 segments, longest anterior dorsal cirri each with 25-31 articles, alternating with shorter ones having 17-23 articles; long ones of middle segments with 15-26, short ones with 8-21 articles. In juvenile specimen measuring 1.3 mm long for 27 setigers, dorsal cirri with limited number of articles in all segments; those of setiger 1 with 8 articles; setiger 2 with 7; setigers 3-4 each with 6; setigers 5-12 with 5; setigers 13-14 with 4; setigers 15-22 with 3; setigers 23-26 with 2; setiger 27 with 1. Ventral cirri digitiform, extending beyond parapodial lobes.

Pygidium with paired anal cirri, each having up to 15-20 articles (Fig. 1.32P).

Remarks. The MMS specimens are generally consistent with the description of *Typosyllis alternata*, particularly in the pattern of alternating long and short dorsal cirri, although the dorsal cirri of the MMS specimens tend to have slightly greater numbers of articles than originally described by Moore (1908), they also have fewer numbers of aciculae per parapodium, some of which project through the body wall; ventral cirri do not project beyond parapodia lobes; and the dorsal simple setae appear to be unidentate. Moore (1908) originally reported the ventral cirri to project beyond the parapodial lobes, although they do not in Japanese specimens (Imajima, 1966d).

Habitat. Mixed sediments, gravel, rocky substrata, to depths of 2560 m.

Distribution. California; Washington; British Columbia; Alaska; Japan.

Typosyllis bella Chamberlin, 1919

Figure 1.33

Typosyllis bella Chamberlin, 1919:7.

Material Examined. California: Western Santa Barbara Channel, east of Point Conception, Sta. BRC-1, rock (1, USNM 170946).

Description. Length about 20 mm, 1.25 mm wide in anterior region excluding parapodia, for about 145 segments (Chamberlin, 1919); MMS specimen incomplete, 5 mm long, 0.7 mm wide excluding parapodia, for 48 setigers. Color in life of mature female yellowish, each anterior segment with 2 transverse reddish-brown lines (Fig. 1.33B; Chamberlin, 1919); 2 transverse rust colored lines per segment through setigers 23-24 in MMS specimen.

Prostomium widest anteriorly; 2 pairs of eyes, elliptical; anterior pair largest; all trapezoidally arranged (Fig. 1.33A). Median antenna arising between anterior pair of eyes, with 21 distinct articles, nearly 2 times longer than prostomium; lateral antennae arising from anterofrontal margin of prostomium, about same length as median antenna, each with 15-18 articles (Fig. 1.33A). Palps nearly as long as prostomium, narrow, distally rounded, not fused basally (Fig. 1.33A). Pharynx extending through setiger 13, with an anterior middorsal tooth. Proventriculus present in setigers 14-23; rows of muscle cells not counted.

Tentacular segment reduced. Two pairs of tentacular cirri, similar in form to median antenna; dorsal pair longest, each longer than median antenna with 32-34 articles; ventral pair slightly less than one-half length of dorsal pair, each with about 15 articles.

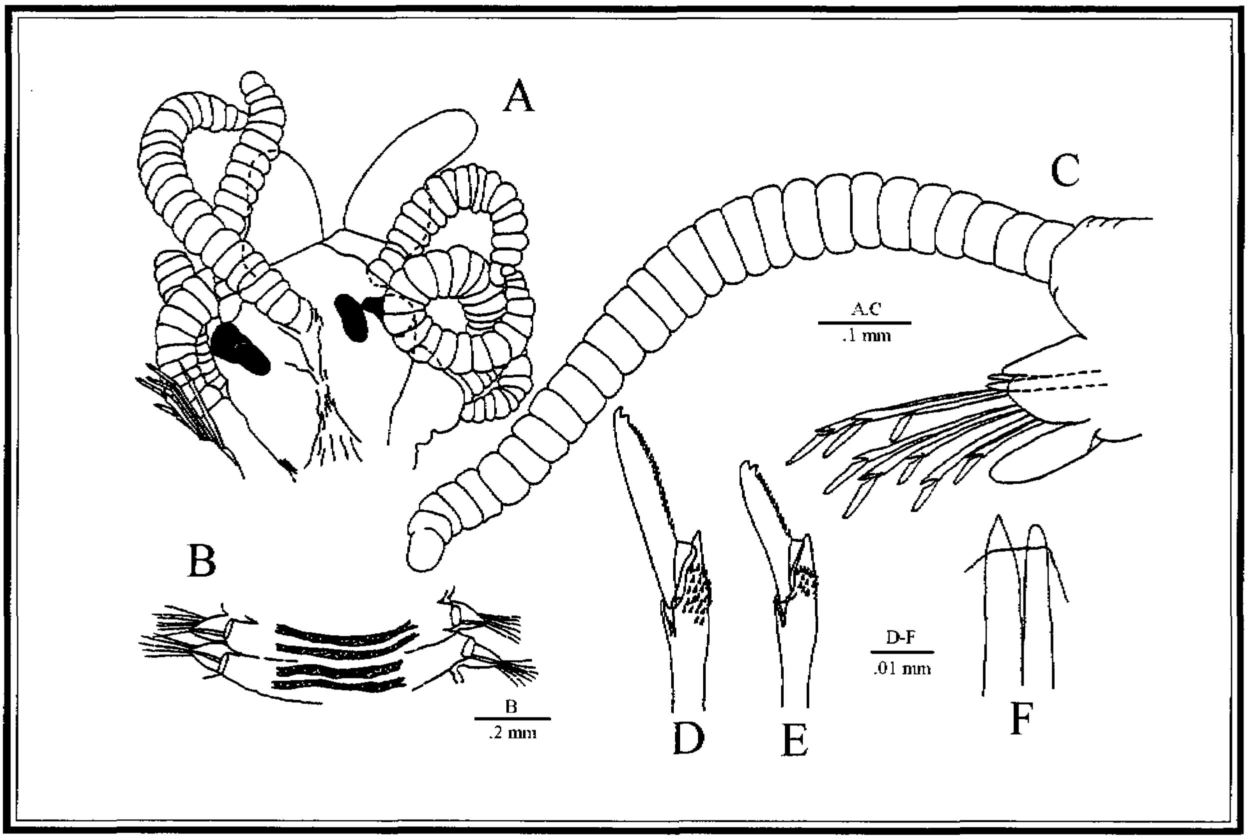

Figure 1.33. *Typosyllis bella*: A, prostomium, dorsal view; B, median segments with paired transverse bars of pigment per segment, dorsal view; C, right parapodium, setiger 2, anterior view; D, superior compound falciger, setiger 2; E, inferior compound falciger, setiger 2; E, paired aciculae, emerging through acicular lobe, superior acicula on right. (A-E, originals by JDK)

Parapodia thick, fleshy, conical in dorsal view; distally incised, forming small superior and larger round inferior lobe (Fig. 1.33C). Setae compound bidentate falcigers (Fig. 1.33C-E), 8-12 per anterior fascicle (11-13 in MMS specimen), decreasing posteriorly. Blades longest superiorly (Fig. 1.33D), 2-2.5 times longer than inferior blades within fascicles (Fig. 1.33E), all decreasing gradually in length inferiorly within fascicles, and posteriorly along body; all with wide angle between the distal and subdistal teeth and finely serrated cutting edges (Fig. 1.33D,E). Setal shafts with numerous subdistal denticles, these gradually decreasing in numbers inferiorly within fascicles (Fig. 1.33D,E). Two to 3 aciculae per parapodium (2 in MMS specimen), inferiormost usually large, pointed, superior ones smaller, distally blunt, middle one enlarged in posterior segments; all projecting through parapodial lobe at and just below distal incision (Fig. 1.33F).

Dorsal cirri extremely well developed, longest in anterior segments (Fig. 1.33C), alternating long with 32 articles, and short with about 18 articles, and gradually decreasing in overall length posteriorly (Chamberlin, 1919); those of MMS specimen generally lost, with dorsal cirri of setiger 1 longest, with 34 articles; setigers 2 and 4 each with 27; setigers 3 and 5 each with 16-17. Ventral cirri slender, digitiform, extending beyond parapodial lobes (Fig. 1.33C).

Pygidium unknown.

Remarks. The present specimen is remarkably consistent with Chamberlin's (1919) original description, especially for the prostomium, dorsal cirri and dorsal segmental pigmentation pattern. The holotype of this species is apparently deposited in the Museum of Comparative Zoology, Harvard, and has not been illustrated or redescribed since first reported, although Hartman (unpublished) did examine the holotype in 1937. The MMS specimen is tentatively referred to *Typosyllis bella* pending re-examination of the holotype.

Habitat. Originally reported from the low intertidal zone of Laguna Beach (Chamberlin, 1919); also associated with rocky substrata in depths of 73.5-78 m.

Distribution. Southern California.

Typosyllis hyalina (Grube, 1863)

Figure 1.34

Syllis (Typosyllis) hyalina Fauvel, 1923:262-263, fig. 98a-c.—Rullier, 1964:159-160.
Syllis hyalina Grube, 1863:45.—Ehlers, 1901:86.—Monro, 1933:30.—Berkeley and Berkeley, 1948: 74, figs. 107-108.—Rioja, 1941:692.—Banse and Hobson, 1974:62, fig. 16m.—Reish, 1968:214.—Westheide, 1974:47-51, pl. 20.—Ben-Eliahu, 1977:9-10.—Núñez, San Martín and Brito, 1992:120.
Typosyllis hyalina: Imajima, 1966e: 271-273, text-fig. 57, a-k.—Hartman, 1968:487-488, figs. 1-3.—Gardiner, 1976:140, fig. 12v-w.—Tebble, 1959:17.—Day, 1967:246, fig.12.2.v-x; 1973:29.
Typosyllis (Typosyllis) hyalina Hartmann-Schröder, 1965:95; 1979:89, figs. 57-61; 1980:50.
Typosyllis aciculata orientalis Imajima and Hartman, 1964:130-132, pl. 3, figs. e,f, pl. 32, figs. a-t. *Fide* Westheide, 1974.

Material Examined. California: Santa Maria Basin, Sta. BRA-21 (1, SBMNH 142710).—Western Santa Barbara Channel, east of Point Conception, Sta. BRC-1 (7, USNM 170947) + (1, USNM 170948); BRC-2 (5); BCC-1 (1).

Description. Body 10-35 mm long, 2 mm wide including parapodia; with over 100 segments (Imajima, 1966e; Hartman, 1968). Color in life variable: translucent, white or occasionally with dorsal pattern of broken or continuous transverse dark lines alternating on every 3 anterior segments (Fig. 1.34A).

Prostomium wider than long, subglobular; 2 pairs of black eyes, set in trapezoidal arrangement, plus an additional pair of frontal eyespots between bases of frontal antennae (Fig. 1.34A). Antennae long, extending beyond palps; median antenna arising from center of prostomium, with 13-14 articles; lateral antennae arising from anterior margin of prostomium, each with 10-12 articles (Fig. 1.34A). Palps large, thick, subtriangular, 1.5 times longer than prostomium, fused basally (Fig. 1.34A). Everted pharynx extending to setiger 9, anterior middorsal tooth conspicuous; with a distal circlet of 10 soft papillae. Proventriculus present in segments 10-21.

Tentacular cirri longer than antennae; dorsal pair each with 20 articles; ventral pair each about as long as median antenna (Fig. 1.34A).

Parapodia fleshy, bluntly conical (Fig. 1.34B,C,H). Setae generally compound falcigers (Fig. 1.34D-G), numbering around 10 per fascicle. Blades distally bidentate. Superior and inferior blades within fascicles subequal in length (Fig. 1.34D-G); those in anterior segments long, slender, conspicuously serrated (Fig. 1.34D,E); in median and posterior segments short, stout, finely serrated (Fig. 1.34F,G). A dorsal superior and a ventral inferior simple seta present in posterior fascicles, both distally bidentate with serrated cutting surfaces (Fig. 1.34I,J). Aciculae numbering 4 per anterior parapodium, decreasing to 1 posteriorly, each distally resembling bird's beak (Fig. 1.34K).

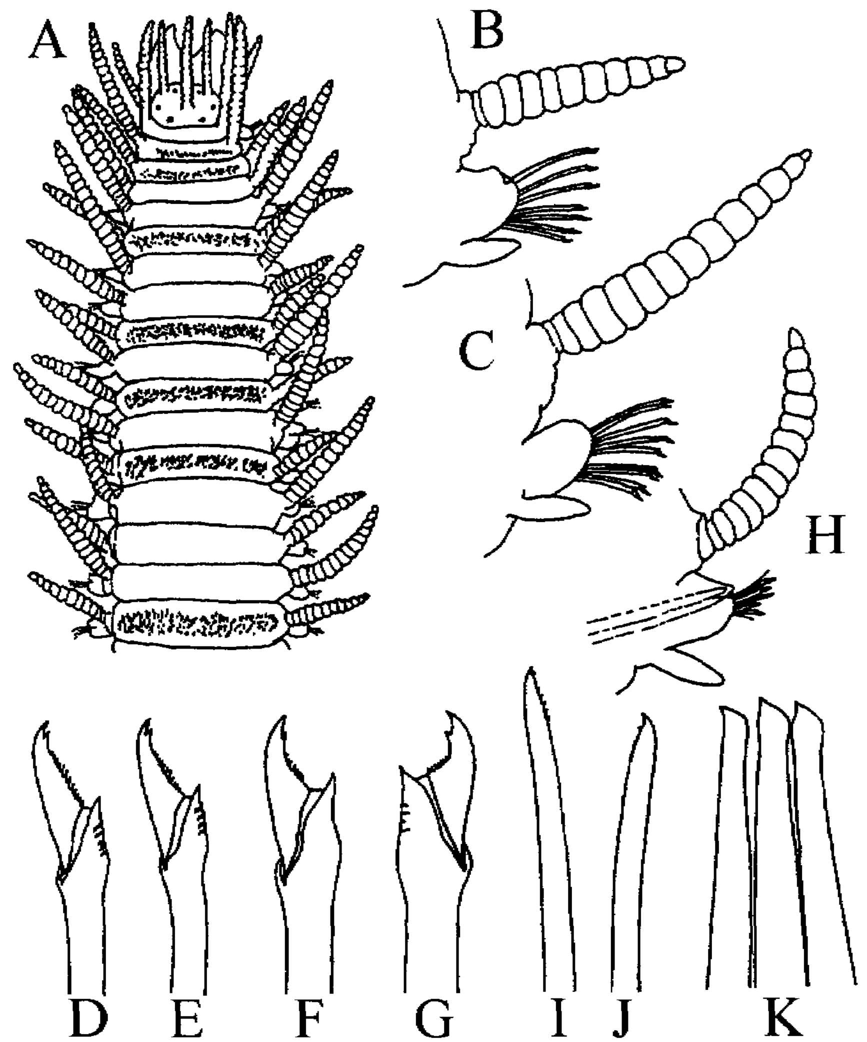

Figure 1.34. *Typosyllis hyalina*: A, anterior end, dorsal view; B, median parapodium with short dorsal cirrus, posterior view; C, median parapodium with long dorsal cirrus, posterior view; D, superior compound falciger, parapodium 10; E, inferior compound falciger, parapodium 10; F, compound falciger, median parapodium; G, compound falciger, posterior parapodium; H, posterior parapodium; I, dorsal simple seta, posterior parapodium; J, ventral simple seta from same parapodium as I; K, aciculae from median parapodium. (A-K, redrawn from Imajima, 1966e)

Dorsal cirri thickest basally, varying in length, strongly annulated; those of setiger 1 longest, with 20 annulations; setigers 2, 3, 5 short, each with 11-14 annulations; setigers 4, 6 long, with 16 annulations; setigers 7, 8 short; setiger 9 long; thereafter regularly alternating short (setiger 10, 11 annulations) and long (setiger 11, 14 annulations) to end of body (Fig. 1.34A). Ventral cirri digitiform, not extending beyond parapodial lobes (Fig. 1.34B,C,H).

Remarks. *Typosyllis hyalina* is a well-recognized, widespread species reported from both the north Pacific and Atlantic basins and the Mediterranean Sea. Local populations of both *T. hyalina* and *T. pulchra* were studied extensively by Piltz (1980).

Habitat. Associated with algae, poriferans and mussel beds in intertidal zones, and hard substrata at MMS stations in depths of 69-90 m.

Distribution. Panama; California north to British Columbia; Japan; North Atlantic Ocean; Mediterranean Sea.

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2. Family Aphroditidae Malmgren, 1867

by

James A. Blake[1]

Introduction

The aphroditids are slow-moving scaleworms commonly called sea mice because of a feltlike dorsal surface that is formed by fine, silky setae and entrapped particles. Aphroditids, because of their size, do not occur in dense populations. They are adapted to burrowing in mud or creeping over the bottom, where they feed on detritus and on sessile or slow moving animals, such as polychaetes (Day, 1967; Fauchald and Jumars, 1979).

Morphology

The body of aphroditids is large, oval, and has relatively few segments (usually less than 60) (Fig. 2.1A, B). Typically, the ventral side is flattened, while the dorsum is arched. The prostomium is spherical and bears a single medial antenna and a pair of long palps (Fig. 2.1D). A well-developed facial tubercle is present above and anterior to the mouth (Fig. 2.1D). Jaws are lacking or poorly developed, but the pharynx is muscular and eversible with several rows of papillae around the opening. Internally, the alimentary canal extends out between the septa to form segmentally arranged caeca. The first segment bears two pairs of tentacular cirri and is uniramous with numerous capillary setae. Parapodia of subsequent segments are biramous, with large internal aciculae. Notosetae include both fine silky setae which entrap silt particles and form the characteristic dorsal felt and stout spines, some of which may be harpoon-shaped (as in *Laetmonice*) (Fig. 2.1C). Neurosetae are simple and sometimes forked. The dorsal surface is covered with 15-20 pairs of elytra (overlapping scales) which occur on segments 2, 4, 5, 7, and alternate segments to 25, then on every third segment. Long dorsal cirri are present on segments which lack elytra (Fig. 2.1E). The pygidium is very small and lacks anal cirri.

Biology

Aphroditids occur from the shallow subtidal to the deep sea. They usually inhabit sandy or muddy bottoms where they are adapted to burrowing or creeping over the surface.

They have a large, muscular eversible pharynx or proboscis and are thought to be active carnivores. Mettam (1980) observed *A. aculeata* Linnaeus feeding on *Nephtys* and *Nereis*. Specimens of *Nereis varians* about three times longer than the *Aphrodita* were swallowed head first indicating an active predatory behavior. *Laetmonice* species may also be active predators, because *L. producta* Grube has been observed with its gut filled with parts of the brittlestar, *Ophiomusium* sp. in Antarctic waters (Hartman, 1967; J.H. Dearborn, personal communication). According to Pettibone (1953), aphroditids eat a great variety of prey items including other annelids, small crustaceans, hydroids, sponges, small molluscs, holothurians, and diatoms. Other animals that use the bodies of aphroditids for support and refuge include other annelids, protozoans, sponges, hydroids,

[1] ENSR Consulting and Engineering, 89 Water Street, Woods Hole, Massachusetts 02543

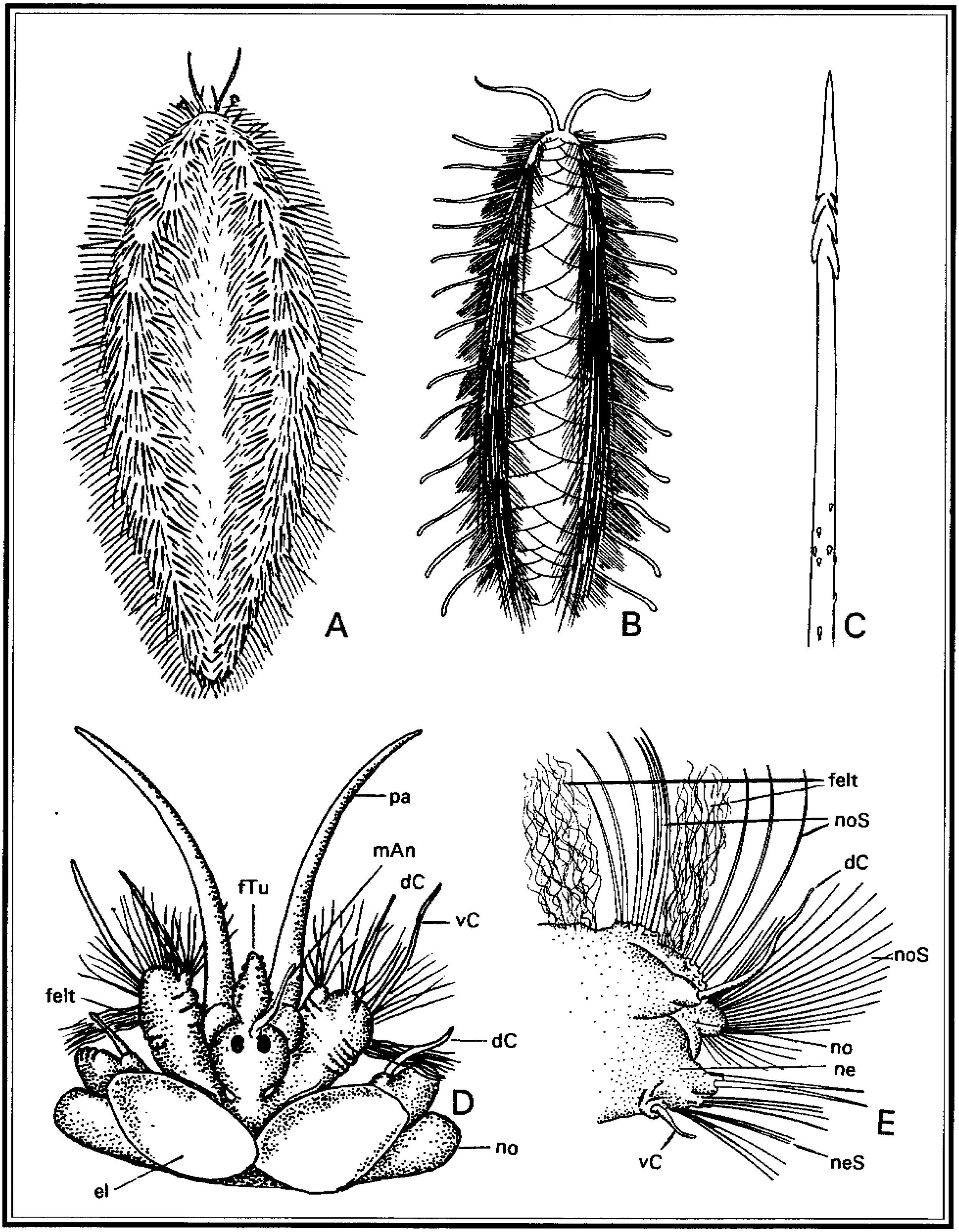

Figure 2.1. Aphroditidae: A, *Aphrodita*, entire animal, dorsal view; B, *Laetmonice*, entire animal, dorsal view; C, harpoon seta; D, *Aphrodita*, anterior end, dorsal view, felt removed; E, parapodium of cirrigerous segment, anterior view. (A-B, after McIntosh; C, after Hartman; D, after Fordham; E, after Pettibone).

echinoderms, bryozoans, molluscs, crustaceans, and tunicates. One particularly interesting association is with the bivalve, *Pseudopythina rugifera* (Carpenter) that lives attached to the ventral surface of *Aphrodita refulgida* Moore. This worm and its commensal clam were collected from off Tomales Point in northern California and studied in the laboratory by Narchi (1969). This small clam attaches to the worm with its byssal threads. Its digestive morphology is well adapted to handling the fine silt particles found in the worm's habitat (Narchi, 1969).

Little is known about the reproduction and development of aphroditids. Paired nephridial or segmental papillae on the posterior face of parapodia between rami serve for the passage of genital as well as excretory products (Pettibone, 1953).

Taxonomic History

In general, there has never been a comprehensive review of the aphroditid polychaetes. Major works by Horst (1916a-b, 1917) on the aphroditids of the *Siboga* Expedition remained for many years the only summaries of this family. Pettibone (1966) redefined some genera, described one new genus, and provided an important key. Some eastern Pacific species were reviewed by Hartman (1939) and Pettibone (1953) and the aphroditids from California were summarized and keyed out by Hartman (1968). Few of these species, however, including most described by Moore (1903, 1905, 1910), have ever been redescribed since their original account. More recently, Watson Russell (1989) revised the genus *Palmyra* and transferred it from the Chrysopetalidae to the Aphroditidae and Hutchings and McRae (1993) published a monograph on the aphroditids of Australia and reviewed the species collected as part of the *Siboga* Expedition. The Hutchings and McRae effort included definitions of five genera and 34 species, seven of which were new to science. This paper is also an important resource and guide to aphroditid morphology and systematic characters.

Key to the Genera of Aphroditidae from California

1A. Dorsal felt well-developed, completely covering elytra with thick mat (Fig. 2.1A); harpoon-shaped notosetae lacking; neurosetae pointed or slightly curved, with or without lateral fringe of soft bristles or basal spur (Fig. 2.2B, D) .... Genus *Aphrodita*

1B. Dorsal felt poorly developed, usually not covering elytra (Fig. 2.1B); harpoon-shaped notosetae present (Fig. 2.1C); neurosetae with lateral fringe of long, stiff bristles and basal spur .... Genus *Laetmonice*

Descriptions of Species

Genus *Aphrodita* Linnaeus, 1758

Type Species: *Aphrodita aculeata* Linnaeus, 1758.

Diagnosis. Body oval, arched dorsally and tapered posteriorly, with 25-45 segments. Prostomium with a single medial antenna and a pair of large sessile eyes. Dorsum covered with tough felt; ventrum usually with numerous small papillae. Dorsum with 15 pairs of elytra under felt. Notosetae including stout acicular spines and long, fine capillaries which form felt; harpoon setae absent. Neurosetae very stout, acicular, arranged in 3 tiers.

Remarks. Eight species were recorded from California by Hartman (1968) and readers should refer to her work for keys to species. Earlier, Pettibone (1953) redescribed *A. japonica* Marenzeller (1879) and *A. negligens* Moore (1905) from the Puget Sound. As part of that work, she included *A. refulgida* Moore (1910) in the synonymy of *A. japonica* and *A. castanea* Moore (1910) and *A. brevitentaculata* Essenberg (1917) in the synonynmy of *A. negligens*. If followed, these synonymies would reduce Hartman's list of species present in California from 11 to 5. Regardless of how many species are actually in the California fauna, all occur on muddy bottoms and should be more commonly taken in trawls than in grabs and box cores. One species, *Aphrodita parva* Moore has been collected in the Santa Maria Basin.

Aphrodita parva Moore, 1905

Figure 2.2

Aphrodita parva Moore, 1905:529-532, pl. 34, figs. 3-7.—Moore, 1908:339; 1910:385-386.—Treadwell, 1914:178.—Berkeley, 1923:211.—Hartman, 1939:22, pl. 1, figs. 9-10; 1968:27, figs. 1-5.

Material Examined. Santa Maria Basin, off Point Estero, Sta. 2, 200 m (1 juvenile); off Point Sal, Sta. PJ-1 (1); off Point Arguello, 900 m (1).

Description. A relatively small species, body short and broad, up to 24 mm long, 15 mm wide for 27 segments. Color in alcohol: flesh. Dorsum covered with greenish silt and debris; ventrum covered with numerous small, spherical papillae.

Prostomium wider than long, bearing 2 pairs small eyes on short frontal peaks; medial antenna slender, about 2.5 times as long as prostomium (Fig. 2.2A); palps thick, about twice as long as medial antennae. Elytra numbering 14-15 pairs, each smooth, thin, transparent without papillae. Parapodia prominent with elevated notopodium and elongated neuropodium (Fig. 2.2C); dorsal cirrus long, threadlike; ventral cirrus thin, tapering, about as long as neuropodium. Notosetae including heavy bristled copper-colored glossy spines and thin pointed setae (Fig. 2.2D, E); neurosetae in 3 rows: dorsalmost row with 1-2 thick spines, middle row with 2-3 spines, and lower row with 3-4 spines; setae diminishing in size ventrally, with lowermost setae bearing prominent spurs (Fig. 2.2B).

Biology. Inhabits bottoms with fine silt.

Remarks. The specimen from Sta. 2 had been identified as *Pontogenia* sp. A in the Phase I reconnaissance. However, the specimen is clearly a juvenile *Aphrodita*, probably *A. parva*. Although *A. parva* is the name applied to these specimens here, it is possible that the species itself is actually a juvenile form of *A. japonica*.

Type Locality. British Columbia, Halibut Bank, Gulf of Georgia, 203-331 m (syntypes, ANSP 2061; USNM 4194).

Distribution. Alaska to western Mexico, 6-1220 m.

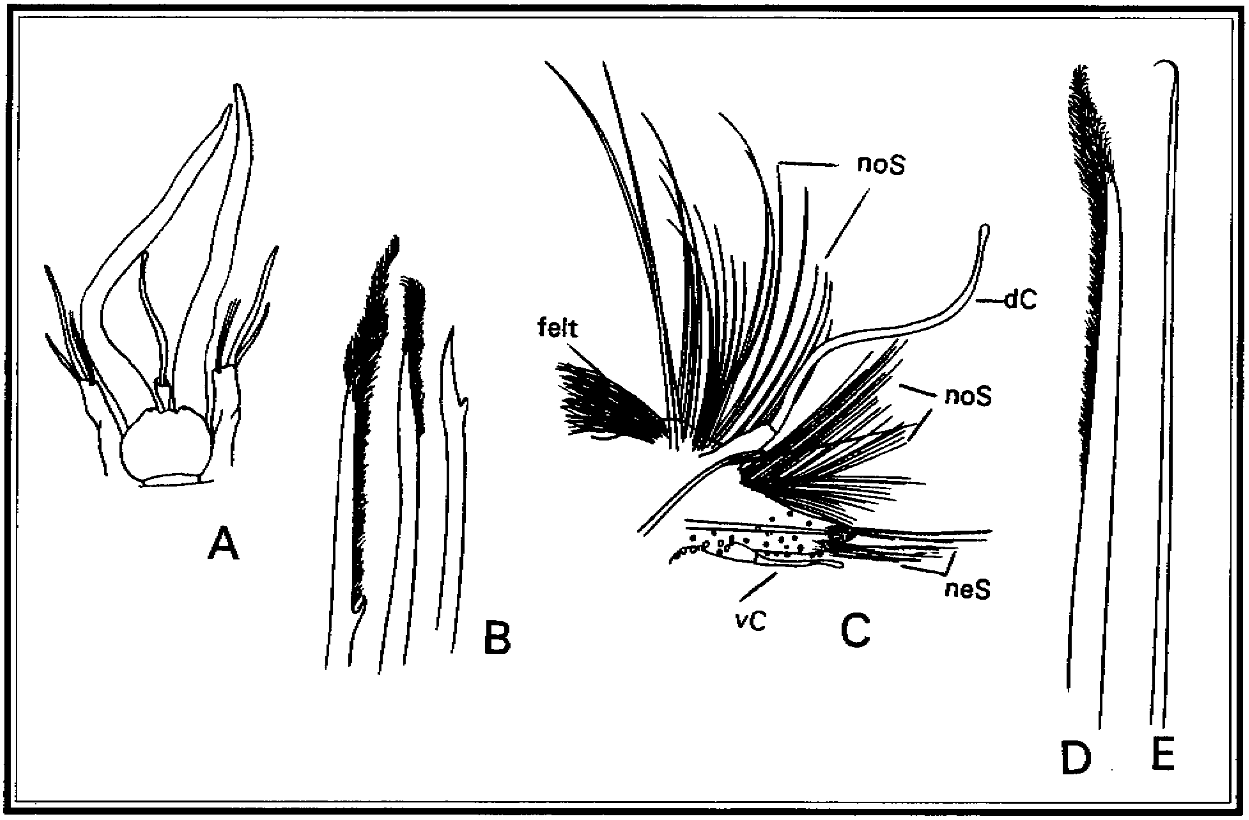

Figure 2.2. *Aphrodita parva*: A, anterior end, dorsal view; B, three types of neurosetae with spurs; C, right parapodium from segment 10; D, bearded neuroseta; E, notoseta. (after Moore, 1905).

Genus *Laetmonice* Kinberg, 1855

Type Species: *Laetmonice filicornis* Kinberg, 1855.

Diagnosis. Body oval, depressed, with 32-46 segments. Prostomium with papillose facial tubercle; rounded with single medial antenna and 2 stout ommatophores. Feltage poorly developed, not completely covering elytra; elytra smooth, covering dorsum, numbering 15-20 pairs. Notosetae of segments with elytra including harpoon-shaped setae, acicular setae, and capillaries; notosetae of cirrigerous segments without harpoon setae, but silky capillaries may be present; neurosetae bifurcate with fringe bristles on edge.

Remarks. Two species, *Laetmonice pellucida* Moore and *L. producta wyvillei* McIntosh have been recorded from off California in deep water (Hartman, 1968). None have been encountered in the Santa Maria Basin and western Santa Barbara Channel.

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3. Family Polynoidae Malmgren, 1867

by

R. Eugene Ruff[1]

Introduction

The family Polynoidae is the largest and most commonly encountered group of scaleworms. The approximately 700 species in this family are characterized by dorsoventrally flattened bodies, simple setae in both notopodial and neuropodial fascicles, and scales alternating with the dorsal cirri down much of the length of the body. Although a few species become quite large (up to 250 mm), the majority of the scaleworms are only a few centimeters in length.

Morphology

In most polynoid species the prostomium is bilobed, with a median furrow between the anterior lobes; the anterolateral corners are sometimes more or less developed into distinct cephalic peaks, or they extend anteriorly to form the ceratophores of the lateral antennae (Fig. 3.1A). There are typically two pairs of eyes arranged in a trapezoidal pattern, although the eyes in deep-water species may be absent. Most species have a median and a pair of lateral antennae which are smooth or covered to a lesser or greater extent with papillae. A pair of tapering palps are attached ventrally to the prostomium, and are normally thicker and longer than the antennae; these structures usually have numerous longitudinal rows of minute sensory papillae. The eversible pharynx is large and muscular, with two pairs of curved, dark, keratinous jaws surrounded by a circlet of marginal papillae.

The tentacular segment (segment 1) has two pairs of tentacular cirri supported on large, forward-projecting basal lobes. These tentaculophores have an internal supporting acicula, and sometimes on the anterior face there are additional projecting setae that are usually similar to the notosetae. The ventral portion of the peristomium forms the upper lip of the mouth (Fig. 3.1B). This is often produced into a ridge which sometimes bears a distinct conical facial tubercle.

The buccal segment (segment 2) bears the first pair of elytra and the first parapodia. Dorsally it may be developed into a nuchal fold that partly covers the prostomium, and ventrally it forms the lateral and lower portions of the mouth. The ventral buccal cirri on this segment are usually well-developed and inserted at the bases of the parapodia.

The paired elytra are flattened, scale-like structures that occur in place of the dorsal cirri, and are normally attached via the elytrophores to segments 2, 4, 5, 7, 9, . . . 21, 23; posterior to this point there are a number of different attachment patterns, and the scales may be lacking in the posteriormost segments. The elytra may overlap and completely conceal the dorsum, or they may be reduced in size. The surface of the scales may be smooth, or it may be covered to a greater or lesser extent with papillae, microtubercles (sclerotized structures that are nodular, pointed, or multipronged, and that are clearly visible only under high magnification)

[1]Ruff Systematics, 11719 Meridian East, Suite 401, Puyallup, WA 98373.

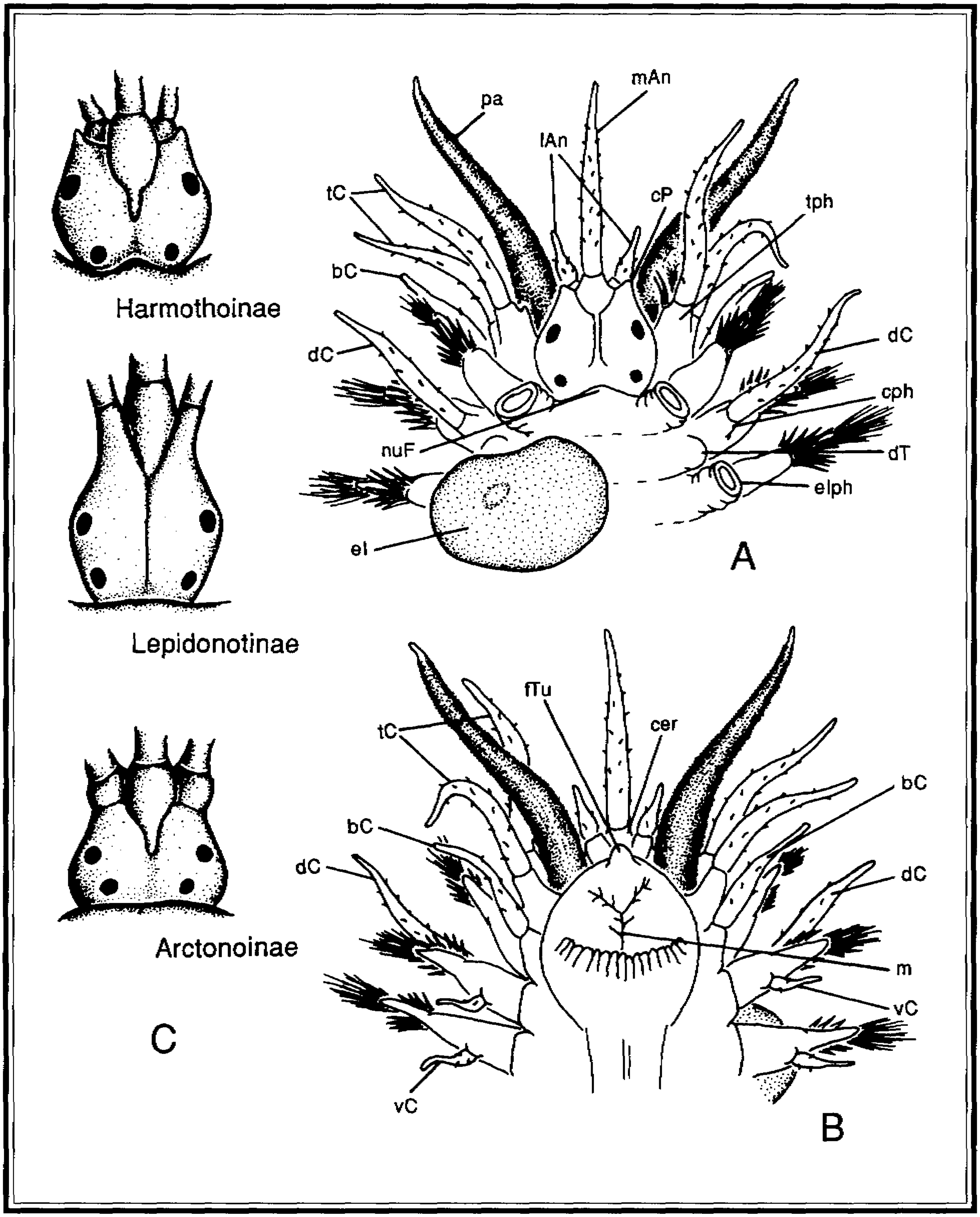

Figure 3.1. Polynoid morphology: A, anterior end of typical harmothoid polynoid, dorsal view; B, ventral view of same; C, prostomia of representatives of three polynoid subfamilies showing insertion pattern of lateral antennae.

or macrotubercles (larger, sclerotized or soft structures that occur irregularly on the surface or near the posterior edges). The borders of the elytra may be smooth, or they may have sparse or dense fringes of clavate or filiform papillae.

The elongated parapodia are biramous or, in some cases, subbiramous. The notopodia are usually located along the dorsal margin of the neuropodia; each has an internal supporting acicula which may be distally emergent. The neuropodia are usually larger than the notopodia, and are distally cleft into a rounded postsetal lobe and a longer, narrower presetal lobe bearing the internal acicula which may emerge distally.

All polynoid setae are simple. Although lacking in a few species, the notosetae range from slender and smooth to stout with subdistal transverse spinous plates. The tips may be capillary, pointed, or blunt with or without a terminal cleft. The neurosetae normally have a long smooth shaft and a curved, subdistal inflated spinous region; the setal tips may be capillary, unidentate, or bidentate with a subequal or small secondary tooth. The shape of the superior neurosetae is often different from those lower in the fascicle, and both uni- and bidentate tips are sometimes found within the same setal bundle.

Dorsal cirri are inserted along the upper margin of the notopodia on segments not bearing elytra; in addition, these segments have a more or less developed dorsal tubercle corresponding in position to the elytrophore. Ventral cirri are normally inserted midway along the ventral edge of the neuropodia after segment 2. Small, cylindrical nephridial papillae occur ventrally at the base of the neuropodia, usually from segment 6; these structures project posteriorly and upward between the parapodia. The pygidium surrounds a dorsally-directed anus, and has a pair of terminal anal cirri that are similar in shape but often longer than the dorsal cirri.

Taxonomic History

For many years, the polynoids were divided into the Iphioninae, Lepidonotinae, and Harmothoinae based essentially on the number and arrangement of the prostomial appendages. Discoveries within the last 20 years, however, including a wealth of material obtained from the deep-sea hydrothermal vents, have prompted the erection of approximately 15 additional subfamilies. Dr. Marian H. Pettibone of the Smithsonian Institution has been instrumental in revising the systematics of the polynoids, and is continuing her revisionary studies to clarify the relationships within the family. Therefore, the subfamilial and generic position of many of the species is currently in a state of flux, a fact reflected in some of the less familiar generic designations listed below.

The insertion of the lateral antennae is of primary importance in distinguishing some of the subfamilies within the Polynoidae, including the four subfamilies represented in the Santa Maria Basin material (Fig. 3.1C). In the Harmothoinae (Horst, 1917), the lateral antennae have small ceratophores that are attached ventrally beneath the anterior prostomial margins and/or to the large ceratophore of the median antenna. In the Lepidonotinae (Willey, 1902) and closely allied Lepidastheniinae (Pettibone, 1989), the lateral antennae are attached terminally to anterior prolongations of the prostomium, without distinct ceratophores. In the Arctonoinae (Hanley, 1989), the lateral antennae have large ceratophores that are inserted subterminally, and are distinctly separated from the prostomium by a transverse groove.

The number and arrangement of the elytra are very important in distinguishing the polynoid genera. Even though the scales are often autotomous, their position can be assessed by counting the distinctive elytrophores along the body. Unfortunately, many species fragment during preservation, and the posterior portion of the body is often lost and not available for examination. Therefore, it is best to narcotize scale worms in a solution of magnesium chloride in seawater immediately after collection. The worms should then be preserved separately if possible to ensure that the elytra are maintained with the correct specimen.

Distribution and Biological Notes

Polynoids are found from the intertidal regions to the abyssal depths on a wide variety of sediment types, although a few are entirely pelagic. Most species are carnivorous or omnivorous, feeding on a large spectrum of smaller invertebrates, plant fragments, and detritus. These species normally creep along the bottom, hiding in crevices, under rocks, and in algal holdfasts. The dorsum and the elytra are often pigmented with a variety of patterns and colors matching the general background. In addition, the elytral surface is sometimes covered with detritus and epiphytes, making the specimens difficult to detect.

A number of polynoids are commensal with other organisms, predominantly the echinoderms, molluscs, or other polychaetes. In many of these species, the elytra and notopodia are reduced in size, and the notosetae are fewer in number or absent altogether. Many of these commensals are pigmented similar to the host organism.

All polynoids are dioecious, with fertilization taking place externally. The eggs may be discharged directly into the water column, but in many species they are brooded beneath the elytra and released into the seawater only after some degree of development. Blake (1975a) illustrates the pelagic larvae of *Halosydna brevisetosa* from Tomales Bay, while other authors (Thorson, 1946; Cazaux, 1968; Daly, 1972) have delineated the reproductive biology and larval development of the widely distributed species *Harmothoe imbricata*. Typically, a larval nectochaete metamorphoses to a bottom dwelling juvenile when it has developed 5-6 pairs of elytra. During metamorphosis the prostomium gains an adult aspect, and the first larval setiger shifts forward to develop into the tentacular segment. In most free-living polynoids, the number of segments is determinant within a small range, and the worms do not grow beyond 30-40 mm in length. A number of the commensal species, however, continue to add segments throughout their lives, and much greater body lengths are attained.

Key to the Species of Polynoidae

1A. Lateral antennae attached terminally to anterior prolongations of the prostomium, without distinct ceratophores 2

1B. Lateral antennae attached subterminally or ventrally, with ceratophores distinctly demarcated from prostomium 10

2A. Anterior elytra with surface tubercles and marginal fringes of papillae; most notosetae ending in long, fine tips 3

2B. Surfaces and margins of anterior elytra smooth; all notosetae (when present) ending in blunt unidentate or notched tips 7

3A. Twelve pairs of elytra with long fringing papillae; numerous notosetae in large tufts 4

3B. Eighteen pairs of elytra with short fringing papillae; relatively few notosetae in small bundles 5

4A. Basal plates of larger tubercles on anterior elytra polygonal; largest tubercles on posterior elytra acutely conical, pointed .... *Lepidonotus spiculus*

4A. Basal plates of larger tubercles on anterior elytra rounded; largest tubercles on posterior elytra digitiform, blunt-tipped .... *Lepidonotus squamatus*[2]

5A. Surfaces of median and posterior elytra smooth; some neurosetae with bidentate tips .... *Halosydna johnsoni*[2]

5B. Elytral surfaces with chitinized conical tubercles; all neurosetal tips unidentate 6

6A. Body broad, oval in outline; conical macrotubercles restricted to region behind attachment scar .... *Halosydna latior*[2]

6B. Body long, linear; conical macrotubercles dispersed across elytral surface .... *Halosydna brevisetosa*[2]

7A. Superior neurosetae thinner than median neurosetae 8

7B. Superior neurosetae thicker than median neurosetae 9

8A. Notopodia elongated; elytra extending across dorsum; proximal ventral margin of neuropodia with row of papillae .... *Lepidasthenia longicirrata*

8B. Notopodia short; elytra leaving median dorsum uncovered; ventral neuropodial margin smooth .... *Lepidasthenia berkeleyae*

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[2]Not represented in the Santa Maria Basin material, but reported from southern California.

9A. Body pigmented dark green or black; neurosetae with large secondary tooth .... *Lepidasthenia virens*[2]

9B. Body pigmented light yellow; secondary neurosetal tooth very small .... *Lepidasthenia gigas*[2]

10A. Lateral ceratophores subterminal, converging at midline on ventral side of prostomium; parapodia subbiramous, notosetae few or absent 11

10B. Lateral ceratophores ventral, attaching to prostomium and/or median ceratophore; parapodia biramous, notosetae numerous 13

11A. Supraacicular neurosetae blunt, bifid; dorsum often with a pigment band across setiger 8 .... *Arctonoe vittata*

11B. Supraacicular neurosetae hooked, similar to subacicular setae; dorsum without pigment band 12

12A. Elytra flat; ventral cirri subulate .... *Arctonoe pulchra*

12B. Elytra with ruffled margins; ventral cirri rudimentary .... *Arctonoe fragilis*[2]

13A. Neurosetae with large semilunar cusp at base of spinous region; notosetae with spinous pockets extending to the tips .... *Subadyte mexicana*

13B. Neurosetae without basal cusp 14

14A. All notosetae ending in capillary tips .... *Tenonia priops*

14B. At least some notosetae ending in blunt or pointed tips 15

15A. Upper notosetae ending in pointed tips; lower notosetae thinner, tapering to very fine points 16

15B. All notosetae ending in blunt or pointed tips 19

16A. Elytra thick, covered with polygonal cells; upper and lower neurosetae similar in shape .... *Gaudichaudius iphionelloides*

16B. Elytra thin, translucent; upper and lower neurosetae differing in shape 17

17A. Dorsum without pigment; margins of elytra with sparse fringe of digitate papillae .... *Hesperonoe laevis*

17B. Dorsum pigmented; elytral margins smooth 18

18A. Dorsum grayish-green; elytra with smooth surface; upper notosetae with coarse serrations .... *Hesperonoe adventor*[2]

18B. Dorsum salmon-colored; elytral surface with scattered conical tubercles; upper notosetae with indistinct serrations .... *Hesperonoe complanata*[2]

19A. Notosetae with longitudinal striations and minute spinules arranged in two longitudinal rows 20

19B. Notosetae with spinules arranged in transverse rows 23

20A. Neurosetae less numerous than notosetae, unidentate or with only indistinct indication of secondary tooth .... *Malmgreniella baschi*

20B. Neurosetae as numerous as notosetae, with well-developed secondary tooth at least in median portion of fascicle 21

21A. Prostomium with acute cephalic peaks; neurosetae with smooth, bare region between distal spinose bracts and base of secondary tooth .... *Malmgreniella macginitiei*

21B. Prostomium with truncate anterior lobes; distal spinose bracts on neurosetae nearly reaching base of secondary tooth 22

22A. Supraacicular lobes small, short; dorsal cirri extending beyond tips of neurosetae; elytral surface without distinct reticulation .... *Malmgreniella scriptoria*

22B. Supraacicular lobes large, digitiform; dorsal cirri extending only to tips of neurosetae; elytral surface distinctly reticulated .... *Malmgreniella nigralba*

23A. Superior neurosetae with deeply incised tips; prostomium without eyes .... *Eucranta anoculata*

23B. Superior neurosetae with tips bifid or entire; prostomium with eyes present 24

24A. All neurosetae with tips entire 25

24B. At least some neurosetae ending in bifid tips 27

25A. Median and lower neurosetae with terminal aristae; elytra thin, appearing smooth .... *Bylgides macrolepidus*

25B. Neurosetae with smooth, slightly hooked tips; elytra thick, with distinct surface macrotubercles 26

26A. Elytra with large, dendritic, acutely-pointed spines; all notosetae with smooth, pointed tips .... *Eunoe senta*

26B. Elytra with knob-like macrotubercles; some notosetae with blunt, sculptured, indistinctly split tips .... *Eunoe oerstedi*[2]

27A. Superior notosetae more slender than most neurosetae; superiormost 1-2 neurosetae greatly enlarged, lance shaped .... *Ysideria hastata*

27B. Superior notosetae thicker than most neurosetae; superiormost 1-2 neurosetae not distinctly enlarged 28

28A. Elytra with multipronged macrotubercles surrounded by large polygonal cells; neurosetae with secondary tooth remote from the tip .... *Harmothoe hirsuta*

28B. Elytra with smooth macrotubercles and without polygonal cells; secondary tooth close to the neurosetal tip 29

29A. Anterior pair of eyes located on forward margin of the prostomium hidden beneath the prostomial peaks; dorsum lightly pigmented or mottled .... *Harmothoe imbricata*[2]

29B. Anterior eyes located on lateral margins of prostomium, visible dorsally; dorsum usually dark brown 30

30A. Elytral surface with large thorn-like curved spines but without filiform papillae; fringing papillae short .... *Harmothoe multisetosa*

30B. Elytral surface with filiform papillae but without large thorn-like curved spines; fringing papillae long .... *Harmothoe fragilis*

Description of Species

Descriptions and illustrations are presented for a total of 22 species distributed among 13 genera that occur in or near the Santa Maria Basin and western Santa Barbara Channel as follows:

Arctonoe fragilis (Baird, 1863)
Arctonoe pulchra (Johnson, 1897)
Arctonoe vittata (Grube, 1855)
Bylgides macrolepidus (Moore, 1905)
Eucranta anoculata (Moore, 1910)
Eunoe senta Malmgren, 1865
Gaudichaudius iphionelloides (Johnson, 1901)
Harmothoe fragilis Moore, 1910
Harmothoe hirsuta Johnson, 1897
Harmothoe imbricata (Linnaeus, 1767)
Harmothoe multisetosa (Moore, 1902)
Hesperonoe laevis Hartman, 1961
Lepidasthenia berkeleyae Pettibone, 1948
Lepidasthenia longicirrata Berkeley, 1923
Lepidonotus spiculus (Treadwell, 1906), **new combination**
Malmgreniella baschi Pettibone, 1993
Malmgreniella macginitiei Pettibone, 1993
Malmgreniella nigralba (Berkeley, 1923)
Malmgreniella scriptoria (Moore, 1910)
Subadyte mexicana Fauchald, 1972
Tenonia priops (Hartman, 1961)
***Ysideria hastata* Ruff, new genus, new species**

An additional polynoid listed as *Herdmanella* sp. in the MMS Phase II voucher material was found to be a 14-segment juvenile and could not be identified to the species level.

Genus *Arctonoe* Chamberlin, 1920

Type Species: *Arctonoe lia* Chamberlin, 1920, by original designation.

Diagnosis. Body elongate, flattened, with more than 100 segments. Bilobed prostomium without cephalic peaks, with well-defined lateral ceratophores inserted at anterior margin and converging ventrally. Antennae, tentacular cirri and dorsal cirri smooth. Facial tubercle poorly developed; buccal segment with or without nuchal fold. Elytra on segments 2, 4, 5, 7, . . . 23, 26, 28, 29, 31, 33, continuing on alternate segments to end of body, often leaving dorsum exposed; elytra without tubercles or papillae. Parapodia subbiramous. Notosetae short, serrated, unidentate or with notched tips; neurosetae stouter, longer, with unidentate hooked tips.

Remarks. The genus *Arctonoe* was recently revised and placed into the new subfamily Arctonoinae by Hanley (1989). A total of three species are known, all of which occur off California.

Arctonoe fragilis (Baird, 1863)

Figure 3.2 A-E

Lepidonotus fragilis Baird, 1863:108.
Polynoe fragilis: Johnson, 1897:179-181, pl. 7, figs. 36, 45, pl. 8, fig. 52.
Arctonoe fragilis: Berkeley and Berkeley, 1948:20, fig. 23.—Pettibone, 1953:64-66, pl. 31, figs 281-290.—Hartman, 1968:45-46, figs. 1-3.—Blake, 1975b:165, pl. 27, fig. 70.—Hanley, 1989:9-12, figs. 4A-F, 5A-F (synonymy).

Material Examined. Washington: San Juan Archipelago (1).—California: off Dillon Beach (1).

Description. Length to 85 mm for 100 segments; body without pigmentation. Prostomium bilobed, wider than long, with four small eyes on posterior half (Fig. 3.2A). Ceratophore of median antenna large, stout; smooth style short, clavate, with filiform tip. Lateral antennae shorter and similar in shape. Palps twice prostomial length, abruptly tapering to short tips, occasionally with brown subterminal bands.

Basal lobes of tentacular segment achaetous, with two pairs of subequal tentacular cirri similar in shape but longer than median antenna. Facial tubercle poorly developed. Cirrophores of ventral buccal cirri large, cylindrical; styles short, clavate, similar to median antenna.

Large elytra nearly touching medially, thin, translucent, smooth, lacking tubercles or marginal papillae, with yellow, reddish, or greenish mottling. Median and posterior borders folded, convoluted (Fig. 3.2B).

Subbiramous parapodia with small digitate notopodia and large, thick, truncate neuropodia (Fig. 3.2C). Notosetae short, slender, with transverse subdistal serrations and unidentate or notched tip (Fig. 3.2D). Neurosetae longer, stout, with faint transverse serrations in swollen subdistal region, narrowing to sharp hooked tip (Fig. 3.2E).

Dorsal cirri thick, clavate, often of varying lengths, with filiform tips. Dorsal tubercles large, rounded. Ventral cirri rudimentary after segment 2. Ventral nephridial papillae low, usually inconspicuous, from segment 6. Short pygidial cirri clavate with filiform tips.

Biology. *Arctonoe fragilis* is commonly found in the ambulacral grooves of the asteroid *Evasterias troschelii*, where the elytra exhibit the general coloration of the host (Morris *et al.*, 1980). When viewed, the dorsal cirri mimic the appearance of the host's tube feet and spines. It has also been reported as a commensal

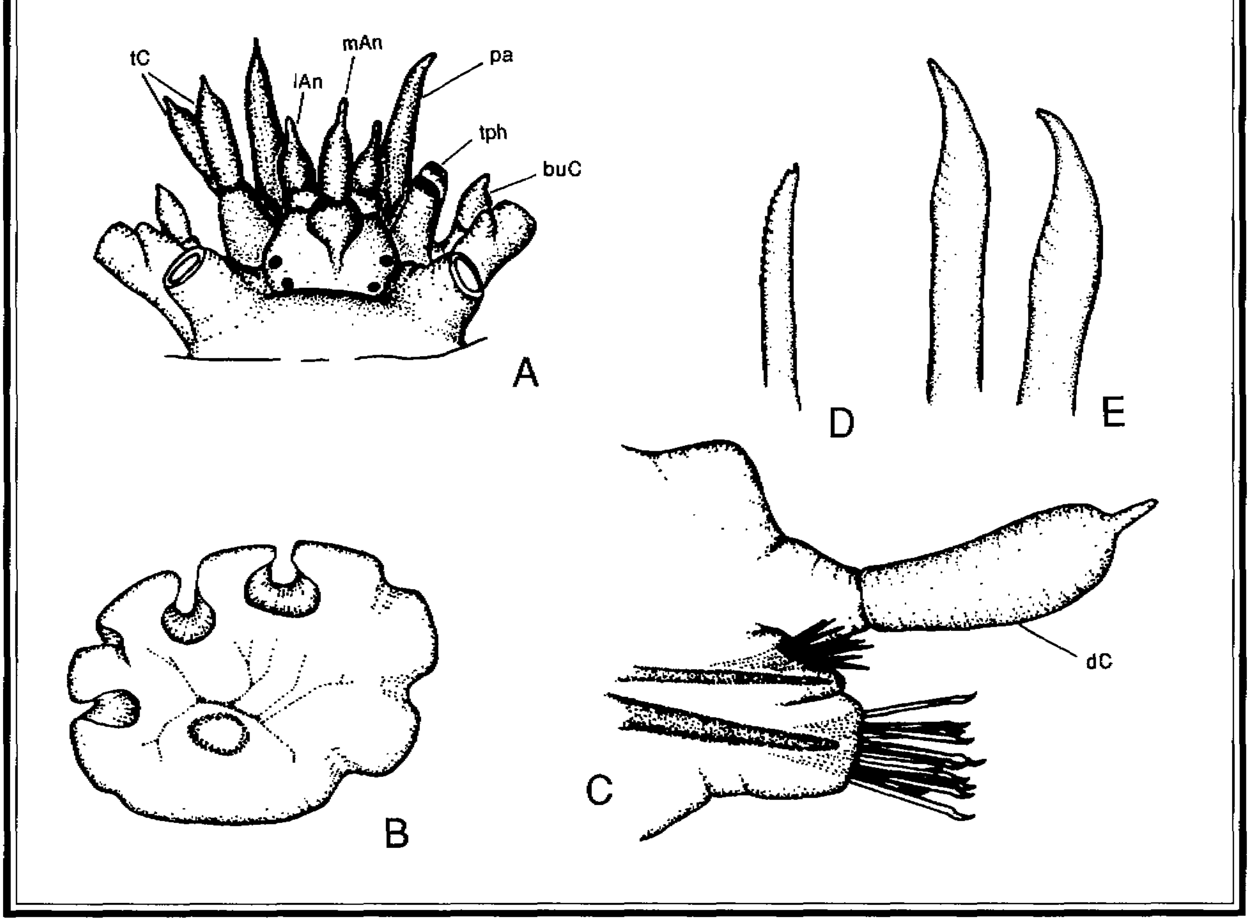

Figure 3.2. *Arctonoe fragilis*: A, anterior end, dorsal view; B, median right elytron; C, median cirrigerous parapodium, anterior view; D, notoseta; E, neurosetae.

with a number of other asteroid species, including *Leptasterias aequalis*, *L. hexactis*, *Luidia foliolata*, *Orthasterias koehleri*, *Pisaster ochraceus*, *P. giganteus*, *Solaster dawsoni*, and *Stylasterias forreri*.

Remarks. *Arctonoe fragilis* is characterized by vestigial ventral cirri and the ruffled posterior margins of the elytra. Because specimens readily fragment and often loose their scales, Baird (1863) provided only a minimal description and he did not mention the convoluted elytral borders. However, subsequent authors have ascribed specimens to Baird's species because of the rudimentary nature of the ventral cirri and the typical association of the worm with asteroids, two features that Baird stressed.

Type Locality and Type Specimens. Esquimalt Harbor, Vancouver Island. Baird (1863) lists the British Museum as the repository for the type specimen, but Hanley (1989) notes that during a recent search it could not be located there.

Distribution. Found in the rocky intertidal and in shelf depths from the Alaskan Peninsula at least as far south as San Francisco, but uncommon in California. Treadwell's (1937) report of the species from Cedros Island off the Baja Peninsula was based upon a mutilated specimen, and is doubtful (Pettibone, 1953).

Arctonoe pulchra (Johnson, 1897)

Figure 3.3 A-E

Polynoe pulchra Johnson, 1897:177-179, pl. 7, figs. 34, 43, 43a, pl. 8, figs. 50, 50a, 50b.
Arctonoe pulchra: Skogsberg, 1942:497-500, fig. D, 6-8; Pettibone, 1953:61-64, pl. 30, figs. 272-280; Hartman, 1968:47-48, figs. 1-4.—Blake, 1975b:175, pl. 27, fig. 69.—Hanley, 1989:12-16, figs. 6A-F, 7A-F (synonymy).

Material Examined. Washington: San Juan Island (3).—California, north of Bodega Bay (2); off Pacific Grove (2 syntypes); Western Santa Barbara Channel, off Point Conception, Sta. BRC-1, 69-74 m (2).

Description. Length to 70 mm for 70 segments; body colorless or mottled with brownish pigment dorsally. Prostomium bilobed, wider than long, with four moderate-sized eyes on posterior half (Fig. 3.3A). Median antenna with large ceratophore and smooth cylindrical style with subdistal swelling and elongated terminal tip; lateral antennae shorter, pyriform, with long filamentous tips. Palps stout, wrinkled, abruptly tapering to short tips, often with brown subterminal pigment bands.

Lateral tentaculophores long, usually achaetous, with two pairs of smooth, subequal tentacular cirri similar in shape but longer than median antenna. Facial tubercle poorly developed. Ventral buccal cirri on segment 2 long, similar to median antenna.

Suboval or reniform elytra covering dorsum. Each elytron thin, flat or slightly undulate, lacking tubercles and marginal papillae, often with reddish-brown pigment concentrated over elytrophore (Fig. 3.3B).

Parapodia subbiramous, with small, digitiform notopodia on anterodorsal side of longer, broader neuropodia; neuropodia with rounded pre- and postsetal lobes (Fig. 3.3C). When present, notosetae short, stout, with spinous edge and blunt, notched tip (Fig. 3.3D). All neurosetae similar in shape, stout, with faint transverse striations in swollen subdistally region, narrowing to sharp hooked tip (Fig. 3.3E).

Ceratophores of dorsal cirri large, cylindrical, tapering; styles long, with subterminal enlargement and long filamentous tip. Dorsal tubercles conspicuous knobs. Ventral cirri short, subulate. Ventral nephridial papillae low, inconspicuous, from segment 6. Pygidium rounded with pair of short, subterminally swollen cirri.

Biology. *Arctonoe pulchra* is normally found commensal with the holothurian *Parastichopus californicus*, using its hooked neurosetae to cling to the epidermis, and crawling into the host's mouth when disturbed (Johnson, 1897; Morris *et al.*, 1980). It is also often associated with the giant gumboot chiton *Cryptochiton stelleri*, the keyhole limpet *Megathura crenulata*, the terebellid *Loimia medusa*, and a number of additional asteroid and gastropod species (Pettibone, 1953).

Remarks. Specimens of *Arctonoe pulchra* exhibit a wide variety of coloration on the elytra and dorsal body that matches the host organisms in cases where the worm is exposed to the environment. These colors, however, usually fade quickly in preservative. Specimens can often be recognized by the dark pigment spot occurring on each elytron, but this pigmentation is variable and may be entirely lacking. Notosetae are usually present in small individuals, but they tend to be lost, especially in the posterior segments, as the specimens grow.

Type Locality and Type Specimens. California, Pacific Grove, 2 syntypes (LACM-AHF Poly 0044). An additional syntype is in the collections of the Zoological Museum of Hamburg in Germany (HZM PE 127b), apparently a gift to Ehlers from either Johnson or the Museum of the University of California (Hanley, 1989).

Distribution. Found from the Gulf of Alaska to Baja California, in low intertidal and shelf depths.

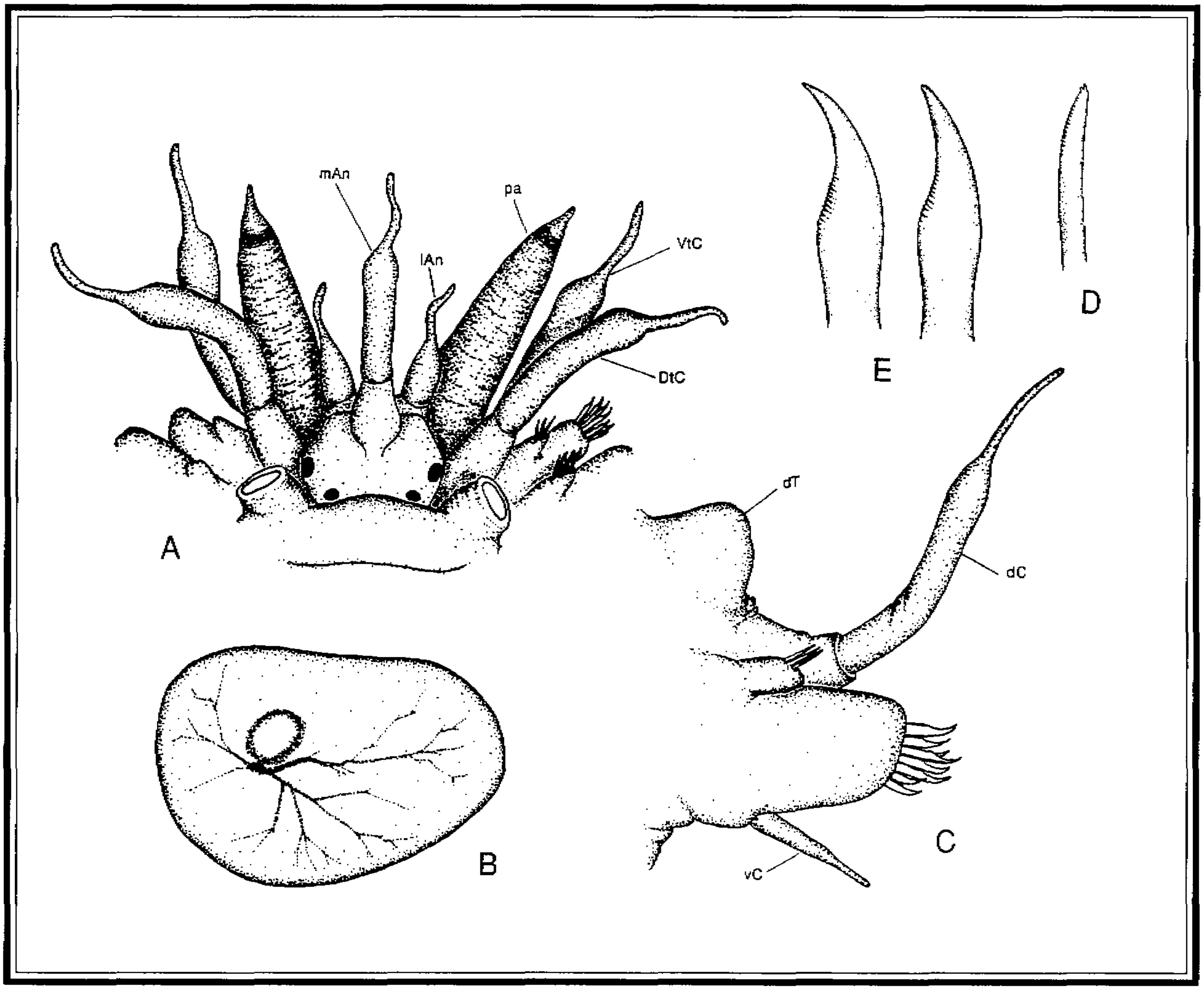

Figure 3.3. *Arctonoe pulchra*: A, anterior end, dorsal view; B, median left elytron; C, median cirrigerous parapodium, anterior view; D, notoseta; E, neurosetae.

Arctonoe vittata (Grube, 1855)

Figure 3.4 A-F

Polynoe lordi: Johnson, 1897:175-177, pl. 7, figs. 35, 44, pl. 8, fig. 51.
Acholoe vittata: Marenzeller, 1902:576-577, pl. 3, fig. 13.
Arctonoe lia Chamberlin, 1920:6-7, pl. 1, figs. 1-4, pl. 2, figs. 1-3.
Halosydnoides vittata: Okuda, 1936:565-68, figs. 4-5.
Arctonoe vittata: Hartman, 1939:29-30, pl. 3, figs. 33-37; 1948:11-12, fig. 2a-f; 1968:49-50, figs. 1-3.—Skogsberg, 1942:489-497, figs. B-D.—Berkeley and Berkeley, 1948:20-21, figs. 24-25.—Pettibone, 1953:57-61, pl. 28, figs. 251-258, pl. 29, figs. 259-271.—Uschakov, 1955:132-133, fig. 23E-J; 1982:116-117, pl. 35, figs. 1-7.—Blake, 1975b:175, pl. 27, figs. 67-68.—Hanley, 1989:4-9, fig. 1A-F, fig. 2A-L (synonymy).

Material Examined. Alaska, Boca de Quadra (3).—Washington, San Juan Island (3).—Oregon, off Tillamook Head (1).—California, off Tomales Point (3); Santa Maria Basin, off Point Sal, Sta. R-8, 90 m (1).

Description. Length to 100 mm for 89 segments; body often with solid pigment band across segment 7 or 8. Prostomium bilobed, wider than long, with four small subequal eyes on posterior half (Fig. 3.4A). Median antenna with thick ceratophore and short, smooth, clavate style with long filiform terminal tip; lateral antennae stubby with long filamentous tips. Palps short, abruptly tapering to short tips, often with dark subterminal pigment bands.

Lateral tentaculophores large, achaetous, with two pairs of subequal cirri similar in length and shape to median antenna. Facial tubercle poorly developed. Ventral buccal cirri of segment 2 with large, cylindrical cirrophore and styles similar to median antenna.

Small suboval or reniform elytra leaving median dorsum uncovered anteriorly, and overlapping in posterior segments; posterior attachment pattern variable and often asymmetrical. Elytra thin, translucent, smooth, lacking tubercles or marginal papillae (Fig. 3.4B), usually white with some degree of black or brown mottling.

Subbiramous parapodia (Fig 3.4C) with small, digitiform notopodia; neuropodia broader, longer, with short, rounded pre- and postsetal lobes. Notosetae short, slender, with subterminal serrations and blunt notched tips (Fig. 3.4D); notosetae often lacking in median and posterior segments. Superior neurosetae after segment 2 similar to notosetae, larger, with fine subterminal spines and notched, blunt tips (Fig. 3.4E); inferior neurosetae stouter, with faint transverse serrations in subterminal inflated region, narrowing distally to pointed hooked tips (Fig. 3.4F).

Dorsal cirri with bulbous cirrophores; styles short, cylindrical to clavate, narrowing to long filiform tips. Dorsal tubercles well-developed. Ventral cirri short, subulate. Small, terete ventral nephridial papillae conspicuous from segment 6 to end of body. Terminal pair of pygidial cirri resembling dorsal cirri in shape, but longer.

Biology. *Arctonoe vittata* is found both free-living and in commensal association with a wide variety of asteroids, gastropods, and polychaetes, where they often tend to match their hosts in body coloration. In California it is most often found with the giant gumboot chiton *Cryptochiton stelleri*, the asteroid *Dermasterias imbricata*, and in the pallial grooves of the keyhole limpet *Diodora aspera* (Morris *et al.*, 1980). Skogsberg (1942) and Pettibone (1953) provide a comprehensive list of hosts.

Remarks. The dark pigment band across the dorsum of segment 8 is not present in all individuals. The size of the elytra is also variable, and tends to be related to the particular host. Specimens associated with *Cryptochiton* and *Diodora* normally have a distinct middorsal gap, while those found with *Dermasterias* may have larger elytra that touch medially.

The number of notosetae in each segment appears to be a function of specimen size. In small specimens, most of the notopodia have setae, although the number per fascicle decreases posteriorly. In larger individuals, however, the notosetae are usually absent in all but the anteriormost segments.

Type Locality and Type Specimens. Sitka, Alaska. Skogsberg (1942) lists the type specimen in the Leningrad Museum.

Distribution. Found from Japan and the Bering Strait along the Pacific coast to Ecuador, in the rocky intertidal zone and shelf depths.

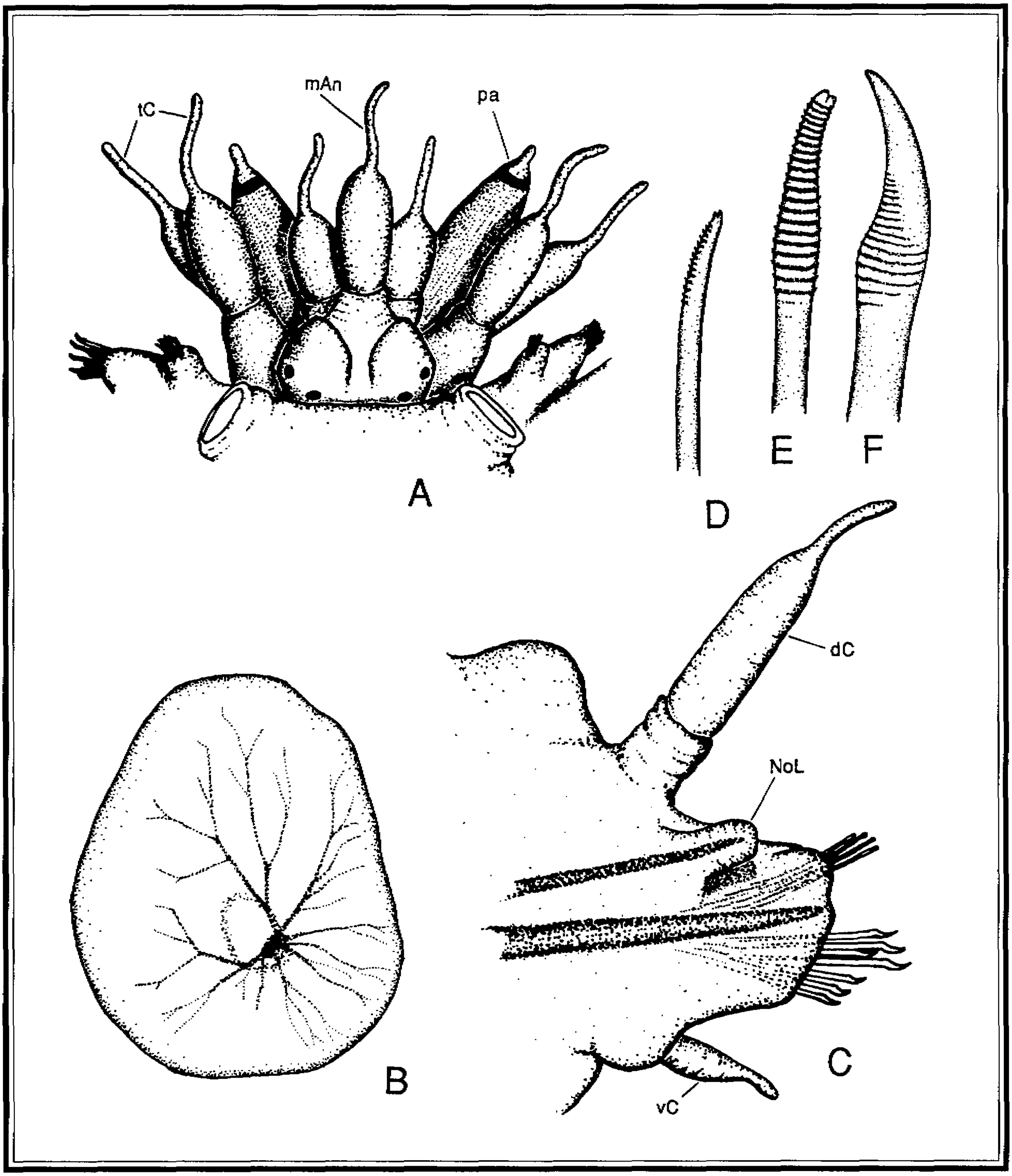

Figure 3.4. *Arctonoe vittata*: A, anterior end, dorsal view; B, median left elytron; C, median cirrigerous parapodium, anterior view; D, notoseta; E, superior neuroseta; F, inferior neuroseta.

Genus *Bylgides* Chamberlin, 1919

Type Species: *Bylgia elegans* Théel, 1879, by monotypy.

Diagnosis. Body short, flattened, with about 40 segments. Prostomium with ceratophores of lateral antennae inserted beneath weak to well-developed cephalic peaks. Antennae, palps, and cirri with small papillae. Fifteen pairs of elytra on segments 2, 4, 5, 7 . . . 23, 26, 29, and 32, completely covering dorsum. Parapodia biramous. Notosetae stout, with transverse rows of spinules and smooth tips; neurosetae thinner, long, with subterminal spines and terminal aristae.

Remarks. Théel (1879) erected the genus *Bylgia* for *B. elegans*, a species with slender, capillary-tipped neurosetae and a prostomium with lateral antennae but lacking the median antenna. Chamberlin (1919), noting that *Bylgia* was preoccupied in crustacea, replaced it with the name *Bylgides*. Later, Augener (1928) proposed the genus *Antinoella* for species that were similar in most respects but that possessed rather than lacked a median antenna. More recent work has shown that the holotype of *Bylgia elegans* has a defective prostomium and was misdiagnosed. Therefore Uschakov (1982) placed *Antinoella* into synonymy with *Bylgides* based upon information provided and subsequently published by Pettibone (1993a). The genus encompasses a number of arctic and boreal species, only one of which is found off California.

Bylgides macrolepidus (Moore, 1905)

Figure 3.5 A-E

Antinoe macrolepida Moore, 1905:538-541, pl. 35, figs. 21-23.—Berkeley and Berkeley, 1948:14, fig. 15.
Antinoella macrolepida: Hartman, 1968:41, figs. 1-3.—Banse and Hobson, 1974:25, fig. 2a..—Lissner *et al.*, 1986:D-7.
Bylgides macrolepida: Uschakov, 1982:157-58, pl. 57, figs. 1-6.
Bylgides macrolepidus: Pettibone, 1993a:21-23, fig. 13a-k.

Material Examined. Alaska, Chatham Strait (holotype, 4 paratypes, and 1 additional specimen); Boca de Quadra (2).—British Columbia, Gulf of Georgia (paratype); off Vancouver Island (paratype).—California, Santa Maria Basin, off Point Estero, Sta. 3, 291 m (1), off Point Arguello, Sta. 59, 216 m (1).

Description. Length to 45 mm for 39 segments; dorsal cirri and body reddish brown with lighter intersegmental transverse lines. Bilobed prostomium broad, anteriorly rounded, with small cephalic peaks (Fig. 3.5A). Anterior eyes large, with well-developed lenses, covering anterior margin of prostomium; posterior eyes smaller, sometimes concealed by base of elytrophores of second segment. Median ceratophore large, cylindrical; style long, tapering, with slight subterminal swelling and scattered papillae. Ceratophores of lateral antennae small, spherical, situated beneath cephalic peaks; subulate styles short, tapering to filamentous tips. Palps about 6 times prostomial length, tapering to acute tips, with numerous small papillae.

Tentaculophores long, lateral to palps, with projecting acicular lobe and several acicular setae. Subequal tentacular cirri similar in shape but shorter than median antenna, with scattered papillae. Facial tubercle not developed. Ventral buccal cirri long, acuminate, with scattered papillae.

Elytra strongly imbricated but easily lost, large, thin, translucent, marbled with pale brown pigment. Each elytron appearing smooth but covered with tiny, curved conical microtubercles and scattered papillae; margin with sparse fringe of minute papillae (Fig. 3.5B).

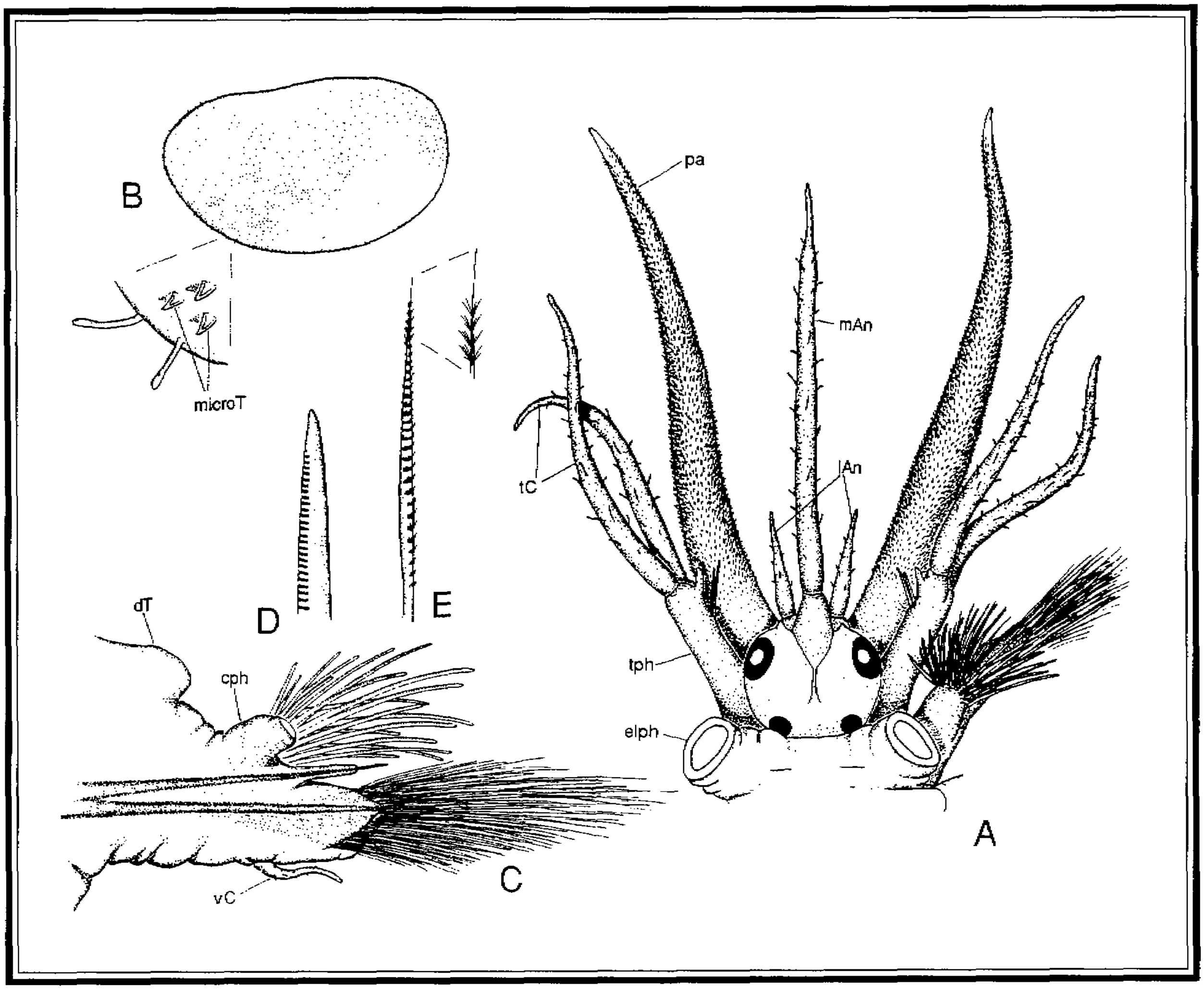

Figure 3.5. *Bylgides macrolepidus*: A, anterior end, dorsal view; B, median left elytron with detail of microtubercles and marginal papillae; C, median cirrigerous parapodium, posterior view; D, notoseta; E, median neuroseta with detail of aristate tip.

Parapodia biramous. Notopodia low, cylindrical, extending into long digitate lobe with emergent acicula. Neuropodia long, slender, with obliquely truncate postsetal lobe and pointed presetal lobe extending into a long digitate cirrus above projecting acicula (Fig. 3.5C). Notosetae numerous, short, thick, nearly straight, with transverse rows of spines and smooth pointed tips (Fig. 3.5D). Neurosetae very numerous, slender, long, with subdistal spines; tips of median and inferior neurosetae with fine hairs and long terminal aristae (Fig. 3.5E).

Dorsal cirri elongate, extending beyond neurosetae, with proximal clavate papillae, subterminal swelling, and smooth distal tips. Dorsal tubercles large, well-developed. Ventral cirri slender, tapering, with scattered papillae. Ventral nephridial papillae cylindrical, from segment 6. Pygidium elongate, with dorsal anus; pygidial cirri similar to dorsal cirri.

Habitat. Known from scattered records in depths from 36-537 m, on bottom types consisting of green mud, fine to coarse sands, and rocks.

Remarks. Most representatives of the genus *Bylgides* are found in the arctic and far north Atlantic. *B. elegans* has been reported from the Bering Sea, but it differs by lacking the large lensed eyes on the anterior prostomial margin beneath the cephalic peaks. These bulbous eyes along with the slender neurosetae with aristate tips are diagnostic features for *B. macrolepidus* in the Santa Maria Basin region.

Type Locality and Type Specimens. Off Freshwater Bay, Chatham Strait, Alaska, 516-536 m, holotype (USNM 5509) and 4 paratypes (USNM 5561-5563, ANSP AD2011). Additional paratypes (USNM 5557, 5559) from the Gulf of Georgia and off Vancouver Island, British Columbia.

Distribution. Found in shelf and upper slope depths from the southern Sakhalin Islands around the Pacific rim as far down as southern California.

Genus *Eucranta* Malmgren, 1865

Type Species: *Eucranta villosa* Malmgren, 1865, by monotypy.

Diagnosis. Body short, strongly arched, with about 40 segments. Prostomium with weak to well-developed cephalic peaks, with ceratophores of lateral antennae inserted beneath anterior margin. Facial tubercle and nuchal fold absent. Fifteen pairs of elytra on segments 2, 4, 5, 7, . . . 23, 26, 29, and 32, completely covering dorsum. Parapodia biramous. Notosetae short, thick, with blunt tips. Most neurosetae slender, long, with coarse spines in subdistal expanded region and unidentate tips; superior and/or inferior neurosetae thinner, with deeply incised tips.

Remarks. The genus *Eucranta* is known from a few species found mainly in arctic and subantarctic waters. The genus is distinguished by having a group of neurosetae in which both forks of the deeply cleft tip are about the same size.

***Eucranta anoculata* (Moore, 1910)**

Figure 3.6 A-F

Antinoe anoculata Moore, 1910:358-361, pl. 30, figs. 34-40.
Antinoella anoculata: Hartman, 1968:39-40, figs. 1-7.
Eucranta anoculata: Fauchald and Hancock, 1981:23.
Bylgides anoculata: Uschakov, 1982: 158-159, pl. 57, figs. 7-11.
Antinoe sp. A: Blake *et al.*, 1988:A-3.
Antinoe sp. C: Steinhauer and Imamura, 1990:F-1 (*partim*).

Material Examined. California, off Monterey Bay (holotype and 2 paratypes); Santa Maria Basin, off Point Buchon, Sta. 16, 591 m (3), off Point San Luis, Sta. R-3, 409 m (1), Sta. 27, 611 m (2), off Point Sal, Sta. R-7, 565 m (8), off Purisima Point, Sta. R-6, 410 m (1); off San Diego (1).

Description. Length to 36 mm for 37 segments; body dusky or colorless, with iridescent cuticle. Prostomium longer than wide, divided into two lobes, with well-developed cephalic peaks; eyes lacking (Fig. 3.6A). Ceratophore of median antenna large, tapering; style slender, acuminate, about twice prostomial length, with numerous minute papillae. Short, tumid ceratophores of lateral antennae attached beneath cephalic peaks, with short, subulate styles. Longitudinally striated palps to four times prostomial length, tapering to slender tips.

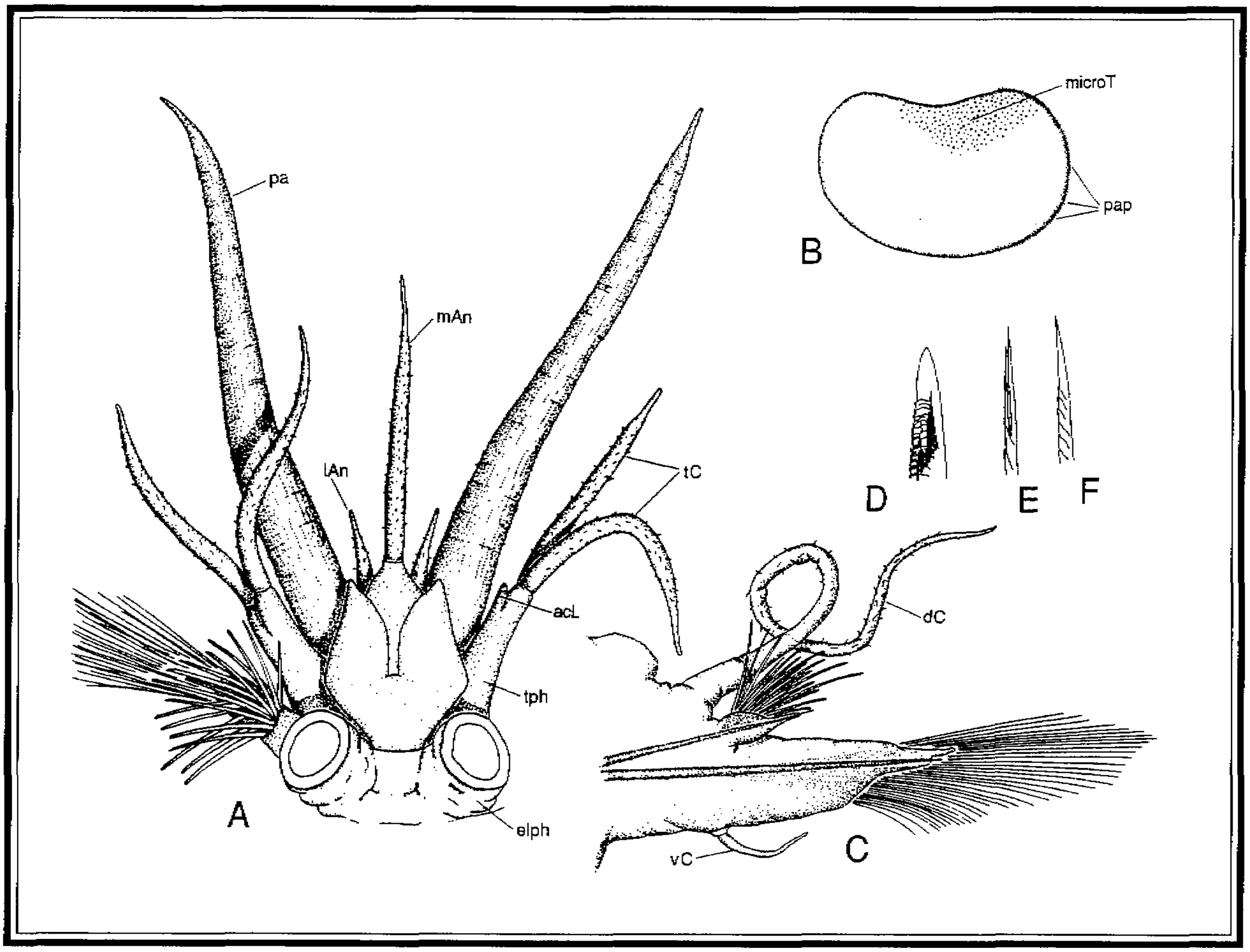

Figure 3.6. *Eucranta anoculata*: A, anterior end, dorsal view; B, median right elytron; C, median cirrigerous parapodium, anterior view; D, tip of notoseta; E, tip of superior neuroseta; F, tip of inferior neuroseta (D-F from Moore, 1910).

Tentaculophores elongated, lateral to palps, each with long acicular lobe and 0-3 stout, curved setae. Dorsal tentacular cirri with numerous minute papillae, similar in length to median antenna; ventral tentacular cirri slightly shorter. Facial tubercle not developed. Ventral buccal cirri on segment two as long as ventral tentacular cirri, tapering to slender tips, with minute papillae.

Elytra large, covering dorsum, colorless or with streaks of greenish-yellow pigment, first pair circular and following pairs reniform, soft, membranous, translucent, with inconspicuous microtubercles anterior to attachment scar; lateral border with very short papillae (Fig. 3.6B).

Notopodia short, stout, extending into long digitate lobe with stout emergent acicula; neuropodia larger, broader, tapering to short digitate cirrus above emergent acicula (Fig. 3.6C). Notosetae stout, slightly curved, with numerous transverse rows of inconspicuous spines, tapering to smooth blunt tips (Fig. 3.6D). Neurosetae more numerous, long, slender. Upper neurosetae with long spinous region and thin, deeply incised tips (Fig. 3.6E); median and inferior neurosetae with prominent serrations on subdistal expanded region, and elongated acute smooth tips (Fig. 3.6F).

Dorsal cirrophores long, slender; styles elongate, evenly tapering, extending well beyond neurosetae, with short clavate papillae. Dorsal tubercles prominent on anterior segments. Short ventral cirri slender, tapering, without papillae. Ventral nephridial papillae long, cylindrical, curving back into intersegmental furrows from segment 6. Pygidium rounded; anal cirri twice length of dorsal cirri, with scattered small clavate papillae.

Habitat. Found in muddy substrates in depths from 565-1600 m.

Remarks. Moore (1910: pl. 30, fig. 38d) figured the tip of a deeply incised neuroseta, but he incorrectly assigned it to a seta in the ventral part of the fascicle. Hartman (1968) perpetuated this error, but later corrected the observation by noting that the species has "deeply incised slender superior neurosetae" (Hartman, 1978).

In some instances the tips of the superior neurosetae appear to be flattened with thickened edges, but with no median split. It is probable that the separate forks appear when the thin center area between the thickened edges has worn away.

Type Locality and Type Specimens. Off Point Piños Light, Monterey Bay, California, 1372-1401 m, holotype (USNM 016882) and 2 paratypes (ANSP AD2900). Although Moore (1910) indicated only one cotype [=paratype] in his publication, the vial at the Academy of Natural Sciences contains two specimens with a label in Moore's handwriting stating "cotypes."

Distribution. Known from bathyal depths off Oregon, California, and northern Mexico. Specimens reported by Uschakov (1982) from the Kurile Islands and the Sea of Okhotsk may be representatives of another genus since incised neurosetae were not observed.

Genus *Eunoe* Malmgren, 1865

Type Species: *Polynoe nodosa* Sars, 1861, designated by Uschakov, 1955.

Diagnosis. Body short, strongly arched, with about 40 segments. Prostomium with weak to well-developed cephalic peaks; ceratophores of lateral antennae inserted beneath anterior margin. Facial tubercle absent; buccal segment with or without nuchal fold. Antennae, palps, and cirri with filiform papillae. Fifteen pairs of elytra on segments 2, 4, 5, 7, . . . 23, 26, 29, and 32, completely covering dorsum. Parapodia with well-developed noto- and neuropodia. Notosetae at least as thick as neurosetae, with blunt or split smooth tips; neurosetae unidentate and subterminally serrated.

Remarks. Approximately 40 species are described in this genus, but most are restricted to the colder waters of the northern and southern hemispheres. Of the two species reported from off California, only one was present in the Santa Maria Basin collections.

Eunoe senta (Moore, 1902)

Figure 3.7 A-F

Gattyana senta Moore, 1902:259-263, pl. 13, figs. 1-13; 1905:525 (correction of type locality).
Eunoe senta: Hartman, 1939:52-53, pl. 10, figs. 128-133; 1968:57-58, figs. 1-6.—Blake, 1975b:175, pl. 28, fig. 78.—Uschakov, 1982:179-180, pl. 67, figs. 5-8.

Material Examined. Alaska, off Icy Cape (holotype and paratype).—California, Santa Maria Basin, off Point Buchon, Sta. 6, 109 m (2), off Purisima Point, Sta. BRC-14, 96-105 m (1).

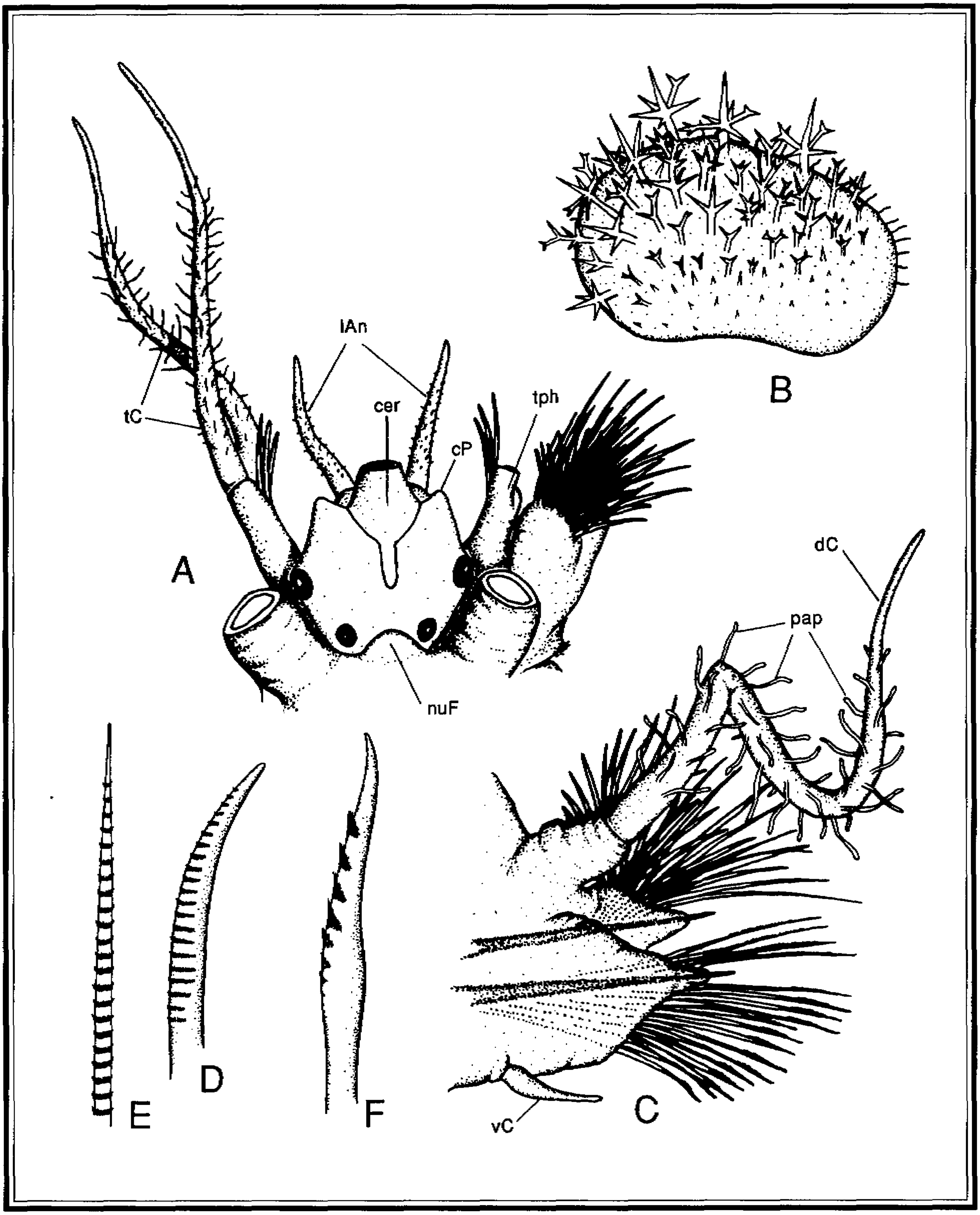

Figure 3.7. *Eunoe senta*: A, anterior end, dorsal view; B, median right elytron; C, median cirrigerous parapodium, posterior view; D, superior notoseta; E, median notoseta; F, distal portion of median neuroseta.

Description. Length to 22 mm for 36 segments; dorsum pale yellow or colorless. Prostomium wider than long, anteriorly divided into two broadly rounded lobes, with low cephalic peaks (Fig. 3.7A). Two pairs of black, circular eyes; anterior pair slightly larger, located on lateral margin of prostomium at widest point. Median ceratophore massive; slender style three times prostomial length, with brown pigment and numerous long papillae basally, and long bare filiform tip. Lateral antennae with stubby ceratophores inserted beneath cephalic peaks, and short, acuminate, papillate styles. Palps stout, with longitudinal rows of digitiform papillae, as long as median antenna, tapering to filiform tip.

Tentaculophores short, broad, lateral to palps, each with pointed acicular lobe and bundle of stout, blunt setae on anterior face. Subequal tentacular cirri papillate, similar in length and shape to median antenna. Facial tubercle absent. Buccal segment with nuchal fold covering posterior margin of prostomium. Cirrophores of ventral buccal cirri large; styles acuminate, papillate, extending to end of neurosetae.

Elytra circular to subreniform, soft, thick, easily detached, colorless or with irregular patches of pigment, darkest on lateral margins. Surface covered with numerous hard, chitinous tubercles increasing in size and complexity toward lateral and posterior borders; smallest spines simple or minutely bifurcate, and largest spines dendritic with acutely pointed branches (Fig. 3.7B). Margin with sparse filiform papillae.

Notopodia stout, extending into conical lobe with long emergent acicula; neuropodia longer, obliquely truncate with similar acicular lobe and protruding acicula (Fig. 3.7C). Numerous notosetae arranged in whorls; upper notosetae short, with close-set transverse rows of spinules and short, smooth tips (Fig. 3.7D); middle and lower notosetae longer, straight, with subterminal region of widely-spaced transverse rows of short spinules encircling shaft, and smooth points (Fig. 3.7E). Neurosetae subequal to notosetae in length and thickness, coarsely serrated in subterminally expanded region, with slightly hooked, smooth tips (Fig. 3.7F).

Dorsal cirrophores large, cylindrical; styles long, digitiform, narrowing to filamentous tips, with numerous long papillae proximally. Dorsal tubercles prominent. Slender, smooth ventral cirri extending only to base of neuropodia. Short cylindrical nephridial papillae present from segment 6, continuing throughout body. Slender pygidial cirri similar to dorsal cirri, with numerous long papillae.

Habitat. Commonly found in shelf depths from 5-346 m on mixed sand and gravel bottoms.

Remarks. The spiny elytra, papillose cirri, and dense bundles of notosetae provide this species with a shaggy aspect. Moore (1902) originally listed the type locality as McCormick Bay in western Greenland. However, this designation was subsequently attributed to a misplaced vial label, and was corrected by Moore (1905) to samples taken in Alaska.

Type Locality and Type Specimens. Icy Cape, Alaska, holotype (ANSP AD266 and slide 2.30) and 1 paratype (ANSP AD5219).

Distribution. Known from the Kurile Islands around the North Pacific rim to southern California. Also reported by Ditlevsen (1937) from western Greenland.

Genus *Gaudichaudius* Pettibone, 1986

Type Species: *Iphione cimex* Quatrefages, 1866, by original designation.

Diagnosis. Body short, flattened, with about 38 segments. Prostomium without cephalic peaks but with ceratophores of lateral antennae inserted beneath anterior margin. Facial tubercle absent; buccal segment with nuchal fold. Fifteen pairs of elytra on segments 2, 4, 5, 7, . . . 23, 26, 29, and 32, completely covering dorsum; surface of elytra with prominent polygonal areas. Parapodia biramous. Upper notosetae short, with transverse spinules and blunt tips; lower notosetae longer, more slender, tapering to fine tips. Neurosetae thicker than notosetae, with expanded subdistal spinous region and bare, slightly hooked tips.

Remarks. Pettibone (1986) erected the genus *Gaudichaudius* to encompass *Iphione cimex* Quatrefages, 1866 (originally described incorrectly), and *Harmothoe iphionelloides* Johnson, 1901. Johnson's species had been placed into the genus *Gattyana* McIntosh, 1897, by Berkeley and Berkeley (1945) based essentially on the characters of the setae, although it was recognized that it differed from other members of the genus in details of the prostomium and elytra (Pettibone, 1953).

Gaudichaudius iphionelloides (Johnson, 1901)

Figure 3.8 A-F

Harmothoe iphionelloides Johnson, 1901:391-92, pl. 1, figs. 2-7.
Gattyana iphionelloides: Berkeley and Berkeley, 1945:321; 1948:12, fig. 12.—Pettibone, 1953:44-45, pl. 22, figs. 194-200.—Uschakov, 1982:155-156, pl. 54, figs. 7-12.
Gaudichaudius iphionelloides: Pettibone, 1986:37-40, fig. 18a-l (synonymy).

Material Examined. Alaska, Icy Strait (1).—British Columbia, off Valdez Island (1).—Washington: Puget Sound (holotype + 1 specimen), Neah Bay (1).—California, Santa Maria Basin, off Point San Luis, Sta. BRA-25, 65-72 m (1).

Description. Length to 35 mm for 36 segments; dorsum generally colorless, ventrum iridescent. Prostomium bilobed, wider than long, without cephalic peaks (Fig. 3.8A). Two pairs of large eyes; anterior pair located on lateral margins of prostomium slightly anterior to widest part, and smaller posterior pair near posterior border. Median ceratophore long, slender, inserted between prostomial lobes; style long, papillate, with subterminal swelling, dark pigment ring, and filiform tip. Ceratophores of lateral antennae short, cylindrical, inserted subterminally; styles acuminate, with scattered papillae, shorter than median antenna. Palps stout, tapering to blunt tips, with numerous short papillae.

Tentaculophores long, lateral to palps, each with short acicular lobe and several long setae on anterior face. Two pairs of subequal tentacular cirri similar in shape and pigmentation to median antenna. Facial tubercle absent. Buccal segment with nuchal fold covering posterior margin of prostomium. Ventral buccal cirri long, acuminate, attached at base of parapodia lateral to mouth.

Elytra strongly imbricated, thick, large, suboval to deeply reniform. Elytral surface light to dark brown, covered with variably-sized polygonal cells, each with central pointed or flattened tubercle, occasionally with black pigment patch (Fig. 3.8B). Lateral and posterior margins with fringe of short papillae. Elytrophores large, elongate, with additional lobe near inner margin.

Parapodia biramous. Notopodia rounded, extending into bluntly pointed acicular lobe; neuropodia broader, longer, diagonally truncate, projecting into thick presetal lobe with short digitate superior cirrus (Fig. 3.8C). Notosetae numerous; upper notosetae short, stout, curved, pointed, with close-set transverse rows of fine spinules (Fig. 3.8D); lower notosetae elongated, slender, tapering to fine points (Fig. 3.8E). Neurosetae thicker than notosetae, numerous, with short subdistal enlarged spinous region tapering to bare hooked tip (Fig. 3.8F).

Dorsal cirri with elongate, basally bulbous cirrophores; styles long, with subterminal swelling and long papillae on distal half. Transversely elongated dorsal tubercles present on cirrigerous segments. Ventral cirri short, acuminate, with sparse papillae. Elongated, cylindrical nephridial papillae projecting between parapodia from segment 6. Terminal pair of pygidial cirri short, papillate.

Habitat. This species is found in intertidal *Zostera* beds, and subtidally on muddy bottoms with rock or shell components.

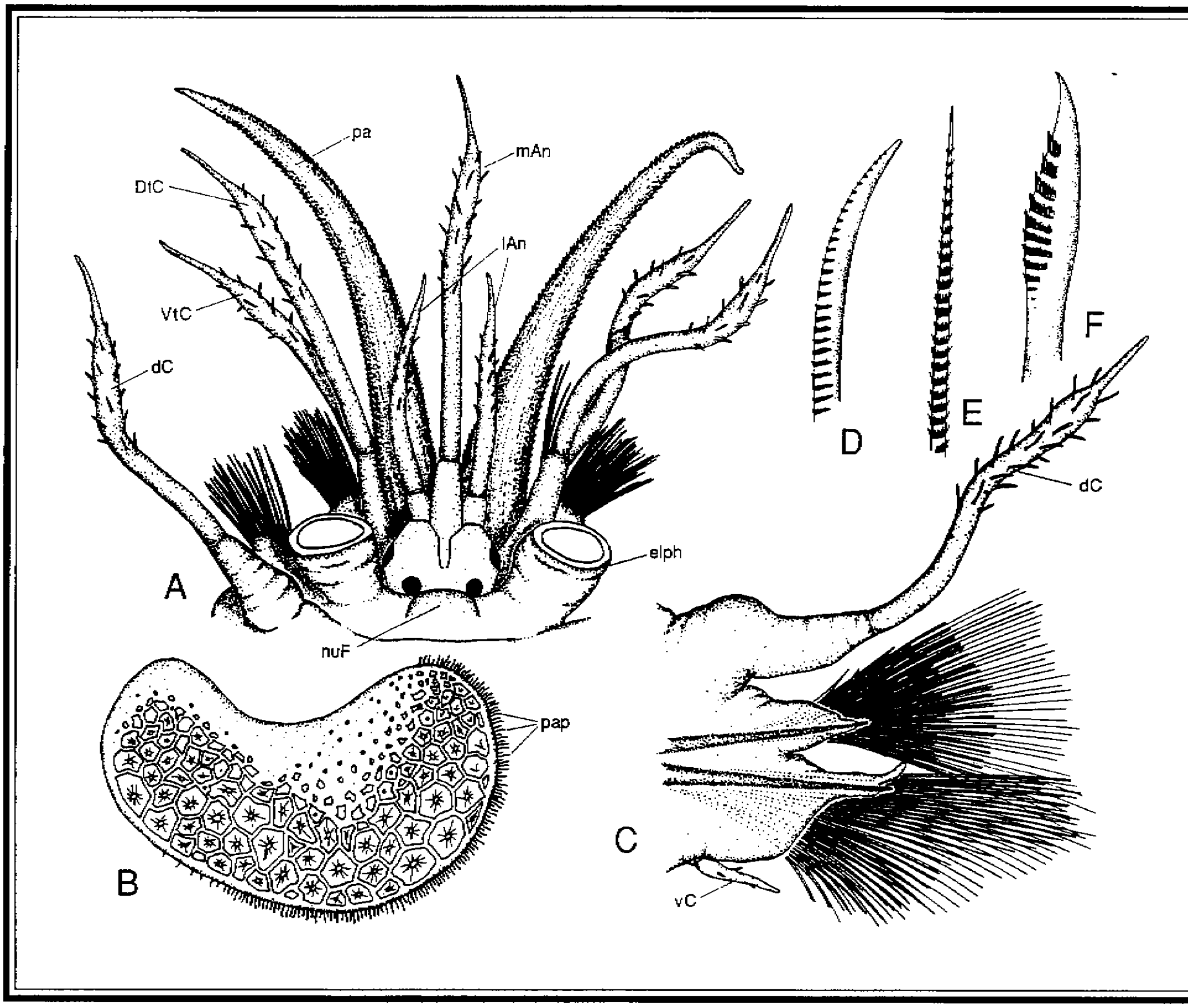

Figure 3.8. *Gaudichaudius iphionelloides*: A, anterior end, dorsal view; B, median right elytron; C, median cirrigerous parapodium, anterior view; D, superior notoseta; E, inferior notoseta; F, distal portion of median neuroseta.

Remarks. *Gaudichaudius iphionelloides* is readily distinguishable from several species of the genus *Gattyana* found in the north Pacific by the presence of polygonal areas surrounding simple, flattened tubercles on the elytra.

Type Locality and Type Specimens. Pleasant Beach near Seattle, Washington. The holotype (MCZ 1897) in the Museum of Comparative Zoology at Harvard has dried out in the past, and now consists of the posterior 18 setigers along with some free elytra.

Distribution. Previously recorded from the Kurile Islands, across the Bering Strait to Alaska, and down to Puget Sound. The specimen from the Phase I hard-substrate station off Point San Luis represents an significant southward extension of the known range.

Genus *Harmothoe* Kinberg, 1855

Type Species: *Harmothoe spinosa* Kinberg, 1855, designated by Bergström, 1916.

Diagnosis. Body short, flattened, with up to 45 segments. Bilobed prostomium with or without cephalic peaks; lateral ceratophores inserted beneath anterior margin. Facial tubercle present or absent; dorsal nuchal fold absent. Fifteen pairs of elytra on segments 2, 4, 5, 7, . . . 23, 26, 29, and 32, occasionally leaving posteriormost segments exposed; elytral surface with or without microtubercles, macrotubercles, and papillae. Parapodia biramous. Notosetae stout, as thick or thicker than neurosetae, with distinct transverse spinous rows and bluntly pointed, glabrous tips. Neurosetae longer, with expanded subdistal spinous region; at least some neurosetae with secondary subterminal tooth.

Remarks. *Harmothoe* is a large genus with over 100 valid species. Several genera have been proposed to split up this large assemblage (e.g. *Lagisca*, *Evarnella*), but the distinctions between these become obscured as additional species are found. Four species of *Harmothoe* occurred in the Santa Maria Basin material, including one species often listed in the genus *Lagisca*.

Harmothoe fragilis Moore, 1910

Figure 3.9 A-F

Harmothoe (*Evarne*) *fragilis* Moore, 1910:353-357, pl. 29, figs. 29-30, pl. 30, figs. 31-33.
Harmothoe impar: Ditlevsen, 1917:12-13, pl. 2, fig. 16, pl. 3, fig. 11.—Uschakov, 1955:157, fig. 41A-E.—Pettibone, 1956:550-551. *Not* Johnston, 1839.
Harmothoe fragilis: Pettibone, 1963:39-41, fig. 9g.—Hartman, 1968:75-76, figs. 1-4.
Antinoe sp. C: Steinhauer and Imamura, 1990:F-1 (*partim*).

Material Examined. Washington, Puget Sound (2).—California, Santa Maria Basin, off Point Buchon, Sta. 6, 109 m (1), off Point Sal, Sta. R-7, 565 m (1), off Point Arguello, Sta. BRA-4, 168-237 m (1); off Santa Catalina (holotype and paratype); off Santa Barbara Island (paratype and 1 additional specimen); off San Clemente Island (paratype).

Description. Length to 26 mm for 41 segments; dorsum pale to deep brown with two thin transverse white stripes converging at elytrophores or dorsal tubercles; ventrum unpigmented. Bilobed prostomium slightly wider than long, with acute cephalic peaks (Fig. 3.9A). Two pairs of large eyes; anterior pair located on lateral margins of prostomium at widest point; posterior pair slightly smaller, at posterior corners of prostomium. Median ceratophore cylindrical, inserted between prostomial lobes, reaching slightly beyond cephalic peaks, pigmented dark brown; cirriform style over twice prostomial length, with numerous long papillae, subterminal swelling, and filiform tip. Lateral ceratophores short, cylindrical, inserted beneath cephalic peaks; styles less than prostomial length, subulate, with scattered papillae. Thick palps as long as median antenna, covered with minute papillae, tapering to short terminal filaments.

Tentaculophores elongate, lateral to palps, each with digitate acicular lobe and several stout setae on anterior face. Subequal tentacular cirri similar in length and shape to median antenna. Facial tubercle and nuchal fold absent. Ventral buccal cirri slender, reaching to end of neurosetae, with small papillae and filiform tips.

Elytra soft, loosely attached, circular to reniform, completely covering dorsum. Elytral surface pale brown, covered with numerous conical or multibranched microtubercles and occasional longer filiform papillae; posterior surface with several large, ovoid, blister-like, darker brown macrotubercles (Fig. 3.9B). Lateral margins with thick fringe of long papillae.

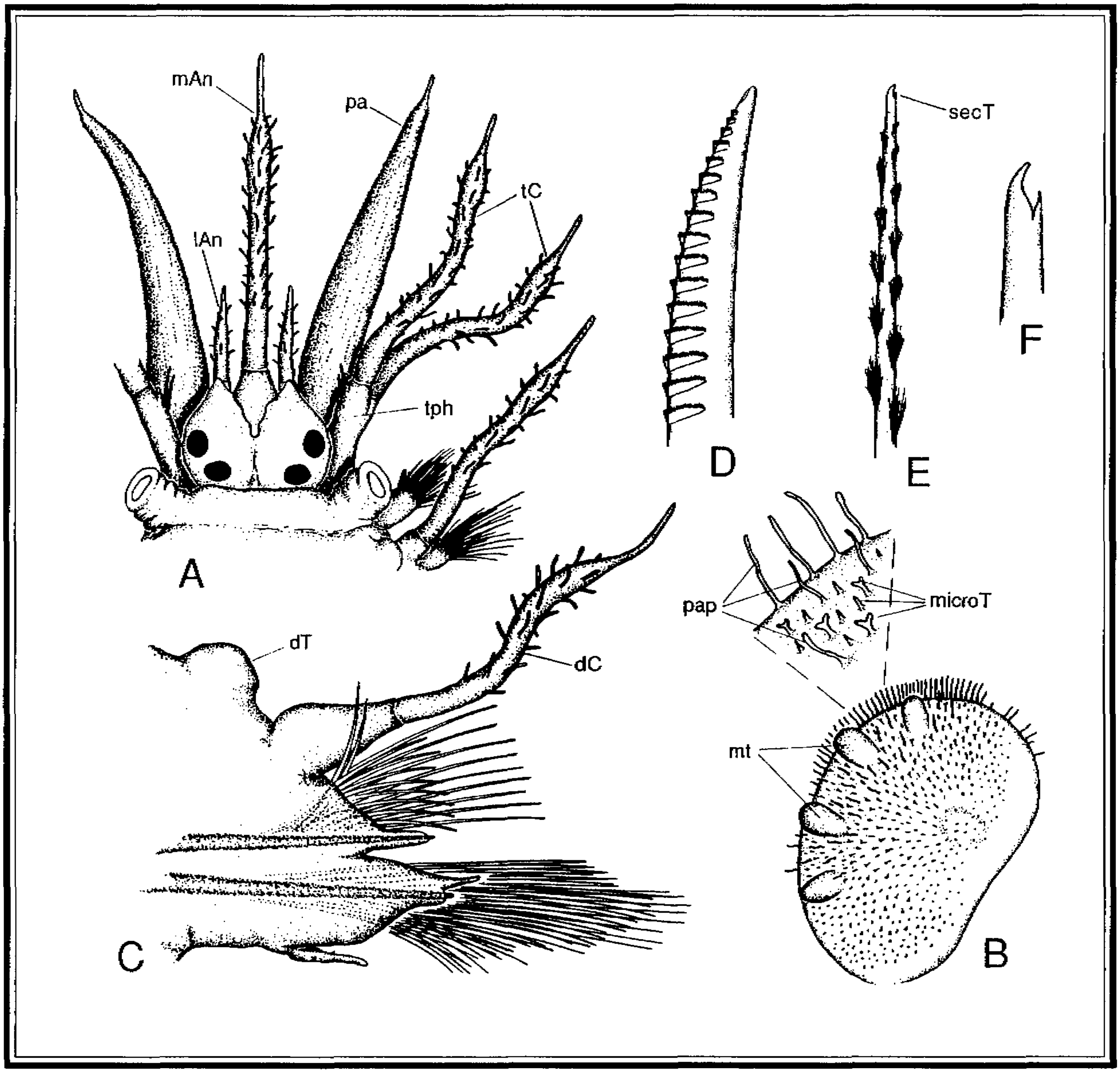

Figure 3.9. *Harmothoe fragilis*: A, anterior end, dorsal view; B, median left elytron with detail of microtubercles and marginal papillae; C, median cirrigerous parapodium, anterior view; D, notoseta; E, distal portion of superior neuroseta; F, tip of median neuroseta.

Notopodia large, extending into acutely pointed lobe with emergent acicula; neuropodia longer, slightly broader, tapering to long digitate terminal cirrus above emergent acicula (Fig. 3.9C). Notosetae stout, curved, with transverse rows of spinules extending to blunt sculptured tips (Fig. 3.9D). Superior neurosetae slender with finely bidentate tip (Fig. 3.9E). Median neurosetae longer, with expanded subdistal spinous region tapering to hooked tip and slender secondary tooth (Fig. 3.9F); inferior neurosetae shorter, often unidentate.

Dorsal cirrophores long, swollen basally; cirri elongate, extending beyond neurosetae, with bare filiform tips and numerous subterminal papillae. Dorsal tubercles prominent, often heavily pigmented. Ventral cirri with low cirrophores; styles short, tapering, with occasional minute papillae. Cylindrical nephridial papillae present at base of parapodia from segment 6. Pygidium with crenulate border surrounding dorsal anus; terminal pygidial cirri longer than dorsal cirri, with numerous long papillae.

Habitat. *Harmothoe fragilis* is found in soft mud, sand and gravel from the shallow subtidal to slope depths of nearly 3000 m.

Remarks. *H. fragilis* is very similar to *H. impar* (Johnston, 1839) from the Atlantic coast of Europe and the Mediterranean, and there is confusion in the literature concerning these two species. Moore's species differs from *H. impar* in having shorter lateral antennae, filiform papillae on the elytral surface, and marginal papillae that are essentially restricted to the lateral border. Moore (1910) illustrated a parapodium studded with small spherical bodies projecting from the surface which are probably parasitic in origin. These spheres were not observed in the Santa Maria Basin specimens.

Type Locality and Type Specimens. Southern California, off Santa Catalina Island, 278-296 m, holotype (USNM 17148) and paratype (USNM 73013); off Santa Barbara Island, 435-567 m, paratype (USNM 17147); off San Clemente Island, paratype (ANSP 2877).

Distribution. Widely distributed throughout the arctic, and into boreal waters in both the Atlantic and Pacific Oceans. It has been reported in the Chukchi Sea and along the Pacific rim as far south as northern Japan and southern California.

Harmothoe hirsuta Johnson, 1897

Figure 3.10 A-E

Harmothoe hirsuta Johnson, 1897:182-3, pl. 6, figs. 27-29, pl. 7, fig. 38, pl. 8, fig. 53.—Chamberlin, 1919:51-54, pl. 2, figs. 2-8, pl. 3, fig. 1.—Hartman, 1968:77-78, figs. 1-6.—Blake, 1975b:176, pl. 28, fig. 75.

Material Examined. California, Western Santa Barbara Channel, off Point Conception, Sta. BRC-1, 69-74 m (2); off San Pedro (holotype); off San Nicolas Island (1).

Description. Length to 32 mm for 40 segments; dorsum dusky, with brown pigment patches anteriorly, or unpigmented; ventrum iridescent. Prostomium bilobed, wider than long, with prominent cephalic peaks and two pairs of large eyes; anterior pair at lateral margins, and posterior pair at posterior margin of prostomium (Fig. 3.10A). Median antenna with large, pigmented ceratophore; style long, cirriform, basally pigmented, with numerous long papillae and filiform tip. Ceratophores of lateral antennae heavily pigmented; styles less than one half length of median antenna, slender, acuminate, with numerous papillae and filiform tips. Palps slightly longer than median antenna, terete, minutely papillated and tapering to fine tips.

Tentaculophores lateral to palps, with 1-3 large curved setae projecting from base; subequal tentacular cirri similar in length and shape to median antenna, with numerous long papillae. Facial tubercle small, rounded. Anterior dorsal margin of buccal segment produced forward as small nuchal fold. Ventral buccal cirri shorter than tentacular cirri, with small papillae, tapering to filiform tips.

Elytra large, strongly imbricated, circular (first pair) or reniform (following pairs); each thin, translucent, with thick lateral fringe and scattered long surface papillae; median and posterior surface divided into large polygonal cells, many with small to large, bulbous, multipronged macrotubercle in center; some cells pigmented dark brown, but most colorless (Fig. 3.10B).

Notopodia short, tapering into acicular lobe with pointed cirrus. Neuropodia longer, broader, extending into thick, pointed presetal acicular lobe, and shorter, diagonally truncate postsetal lobe; ventral margin proximal to ventral cirrophore rugose (Fig. 3.10C). Notosetae stout, numerous, with long spinous regions tapering to blunt tips (Fig. 3.10D). Neurosetae slightly more slender than notosetae, with long subdistal spinous region tapering to long, bare hooked tip with remote incision forming small secondary tooth (Fig. 3.10E).

Dorsal cirrophores long, tapering; styles cirriform, extending well beyond neurosetae, with numerous long papillae, broad basal band of dark pigment, and filiform tips. Dorsal tubercles well-developed, knoblike.

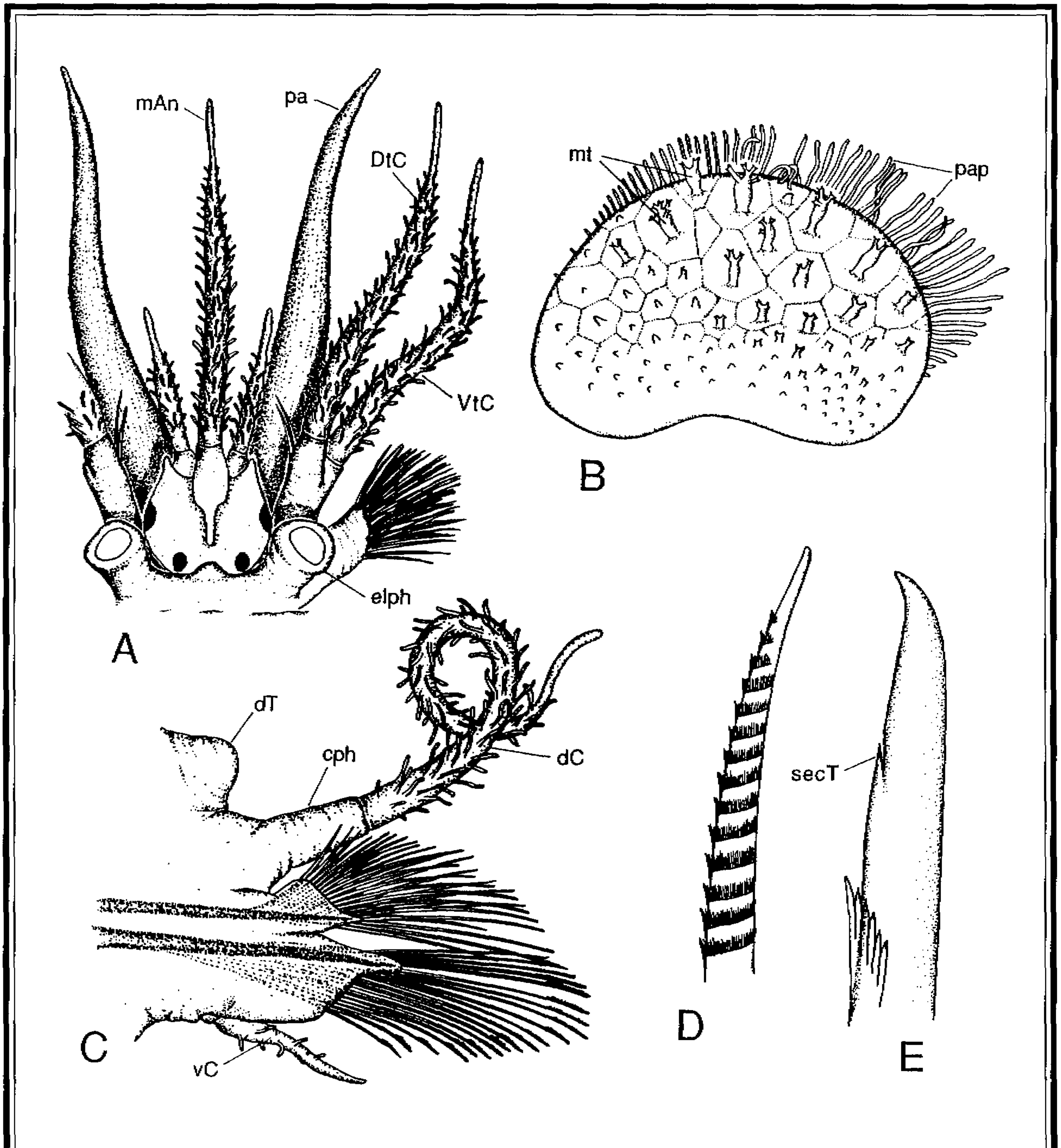

Figure 3.10. *Harmothoe hirsuta*: A, anterior end, dorsal view; B, median left elytron; C, median cirrigerous parapodium, anterior view; D, notoseta; E, tip of median neuroseta.

Ventral cirrophores small, bulbous; styles short, acuminate, with scattered short papillae along dorsal margin. Nephridial papillae short, bulbous, beginning on segment 6, inconspicuous on posterior segments. Pygidial cirri twice as long as dorsal cirri, with numerous long papillae.

Habitat. This is a shallow-water species, normally found in the rocky intertidal and shallow subtidal areas.

Remarks. The setae, cirri, and elytra of *H. hirsuta* are usually coated with sediment and debris, giving the organism a very shaggy appearance.

Essenberg (1918) noted that this species had been reported from Icy Strait, Alaska, and from Port Townsend, Washington. These specimens were located in the collections of the Academy of Natural Sciences in Philadelphia, and were found to be one example of *Gaudichaudius iphionelloides* (Johnson, 1901) [ANSP 2027], and the missing holotype of *Eunoe barbata* Moore, 1910 [ANSP 2028] (Spamer & Bogan, 1991).

Type Locality and Type Specimens. California, San Pedro, at the low water mark, holotype (LACM-AHF Poly 0017).

Distribution. Known from southern California and Panama, in intertidal regions out to 98 m.

Harmothoe imbricata (Linnaeus, 1767)

Figure 3.11 A-E

Harmothoe imbricata: Johnson, 1897:181, fig. 37.—Izuka, 1912:43-49, pl. 5, figs. 1-4, pl. 6, fig. 1.—Fauvel, 1923:55, fig. 18f-l.—Berkeley and Berkeley, 1948:11, fig. 9.—Pettibone, 1953:32-36, pl. 13, figs. 114-20, pl. 14, figs. 121-31; pl. 15, figs. 132-37; pl. 16, figs. 138-46 (synonymy); 1963:36-38, fig. 7a-d.—Hartman, 1968:79-80, figs. 1-4.—Blake, 1975a:29; 1975b:176, pl. 28, figs. 76-77.—Uschakov, 1982:165-166, pl. 59, figs. 1-5 (synonymy).—Tebble and Chambers, 1982:30-31, figs. 7a, 9a-b, 31.

Material Examined. Alaska, Boca de Quadra (3).—Washington, Lopez Island (2).—California, Tomales Bay (4).

Description. Length to 65 mm for 39 segments; dorsum usually mottled, with darker areas around cirrophores and elytrophores; ventrum dusky or colorless. Prostomium wider than long, with prominent cephalic peaks (Fig. 3.11A). Two pairs of large eyes; anterior pair located forward beneath cephalic peaks but usually visible through prostomium; posterior pair slightly smaller, near posterior corners. Median antenna with large, pigmented ceratophore; long style with subterminal swelling, scattered papillae, and filiform tip. Lateral ceratophores short, inserted ventrally on prostomium; styles short, acuminate, with scattered papillae and filamentous tips. Palps to 5 times length of prostomium, tapering, with longitudinal rows of small papillae and short tips.

Basal lobes of tentacular cirri elongate, with 1-2 setae projecting from base. Two pairs of subequal tentacular cirri similar in length and shape to median antenna. Facial tubercle and nuchal fold absent. Ventral buccal cirri with large cirrophores; styles shorter than tentacular cirri, papillate, tapering to filiform tips.

Elytra large, thick, suboval to subreniform, strongly imbricated and covering dorsum, but easily detached. Elytral surface with numerous blunt microtubercles, scattered surface papillae, and, in larger specimens, globular macrotubercles near posterior margin (Fig. 3.11B); lateral and posterior borders with fringe of short papillae, or fringe absent.

Notopodia rounded, tapering into pointed acicular lobe; neuropodia longer, broader, extending into thick presetal lobe with emergent acicula (Fig. 3.11C). Notosetae stout, moderately thick, with long spinous regions tapering to blunt, bare tips (Fig. 3.11D). Neurosetae slightly more slender than notosetae, with short, expanded, subdistal spinous region tapering to long, bare hooked tip with or without small secondary tooth (Fig. 3.11E).

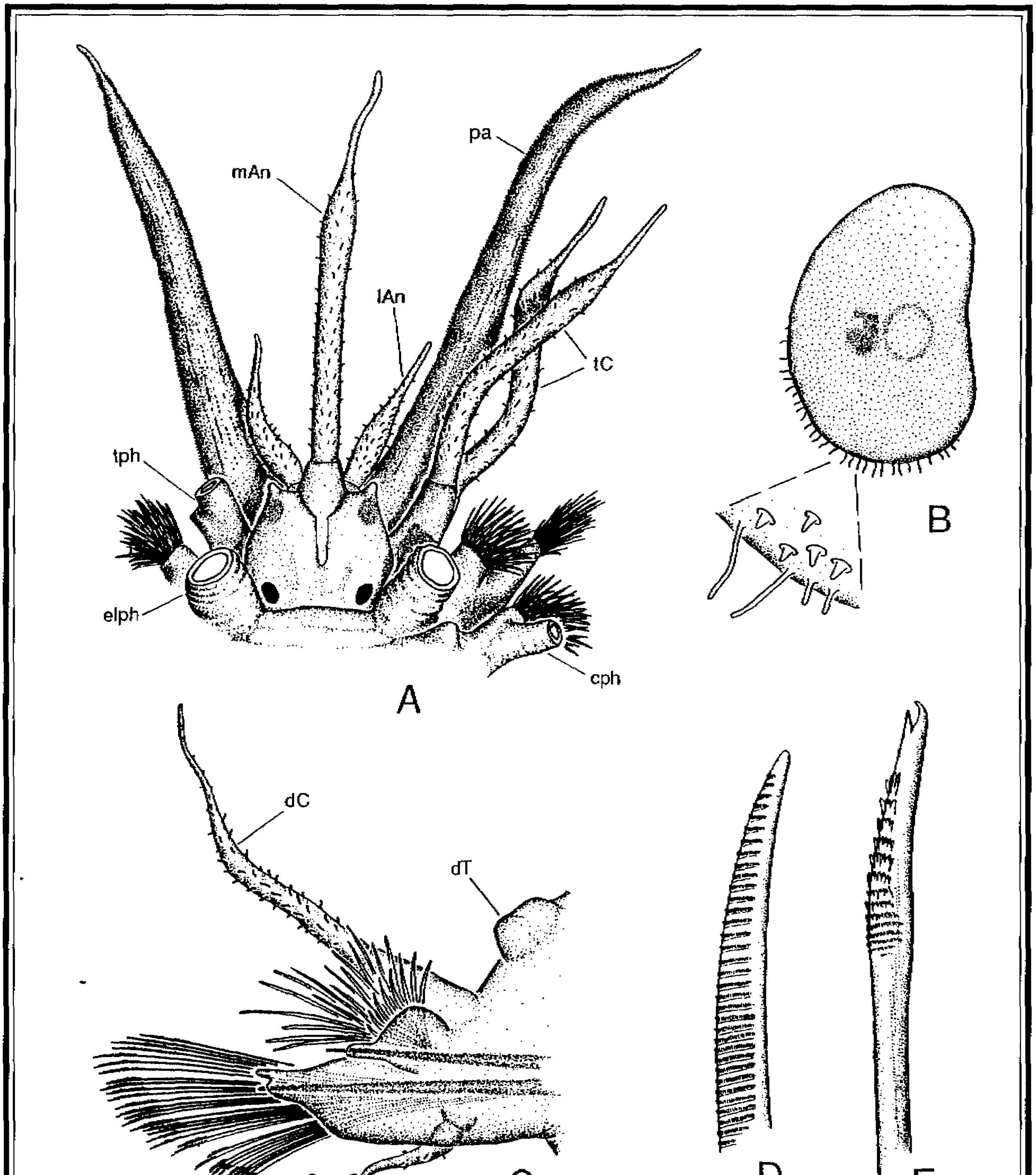

Figure 3.11. *Harmothoe imbricata*: A, anterior end, dorsal view; B, median right elytron with detail of microtubercles and marginal papillae; C, median cirrigerous parapodium, anterior view; D, distal portion of median notoseta; E, distal portion of median neuroseta.

Dorsal cirri with long, cylindrical cirrophores; styles basally pigmented, papillate, with subdistal swelling and filiform tips extending well beyond neurosetae. Dorsal tubercles prominent, bluntly conical. Ventral cirri short, acuminate, with numerous small papillae. Cylindrical nephridial papillae long, projecting between parapodia from segment 6. Terminal pair of pygidial cirri up to twice dorsal cirri length.

Biology. *Harmothoe imbricata* is a successful cosmopolitan found throughout the arctic and in boreal seas. The species utilizes a wide variety of habitats, and is found intertidally under rocks and in eelgrass beds, and subtidally on rocky, muddy, or sandy substrates, in kelp holdfasts, mussel beds and old *Sabellaria* reefs. It is an active swimmer and can tolerate a wide range of salinities. It is found both free-living and in commensal association with echinoderms and other polychaetes. Blake (1975a) recorded egg diameters of 120-123 μm in specimens from Tomales Bay. The eggs are brooded under the elytra throughout much of the year, and after hatching, the California larvae of this species have a prolonged pelagic life before settling and metamorphosis. In other oceans, however, *H. imbricata* has been found to exhibit a full range of developmental types from direct development under the elytra to direct spawning into seawater (Blake, 1975a). This plasticity in mode of reproduction, coupled with the apparently diverse habitats in which the species is able to live, undoubtedly contribute toward making *H. imbricata* one of the most widely-distributed species of polynoids.

Remarks. The elytra of *H. imbricata* exhibit great variations both in pigment pattern and in coloration. The first pair are often colorless, and following pairs have various mottled or solid patterns in shades ranging from white, light tan, red, green, brown, grey, and black.

The secondary tooth on the neurosetae is usually well-developed in the middle portion of the fascicle, and is often broken, worn, or not developed on the upper and lower neurosetae. Very few bidentate setae are present in juvenile or subadult specimens, and most of the neurosetae appear unidentate.

Type Locality and Type Specimens. The species currently accepted as *Harmothoe imbricata* was described by Linnaeus in 1767 based upon material sent from Iceland, although it is unclear whether this material was an actual specimen or merely a drawing (Chambers and Heppell, 1989). No type specimen is known to exist.

Distribution. Widespread throughout the northern hemisphere, extending down to the Mediterranean and to New Jersey in the Atlantic, and from the Yellow Sea around the Pacific rim to southern California. It is abundant in the intertidal and shallow subtidal, but is also found out to abyssal depths.

Harmothoe multisetosa (Moore, 1902)

Figure 3.12 A-F

Lagisca multisetosa Moore, 1902:267-69, pl. 14, figs. 29-36.—Berkeley and Berkeley, 1945:322; 1948:15-16, fig. 17.—Hartman 1968:105-106, figs. 1-6.
Harmothoe multisetosa: Moore, 1910:340-41.—Pettibone, 1953:29-31, pl. 12, figs. 104-113 (synonymy).

Material Examined. Alaska, Icy Cape (holotype).—Washington, off San Juan Island (9).—California, Santa Maria Basin, off Point Buchon, Sta. 6, 109 m (1), off Purisima Point, Sta. BRA-13, 89-101 m (1).

Description. Length to 35 mm for 43 segments; dorsum dark brown with two thin transverse white bands per segment converging at elytrophores or dorsal tubercles; ventral surface colorless, iridescent. Prostomium wider than long, with prominent cephalic peaks (Fig 3.12A). Two pairs of large eyes; anterior pair slightly larger, located near lateral borders at widest point of prostomium. Median antenna with long, tapering, pigmented ceratophore; style more than twice prostomium length, with numerous scattered papillae, subterminal swelling, and long filiform tip. Lateral ceratophores short, inserted beneath cephalic peaks; styles about length of prostomium, acuminate, with scattered papillae and filiform tips. Palps longer than median antenna, tapering to filiform tips, with minute papillae.

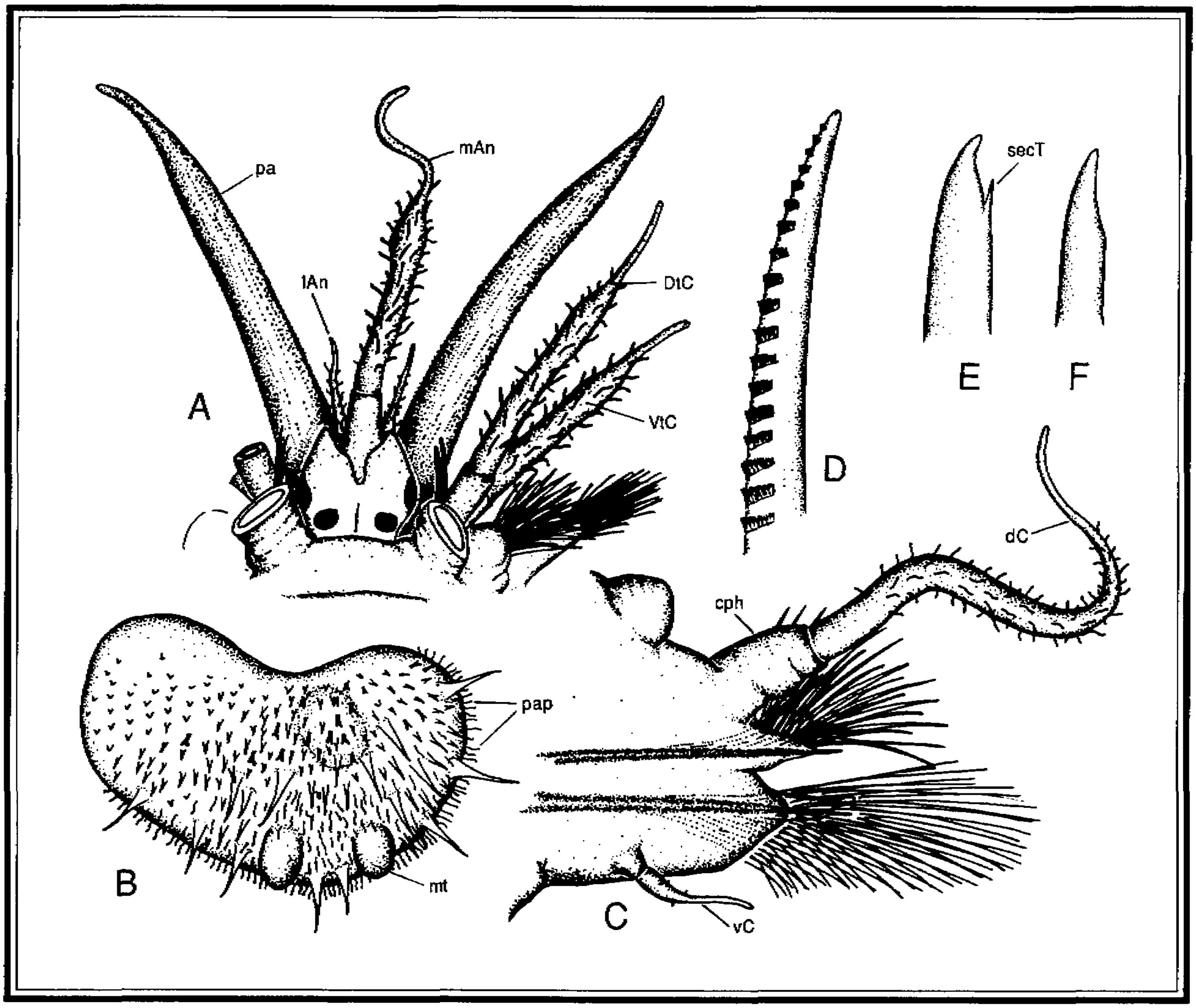

Figure 3.12. *Harmothoe multisetosa*: A, anterior end, dorsal view; B, median right elytron; C, median cirrigerous parapodium, posterior view; D, notoseta; E, tip of median neuroseta; F, tip of inferior neuroseta.

Basal lobes of tentacular cirri with digitate acicular lobe and 1-3 stout, curved setae on anterior face. Upper pair of tentacular cirri similar in length and shape to median antenna; lower pair about ¾ as long. Facial tubercle absent. Ventral buccal cirri with long, cylindrical cirrophores; styles similar to lower tentacular cirri.

Large suboval to subreniform elytra covering dorsum except for posteriormost segments. Elytra thin, translucent, with blunt or bifid microtubercles, numerous larger thorn-like curved spines with acutely pointed tips, and occasional large, blister-like macrotubercles near posterior border; lateral and posterior borders with fringe of short papillae (Fig. 3.12B). Elytral surface uniformly tan or gray, or mottled with brownish pigment; macrotubercles darker brown.

Notopodia obliquely truncate, with inferior acutely pointed acicular lobe; neuropodia longer, extending into pointed presetal lobe with protruding acicula and long digitiform superior cirrus (Fig. 3.12C). Notosetae stout, curved, with transverse rows of spinules and blunt to pointed smooth tips (Fig. 3.12D). Neurosetae about as thick as notosetae, enlarged subdistally; superior neurosetae with long subdistal spinous region tapering to smooth points; median neurosetae with shorter spinous region, hooked smooth tip, and small secondary tooth (Fig. 3.12E); inferior neurosetae shorter, unidentate (Fig. 3.12F).

Dorsal cirri extending beyond neurosetae, with long, tapering cirrophores, and styles similar to median antenna. Dorsal tubercles knoblike, often with brown pigment. Ventral cirri short, basally inflated, tapering to filiform tip, with occasional small papillae. Bulbous nephridial papillae short, projecting between parapodia from segment 6. Terminal pair of pygidial cirri similar in shape and longer than dorsal cirri.

Habitat. This species is common in intertidal areas on pilings, and across the continental shelf out to 250 m in regions with rocks, algae, barnacles, or mollusc shells.

Remarks. Although the dark brown dorsal pigmentation may fade over time in preservative, the thin transverse white stripes on each segment remain visible.

A number of authors (Ditlevsen, 1917; Augener, 1928; Annenkova, 1937; Wesenberg-Lund, 1950) have synonymized *Harmothoe multisetosa* with *H. aspera* (Hansen, 1878) from arctic and boreal waters. However, the elytra of the latter species lack both the bifid microtubercles and the large, soft macrotubercles found in *H. multisetosa*. These structures were observed in the California material, and Moore's species is regarded as distinct pending further investigation.

Type Locality and Type Specimens. The original assignment of the type locality to McCormick Bay in western Greenland was subsequently corrected to Icy Cape, Alaska (Moore, 1905), holotype (ANSP AD267 and slide 3.7).

Distribution. Known along the Pacific coast of North America from Alaska to Mexico.

Genus *Hesperonoe* Chamberlin, 1919

Type Species: *Harmothoe complanata* Johnson, 1901, by monotypy.

Diagnosis. Body short, flattened, with about 40 segments. Bilobed prostomium with cephalic peaks; ceratophores of lateral antennae inserted beneath anterior margin. Facial tubercle and nuchal fold absent. Fifteen pairs of elytra on segments 2, 4, 5, 7, . . . 23, 26, 29, and 32, completely covering dorsum. Parapodia biramous. Upper notosetae thicker than neurosetae, with transverse striations and blunt tips; lower notosetae longer, more slender, tapering to capillary tips. Superior neurosetae slender, with long spinous region tapering to fine tips; inferior neurosetae thicker, with expanded subdistal spinous region and smooth, slightly hooked tips.

Remarks. *Hesperonoe* is similar to the genus *Harmothoe*, but it differs in having two different kinds of setae in both the notopodia and neuropodia. Three species, *Hesperonoe laevis* Hartman, 1961, *H. complanata* (Johnson, 1901), and *H. adventor* (Skogsberg, 1928), occur off California.

Hesperonoe laevis Hartman, 1961

Figure 3.13 A-F

Hesperonoe laevis Hartman, 1961:47-48, pl. 1, figs. 1-6; 1968:95-96, figs. 1-5.

Material Examined. Washington, Puget Sound (1).—Oregon, off Coos Bay (2).—California, Santa Maria Basin, off Point Sal, Sta. 38, 197 m (1), Sta. 40, 392 m (1); off Santa Barbara (syntype).

Description. Length to 40 mm for 38 segments; dorsum pale. Bilobed prostomium about as long as wide, dusky gray, produced anteriorly into cephalic peaks (Figs. 3.13A). Anterior pair of eyes located near widest point of prostomium; posterior pair smaller, closer together. Ceratophore of median antenna large,

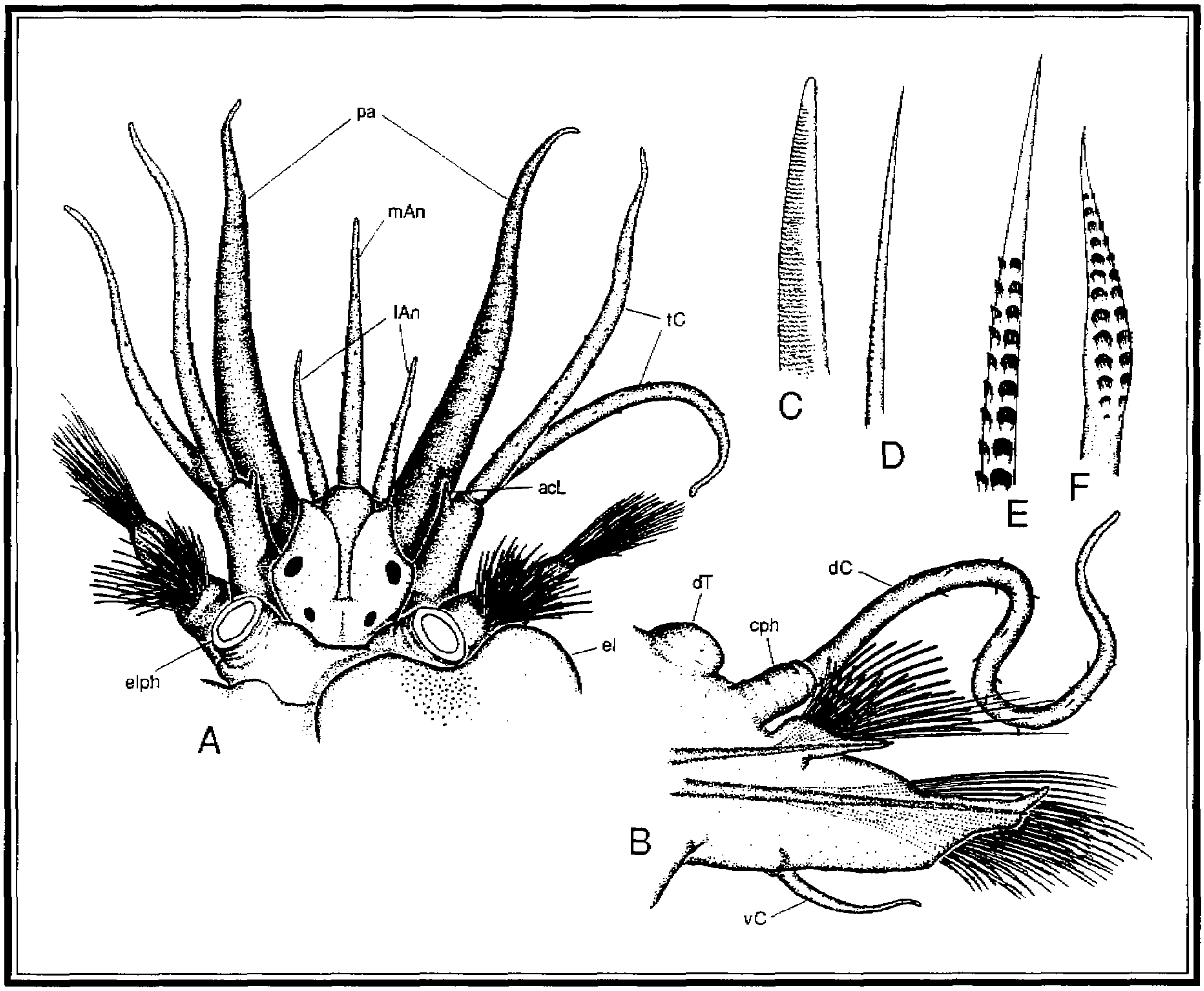

Figure 3.13. *Hesperonoe laevis*: A, anterior end, dorsal view; B, median cirrigerous parapodium, anterior view; C, superior notoseta; D, inferior notoseta; E, distal portion of superior neuroseta; F, distal portion of inferior neuroseta.

extending beyond cephalic peaks; style about twice prostomium length, tapering to filiform tip, with tiny scattered papillae. Lateral ceratophores small, inserted beneath cephalic peaks; styles tapering, half as long as median antenna. Palps three times prostomial length, tapering to filiform tips, with minute papillae.

Basal lobes of tentacular cirri large, with digitiform acicular lobe. Dorsal pair of tentacular cirri evenly tapering, reaching to end of palps, with small scattered papillae; ventral pair slightly shorter. Facial tubercle absent. Cylindrical cirrophores of ventral buccal cirri inserted at base of first parapodia; styles long, tapering, similar to ventral tentacular cirri.

Elytra large, subcircular to subreniform, completely covering dorsum. Each elytron thin, smooth except for inconspicuous microtubercles anterior to attachment scar, pale or with white, gray, or reddish-brown mottling; margins with occasional digitate papillae.

Notopodial lobe nearly as large as neuropodia in first segment; thereafter notopodia small, tapering to digitate lobe with emergent acicula. Neuropodia larger, longer, extending into short digitate lobe above protruding acicula (Fig. 3.13B). Superior and median notosetae moderately thick, tapering to blunt points, with fine, scarcely discernable transverse striations (Fig. 3.13C); inferior notosetae thinner, longer, tapering to fine points (Fig. 3.13D). Upper neurosetae thin, with long, coarsely serrated region, tapering to smooth, sharp tips (Fig. 3.13E); neurosetae in median and lower portion of fascicle thicker, with subterminal swelling, shorter serrated region, and pointed or sharp tips (Fig. 3.13F).

Dorsal cirri with large, elongated cirrophores; long tapering styles extending beyond neurosetae, with scattered clavate papillae. Dorsal tubercles well-developed, projecting laterally. Acuminate ventral cirri smooth. Digitiform nephridial papillae present from segment 6, continuing to end of body. Pygidium low, broad; pygidial cirri nearly twice as long as dorsal cirri.

Habitat. Found in muddy sediments from 20-410 m in association with the echiuran *Listriolobus pelodes*.

Remarks. Two additional species of *Hesperonoe* occur in California, but both are restricted to intertidal areas. *H. complanata* is bright yellowish orange in life and is commensal with the ghost shrimp *Callianassa californiensis*. *H. adventor* is grayish-green and is found in the burrows of the echiuran *Urechis caupo*.

Type Locality and Type Specimens. California, off Santa Barbara, 42 m, holotype (LACM-AHF Poly 0026) and numerous paratypes (LACM-AHF Poly 0027).

Distribution. Known from Puget Sound to southern California.

Genus *Lepidasthenia* Malmgren, 1867

Type Species: *Polynoe elegans* Grube, 1840, by monotypy.

Diagnosis. Body elongate, flattened, with more than 100 segments. Bilobed prostomium extending anteriorly into ceratophores of terminally-attached lateral antennae; antennae and cirri smooth. Facial tubercle present; buccal segment with or without nuchal fold. Elytra on segments 2, 4, 5, 7, . . . 23, 26, 29, 32 (or 31), 34, 37, normally continuing on every third segment to end of body. Parapodia subbiramous; well-developed neuropodium with dorsal cleft between pre- and postsetal lobes. When present, notosetae short, slender, blunt; neurosetae stouter, longer, with subdistal spinous region and uni- or bidentate tips.

Remarks. The genus *Lepidasthenia* includes approximately 40 valid species, most of which are tropical or subtropical in distribution. Members of the genus apparently continue to add segments throughout their lives, and individuals with nearly 200 setigers have been reported. Four species have been reported from California, two of which were found in the Santa Maria Basin material.

Lepidasthenia berkeleyae Pettibone, 1948

Figure 3.14 A-E

Lepidasthenia berkeleyae Pettibone, 1948:413-416, fig. 2a-f; 1953:53-54, pl. 26, figs. 237-239.—Lie, 1968:368-369.

Lepidasthenia interrupta: Hartman, 1968:115-116.—Blake, 1975b:176, pl. 27, fig. 71. *Not* Marenzeller, 1902.

Material Examined. British Columbia, Deep Bay, topotype of *L. longicirrata*.—Washington, Puget Sound (holotype, 2 paratypes, and 3 additional specimens).—California, off Point Arena (1); Tomales Bay (3); Santa Maria Basin, off Point San Luis, Sta. 21, 49 m (1), Sta. 23, 99 m (1), off Purisima Point, Sta. R-5, 154 m (1).

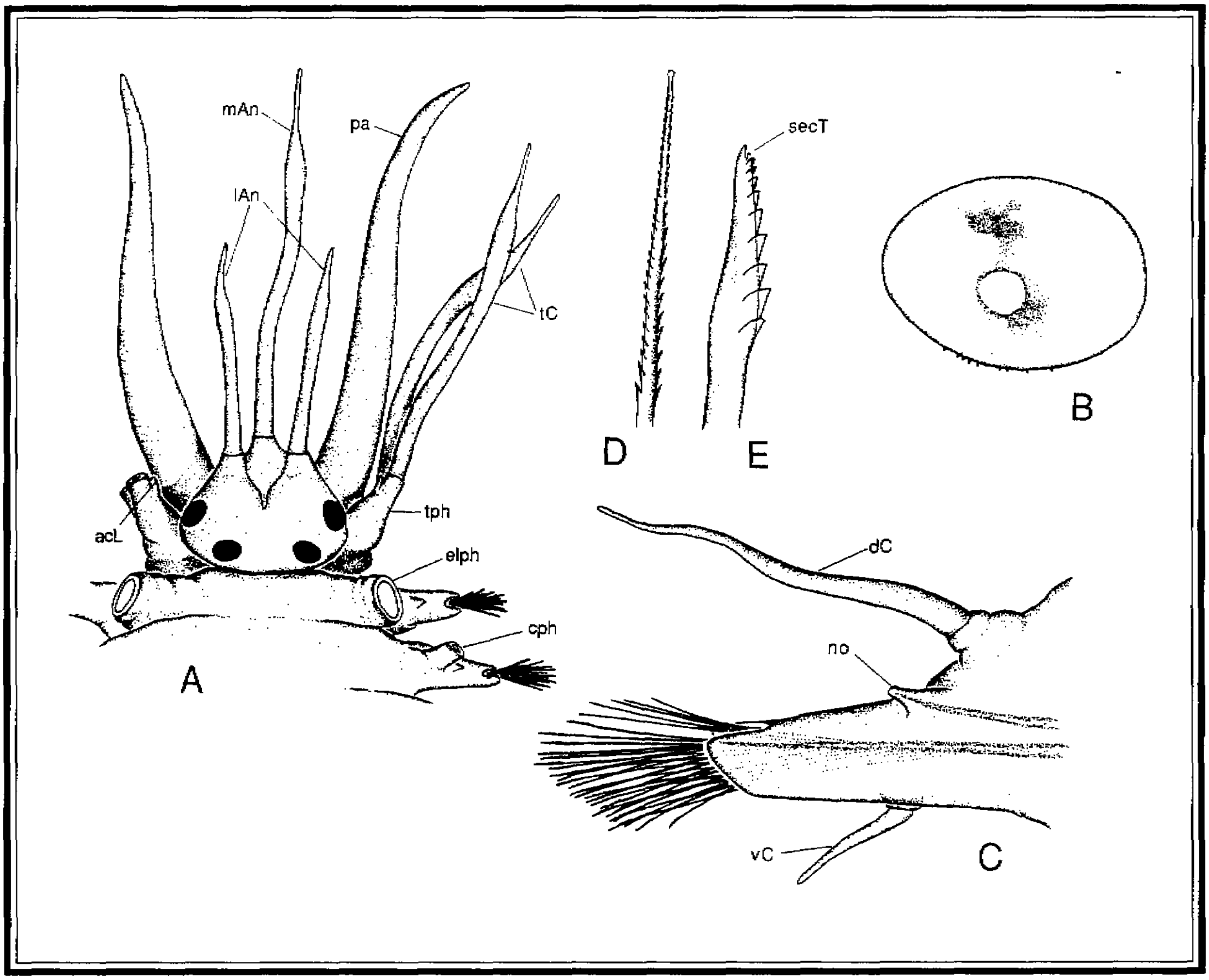

Figure 3.14. *Lepidasthenia berkeleyae*: A, anterior end, dorsal view; B, median left elytron; C, median cirrigerous parapodium, anterior view; D, superior neuroseta; E, distal portion of median neuroseta.

Description. Length to 75 mm for 100 segments; dorsum colorless or with wide transverse bands of brown pigment, and darker pigment at bases of parapodia, cirrophores, and elytrophores; ventrum unpigmented. Prostomium wider than long, projecting anteriorly into ceratophores of lateral antenna (Fig. 3.14A). Four large eyes; anterior pair near widest part of prostomium; posterior pair closer together and near posterior margin. Median antenna with short ceratophore; style up to three times prostomial length, slender, cylindrical, smooth, with slight subdistal swelling and filiform tip. Lateral antennae less than twice prostomial length, similar in shape to median antenna. Palps long, subulate, without pigment or papillae.

Tentaculophores large, lateral to palps, achaetous but with digitiform acicular lobe on anterior face. Two pairs of subequal tentacular cirri similar in length and shape to median antenna. Facial tubercle bulbous; nuchal fold lacking. Ventral buccal cirri long, slender, with filiform tip and slight subdistal swelling.

Suboval elytra leaving median dorsum uncovered. Each elytron thin, translucent, with occasional minute sensory papillae along outer edge; surface smooth, lacking tubercles or papillae, with dark pigment concentrated around elytrophore and extending in band toward middorsum (Fig. 3.14B).

Parapodia subbiramous. Notopodia short, digitiform, not reaching to base of neuropodial lobes; neuropodia long, slender, with rounded pre- and postsetal lobes separated by deep dorsal cleft (Fig. 3.14C). Superior neurosetae slender, with long subdistal spinous region tapering to fine knobbed tip (Fig. 3.14D). Median and inferior neurosetae stouter, with short spinous region tapering to blunt bifid tip (Fig. 3.14E).

Dorsal cirrophores basally bulbous; styles smooth, slender, similar to median antenna in anterior segments, and tapering evenly to filiform tips in median and posterior segments. Dorsal tubercles poorly developed. Ventral cirri short, smooth, subulate. Ventral nephridial papillae small, short, from segment 6. Pygidium with terminal pair of acuminate cirri similar to dorsal cirri.

Biology. *Lepidasthenia berkeleyae* has been reported as a commensal with *Praxillella pacifica* and *Maldanella robusta*, living in the thick mud tubes of these maldanids. Generally, this species is found in areas with muddy bottoms, in water depths from 49-480 m.

Remarks. Hartman (1968:115) recognized *Lepidasthenia interrupta*, originally described by Marenzeller (1902) from off Japan, as the California species with thin superior neurosetae and no ventral neuropodial papillae. However, she incorrectly inserted Marenzeller's drawing of the anterior end of *Lepidonotus elongatus* rather than his sketch of the parapodium of *Lepidasthenia interrupta* as her figure 2. Although Marenzeller does not mention it in his text, this drawing of the 23rd parapodium clearly shows a papilla on the ventral margin of the neuropodium. Therefore, the California specimens that lack these papillae cannot be the same as Marenzeller's species.

The secondary tooth on the median and inferior neurosetae is often screened by the subterminal spines which extend nearly to the tip of each seta.

Type Locality and Type Specimens. Washington, Puget Sound, off Green Point, 92 m, holotype (USNM 21099, specimen dried); near Gertrude Island, 126 m, paratype (USNM 21100); off Heron Island, 63 m, paratype (USNM 32293, gravid female).

Distribution. Reported from British Columbia to southern California.

Lepidasthenia longicirrata Berkeley, 1923

Figure 3.15 A-E

Lepidasthenia longicirrata Berkeley, 1923:214-15, pl. 1, figs. 8-13.—Pettibone, 1953:51-53, pl. 26, figs. 229-236.—Hartman, 1968:117-118, figs. 1-5.—Uschakov, 1982:89-90, pl. 22, figs. 4-6.
Lepidametria longicirrata: Berkeley and Berkeley, 1948:18-19, fig. 22.

Material Examined. British Columbia, off Jesse Island (holotype); off Port Albion (topotype).—Washington: Puget Sound (1).—California, Santa Maria Basin, off Purisima Point, Sta. R-4, 92 m (1), Sta. BRA-21, 75-90 m (1), off Point Arguello, Sta. 70, 200 m (1).

Description. Length to 120 mm for 118 segments; dorsum with wide bands of light brown pigment, and darker pigment at bases of parapodia, cirrophores, and elytrophores; ventrum unpigmented, iridescent. Prostomium wider than long, bilobed, extending into ceratophores of lateral antennae, with four moderate-sized eyes (Fig. 3.15A). Ceratophore of median antenna small; style long, smooth, cylindrical, with filiform tip and pigmented subterminal swelling; lateral antennae shorter, similar in shape. Palps long, thick, tapering to filamentous tips, without pigment or papillae.

Tentaculophores large, lateral to palps, achaetous but with digitiform acicular lobes. Two pairs of smooth, slender tentacular cirri; upper pair similar in shape and slightly longer than median antenna. Small papilla present beneath each palp and lateral to bulbous facial tubercle. Nuchal fold absent. Ventral buccal cirri long, slender, tapering.

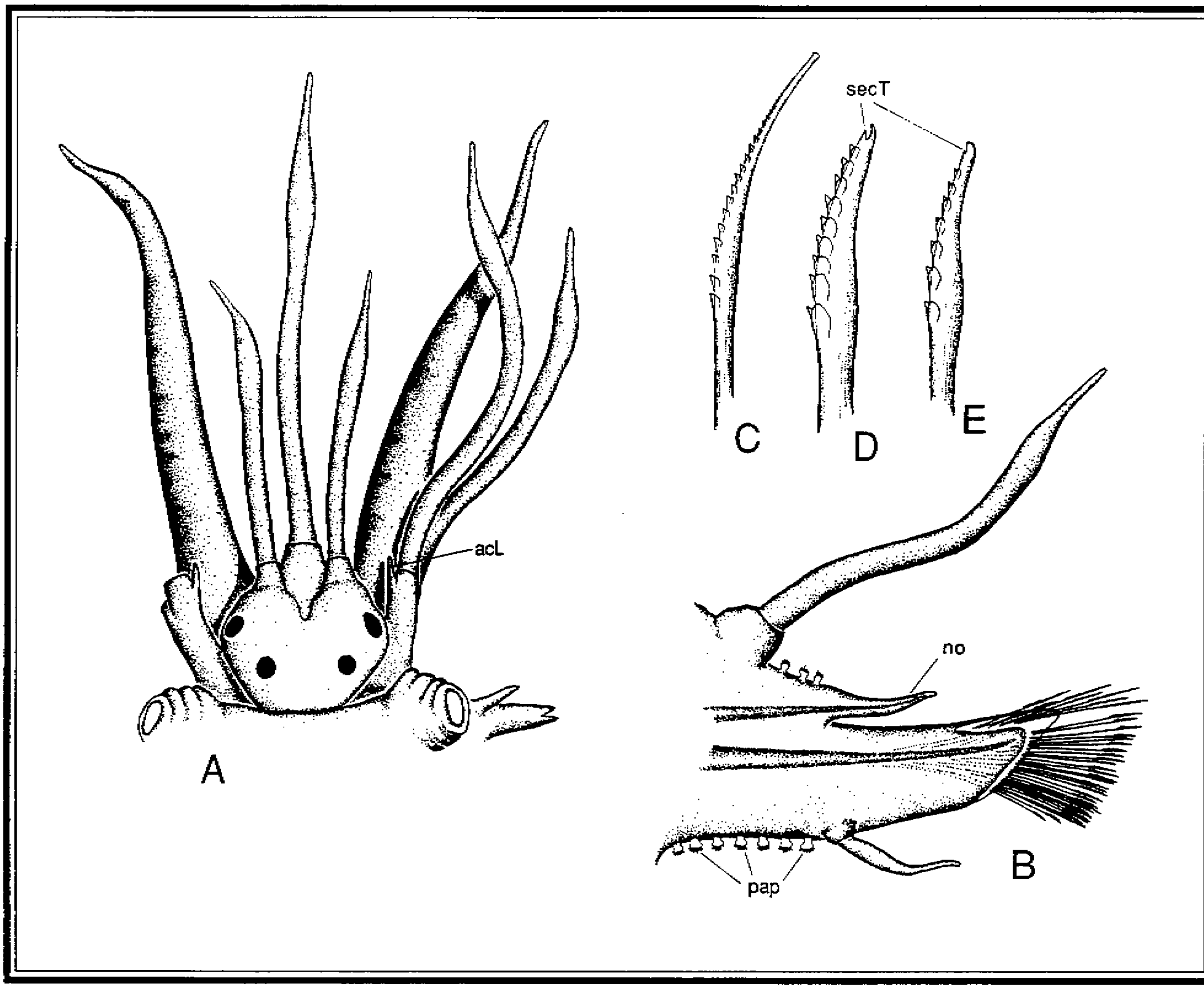

Figure 3.15. *Lepidasthenia longicirrata*: A, anterior end, dorsal view; B, anterior cirrigerous parapodium, posterior view; C, superior neuroseta; D, distal portion of median neuroseta; E, distal portion of inferior neuroseta.

Large suboval elytra nearly covering dorsum; each elytron thin, translucent, smooth, lacking tubercles or marginal papillae, with brown pigment especially around elytrophore.

Parapodia subbiramous. Notopodia digitiform, elongated and reaching nearly to base of neuropodial lobes; neuropodia long, slender, with dorsal cleft between elongate, rounded presetal lobe and slightly shorter postsetal lobe (Fig. 3.15B). Proximal ventral margin of neuropodia with fringe of short, squat papillae having terminal cilia; similar fringe also present dorsally between notopodia and elytrophore or cirrophore on anterior segments. Superior neurosetae long, slender, with long subdistal spinous region tapering to fine knobbed tip (Fig. 3.15C); median neurosetae stouter, with short spinous region tapering to bare bifid tip with distinct secondary tooth (Fig. 3.15D); inferior neurosetae shorter, slender, curved, minutely bidentate (Fig. 3.15E).

Dorsal cirri slender, long in anterior region with slight subdistal swelling, and shorter, acuminate in posterior setigers. Dorsal tubercles not developed. Ventral cirri short, subulate, smooth. Ventral nephridial papillae small, short, from segment 6. Terminal pair of pygidial cirri slender, resembling posterior dorsal cirri.

Biology. *Lepidasthenia longicirrata* is normally found free-living in muds, among rocks, or in shelly substrata, from the intertidal to 330 m. It is also sometimes found associated with parchment-like, sand and shell-covered tubes which the worm apparently constructs.

Remarks. The fringe of papillae on the proximal ventral margin of the neuropodia is easily abraded, and is not always present on all segments. The similar row on the dorsal margin has not been previously reported in the literature; this feature is apparently restricted to the anterior region, and was not observed posterior to segment 21. A single short, blunt notoseta was observed on an anterior parapodium in the small specimen from Puget Sound.

The holotype consists of a median and posterior fragment, but the anterior end is missing. Therefore, Edith Berkeley selected two topotypes from the Berkeley private polychaete collection, and these were transferred to the Smithsonian in 1964 (Pettibone, 1967). One of these (USNM 32851) was considered by the Berkeleys to be the commensal form of *L. longicirrata*, but it is now generally accepted as *L. berkeleyae*.

Type Locality and Type Specimens. British Columbia, dredged from a sponge bed off Jesse Island near Nanaimo, 27 m, holotype (USNM 32853); off Port Albion, topotype (USNM 32852).

Distribution. Known along the North American coast from Vancouver Island to southern California, and also reported from the Gulf of Tonkin in the western Pacific (Uschakov, 1982).

Genus *Lepidonotus* Leach, 1816

Type Species: *Aphrodita squamata* Linnaeus, 1767, designated by Malmgren, 1867.

Diagnosis. Body short, arched, with 26 segments. Bilobed prostomium extending anteriorly into ceratophores of terminally-attached lateral antennae. Antennae and cirri smooth. Facial tubercle present; buccal segment with or without nuchal fold. Twelve pairs of elytra on segments 2, 4, 5, 7, . . . 21 and 23; elytra with or without tubercles and papillae. Notopodia small or vestigial; unidentate notosetae short, slender, spinose, or notosetae lacking. Neuropodia large, with or without acicular lobe; neurosetae stout, long, with subdistal spines and unidentate or occasionally bidentate tips.

Remarks. The genus *Lepidonotus* contains over 70 species. As currently defined, the generic diagnosis is very broad, and several groups will undoubtedly be split away from the genus after revision. Only one species was seen in the Santa Maria Basin material.

***Lepidonotus spiculus* (Treadwell, 1906) new combination**

Figure 3.16 A-H

Polynoe spicula Treadwell, 1906:1151-1152, fig. 11.
Lepidonotus caeloris [*sic*]: Moore, 1908:331 (*partim*); 1910:333-334 (*partim*).—Berkeley, 1923:213 (*partim*). *Not* Moore, 1903.
Lepidonotus caelorus: Hartman, 1938:108-9, fig 35b-d (*partim*).—Berkeley and Berkeley, 1948:9-10, fig. 6-7 (*partim*).—Pettibone, 1953:15-16, pl. 1, figs 1-8, pl. 2, figs. 9-19 (*partim*). *Not* Moore, 1903.
Lepidonotus squamatus: Berkeley and Berkeley, 1954:455-456 (*partim*).—Khlebovich, 1961:165.—Imajima and Hartman, 1964:26-27, pl. 1, figs. g-j (*partim*). *Not* Linnaeus, 1767.

Material Examined. Washington, Puget Sound (10).—California, Monterey Bay (2); Santa Maria Basin, off Point Buchon, Sta. BRA-27, 96-126 m (19), off Point Arguello, Sta. BRA-6, 54-63 m (44).

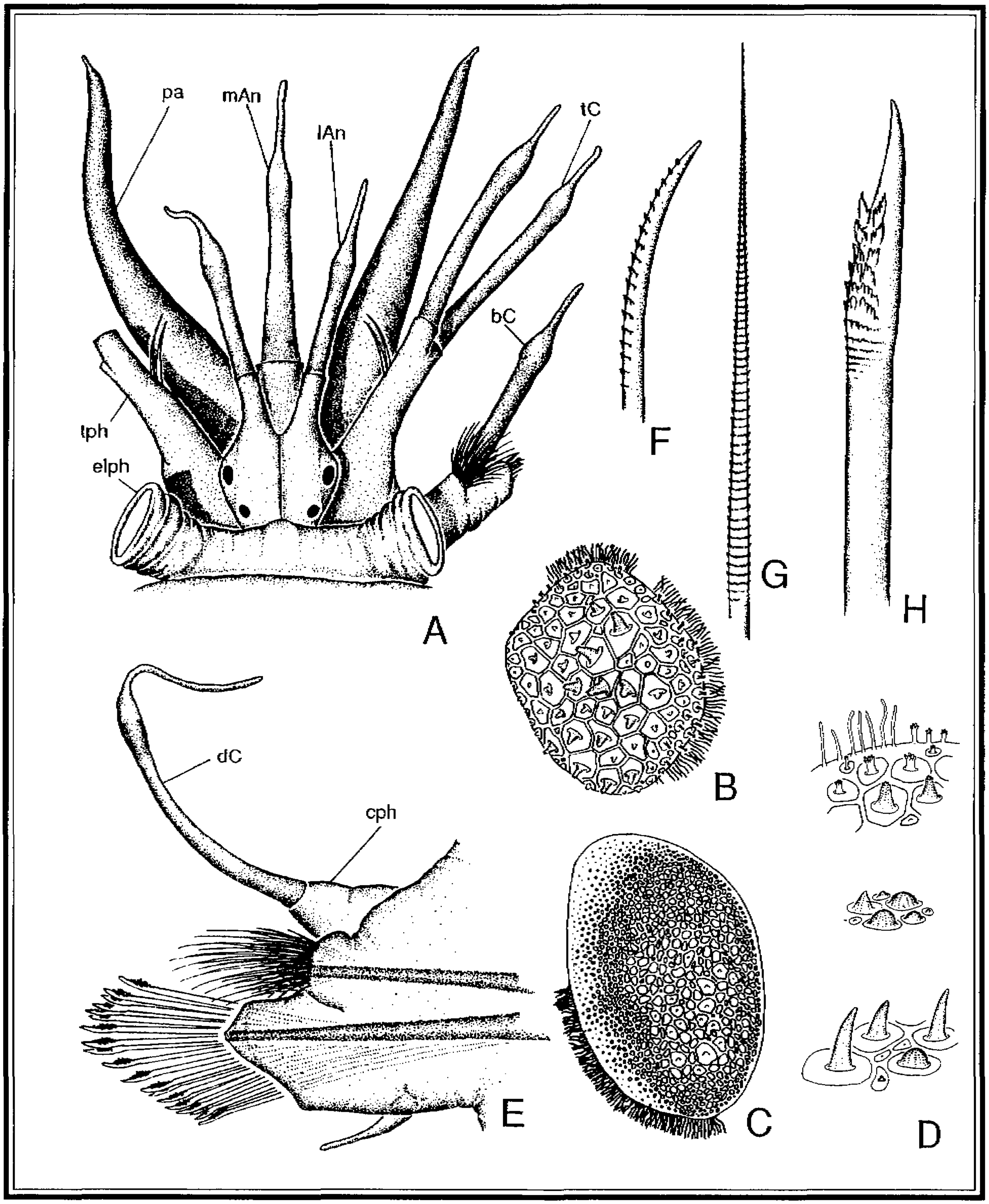

Figure 3.16. *Lepidonotus spiculus*, new combination: A, anterior end, dorsal view; B, first right elytron; C, median left elytron; D, detail of elytral surface from anterior elytron (top group), median elytron, and posterior elytron; E, median cirrigerous parapodium, anterior view; F, superior notoseta; G, inferior notoseta; H, distal half of median neuroseta.

Description. Length to 20 mm for 26 segments; most body surfaces colorless except for dark middorsal pigment patch on segment 23. Prostomium slightly wider than long, bilobed with anterior portions projecting forward as ceratophores of lateral antenna (Fig. 3.16A). Two pairs of dark eyes; anterior pair located at widest part of prostomium, and slightly smaller posterior pair near posterior margin. Median antenna with large, cylindrical, basally pigmented ceratophore; style smooth, with ring of brown pigment around subterminal enlargement and with long filiform tip; styles of lateral antennae similar but shorter. Palps smooth, colorless, longer than median antenna, tapering to short filiform tips.

Long tentaculophores with 1-2 spinose setae; two pairs of subequal tentacular cirri similar in shape and pigmentation to median antenna. Facial tubercle small, bulbous. Buccal segment with pair of smooth ventral buccal cirri similar in shape to tentacular cirri; dorsal anterior margin produced forward as small nuchal fold.

Twelve pairs of tough, leathery, firmly attached elytra, strongly imbricated and completely covering dorsum; surface studded with numerous light orange to dark tan-colored tubercles, becoming small and sparse under areas of overlap. Anterior elytra suboval, with small to large tubercles centered on polygonal, closely packed basal plates (Fig. 3.16B); largest tubercles conical with sculptured sides and spinose tips; smaller tubercles near anterior and lateral borders columnar with spinose tips. Median elytra subreniform to pyriform, with smaller, lower tubercles on more rounded basal plates (Fig. 3.16C). Posterior elytra pyriform to subtriangular, with numerous tall, acutely conical tubercles on round basal plates (Fig. 3.16D). Lateral and posterior margins with thick fringe of long filiform papillae.

Parapodia biramous; notopodial lobe short, rounded, located on anterodorsal surface of neuropodia; neuropodia larger, truncate, distally cleft with presetal lobe slightly longer than postsetal lobe (Fig. 3.16E). Notosetae spinous; superior row slender, short, curved, with blunt tips (Fig, 3.16F); median and inferior rows slender, longer, tapering to capillary tips extending beyond end of neuropodium (Fig. 3.16G). Neurosetae thicker than notosetae, amber colored, with slight subterminal enlargement tapering to long, smooth, slightly hooked tips; enlarged region with two rows of bracts becoming progressively larger distally (Fig. 3.16H).

Dorsal cirri with large, basally inflated cirrophores; styles slender, smooth, extending well beyond neurosetae, with pigmented subterminal swelling and long filiform tips. Dorsal tubercles large, well developed. Ventral cirri short, subulate, reaching to base of lower neurosetae. Nephridial papillae beginning on segment 8, prominent from segment 10, continuing through next to last segment. Anus dorsal, centered on longitudinally striated median ridge extending through last three segments. Pygidium with two very long, smooth, slender cirri with pigmented subterminal swellings and filiform tips.

Remarks. This species was originally described by Treadwell (1906) in the genus *Polynoe*, but it was subsequently referred to *Lepidonotus caelorus* Moore, 1903 by Hartman (1938), and most subsequent authors have accepted this synonymy. However, as part of her extensive work of the family Polynoidae, Dr. Marian H. Pettibone at the Smithsonian Institution has reexamined Treadwell's material and noted that the ornamentation of the elytra is distinctive. The largest anterior tubercles are conical with spiny tips rather than bluntly digitiform, and they are situated on polygonal rather than rounded basal plates. In the posterior region, the largest tubercles are acutely conical rather than bluntly digitiform. Dr. Pettibone has graciously provided some of her extensive notes and sketches on this genus, permitting the resurrection of Treadwell's species in this volume.

Type Locality and Type Specimens. California, Monterey Bay, 84-126 m, 3 syntypes (USNM 5203).

Distribution. Found from Japan north around the Pacific rim and down the west coast of North America as far as southern California.

Genus *Malmgreniella* Hartman, 1967

Type Species: *Malmgreniella dicirra* Hartman, 1967, by original designation.

Diagnosis. Body flattened, with up to 46 segments. Bilobed prostomium with or without cephalic peaks; lateral ceratophores inserted subterminally, joining beneath median ceratophore. Facial tubercle present or absent; dorsal nuchal fold absent. Fifteen pairs of elytra on segments 2, 4, 5, 7, . . . 23, 26, 29, and 32, smooth or with microtubercles confined to anterior region. Parapodia biramous. Notosetae stout, as thick or thicker than neurosetae, with transverse or longitudinal spinous rows, and blunt or pointed tips. Neurosetae with expanded subdistal spinous region and bare, hooked, bidentate or unidentate tips.

Remarks. *Malmgreniella* was originally established by Hartman (1967) for a polynoid found living commensally with stylasterine hydrocorals in the Antarctic. Recently, Pettibone (1993b) has emended the genus and expanded it to include many of the species previously referred to *Malmgrenia* McIntosh, 1874, which is now considered indeterminable. The genus is close to *Harmothoe* Kinberg, 1856, and encompasses a number of species having a commensal relationship with other invertebrates. It is represented off southern California by a group of closely-related species that are all characterized by having nearly smooth elytra with microtubercles confined to a small anterior patch, and notosetae with fine spinules arranged in two longitudinal rows. These species have two distinct types of body pigmentation. A dark brownish or nearly black pigment occurs on the epithelial surface of the posterior dorsal and ventral body, on the cirrophores and basal portions of the cirri, and in broad arcs across the elytra. Beneath the surface are reddish-brown pigment granules that occur on the posterior portion of the prostomium, scattered across the elytra, and occasionally in the parapodia, dorsal and ventral cirri, and around the nephridia. The expression of these two pigments varies widely between individual specimens, and one or the other of the pigments may at times be virtually absent. Therefore, individuals of the same species may superficially appear to be quite different from one another. The details of the prostomium, parapodia, and the setae must be assessed in order to correctly identify specimens within this genus.

Malmgreniella baschi **Pettibone, 1993**

Figure 3.17 A-E

Eunoe sp. C: Lissner *et al.*, 1986:D-7.
Harmothoe sp. A: Lissner *et al.*, 1986:D-7.
Harmothoe nr. *lunulata*: Steinhauer and Imamura, 1990:F-1 (*partim*). *Not* delle Chiaje, 1830.
Malmgreniella baschi Pettibone, 1993b:72-75, fig. 47a-i.

Material Examined. California, Santa Maria Basin, off Point San Luis, Sta. 22, 99 m (1), off Point Sal, Sta. PJ-1, 145 m (2), Sta. PJ-6, 148 m (3), PJ-9, 169 m (2), PJ-13, 144 m (2), off Purisima Point, Sta. R-4, 92 m (2); Western Santa Barbara Channel, off Point Conception, Sta. 79, 98 m (1), Sta. 86, 197 (1); off Santa Catalina Island (holotype and 2 paratypes); off San Diego (3).

Description. Length to 14 mm for 38 segments; posterior dorsum and ventrum often with black transverse pigment bands. Bilobed prostomium about as long as wide, with indistinct cephalic peaks and two pairs of black, lensed eyes; anterior pair larger, situated ventrolaterally in front of widest point of prostomium; posterior pair near posterior margin (Fig. 3.17A). Short, broad median ceratophore inserted in anterior prostomial notch; style about twice prostomial length, tapering, with occasional clavate papillae and long filiform tip. Ceratophores of lateral antennae short, thick, joining beneath median ceratophore; styles short, basally stout, tapering to filiform tips. Palps smooth, acuminate, as long or longer than median antenna, tapering to short filiform tips.

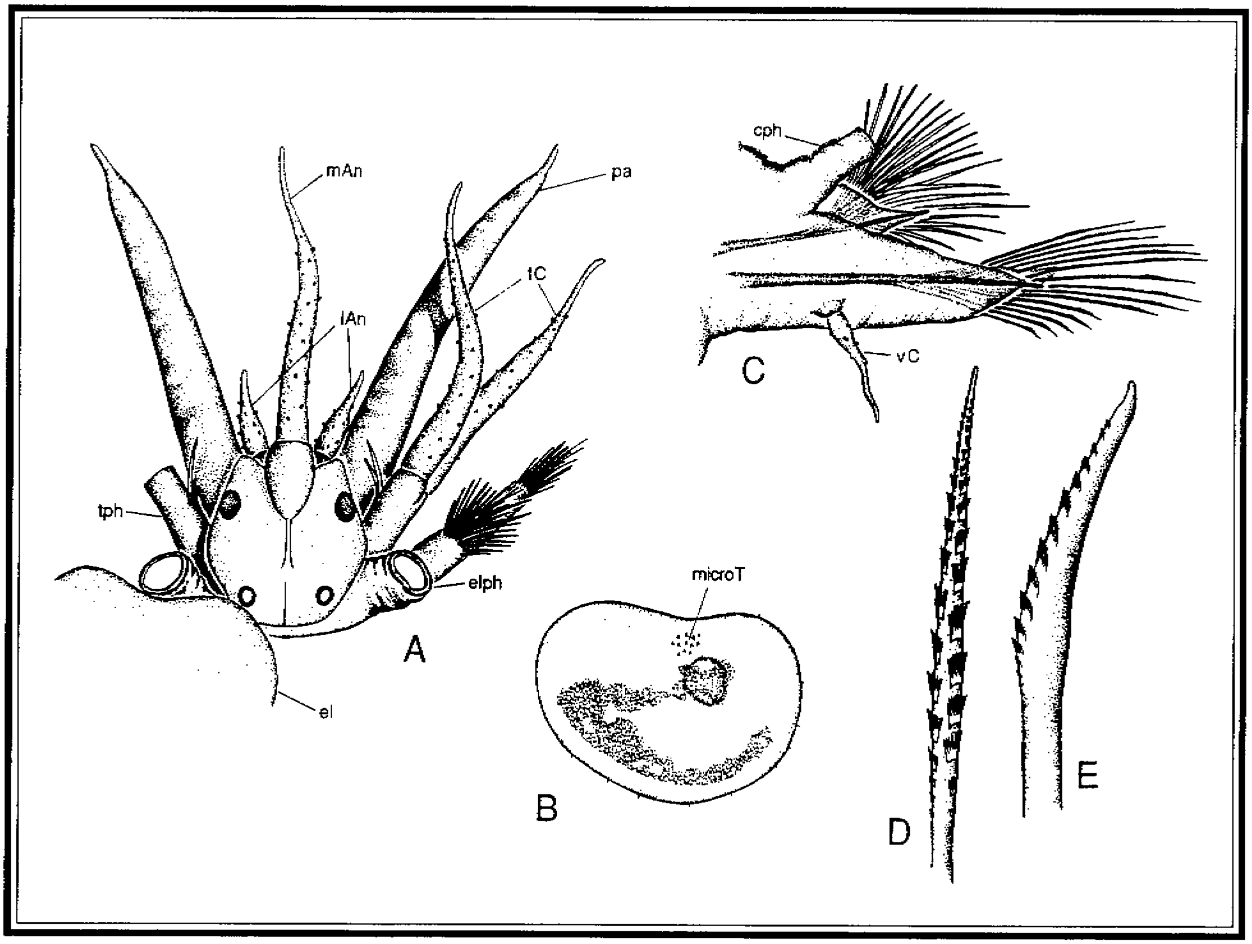

Figure 3.17. *Malmgreniella baschi*: A, anterior end, dorsal view; B, median right elytron; C, median cirrigerous parapodium, posterior view; D, superior neuroseta; E, distal portion of median neuroseta.

Tentaculophores terete, lateral to prostomium, occasionally pigmented, with 0-2 stout, curved setae on anterior face. Tentacular cirri similar to median antenna, with basal pigment and scattered papillae; lower pair slightly shorter. Facial tubercle bulbous, pigmented. Cirrophores of ventral buccal cirri short, broad; styles similar to inferior tentacular cirri.

Fifteen pairs of thin, oval to reniform elytra with occasional micropapillae on lateral and posterior borders (Fig. 3.17B). Surface smooth except for small area of short rounded microtubercles anterior to attachment scar on some anterior elytra; surface with or without mottled dark pigment over attachment point and in irregular C-shaped band along median, posterior, and lateral areas; additional reddish-brown pigment granules sometimes present.

Notopodia short, rounded, tapering into distally pointed acicular lobe (Fig. 3.17C). Neuropodia elongated, extending into short, rounded postsetal lobe, and triangular presetal lobe with tapering extension above emergent acicula. Curved notosetae more numerous and about as stout as neurosetae, with longitudinal striations, two faint longitudinal rows of minute spinules, and bluntly pointed tips. Superior neurosetae with prominent spinules on long spinose region, tapering to pointed tips (Fig. 3.17D); median and inferior neurosetae with shorter enlarged spinous region and less prominent spinules, tapering to bare hooked tips with only indistinct indication of secondary tooth (Fig. 3.17E).

Dorsal cirrophores large, cylindrical, with cilia on upper margin and often with pigment on ventral side; tapering styles extending to tips of neurosetae, with scattered clavate papillae. Prominent dorsal tubercles knob-like. Ventral cirri short, acuminate, with scattered papillae. Pygidium with dorsally-directed anus and pair of long, tapering cirri.

Biology. *Malmgreniella baschi* is commensal with the ophiuroid *Ophiopsila californica*, and has been collected in sands and in the tubes of *Chaetopterus variopedatus* (Pettibone, 1993b).

Remarks. The shape of the anterior prostomium is somewhat variable, but the lobes are not produced into acute peaks. This species differs from its congeners mainly in possessing relatively few neurosetae, the tips of which are unidentate with only the suggestion of a secondary tooth. On a few specimens, the longest median neuroseta could occasionally be found with a thin secondary tooth.

Type Locality and Type Specimens. California, Santa Catalina Island, holotype (USNM 133581) and 7 paratypes (USNM 133582-133585).

Distribution. Found in shelf depths in southern California.

Malmgreniella macginitiei Pettibone, 1993

Figure 3.18 A-D

Harmothoe lunulata: Berkeley and Berkeley, 1941:21 (*partim*).—Blake, 1975b:176, figs. 72-74. *Not* delle Chiaje, 1830.
Malmgrenia lunulata: Pettibone, 1953:25 (*partim*), pl. 9, fig. 77, pl. 10, figs. 80-82, 85, 87, pl. 11, figs. 92-95. *Not* delle Chiaje, 1830.
Harmothoe crassicirrata: Lissner *et al.*, 1986:D-7. *Not* Johnson, 1897.
Harmothoe cf. *lunulata*: Kudenov, 1975:42, fig. 1a-g; Lissner *et al.*, 1986:D-7 (*partim*). *Not* delle Chiaje, 1830.
Malmgreniella macginitiei Pettibone, 1993b:70, fig. 45a-j.

Material Examined. California, Tomales Bay (holotype and 1 paratype); Santa Maria Basin, off Point San Luis, Sta. 21, 49 m (1); off Newport Beach (1); off San Diego (7).

Description. Length to 13 mm for 35 segments; posterior dorsum and ventrum usually with transverse bands of dark pigment. Bilobed prostomium slightly longer than wide, with reddish-brown pigment often concentrated in median furrow; cephalic peaks acute (Fig. 3.18A). Two pairs of moderate-sized eyes; anterior pair situated in front of widest point of prostomium; slightly smaller posterior pair closer together, located near posterior margin. Median ceratophore short, broad, pigmented; style less than twice prostomial length, basally pigmented, with occasional clavate papillae and long filiform tip. Ceratophores of lateral antennae short, thick, joining beneath median ceratophore; styles short, tapering, with scattered papillae and filiform tips. Stout palps about as long as median antenna, smooth, tapering to short filiform tips.

Cylindrical tentaculophores lateral to prostomium, pigmented, with 1-2 stout, curved setae on anterior face. Tentacular cirri basally pigmented, with scattered papillae; upper pair slightly longer than median antenna, and lower pair somewhat shorter. Facial tubercle as prominent pigmented ridge. Cirrophores of ventral buccal cirri bulbous, pigmented; styles long, tapering, with scattered clavate papillae.

Fifteen pairs of thin, strongly imbricated, subcircular to reniform elytra with occasional tiny bordering papillae (Fig. 3.18B). Elytral surface smooth except for small area of short rounded microtubercles anterior to attachment scar on some anterior scales; surface usually with mottled dark pigment in irregular band along median and posterior areas and over attachment point; additional granules of reddish-brown pigment often present throughout.

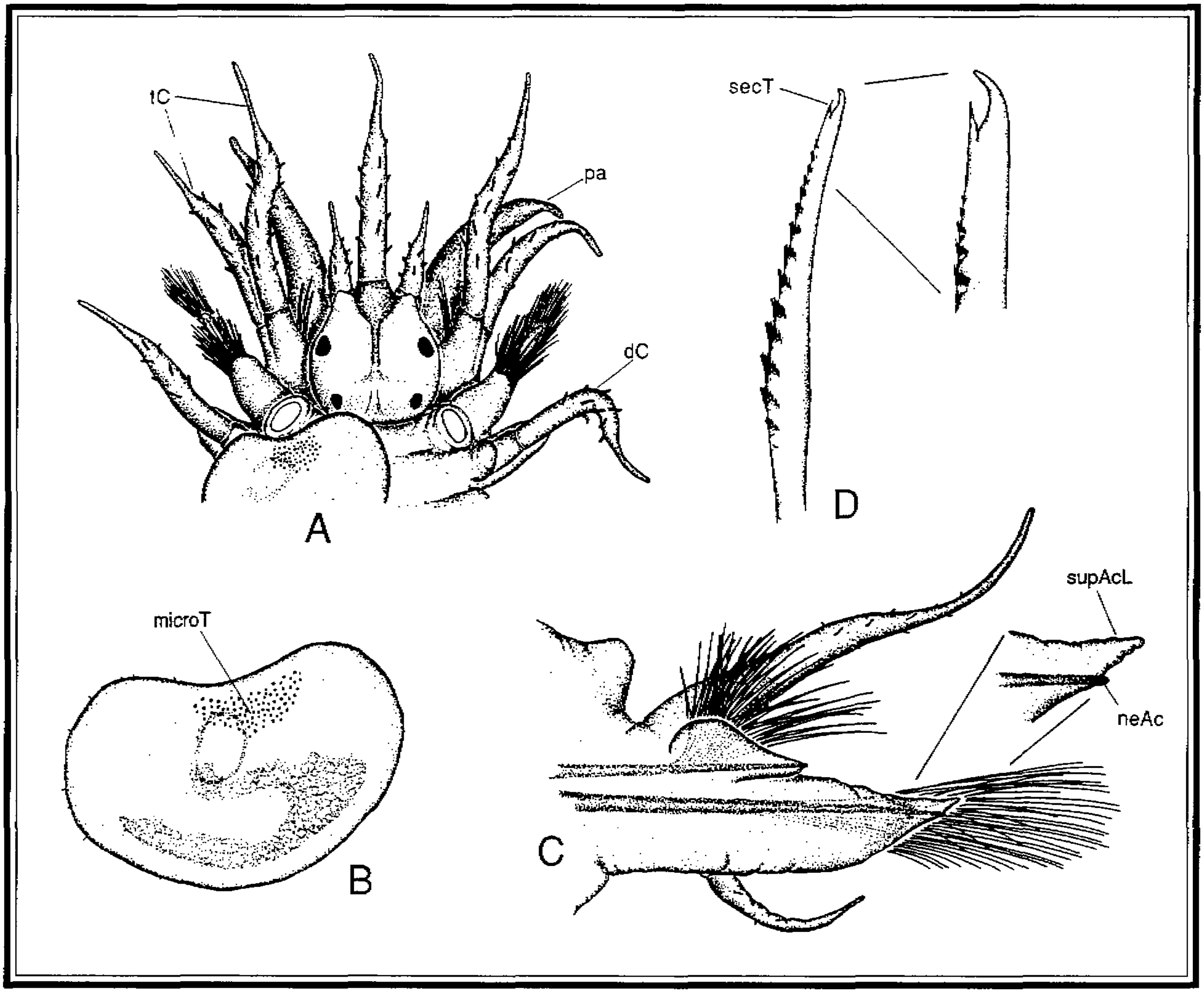

Figure 3.18. *Malmgreniella macginitiei*: A, anterior end, dorsal view; B, median left elytron; C, median cirrigerous parapodium, anterior view, with detail of neuropodial supraacicular lobe; D, distal portion of median neuroseta with detail of tip.

Notopodia short, broad, tapering into pointed inferior lobe with emergent acicula (Fig. 3.18C). Neuropodia elongated, extending into short digitate lobe above emergent acicula. Notosetae numerous, stout, curved, longitudinally striated, with two rows of minute spinules and bluntly pointed tips. Neurosetae numerous and slightly more slender; superior neurosetae with pointed or minutely bifid tips; median neurosetae with shorter enlarged spinous region and bare hooked tips, each with moderate secondary tooth tapering to slender tip (Fig. 3.18D); inferiormost neurosetae with slightly hooked tips and reduced or absent secondary teeth. Distal spinous bracts not approaching base of secondary tooth.

Cirrophores of dorsal cirri large, cylindrical; styles tapering, basally pigmented, with occasional small clavate papillae, extending nearly to tips of neurosetae. Dorsal tubercles prominent, knob-like. Ventral cirri short, acuminate, with occasional papillae. Pygidium small, with low lobes surrounding the dorsally-directed anus; two pygidial cirri similar in size and shape to dorsal cirri.

Biology. *Malmgreniella macginitiei* is a commensal polynoid that has been collected in the burrows of the ghost shrimp *Callianassa californiensis*, in the tubes of the maldanid *Axiothella rubrocincta*, and on the arms of the ophiuroid *Amphiodia urtica* (Pettibone, 1993b).

Remarks. This species differs from its congeners mainly in possessing acutely pointed cephalic peaks on the prostomium, and in details of the neurosetae. The tips of the secondary teeth are drawn into long, fine points, although these are often broken off. In addition, the region just beneath each secondary tooth is bare and devoid of the transverse spinous bracts.

Type Locality and Type Specimens. California, Tomales Bay, intertidal, holotype (USNM 24933), 1 paratype (LACM-AHF Poly 1119); Newport Bay, 1 paratype (USNM 55059).

Distribution. Washington to southern California, in intertidal and shelf depths.

Malmgreniella nigralba (Berkeley, 1923)

Figure 3.19 A-E

Malmgrenia nigralba Berkeley, 1923:213, pl. 1, figs. 5-7; 1924:193.—Hartman, 1968:133, figs. 1-3.
Malmgrenia lunulata: Pettibone, 1953:25 (*partim*), pl. 11, figs. 96-103. *Not* delle Chiaje, 1830.
Harmothoe nr. *lunulata*: Lissner *et al.*, 1986:D-7 (*partim*). *Not* delle Chiaje, 1830.
Harmothoe nigralba: Hanley, 1987:153, figs. 3f, h.
Malmgreniella nigralba: Pettibone, 1993b:60, figs. 39, 40.

Material Examined. Alaska, Prince William Sound (1).—British Columbia, near Nanaimo (3 syntypes).—California, Western Santa Barbara Channel, off Point Conception, Sta. 79, 98 m (6); off San Diego (5).

Description. Length to 24 mm for 40 segments; dorsum and ventrum colorless or with light or dark pigment bands especially in posterior segments. Prostomium bilobed, about as long as wide, with median furrow and truncate anterior lobes (Fig. 3.19A). Two pairs of moderate eyes; slightly larger anterior pair on lateral margin anterior to widest portion of prostomium. Ceratophore of median antenna short, bulbous; style slightly longer than prostomium, with short clavate papillae, tapering to filiform tip. Ceratophores of lateral antennae short, broad, inserted subterminally and converging beneath median ceratophore; styles half prostomial length, pyriform, with clavate papillae. Palps about length of median antenna, tapering, wrinkled, with short tips and minute papillae.

Tentaculophores large, lateral to prostomium, with or without stout, curved seta on anterior face; dorsal and ventral tentacular cirri subequal, similar to median antenna, with short clavate papillae. Facial tubercle prominent, often with brownish pigment; nuchal fold absent. Ventral buccal cirri long, tapering, with scattered clavate papillae.

Fifteen pairs of thin, subcircular to subreniform elytra covering dorsum. First pair and posterior pairs essentially smooth; median pairs with small area of rounded microtubercles anterior to attachment scar and occasional minute marginal papillae (Fig 3.19B). First pair with circle of dark pigment on reticular background; following pairs with pigment and reticulation generally confined to posterior half of elytral surface.

Notopodia small, rounded, tapering into digitate inferior lobe with emergent acicula; neuropodia larger, tapering to subconical presetal acicular lobe with short, broad, distally rounded supraacicular cirrus (Fig. 3.19C). Notosetae slightly curved, with longitudinal striations and faint subdistal spines arranged in two longitudinal rows, tapering to blunt tips (Fig. 3.19D). Neurosetae similar to notosetae in number and thickness; superior neurosetae with long subdistal spinous region and rounded or bidentate tips (Fig. 3.19E); median neurosetae with shorter subdistal spinous region, tapering to strongly hooked tip and prominent secondary tooth diverging slightly from axis of seta; distal spinous bracts reaching very close to base of secondary tooth (Fig. 3.19F); inferior neurosetae smaller, bidentate or ending in knobbed tip (Fig. 3.19G).

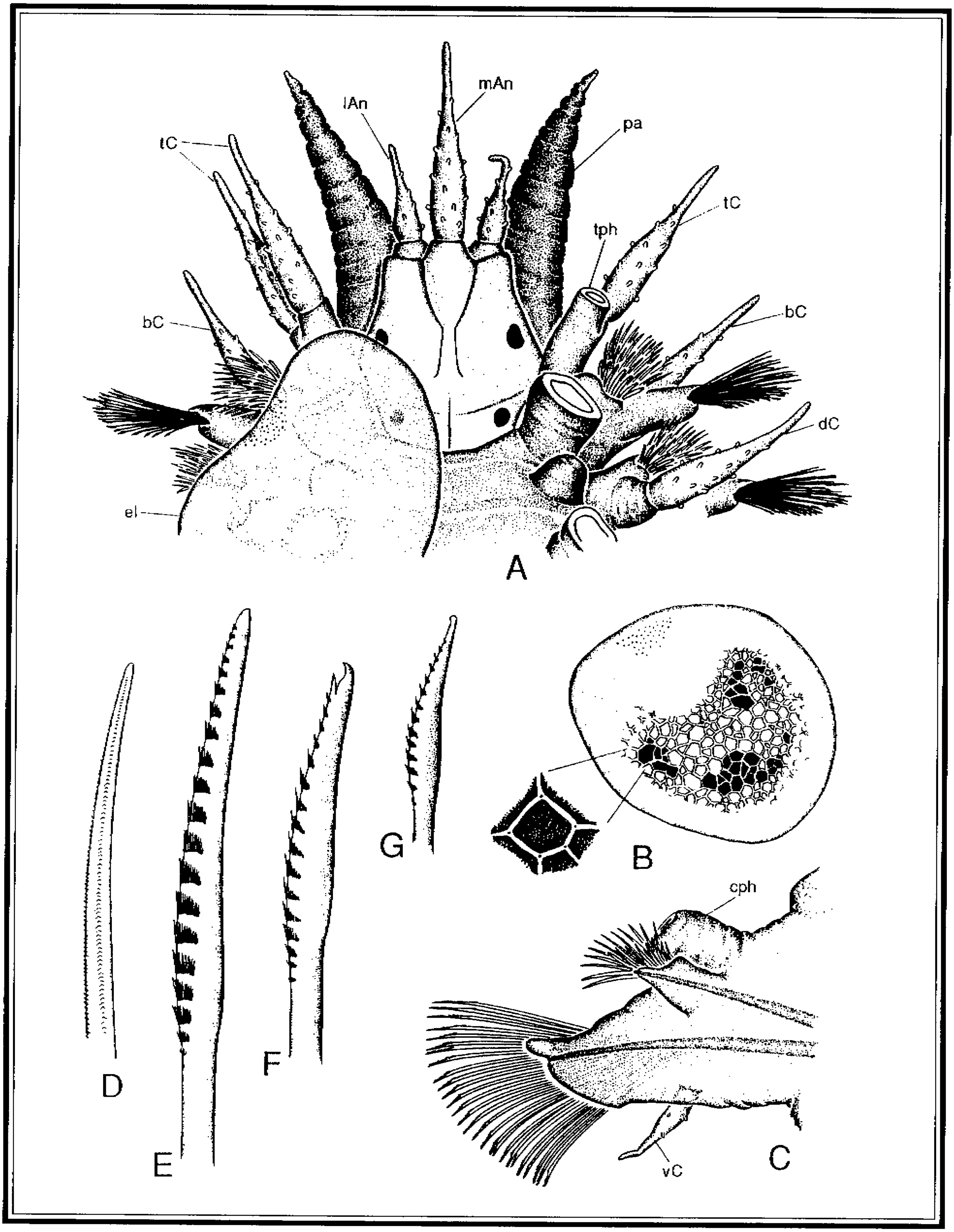

Figure 3.19. *Malmgreniella nigralba*: A, anterior end, dorsal view; B, posterior right elytron with detail of pigmented reticular cell; C, median cirrigerous parapodium, anterior view; D, notoseta; E, distal portion of superior neuroseta; F, distal portion of median bifid neuroseta; G, distal portion of inferior knob-tipped neuroseta.

Dorsal cirrophores large, cylindrical; styles tapering, extending about to tips of neurosetae, with scattered small clavate papillae. Dorsal tubercles prominent, nodular. Ventral cirri short, with scattered papillae, tapering to filiform tips. Nephridial papillae short, cylindrical, evident by segment 11. Pygidium with low lobe surrounding dorsally directed anus, with pair of long, tapering anal cirri.

Biology. *Malmgreniella nigralba* has been found in California, Washington, and British Columbia living in the vertical burrows of the holothuroid *Leptosynapta clarki*. It appears to prefer coarse gravelly sands from the low intertidal out to approximately 100 m.

Remarks. The elytra of this species are distinctly reticulated although this feature is not always obvious if the black pigmentation has faded. The transverse spinous bracts on the neurosetae are present distally to the base of the secondary tooth. This tooth was seen to be much longer in the California specimens than in material from colder waters further to the north.

Type Locality and Type Specimens. British Columbia, Vancouver Island, Piper's Lagoon, 3 syntypes (USNM 32875-32876).

Distribution. Southern Alaska to southern California, in intertidal and shelf depths.

Malmgreniella scriptoria (Moore, 1910)

Figure 3.20 A-E

Harmothoe scriptoria Moore, 1910:344-346. pl. 28, figs. 13-17.—Hartman, 1961:49; 1968:85-86, figs. 1-5.

Malmgrenia lunulata: Pettibone, 1953:25-28 (*partim*), pl. 9, figs. 73-76, pl. 10, figs. 78-79, 83-84, 86, pl. 11, figs. 88-91. *Not* delle Chiaje, 1830.

Harmothoe nr. *lunulata*: Lissner *et al.*, 1986:D-7 (*partim*).—Steinhauer and Imamura, 1990:F-1 (*partim*). *Not* delle Chiaje, 1830.

Malmgreniella scriptoria: Pettibone, 1993b:68-69, fig. 44A-K.

Material Examined. California, Monterey Bay (holotype and 1 additional specimen); Santa Maria Basin, off Point Sal, Sta. 33, 396 m (2), off Purisima Point, Sta. R-2, 161 m (3), Sta. R-3, 409 m (1), Sta. R-6, 410 m (1), off Point Arguello, Sta. 74, 201 m (3); Western Santa Barbara Channel, off Point Conception, Sta. 80, 196 m (1).

Description. Length to 22 mm for 40 segments; dorsum dusky brown or colorless. Prostomium slightly longer than wide, with median furrow and truncate anterior lobes (Fig. 3.20A). Two pairs of small to moderate eyes; slightly larger anterior pair on lateral margin of prostomium near widest point. Reddish-brown pigment granules sometimes present near anterior margin of prostomium and between posterior pair of eyes. Ceratophore of median antenna short, thick; style acuminate, longer than prostomium, basally pigmented, with minute papillae, tapering to filiform tip. Ceratophores of lateral antennae inserted subterminally, joining beneath median ceratophore; styles short, tapering, with occasional minute papillae. Palps about length of median antenna, tapering, wrinkled, with short tips and minute papillae.

Tentaculophores large, projecting forward, with or without stout, curved seta on anterior face. Upper pair of tentacular cirri similar to median antenna, with basal pigment and minute papillae; lower pair slightly shorter. Facial tubercle prominent, often with brownish pigment. Nuchal fold absent. Cirrophores of ventral buccal cirri large, directed forward; styles long, tapering, with scattered papillae.

Elytra covering dorsum, easily detached, subcircular to reniform. Elytra thin, delicate, with occasional minute marginal papillae (Fig. 3.20B); surface smooth except for small area of rounded microtubercles anterior to attachment scar, with crescent of brownish pigment near posterior margin and around attachment scar, or pigment absent.

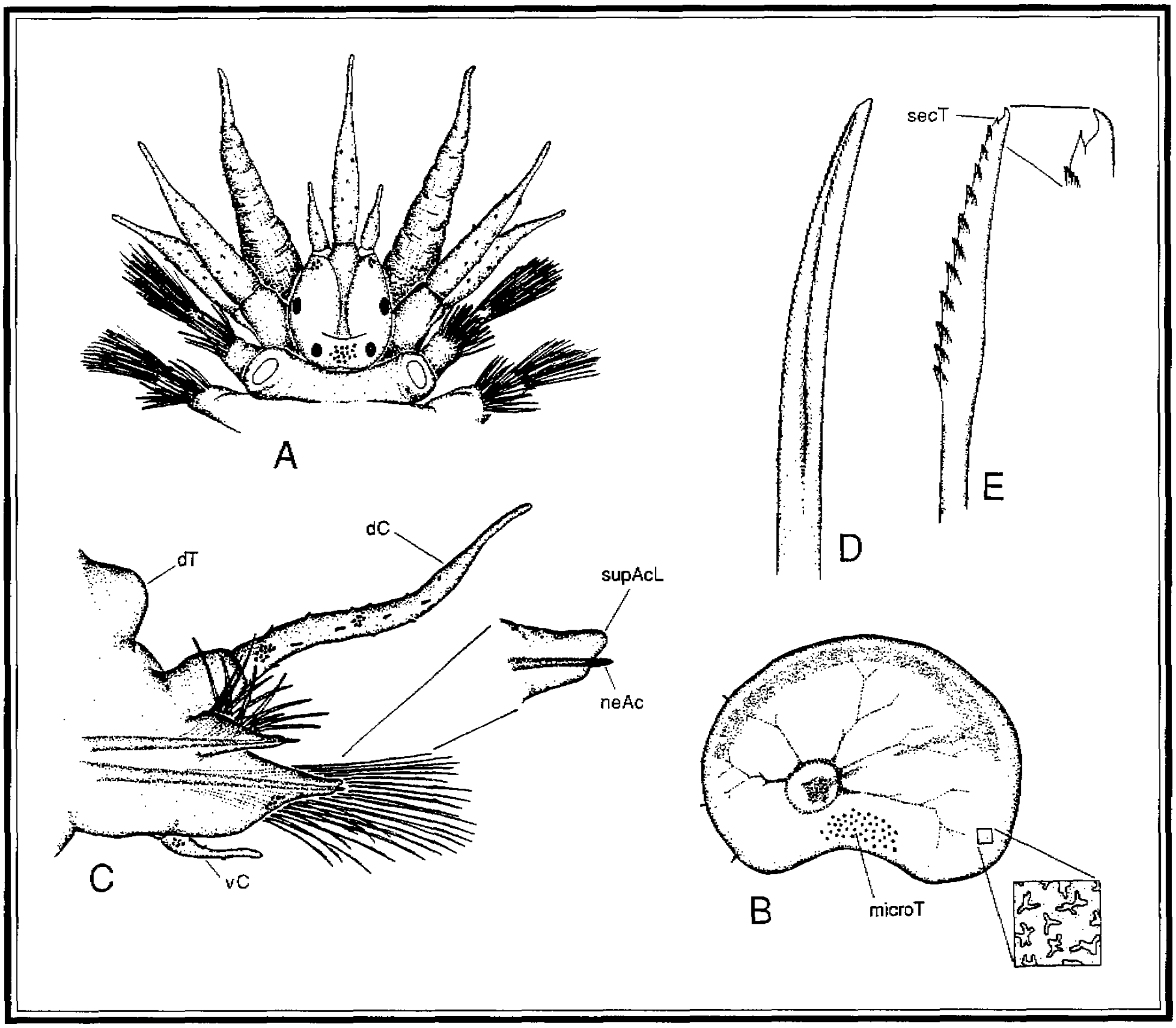

Figure 3.20. *Malmgreniella scriptoria*: A, anterior end, dorsal view; B, median right elytron with detail of surface; C, median cirrigerous parapodium, anterior view, with detail of neuropodial supraacicular lobe; D, notoseta; E, distal portion of median neuroseta with detail of tip.

Notopodia low, rounded, tapering into digitate inferior lobe with long emergent acicula; neuropodia prominent, triangular, tapering to presetal lobe with short cirrus above emergent acicula; pre- and postsetal margins often pigmented (Fig. 3.20C). Notosetae stout, slightly curved, tapering to blunt tips, with longitudinal striations and faint subdistal spines arranged in two longitudinal rows (Fig. 3.20D). Neurosetae more numerous and slightly more slender than notosetae; upper neurosetae with long subdistal spinous region and knobbed or bidentate tips; median and lower neurosetae with shorter subdistal spinous region, tapering to strongly hooked tip and prominent, short secondary tooth (Fig. 3.20E). Distal spinous bracts reaching very close to base of secondary tooth.

Dorsal cirrophores large, tapering; styles acuminate, extending to or beyond tips of neurosetae, with scattered small papillae and granules of brownish pigment. Dorsal tubercles prominent, pigmented. Ventral cirri short, with pigment granules basally, tapering to filiform tip. Nephridial papillae short, cylindrical, present by segment 9. Pygidium with low lobe surrounding dorsal anus; pygidial cirri similar to and slightly longer than dorsal cirri.

Biology. Found in the ambulacral grooves of the heart urchin *Brisaster latifrons*, in middle shelf to upper slope depths in areas of green muds having a sand or gravel component.

Remarks. Examination of the type material confirms that *Malmgreniella scriptoria* has papillate rather than smooth antennae and cirri as illustrated by Moore (1910: figs. 13-14). The specimen in the U.S. National Museum (USNM 17156) is a gravid female in which the numerous eggs have distorted the parapodia, causing the dorsal tubercles to appear less conspicuous than normal. The "close and curious fine pencil-like white markings" (Moore 1910) are clearly visible in the elytra of the specimen at the Academy of Natural Sciences of Philadelphia, and appear to be regions devoid of any subsurface pigment granules.

Type Locality and Type Specimens. Off the Point Piños Light, Monterey Bay, 101-305 m, holotype (USNM 17156 and ANSP AD4602X slide 6.7). Moore (1910) examined two specimens from Monterey Bay, and he made an error in his manuscript when he designated the specimen from *Albatross* Station 4452 as the type (p. 346). That specimen is in the Philadelphia collection (ANSP AD2893) with an internal label in Moore's handwriting stating it to be a "cotype." The specimen from *Albatross* Station 4460 in the collections of the U.S. National Museum is a gravid female and was indicated by Moore to be the type on page 344 of his manuscript. Loi (1980) and Pettibone (1993b) have recognized this specimen (USNM 17156) as the holotype.

Distribution. Known from Puget Sound to southern California.

Genus *Subadyte* Pettibone, 1969

Type Species: *Polynoe pellucida* Ehlers, 1864, by original designation.

Diagnosis. Body elongate, flattened, with about 40 segments. Bilobed prostomium with or without cephalic peaks; lateral ceratophores inserted ventrally. Antennae, palps, and cirri with papillae. Facial tubercle present or absent; buccal segment with small nuchal fold. Fifteen or sixteen pairs of elytra on segments 2, 4, 5, 7, . . . 23, 26, 29, 32, and occasionally 34; elytra without microtubercles but with vesicular papillae. Parapodia biramous. Notosetae as thick or thicker than neurosetae, curved, with spinous pockets and blunt unidentate or bidentate tips. Neurosetae longer, with distinct basal cusp, spinose subdistal region, and unidentate or bidentate tips.

Remarks. Pettibone (1969) erected the genus *Subadyte* for a group of short-bodied species previously included in *Scalisetosus* McIntosh, 1885. Members of this genus are distinguished by the presence of spinous pockets along the notosetae, and neurosetae with a large cusp at the base of the spinous region. Currently there are about 7 species known, including several recently described from Australian waters (Hanley and Burke, 1990; 1991). A single species was recognized in the Santa Maria Basin material.

Subadyte mexicana **Fauchald, 1972**

Figure 3.21 A-G

Subadyte mexicana Fauchald, 1972:27-29, pl. 1 figs. a-e.—Steinhauer and Imamura, 1990:F-1.—Pettibone, 1993c:685-687, figs. 4-5.
Subadyte sp. A: Lissner *et al.*, 1986:D-7.—Blake *et al.*, 1988:A-3.—Steinhauer and Imamura, 1990:F-1.
Subadyte sp. B: Lissner *et al.*, 1986:D-7.

Material Examined. California, off Point Buchon, Sta. 10, 690 m (1), off Point San Luis, Sta. R-1, 91 m (3), Sta. R-2, 161 m (1), Sta. R-3, 409 m (2), off Point Sal, Sta. 41, 495 m (1), Sta. R-8, 90 m (7), Sta. R-9, 410 m (24), Sta. PJ-1, 145 m (5), Sta. PJ-7, 123 m (4), Sta. PJ-8, 142 m (3), Sta. PJ-10, 147 m (7), Sta. PJ-14, 134 m (1), Sta. PJ-15, 155 m (2), Sta. PJ-16, 130 m (2), Sta. PJ-23, 143 m (3), off Purisima Point, Sta.

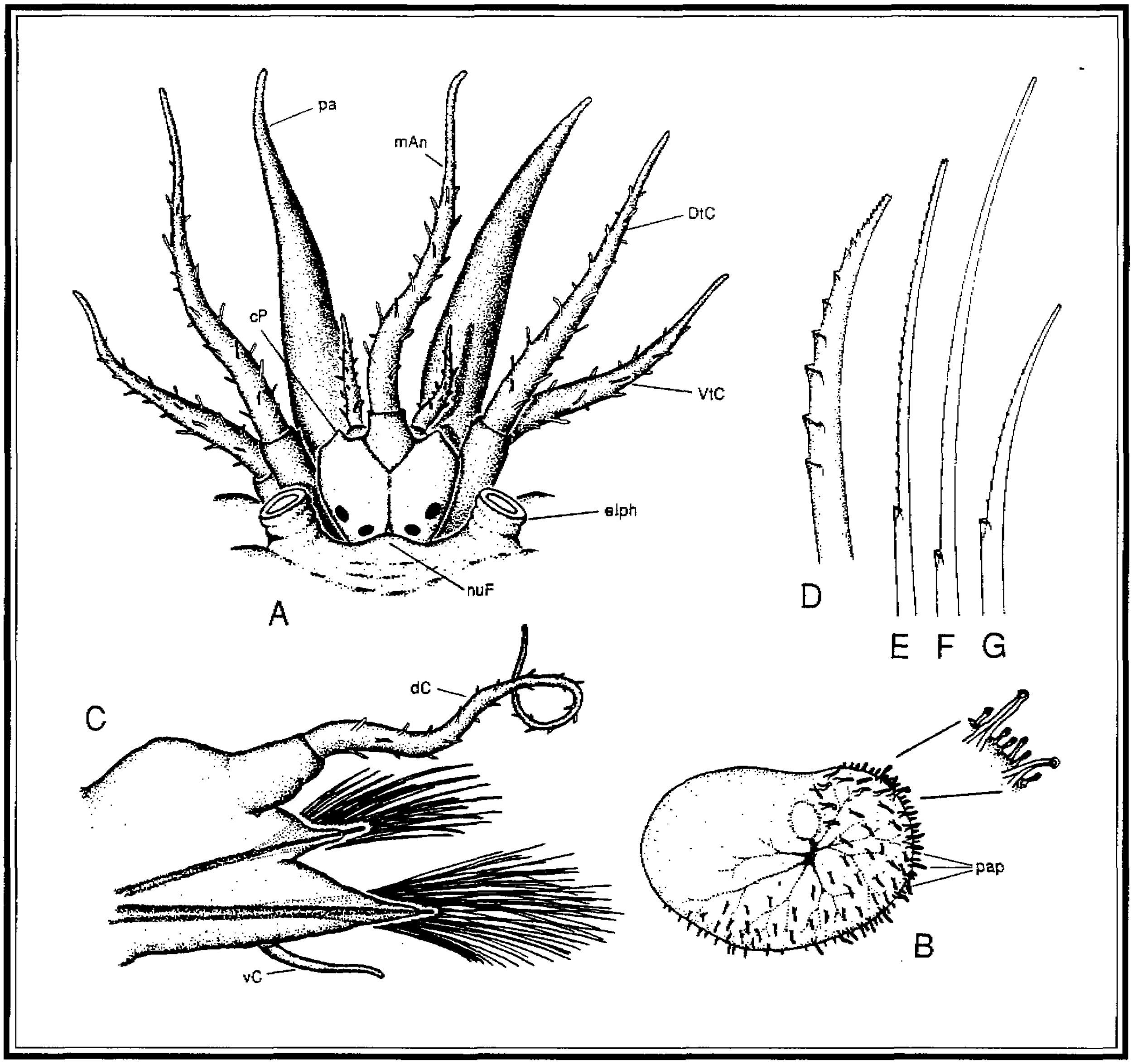

Figure 3.21. *Subadyte mexicana*: A, anterior end, dorsal view; B, median right elytron with detail of marginal papillae; C, median cirrigerous parapodium, anterior view; D, notoseta; E, superior neuroseta; F, median neuroseta; G, inferior neuroseta.

46, 597 m (1), Sta. R-4, 92 m (14), Sta. R-5, 154 m (8), Sta. R-6, 410 m (57), off Point Arguello, Sta. 65, 107 m (1), Sta. 72, 401 m (3); off San Diego, Sta. E (1).

Description. Length to 6.8 mm long for 30 segments, width including parapodia 2.0 mm; dorsum with dusky pigment tending to concentrate in two longitudinal bands above elytrophores and cirrophores; ventrum colorless. Prostomium strongly bilobed, wider than long, with distinct cephalic peaks; two pairs of moderate reddish eyes arranged in trapezoidal pattern on posterior half (Fig. 3.21A). Median ceratophore large, cylindrical, inserted between anterior prostomial lobes; style three times prostomial length, tapering, with scattered long papillae and long filiform tip. Ceratophores of lateral antennae bulbous, inserted beneath cephalic peaks, nearly meeting beneath median ceratophore; styles slender, about length of prostomium, acuminate, with numerous papillae. Palps long, tapering, with longitudinal rows of minute papillae. Pharynx with border of soft, distally pointed papillae, 11 in dorsal arc and 11 in ventral; lateral two pairs minute.

Tentaculophores lateral to palps; upper lobe long, cylindrical, with emergent acicula; lower lobe shorter; 1-2 curved setae with spinous pockets occasionally present on anterior face. Tentacular cirri similar in shape to median antenna, with scattered papillae; upper cirri distinctly longer than lower pair. Facial tubercle present, with upper lip produced into prominent longitudinal ridge. Buccal segment with small nuchal fold extending over posterior margin of prostomium. Ventral buccal cirri tapering, with long filiform tips and scattered papillae.

Suboval to subreniform elytra on segments 2, 4, 5, 7, . . . continuing on alternate segments to end of body, strongly imbricated and covering dorsum. Elytra thin, translucent, with scattered papillae on surface and along lateral and posterior margin (fig 3.21B). Some surface papillae vesicular, enlarged proximally, and all with clavate tips.

Parapodia biramous; notopodia low, rounded, extending into long, slender presetal lobe with emergent acicula (Fig. 3.21C). Neuropodia longer, broader, tapering into long pointed lobe with terminal emergent acicula. Notosetae thick, curved; each seta with proximal smooth shaft and median region of spinose pockets becoming progressively smaller and closer together toward blunt, notched tip (Fig. 3.21D). Neurosetae numerous, slender, longer than notosetae, with basal cusp proximal to spinous region. Superior neurosetae coarsely serrated, tapering to notched tips (Fig. 3.21E); median neurosetae longer, with indistinct serrations and unidentate tips (Fig. 3.21F); inferior neurosetae with small distinct serrations on short distal region, tapering to unidentate tips (Fig. 3.21G).

Ceratophores of dorsal cirri cylindrical, enlarged basally; styles long, tapering, with scattered papillae, extending beyond tips of neurosetae. Dorsal tubercles not developed. Ventral cirri short, slender, smooth. Nephridial papillae short, cylindrical, from segment 6. Pygidium rounded, with terminal anus; terminal cirri not observed.

Biology. Found in sandy and muddy sediments on the continental shelf and slope, and reported from a whale-fall community in the Santa Catalina Basin (Pettibone, 1993c).

Remarks. *Subadyte mexicana* is extremely fragile, and unbroken adult specimens are rarely found. The eyes are often indistinct, and at times the visual pigment is barely discernable. This is especially true of the specimens from the deeper stations, indicating that the visual pigments may not fully develop at depth. Some specimens exhibit distinct longitudinal bands of pigment along the dorsum, while others appear colorless. In the smaller specimens, a relatively greater proportion of the neurosetae exhibit distal serrations and notched tips. Presumably the nearly smooth neurosetae with unidentate tips are acquired later as the worm grows larger.

Type Locality and Type Specimens. Baja California, 15.5 miles from Natividad Island light, 844 m, holotype (LACM-AHF Poly 1008).

Distribution. Southern California and Mexico as far south as Cedros Island, in mid-shelf to mid-slope depths.

Genus *Tenonia* Nichols, 1969

Type Species: *Tenonia kitsapensis* Nichols, 1969, by monotypy.

Diagnosis. Body short, flattened, widest anteriorly and tapering posteriorly, with up to about 39 segments. Bilobed prostomium with cephalic peaks; ceratophores of lateral antennae inserted beneath anterior margin. Antennae, palps, and cirri without papillae. Facial tubercle absent; buccal segment with small nuchal fold. Fifteen pairs of elytra on segments 2, 4, 5, 7, . . . 23, 26, 29, and 32, completely covering dorsum. Parapodia biramous. All setae of similar thickness; notosetae and superior neurosetae long, slender, serrated, tapering to capillary tips; inferior neurosetae with expanded subdistal spinous region and bifid tips.

Remarks. *Tenonia* is similar to the genus *Harmothoe* in which the sole species was originally described. It differs, however, in having notosetae that are slender and capillary-tipped rather than thick and pointed.

Tenonia priops (Hartman, 1961)

Figure 3.22 A-E

Harmothoe priops Hartman, 1961:50-51; 1966:193-194, pl. 1, figs. 4-6; 1968:83-84, fig. 1.
Tenonia kitsapensis Nichols, 1969:205-208, fig. 1 A-J.
Tenonia priops: Barreca, 1984:801-803.

Material Examined. Washington, off Port Madison (holotype and 15 paratypes of *Tenonia kitsapensis*).—Oregon, off Coos Bay (2).—California, Monterey Bay (1); Santa Maria Basin, off Point Sal, Sta. R-8, 90 m (2).

Description. Length to 12 mm for 39 segments; dorsum with distinctive wide transverse bands and narrower intersegmental bands of dark reddish brown pigment. Prostomium trapezoidal, bilobed, with weakly-developed cephalic peaks and pigment speckles on wide posterior portion (Fig. 3.22A). Two pairs of large eyes; anterior pair located beneath cephalic peaks and visible through transparent prostomium. Median antenna with large ceratophore inserted in notch between prostomial lobes; smooth, acuminate style pigmented basally, about twice prostomial length. Ceratophores of lateral antennae inserted beneath median ceratophore; smooth pigmented styles short, basally bulbous, tapering to filiform tips. Palps longer than median antenna, thick, tapering abruptly to filiform tips, without papillae.

Tentaculophores short, lateral to palps, without setae or acicular lobe. Two pairs of subequal tentacular cirri similar in length and shape to median antenna, with dark pigment basally. Facial tubercle absent. Buccal segment with small dorsal nuchal fold. Ventral buccal cirri smooth, pigmented, tapering, inserted on short cirrophores at bases of parapodia.

Fifteen pairs of circular elytra not covering dorsum in anterior setigers. Elytra thin, translucent, easily detached, nearly smooth except for occasional inconspicuous microtubercles, with brown pigment around attachment scar; elytral margins smooth (Fig. 3.22B).

Notopodia short, tapering into pointed lobes with emergent acicula; neuropodia much longer, extending into slender triangular lobe with digitate cirrus above emergent acicula (Fig. 3.22C). Notosetae uniformly thin, with fine serrations, tapering to capillary tips (Fig. 3.22D); superior notosetae bent, and inferior notosetae longer and straight. Superior neurosetae resembling lower notosetae; inferior neurosetae slightly thicker, coarsely serrated in subdistal expanded region, with bifid tips (Fig. 3.22E).

Dorsal cirri with large, cylindrical cirrophores and long, acuminate styles without papillae or pigment. Dorsal tubercles not developed. Ventral cirri short, tapering, inserted at midlength of parapodia. Short nephridial papillae present by segment 8, and well-developed in posterior segments. Pygidium blunt, with dark pigment terminally, and pair of long, smooth, basally inflated cirri.

Habitat. Found in soft sediments ranging from muds to clean, fine sands with shell fragments or gravel, in 2-170 m.

Remarks. This small species readily fragments and is rarely encountered whole, making it difficult to accurately determine the number of pairs of scales. In addition, Nichols (1969) reports that nearly mature females may have only 13 or 14 elytral pairs. The distinctive barred dorsal pigment pattern may fade and disappear with prolonged storage in alcohol.

Type Locality and Type Specimens. California, off Santa Barbara Point Light, 25 m, holotype (LACM-AHF Poly 0019) and paratype (LACM-AHF Poly 0020).

Distribution. Recorded along the Pacific coast of the U.S. from Puget Sound to southern California.

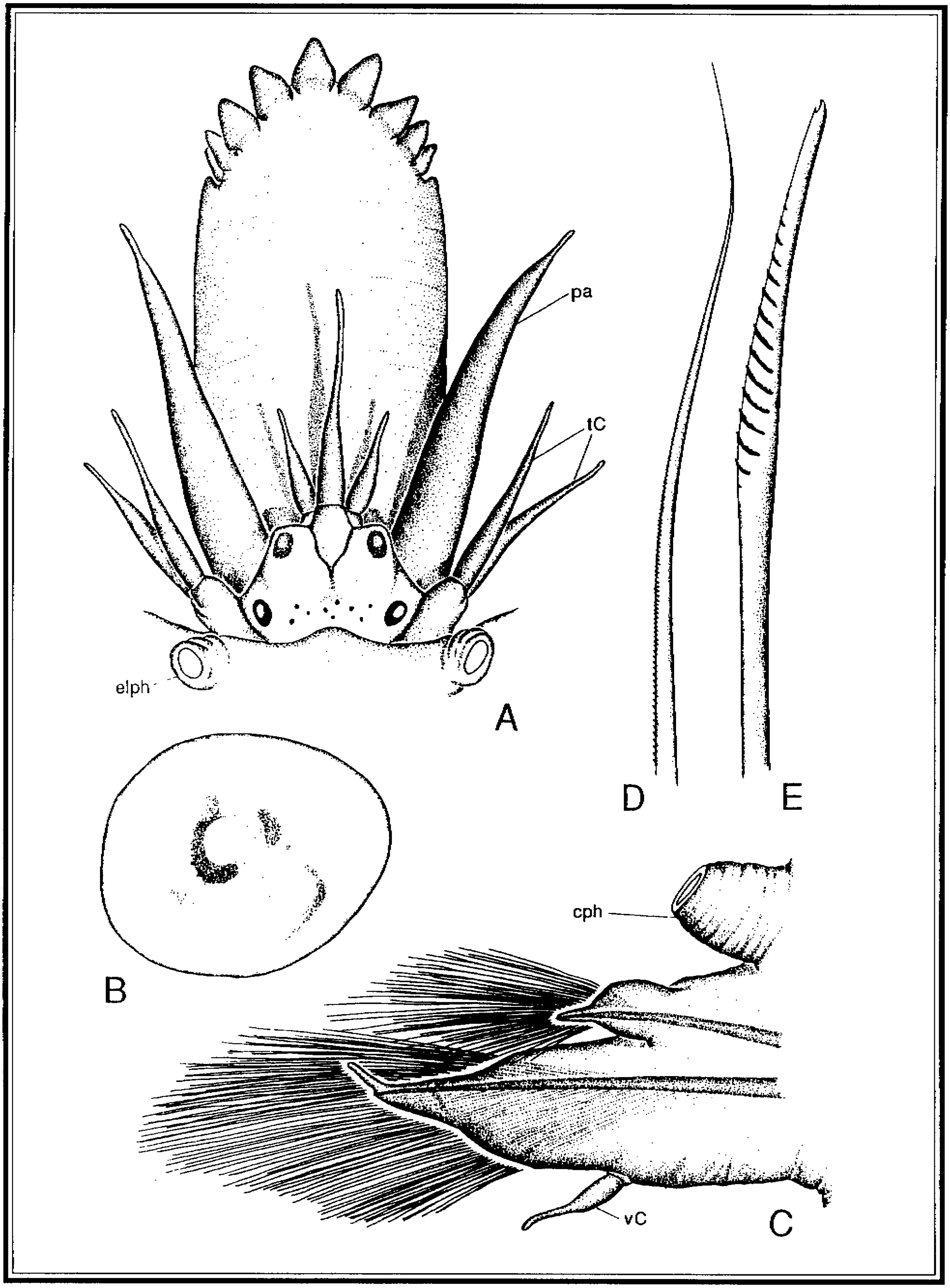

Figure 3.22. *Tenonia priops*: A, anterior end, dorsal view, with pharynx everted; B, median left elytron; C, median cirrigerous parapodium, anterior view; D, notoseta; E, distal portion of inferior neuroseta.

Genus *Ysideria* Ruff, new genus

Type Species: *Ysideria hastata* Ruff, new species. Gender: feminine.

Diagnosis. Body dorsally flattened, with up to 37 segments. Bilobed prostomium with cephalic peaks, with 3 antennae, 2 palps, and 2 pairs of eyes; ceratophore of median antenna in anterior notch; ceratophores of lateral antennae inserted beneath anterior margin. Tentaculophores of first segment lateral to prostomium, with pair of dorsal and ventral tentacular cirri, and with acicular lobe on inner face with 0-2 setae. Second segment with first pair of elytrophores, biramous parapodia, and long ventral buccal cirri. Fifteen pairs of elytra on segments 2, 4, 5, 7, . . . 23, 26, 29, and 32. Parapodia biramous, with small notopodia inserted on superior margin of large neuropodia, each with projecting acicular lobe. Notosetae more slender than neurosetae, with transverse spinous rows, tapering to blunt glabrous tips. Superior neurosetae thick, lancelike, with enlarged subterminal spinous region and entire, blunt tips; median and inferior neurosetae thinner, with enlarged subterminal spinous region and hooked bifid or entire tips. Dorsal cirri on nonelytrigerous segments, with basally enlarged cirrophores and cylindrical styles; dorsal tubercles nodular; ventral cirri short. Pygidium with pair of cylindrical anal cirri.

Etymology. The name is of arbitrary derivation.

Remarks. *Ysideria* is distinguished from most of the genera within the Harmothoinae by having notosetae that are more slender than the neurosetae. It is similar in many characters to the genus *Arcteobia*, but it differs in having notosetae that are all pointed rather than having some that taper to capillary tips, and in having thick, stout, uniramous superior neurosetae.

Ysideria hastata Ruff, new species

Figures 3.23 A-B, 3.24 A-G

Material Examined. California, Monterey Bay, off Santa Cruz, Sta. 1 36°56.13'N, 122°04.13'W, 31 m, 18 Oct 1992; —off Point Loma, San Diego, Sta. A-8, 32°39.84' N, 117°16.84' W, 62 m, 22 May 1980 (holotype, USNM 171057, 1 paratype, LACM-AHF Poly 1720); Sta. A-10, 32°39.50' N, 117°16.13' W, 48 m, 14 Jan 1986 (1 paratype, SBMNH 142933); Sta. A-11, 32°39.98' N, 117°16.27' W, 48 m, 19 Jul 1988 (1 paratype, USNM 171059), 3 Apr 1989 (1 paratype, USNM 171058); Sta. A-13, 32°40.97' N, 117°16.57' W, 43 m, 3 Apr 1989 (1 paratype, LACM-AHF Poly 1721); Sta. B-3, 32°45.42' N, 117°18.38' W, 59 m, 4 Jan 1993 (1 paratype, MCZ 4014).

Description. Holotype complete, in two pieces, 22 mm long for 37 segments, width excluding setae 5 mm. Body elongate, flattened dorsally, arched ventrally, of nearly constant width through median region. Dorsum with transverse triangular area of brown pigment on each setiger, becoming darker posteriorly; ventrum with similar triangular pattern plus patch of pigment at base of nephridia, or pigment in broad transverse band spreading onto parapodia. Prostomium trapezoidal, bilobed, with moderate to distinct cephalic peaks (Fig. 3.23A). Two pairs of dark eyes; anterior pair larger, anterior to widest part of prostomium; posterior pair adjacent to first elytrophores. Median antenna with large, cylindrical, slightly tapering ceratophore in anterior prostomial notch; style tapering, about as long as prostomium, with filiform tip and scattered short, clavate papillae. Lateral ceratophores short, inserted ventrally on prostomium; styles short, subulate, with filiform tips and scattered papillae. Palps stout, tapering, about prostomial length, with minute papillae and short tips.

Tentaculophores elongate, lateral to prostomium and adjacent to palps, with acicular lobe on inner face with 0-2 stout, curved setae. Two pairs of subequal tentacular cirri similar in shape and slightly longer than median antenna, with scattered clavate papillae. Second (buccal) segment with pair of large elytrophores and first biramous parapodia; ventral buccal cirri similar to tentacular cirri, situated on basally enlarged cirrophores lateral to ventral mouth. Antennae, tentacular cirri, and buccal cirri with brown pigment proximally.

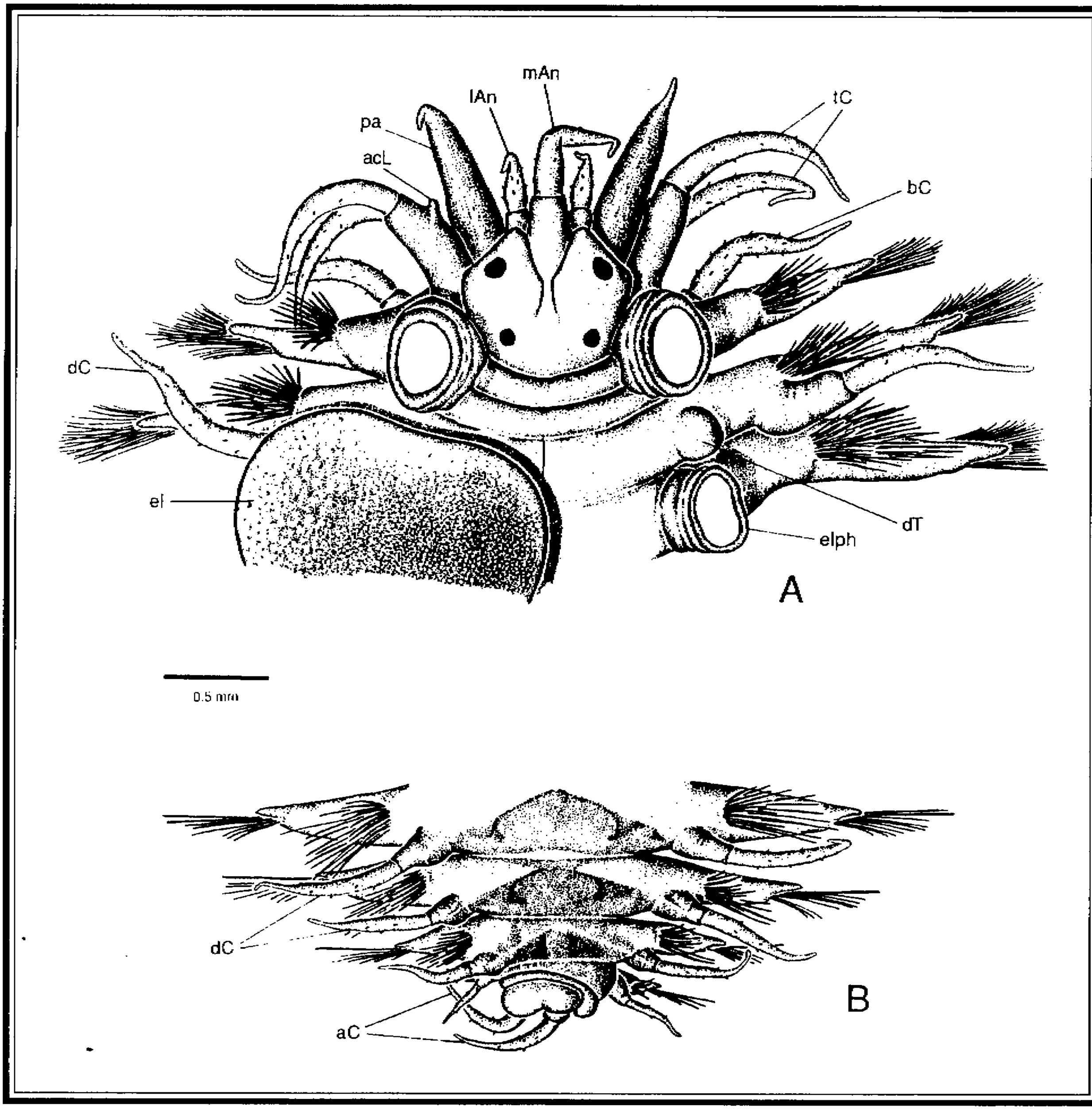

Figure 3.23. *Ysideria hastata*, new species, holotype: A, anterior end, dorsal view; B, posterior end, dorsal view, left posteriormost parapodium underdeveloped.

Fifteen pairs of large elytra completely covering dorsum; first pair suboval, slightly thicker, with shiny surface; subsequent pairs subreniform (anterior) to subcircular (posterior), thin, dull, often wrinkled. Elytra smooth except for occasional micropapillae, without tubercles or fringing papillae; entire surface mottled with brown pigment, or pigmentation restricted to median and posterior regions and area around attachment point (Fig. 3.24A). Notopodia small, much shorter than neuropodia, tapering into acutely conical acicular lobe on lower side (Fig 3.24B). Neuropodia large, broad, extending into presetal lobe with emergent acicula and small, short, blunt supraacicular process; postacicular lobe shorter, subtriangular. Notosetae moderate in number, arranged in several whorls, slightly curved, uppermost short and lowermost longer, reaching nearly to tip of neuropodia; each notoseta pale yellow, slender, with distinct transverse spinous rows,

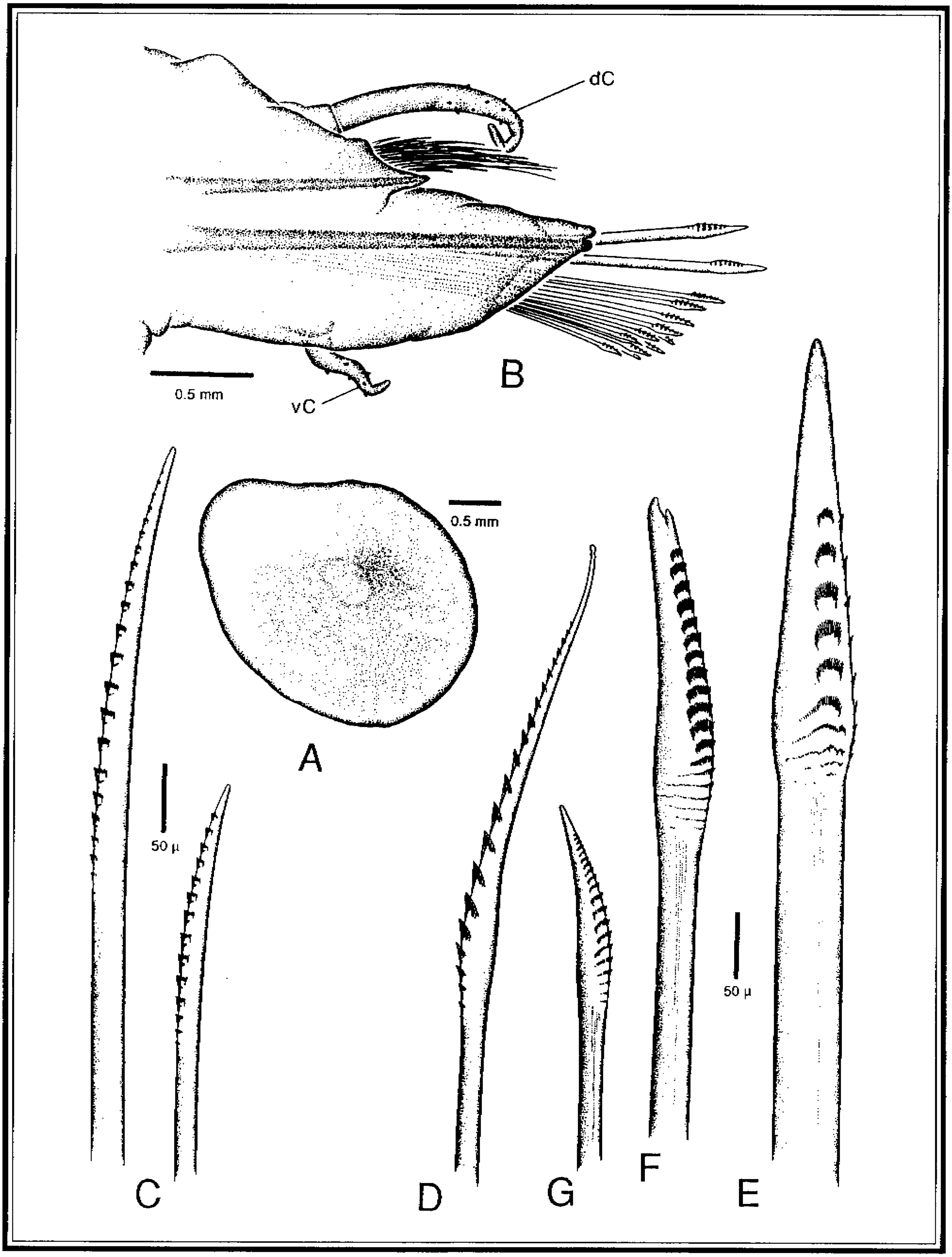

Figure 3.24. *Ysideria hastata*, new species, holotype: A, right eighth elytron from segment 15; B, left cirrigerous parapodium from segment 18, anterior view; C, inferior and superior notosetae, segment 18; D, median neuroseta from 2nd segment; E, superior neuroseta, segment 18; F, median neuroseta; G, inferior neuroseta.

tapering to blunt, glabrous tip (Fig. 3.24C). Neurosetae less numerous than notosetae, arranged in vertical series; those on first two parapodia slender, with long, basally expanded spinous region, tapering to thin knobbed tips (Fig. 3.24D). Thereafter superior 1-2 neurosetae massive, harpoon shaped, amber colored, with short expanded region of spinous bracts, tapering to glabrous, blunt tips (Fig. 3.24E); median neurosetae thicker than notosetae, light amber, with short, slightly curved spinous region tapering to glabrous, slightly hooked, bifid tips (Fig. 3.24F); inferior neurosetae more slender, tapering to entire blunt tips (Fig, 3.24G).

Cirrophores of dorsal cirri cylindrical, with pigmented basal enlargement on posterior side; styles cylindrical, heavily pigmented, sparsely papillate, tapering to filiform tips not extending beyond neurosetae. Dorsal tubercles low to bluntly conical, with little pigment. Ventral cirri short, acuminate, with scattered small papillae; ventral cirrophores low, with dark brown pigment patch on median side. Cylindrical nephridial papillae projecting between parapodia from segment 6. Pygidium with anus medial to last parapodia (Fig. 3.23B), with terminal pair of short, sparsely papillate pygidial cirri tapering to filiform tips.

Etymology. Latin *hastatus*, armed with a spear, in reference to the large spear-shaped superior neurosetae.

Remarks. The elytra of *Ysideria hastata* exhibit a large variation in the distribution of pigments. This elytral mottling along with the presence of pigment on the posterior ventrum and the heavy specialized neurosetae are suggestive of a commensal mode of living. To date, however, no potential host organisms have been reported.

Most of the specimens examined have the notosetae encased in a golden yellowish substance of unknown origin and composition. This material does not appear on the neurosetae. A similar substance occasionally occurs on the notosetae of *Malmgreniella scriptoria*.

This species is recorded as *Harmothoe* sp. A in the SCAMIT listing of soft bottom macroinvertebrates from infaunal monitoring programs in the Southern California Bight.

Distribution. Reported from central and southern California from Monterey Bay southward to Point Loma in shelf depths between 29-62 m.

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4. Family Acoetidae Kinberg, 1865

by

James A. Blake[1]

Introduction

The Acoetidae (=Polyodontidae) are scaleworms with large bodies that are elongated and dorsoventrally flattened. They typically have 300 or more segments, and some may reach gigantic proportions with more than 600 segments and lengths of up to a meter or more and widths of up to 40 mm. These worms live in long tubes constructed of thin interwoven threads that are combined with adhering particles of mud or sand. They are carnivorous and extend out of their tubes to catch prey. Acoetids are generally tropical in distribution and include eight genera and about 45 species.

Morphology

Acoetids have bodies that are partially covered with numerous dorsal elytra. The dorsal surface of the body is usually transversely grooved, often obscuring segmental boundaries. The ventral surface is smooth. The head region is well developed. The prostomium and tentacular segment are more or less fused and bear long ventral palps, antennae, tentacular cirri, and eyes (Fig. 4.1A, 4.2A). The prostomium is oval or slightly bilobed, and bears a pair of lateral antennae and sometimes a median antenna. In most genera, including *Acoetes* and *Polyodontes*, the anterior pair of eyes is large and located on a stalked structure called the ommatophore (Fig. 4.1A, 4.2A). These eyes are very characteristic and readily distinguish acoetids from other scaleworms. The tentacular segment bears one or two aciculae and a pair of dorsal and ventral tentacular cirri; setae may be present or absent. Elytra are first present on the second segment which is biramous and forms the lateral lips of the mouth. The pharynx is eversible, large, muscular, and bears two pairs of jaws. There is usually a pair of papillae around the oral opening.

The elytra overlap along the sides of the body, leaving the mid-dorsum uncovered. They are attached to large elytrophores on segments 2, 4, 5, and 7, continuing on alternating segments down the body (Fig. 4.1E, 4.2I). Individual elytra are relatively small, rounded and smooth (Fig. 4.1B). Dorsal cirri are present on those segments lacking elytra (Fig. 4.2E). Branchiae are reported for some species of *Polyodontes*. When present, the branchiae have a thickened cuticle and represent non-vascular coelomic extensions on the parapodia and the bases of the elytra. They may be papilliform, filamentous, or arborescent.

Setae are all simple. Notopodia are reduced anteriorly, with a bundle of notosetae present or absent. Notopodia of middle body segments form enlarged flattened lobes on the anterodorsal sides of the neuropodia (Fig. 4.1E). Again, notosetae may be present or absent; coiled spinning glands (=web glands) are present, producing soft silky threads that are used in tube building. The silken fibers are actually modified setae which emerge from the notopodium. Neuropodia are well developed and accessory bracts may be present. Neurosetae include stout acicular spines with spinelets, thin hirsute pointed setae, and thin, spirally coiled setae with

[1] ENSR Consulting and Engineering, 89 Water Street, Woods Hole, Massachusetts 02543

various types of serrations (Fig. 4.1G-J, 4.2D, F-H); some neurosetae have terminal hairs (Fig. 4.1K). From segment 9, the upper group of neurosetae form a low anterodorsal bract on the neuropodium opposite the place where the spinning fibers arise. According to Pettibone (1989), these setae may function in the separation of the spinning fibers. Two types of neurosetae are present: (a), stout and long (Fig. 4.1Ka; 4.2Ja); and (b), shorter, more slender (Fig. 4.1Kb; 4.2Jb). The structure of these setae differ among genera and species, and Pettibone (1989) has greatly emphasized them as taxonomic characters. Ventral cirri are short and pointed (Fig. 4.1C-E; 4.2B, E, I). The pygidium bears 2 long anal cirri.

Biology

The Acoetidae are tube dwellers. They line the walls of their tubes with fine collagenous threads. These threads are secreted by the spinning glands and are woven into a criss-cross, spiralled pattern. They are usually combined with mud, clay, or sand particles, forming very strong, thickened tubes that may extend up to a meter or more in length and be up to 4 cm in width. The tubes of acoetids are unique among the polychaetes for the complete absence of a membranous lining. According to Pettibone (1989), the felted appearance formed from the threads are homologous with the fibers comprising the dorsal felt of *Aphrodita.*

The tube and body of acoetids provides habitat for a variety of commensals. Entoprocts are attached to the walls of the tubes (Franzén, 1962; Nielsen, 1966; Pettibone, 1989), gastropods live under the elytra (Moore, 1972), montacutid bivalves live between parapodia (Rullier, 1965; Intes and Le Loeuff, 1975), and other polychaetes live within the tubes (Fox and Ruppert, 1985). The entoprocts use the respiratory currents generated in the tubes to filter food particles.

Acoetids are carnivorous, using their tubes as retreats from which they extend, grab their prey, and pull back. Pettibone (1989) describes reports from the Mediterranean where large specimens of *Polyodontes macillosus* have been captured on fishing lines. The worms were attached to the bait (hermit crabs, worms, and small fish) by the everted proboscis.

Sexes are separate. Nothing is known about the reproduction and development of species of Acoetidae. Pettibone (1989) describes juveniles of two species.

Taxonomic History

The most important review and revision of the Acoetidae is by Pettibone (1989). In this work the entire taxonomic history of the family is reviewed along with keys, descriptions, and illustrations of all of the known species. All available information on the biology and natural history of these scaleworms is also reviewed.

The species of the Acoetidae have been included in virtually every scale worm family at one time or another. In most recent keys or monographs, including Hartman (1968), species of this group have been included in the family Polyodontidae. Pettibone (1989), however, points out that the Acoetidae Kinberg, 1856, based upon *Acoetes* Audouin and Milne-Edwards, 1832 has priority because the family name Polyodontidae Augener, 1918, based upon *Polyodontes* Renieri in Blainville, 1828, is preoccupied in Fishes by Polyodontidae Bonaparte, 1837, that is based on the genus *Polyodon* Schneider, 1801.

Most Acoetidae are tropical or subtropical. However, Hartman (1968) records three species of acoetids (as Polyodontidae) from southern California. *Peisidice aspera* Johnson, also included with this group by Hartman (1968), belongs to the genus *Pholoides* in the family Pholoidae (Blake, 1995, this volume).

One species, *Acoetes pacifica* has been collected from the Santa Maria Basin. Two additional species, *Polyodontes lupinus* and *P. panamensis*, have been reported from southern California (Hartman, 1968; Pettibone, 1989).

Key to the Genera and Species From California

1A. Upper neurosetae of type a from segment 9 long, tapering to fine tips, thickly spinous distally (Fig. 4.1Ka); type b neurosetae shorter than type a (Fig. 4.1Kb) but not completely hidden by notopodia .... Genus *Acoetes: A. pacifica*

1B. Upper neurosetae of type a from segment 9 long, abruptly tapering to slender tips (Fig. 4.2Ja), plumose subdistally and short spinous rows basally; type b neurosetae very short (Fig. 4.2Jb), hidden by notopodia .... Genus *Polyodontes* ... 2

2A. With numerous elongate oval branchiae on elytrophores and dorsal cirrophores from about segment 10, replaced by few digitiform branchiae from about segment 34 .... *Polyodontes lupinus*

2B. Branchiae absent, or with single digitiform branchiae on some segments from segment 30 .... *Polyodontes panamensis*

Descriptions of Species

Genus *Acoetes* Audouin and Milne-Edwards, 1832

Type Species: *Acoetes pleei* Audouin and Milne-Edwards, 1832, by monotypy.

Diagnosis. Prostomium bilobed, with pair of bulbous stalked ommatophores directed anteriorly and pair of small eyes; median antenna with ceratophore in middle of prostomium. First or tentacular segment distinct dorsally; tentaculophores lateral to prostomium, each with 2 aciculae, 2-4 groups of capillary setae and pair of tentacular cirri. Second segment with first pair of elytra and long ventral buccal cirri; biramous parapodia with bundle of notosetae; neurosetae slender, spinous, lanceolate. Acicular neurosetae from segment 3. Dorsal cirri with short cirrophores and short styles on segments lacking elytra; ventral cirri short, subulate. Notopodium from segment 9 wide, flattened, anterodorsal to neuropodium, with notoacicula, internal spinning glands, and small row of delicate notosetae; neuropodium with lower group of neurosetae within anteroventral bract, neurosetae curved, spinous, lanceolate; middle row of stout acicular neurosetae, with or without aristae; upper group of neurosetae, emanating from low anterodorsal bract (hidden by notopodium), of 2 types: a) longer, abruptly tapered to slender spinous tips, long spines subdistally and short spinous rows basally, b) short (hidden by notopodium), bipinnate. Distal border of large muscular pharynx with 13-15 pairs of papillae, middorsal and midventral ones on wide lobulated bases, middorsal one longer than others; 2 pairs of hooked jaws, each with 5-9 lateral teeth.

Remarks. The genus *Acoetes* contains 12 species, one of which is known from California and has been found in the Santa Maria Basin. All of the known species were described by Pettibone (1989) and a key provided.

Acoetes pacifica (Treadwell, 1914)

Figure 4.1

Panthalis pacifica Treadwell, 1914:184, pl. 11, figs. 1-7.—Hartman, 1939:87, pl. 26, figs. 309-312.—Berkeley and Berkeley, 1941:24.—Emerson, 1971:137.—Fauchald, 1972:29; 1977:9.

Acoetes pacifica: Pettibone, 1989:87-91, figs. 63-64 (synonymy).

Material Examined. California, western Santa Barbara Channel, Sta. 73, 98 m (1); Santa Maria Basin, off Point Sal, Sta. R-8, 90 m (1).

Description. A relatively small species, recorded up to 40+ mm long and 10 mm wide for 53+ segments (Pettibone, 1989); Santa Maria Basin specimens smaller, 31 mm long, 7 mm wide, for 62 segments on complete specimen from Sta. R-8. Body broad, dorsoventrally flattened. Anterior few pairs of elytra large, oval, covering dorsum, following ones leaving middorsum uncovered; elytra delicate, thin, more or less pigmented with brown on medial part, with lateral pouch from about segment 9 (Fig. 4.1B). Color in alcohol: flesh.

Prostomium bilobed with pair of rounded ommatophores, without distinct neck (Fig. 4.1A); median antennae with or without papillae on sides of ceratophore; lateral antennae arising ventral to ommatophores, with tips extending beyond ommatophores; posterior pair of eyespots lateral to ceratophore of median antenna; ventral palps long, smooth, tapered, 2-3 times longer than prostomium (Fig. 4.1A). Tentacular segment with bundle of slender setae on inner side, row of globular papillae, and pair of dorsal and ventral tentacular cirri, each longer than median antenna. Distal border of extended pharynx with 13-15 pairs of papillae, middorsal one much longer than others, midventral one longer than others but shorter than middorsal one; 2 pairs of hooked jaws, each with 6-8 lateral teeth.

Second segment with first pair of elytrophores (Fig. 4.1A), ventral buccal cirri longer than following ventral cirri, and biramous parapodia; notopodium small digitiform lobe (Fig. 4.1C) with bundle of long, slender, finely spinous notosetae (Fig. 4.1F); neuropodium with longer presetal acicular lobe, shorter, rounded postsetal lobe, and ventral bract; neurosetae slender spinous capillaries (Fig. 4.1G).

Third segment with first pair of dorsal cirri, each with short cirrophore and style extending beyond setae (Fig. 4.1D); parapodia similar to segment 2 except presetal neuropodial lobe shorter and middle neurosetae stout, acicular, aristate (Fig. 4.1I). Parapodia of segments 4-8 with fewer, shorter notosetae; upper neurosetae similar to anterior parapodia; lower neurosetae slender, with larger spines more basally and close-set spinous rows distally on tapered capillary tips (Fig. 4.1J); middle stout acicular neurosetae with distal hairs on bases of aristae.

Notopodia becoming larger, rounded, flattened from segment 9 with appearance of notoacicula, spinning glands, and few short notosetae (Fig. 4.1E); neuropodium with slightly bilobed presetal acicular lobe, truncate postsetal lobe and distinct anteroventral bract; lower neurosetae numerous, similar to anterior parapodia; middle row of stout acicular neurosetae with distal hairs on bases aristate, some in more posterior parapodia with additional subdistal spines along one side; upper group of neurosetae, emerging from low anteroventral bract, of 2 types: a) long, slender, abruptly tapered to slender tip, with subdistal long hairs and rows of shorter spines more basally (Fig. 4.1Ka); b), short, slender, aristate (Fig. 4.1Kb), hidden by notopodium. Branchiae absent. Pygidium with two long, tapering anal cirri.

Biology. Constructs tubes in fine, green muds; recorded from continental shelf depths in California, 90-163m.

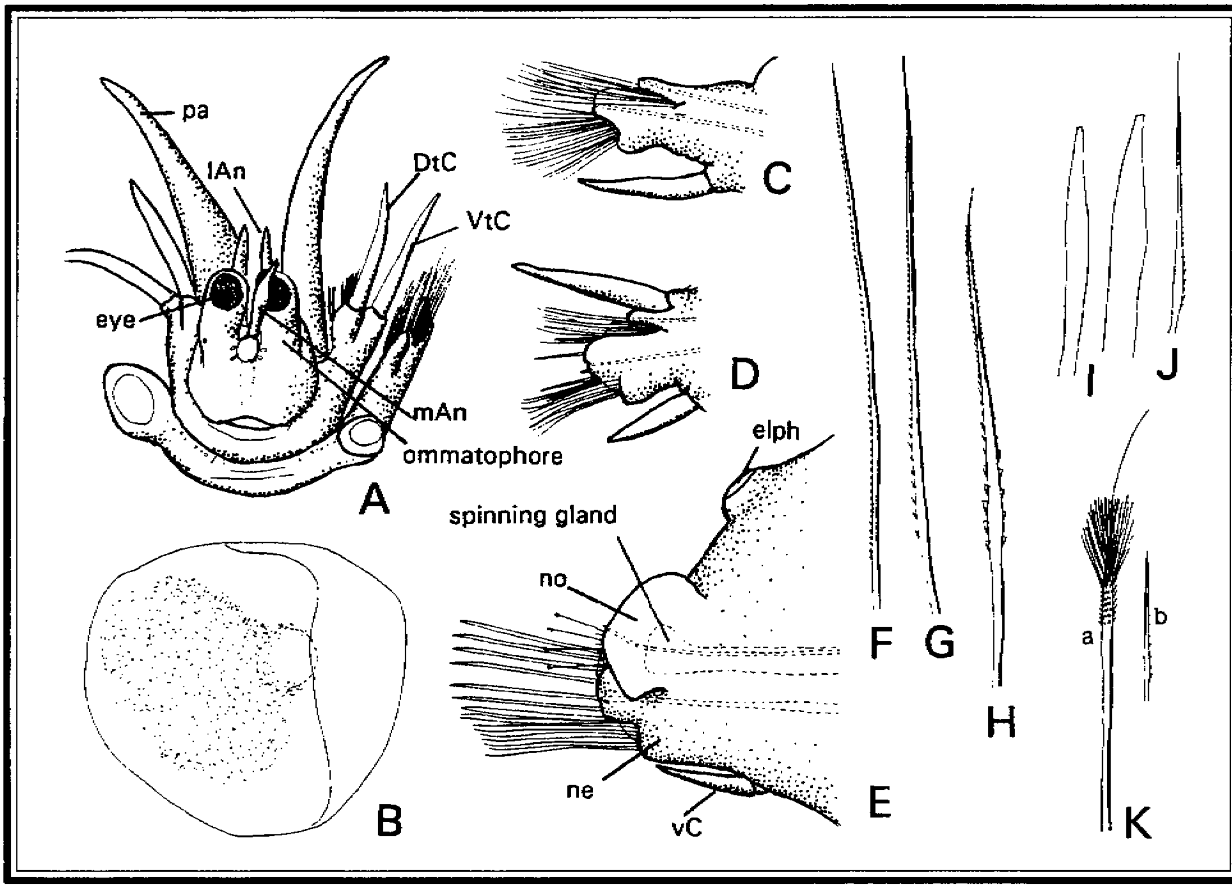

Figure 4.1. *Acoetes pacifica*: Anterior end, dorsal view, left parapodium of segment 2 omitted; B, elytron from segment 25; C, elytragerous parapodium of segment 2, anterior view; D, cirrigerous parapodium of segment 3, anterior view; E, elytragerous parapodium of segment 25, anterior view, acicula and spinning gland dotted; F, notoseta from segment 2; G, neuroseta from segment 2; H, upper neuroseta from segment 3; I, middle neuroseta from segment 3; J, lower neuroseta from segment 3; K, upper neurosetae from segment 9 (types a and b indicated). (after Pettibone, 1989).

Type Locality. California, off San Diego, 91-163 m (holotype, LACM-AHF Poly 52; 2 paratypes AMNH 769, 771).

Remarks. *Acoetes pacifica* differs from *A. mortenseni* from off Panama in having cylindrical ommatophores on the prostomium without distinct necks instead of ones with necks and smooth palps instead of ones which are papillated.

Distribution. Central California to Lower California; Panama; Gulf of Mexico; 10-640 m.

Genus *Polyodontes* Renieri, 1828

Type Species: *Phyllodoce maxillosa* Ranzani, 1817, by monotypy.

Diagnosis. Prostomium bilobed, with pair of large ommatophores on anterior part of prostomium and pair of small eyespots; median antenna with ceratophores in middle of prostomium. First or tentacular segment distinct dorsally; tentaculophores lateral to prostomium, each with 2 aciculae, 2 groups of capillary setae and pair of tentacular cirri. Second segment with first pair of elytra and long ventral buccal cirri; biramous parapodia with bundle of capillary notosetae; neurosetae both stout and slender, spinous, tapering to slender tips. Stout acicular neurosetae, with or without aristae, beginning on segment 3 or more posteriorly. Dorsal cirri on non elytra-bearing segments, with short, subulate cirrophores and short styles; ventral cirri short, subulate. Notopodium from segment 9 wide, flattened, anterodorsal to neuropodium, with notoacicula, internal spinning glands, and small bundle of short capillary notosetae on inner side of notopodium; neuropodium truncate, with lower group of neurosetae within more or less distinct anteroventral bract; middle row of stout acicular neurosetae; upper group of neurosetae, emanating from low anterodorsal bract (hidden by notopodium), of 2 types: a) long, stout, thickly spinous, tapering to fine tips and b) short, slender, tapering to sharp tips, bipinnate. With or without parapodial branchiae. Distal border of large muscular pharynx with 13-19 pairs of papillae, middorsal and midventral ones on wide lobulated bases, longer than others; 2 pairs of hooked jaws, each with 2-10 lateral teeth.

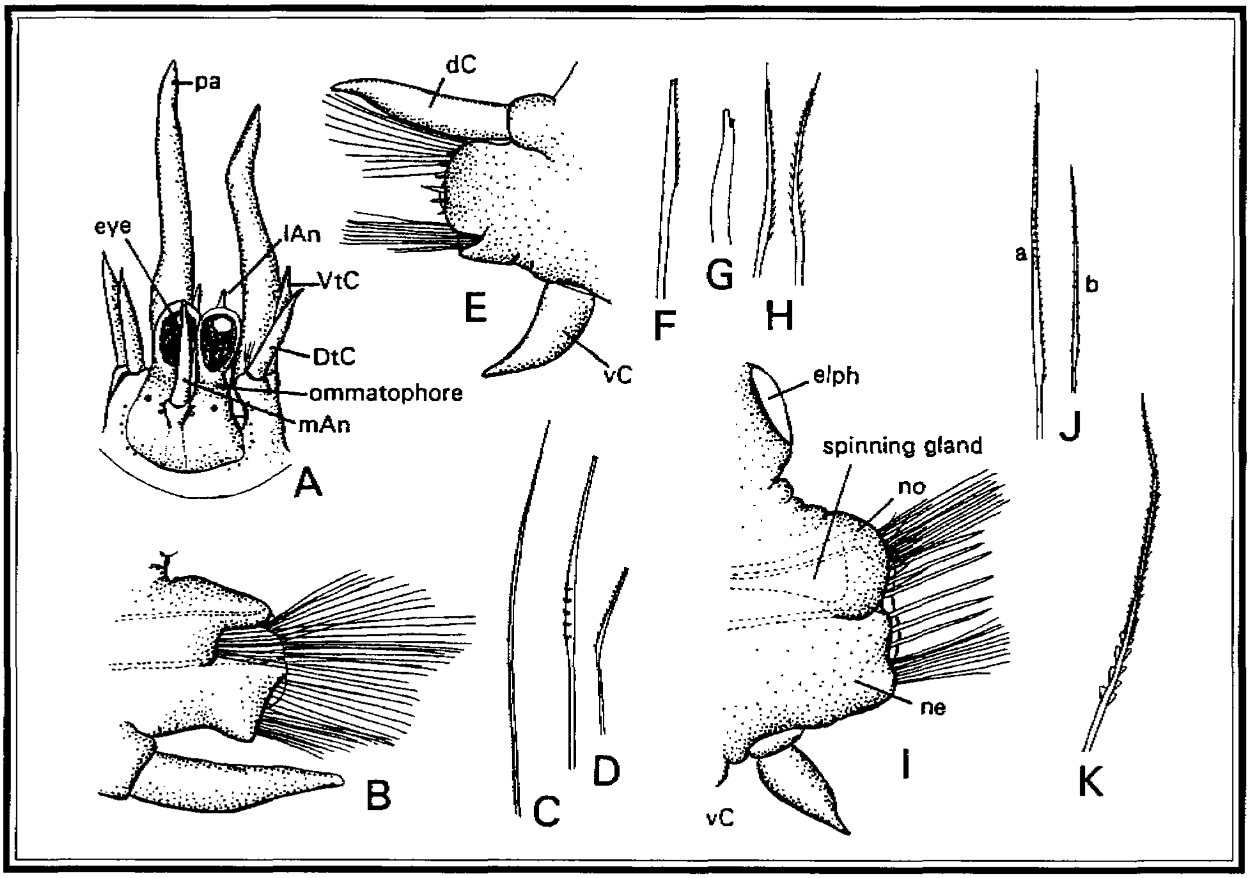

Figure 4.2. *Polyodontes panamensis*: A, anterior end, dorsal view; B, elytragerous parapodium of segment 2, anterior view; C, notoseta from segment 2; D, middle and lower neurosetae from segment 2; E, cirrigerous parapodium of segment 3, posterior view; F-H, upper (F), middle (G), and lower (H) neursetae from segment 3; I, elytragerous parapodium of segment 9, anterior view, aciculae and spinning gland dotted; J-K, upper (J, types a and b indicated) and lower (K) neurosetae from segment 9. (after Pettibone, 1989).

Remarks. The genus *Polyodontes* contains 12 species, two of which have been recorded from California (Pettibone, 1989). *Polyodontes lupinus* (Stimpson), and *P. panamensis* (Chamberlin) have been reported from southern California (Hartman, 1968; Pettibone, 1989). Both species are separated in the key (see above) and detailed descriptions may be found in Pettibone (1989). Figure 4.2 depicts some morphological features of a typical species of *Polyodontes*.

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5. Family Pholoidae Kinberg, 1858

by

James A. Blake[1]

Introduction

The Pholoidae includes small crawling scaleworms that are found in algal holdfasts, under rocks and in crevices among oysters and mussels, and creeping over the surface of muddy sediments littered with shell hash. Some species are interstitial. They are widely distributed and occur from the intertidal zone to great depths.

Morphology

The bodies of pholoids are small, flattened, with 19 to 90 segments. The dorsum may have adhesive tubercles and the ventrum may bear papillae. The prostomium is fused to the first or tentacular segment, and bears a single median antenna, a pair of palps and often two pairs of sessile eyes; two short lateral antennae are present or absent. A facial tubercle is usually present on the dorsal face of the mouth opening. The muscular pharynx is eversible, and has two pairs of interlocking jaws and a circlet of papillae around the opening. The tentaculophores represent the first segment, are lateral and anterior to the prostomium and bear 1-2 pairs of tentacular cirri; setae may be present or absent on the tentacular segment. The elytra are present from segments 2, 4, 5, 7, continuing on alternate segments to segment 23, after which they are present on every segment, or on alternating segments. Elytra are soft and delicate, with surface and marginal papillae; or stiff and rigid with concentric rings, and fringes of marginal papillae; they cover the dorsum or leave the mid-dorsum uncovered. Parapodia are biramous and supported by acicula. Bracts are present, but basal ones are absent in the neuropodia. Notopodia are smaller than neuropodia. Notosetae are finely spinous capillaries, and neurosetae are compound falcigers with short blades. Dorsal cirri and branchiae are completely absent, but prominent, knoblike dorsal tubercles are present on segments lacking elytra. Ventral cirri are short and tapered. The pygidium is small, and bears two anal cirri. The aberrant interstitial genus *Metaxypsamma* Wolf, 1986, has uniramous parapodia with a single neuroacicula, and papillated nodular lobes instead of elytra (Pettibone, 1992).

Taxonomic History

The species of Pholoidae have been included in the Sigalionidae, Acoetidae, and Polyodontidae by various authors. Hartman (1959; 1968) placed *Peisidice* Johnson, 1895 in the Polyodontidae and *Pholoe* Johnston, 1839 in the Sigalionidae. She also included *Pholoides* Pruvot, 1895 as a synonym of *Pholoe*. The family Peisidicidae was established by Darboux (1900) for *Peisidice* but was largely ignored until resurrected by Hartman and Fauchald (1971). Fauchald (1977) established the family Pholoididae, based upon *Pholoides* Pruvot as a new name for Peisidicidae. Fauchald included *Parapholoe* Hartmann-Schröder, 1965 in this family, but placed *Pholoe* in the Sigalionidae.

[1] ENSR Consulting and Engineering, 89 Water Street, Woods Hole, Massachusetts 02543

Pettibone (1982) resurrected the family Pholoidae Kinberg, 1858[2] in which she included *Pholoe* and *Pholoides* (including *Peisidice*). In a recent monograph, Pettibone (1992) synonymized *Paraeupholoe* Hartmann-Schröder, 1962 and *Parapholoe* Hartmann-Schröder, 1965 with *Pholoides* Pruvot and added *Metaxypsamma* Wolf, 1986, and three new genera to the Pholoidae. In this same work, she provided a definition of the family Pholoidae, keys to the genera, and complete accounts of the species in all genera except *Pholoe* within which, two species were treated. No review of the species of *Pholoe* has been published.

The Pholoidae are separated from the Sigalionidae by the characters listed in Table 5.1. The key separates the two genera *Pholoe* and *Pholoides* which occur in California and Santa Maria Basin. A review and partial revision of the genus *Pholoe* is in preparation by M. E. Petersen, personal communition).

Table 5.1. Comparative Characteristics of the Families Pholoidae and Sigalionidae (after Pettibone, 1992).

Characteristic/Family	Pholoidae	Sigalionidae
Body	Short, subrectangular, with segments few to moderate (<90); crawling forms	Long, narrow, slender, with segments numerous (>300); burrowing forms
Branchiae	Absent	Present, attached to lateral sides of elytrophores and dorsal tubercles
Tentaculophores of segment I	Medial to palps	Dorsal to palps
Neuropodia	Without basal bracts and distal stylodes	With basal bracts (absent in Sigalion) and/or distal stylodes
Compound neurosetae	Blades short, falcate	Blades short and long, multi-articulated, falcigers or spinigers

[2] Family Pholoidae Kinberg, 1858. Type genus: *Pholoe* Johnston, 1839. Original spelling: Pholoidea, corrected by Pettibone 1982.

Biology

Pholoids have a proboscis equipped with four jaws, suggesting that they are carnivorous (Fauchald and Jumars, 1979). Direct evidence for a carnivorous feeding mode has been provided by Pleijel (1983), who described feeding habits of *Pholoe minuta* (Fabricius) from the west coast of Sweden. Pleijel was able to make observations on living animals in an aquarium and also examined gut contents and feces. He found the most common prey organism to be sedentary polychaetes and small crustaceans. *P. minuta* encounters prey items as they move through the sediment. The worm then attacks by rapidly everting its armed proboscis. An important prey species was the spionid *Prionospio*, which was either eaten whole or in part. Heffernan (1988) described the fine structure of the digestive system of *P. minuta*, including histochemistry of secretory cells associated with the proboscis and jaws. The digestive tract of *P. minuta* is composed of an anterior foregut or oesophagus (mouth to segment 6), a muscular pharynx (6 to 16th segment), and the intestine which continues to the anus. During feeding, the pharynx is everted and overlain with the oesophagus. Mucoid secretions produced by the oesophagus probably serve to lubricate the pharynx during eversion and inversion and its tough cuticular surface is a protection against abrasion by the sediment particles in which the worm lives (Heffernan, 1988). Secretions in the pharynx assist in movement of the prey along the digestive tract.

Aspects of the life history of *Pholoe* spp. are provided by Christie (1982), Heffernan *et al.* (1983), Heffernan (1985), and Heffernan and Keegan (1988a-b). Christie (1982) dealt with two species: *P. minuta* and *P. pallida* Chambers, 1985 (as *P.* cf. *anoculata* Hartman) from England, while the various studies conducted by Heffernan dealt with *P. minuta* from Galway Bay, Ireland. *Pholoe minuta* has been found to be a polytelic species, that reaches sexual maturity by the third year, then annually spawning two or three times (Heffernan and Keegan, 1988a). The worms live at least four years. Christie (1982) found both *P. minuta* and *P. pallida* to retain their gametocytes in the gonads until maturity. Gametogenesis was well synchronized and followed by a restricted breeding season. Christie found that the two species differed in the size of the gametes, time of spawning, and the type of larval development. Small eggs (120-150 µm) were produced by *P. minuta* in April that developed into planktotrophic larvae. In contrast, *P. pallida* produced large, yolky eggs (180-200 µm in diameter) in November that developed into lecithotrophic larvae. Males of *P. minuta* produced small-headed, primitive sperm, whereas males of *P. pallida* produced long-headed aberrant sperm. Primitive sperm are associated with a dispersal type of spawning mechanism and normally planktotrophic larvae, while aberrant sperm are associated with some form of brood protection and non-planktotrophic development (Franzén, 1956). Spawning times for *P. minuta* in Ireland (March-April) reported by Heffernan and Keegan (1988a) agreed with the observations by Christie (1982) in England. Lacalli (1980, 1981) found pelagic larvae of *P. minuta* in May-June in New Brunswick, Canada. Curtis (1977) reported that spawning of *P. minuta* occurred in March-April in west Greenland and suggested that the larvae were lecithotrophic.

Pholoe anoculata Hartman, 1965 was determined to be a dominant infaunal species in Atlantic continental slope depths from the Canadian border to off North Carolina (Blake, 1993). The species was found to reproduce year round, but sexually mature specimens were only encountered in upper slope (600-1000 m) sediments, while specimens from depths of 2000 m or greater were not gravid. These results suggested that recruitment to the lower slope depths was by larvae that came from shallower depths.

Actual observation on the morphology of embryos and larvae of pholoids is limited to *Pholoe minuta* (Åkesson, 1963; Sveshnikov,1967; Lacalli, 1980; Heffernan and Keegan, 1988b), *Pholoe synophthalmica* (Cazaux, 1968), *Pholoides asperus* (Blake, 1975a as *Pholoe minuta*), and for several of the smaller interstitial species (Laubier, 1975; Wolf, 1986; Pettibone, 1992). Four patterns are apparent: (1) species with small eggs and planktotrophic larvae; (2) species with large eggs and lecithotrophic larvae; (3) species with large eggs, special forms of brooding under the elytra with direct development; and (4) species with large eggs and viviparity. Pelagic larvae of pholoids pass through trochophore, metatrochophore, and nectochaete stages similar to those of the Polynoidae and Sigalionidae. Species with direct development or viviparity do not exhibit any of the traditional morphology associated with pelagic larvae.

Key to the Genera and Species of Pholoidae

1A. Prostomium oval, bilobed, with median antenna on ceratophore in anterior notch (Fig. 5.1A, 5.2A); with or without lateral antennae; tentaculophores achaetous, with dorsal and ventral tentacular cirri; elytra on segments 2, 4, 5, 7, and continuing on alternate segments to segment 23, then on every segment to end of body; elytra delicate, with border and surface papillae (Fig. 5.1C-D, 5.2D-E) .... Genus *Pholoe* 2

1B. Prostomium subrectangular, with median antenna on ceratophore on anterior border; without lateral antennae (Fig. 5.3B); tentaculophores with notosetae and single tentacular cirrus; elytra on segments 2, 4, 5, 7, and continuing on alternate segments to end of body; elytra thick, with concentric rings and numerous long border papillae (Fig. 5.3B, G) .... Genus *Pholoides*

2A. Eyes present; median antenna and dorsal and ventral tentacular cirri short, with pseudoarticulated tips (Fig. 5.1A); papillae on elytra with weak folds or joints, not expanded attip, more or less of the same length on elytra throughout body (Fig. 5.1D,E) .... *Pholoe glabra*

2B. Eyes absent; median antenna and dorsal and ventral tentacular cirri long, with thin tapering tips (Fig. 5.2A); papillae on elytra simple, with weakly expanded tip, short on anterior elytra, becoming very long on middle and posterior elytra (Fig. 5.2E) .... *Pholoe courtneyae*

Descriptions of Species

Genus *Pholoe* Johnston, 1839

Type Species: *Pholoe inornata* Johnston, 1839.

Diagnosis. Body small, linear, up to 90 segments. Elytra on segments 2, 4, 5, 7, and continuing on alternate segments to 23, then on every segment to end of body. Elytra delicate, with papillae on border and surface. Prostomium and first tentacular segment fused, ventrally forming anterior lip of mouth, with projecting facial tubercle; or facial tubercle lacking. Prostomium rounded, bilobed, with median antenna on ceratophore in anterior notch, with or without lateral antennae; eyes present or absent, sometimes fused. Parapodia biramous; notopodial lobe conical, acicular, with subdistal bract on dorsal face; neuropodial lobe larger, conical, acicular, sometimes with distal papillae. Notosetae simple, slender, capillary, finely spinose, of 2 types: shorter, strongly bent or geniculate, and longer, slightly curved or straight. Neurosetae stouter than notosetae, compound, with shafts spinose subdistally and blades short, spinose, falcate, and unidentate. Pygidium with pair of anal cirri.

Remarks. *Pholoe glabra* appears to be the most common species in California (see below). *Pholoe minuta* (Fabricius) is a widespread species and may be present in California estuaries and other nearshore habitats, but it has not been encountered in this study. Several species appear to have been confused with *P. minuta* in the North American literature and a review of these records is needed. Pettibone's (1953) description of *P. minuta* from the Puget Sound appears to be of *P. glabra*.

Specimens of a deep-water species of *Pholoe* have been encountered in the MMS collections as well as in samples taken from the continental slope off northern California. The species is identified as *Pholoe courtneyae*, new species.

Pholoe glabra Hartman, 1961

Figure 5.1

Pholoe glabra Hartman, 1961:51-54, pl. 2, figs. 1-8.—1968:157, figs. 1-6.—Blake, 1975b:172, 176-177, fig. 82.

Material Examined. California, Santa Maria Basin, off Port San Luis, Sta. 21, 49 m (41); off Point Sal, Stas. PJ-1, 145 m, (21); PJ-2, 142 m, (25+); PJ-3, 138 m, (25+); PJ-4, 150 m (25+); PJ-5, 152 m (8); PJ-6, 148 m, (40+); PJ-7, 123 m, (100+); R-8, 90 m (40+); Sta. 103, 197 m (1).

Description. Body small, linear, depressed, with about 38 segments; 10-15 mm long, 2 mm wide. Middorsum completely covered by overlapping elytra. Elytra oval anteriorly (Fig. 5.1C), becoming subquadrate posteriorly (Fig. 5.1D); each elytron with short marginal papillae; papillae simple, slender with narrow folds or articles, several small sensory hairs on tip. Color: white with rust-colored dorsum.

Prostomium with 2 anterior triangular-shaped lobes, separated by a deep notch (Fig. 5.1A); with 2 pairs of small, closely set, black eyes; median antenna short, thick, tapering distally, with 3-4 pseudoarticulated joints; palps massive, tapering. Facial tubercle short, triangular. Proboscis with 18 terminal papillae and 2 pairs of dark jaws. Two pairs of thick tentacular cirri, similar in appearance to median antenna, with pseudoarticulations.

Notopodium small, distally rounded; neuropodium large, distally pointed, with small surficial papillae; ventral cirrus thin, fingerlike (Fig. 5.1B). Both podial lobes bearing stout aciculae and dense fascicles of setae; notosetae simple, with 6-12 serrated, geniculate setae in supra-acicular position (Fig. 5.1E) and 5-12 long, smooth capillaries in sub-acicular position. Neurosetae all compound falcigers, with short blade and fine serrations on base of blade and tip of shaft (Fig. 5.1F). Pygidium with pair of long, cirriform anal cirri.

Biology. This small carnivorous species is widespread and abundant from central California to Mexico in continental shelf and slope depths in sediments of olive green silt. In the Phase II monitoring program the species was one of more abundant polychaete species, with densities of 154 and 259 individuals m^{-2} at stations R-5 and PJ-1, respectively.

As part of a life history study that was based on specimens from the MMS Phase II Santa Maria Basin samples, Kropp and Carroll (1990) found gravid females during all seasons except July and October 1987. Males exhibited a similar pattern. No data were presented on egg diameter, precluding an assessment of reproductive maturity in the population. One specimen collected at PJ-1 during May 1987 had both eggs and sperm. Recruitment apparently occurred at station PJ-1 during October of 1986 and 1987 and again in January 1988.

Remarks. *Pholoe glabra* is characterized by having a short, triangular facial tubercle, short elytral papillae that have several folds or articles, pseudoarticulated joints on the tips of the median antenna and the dorsal and ventral tentacular cirri, and very few papillae on the surface of the body. Further, the serrations on the blades of the compound setae are very distinct; in related species these are either absent or very difficult to discern.

Distribution. California, intertidal beaches; subtidal on the continental shelf and upper slope, to approximately 300 m.

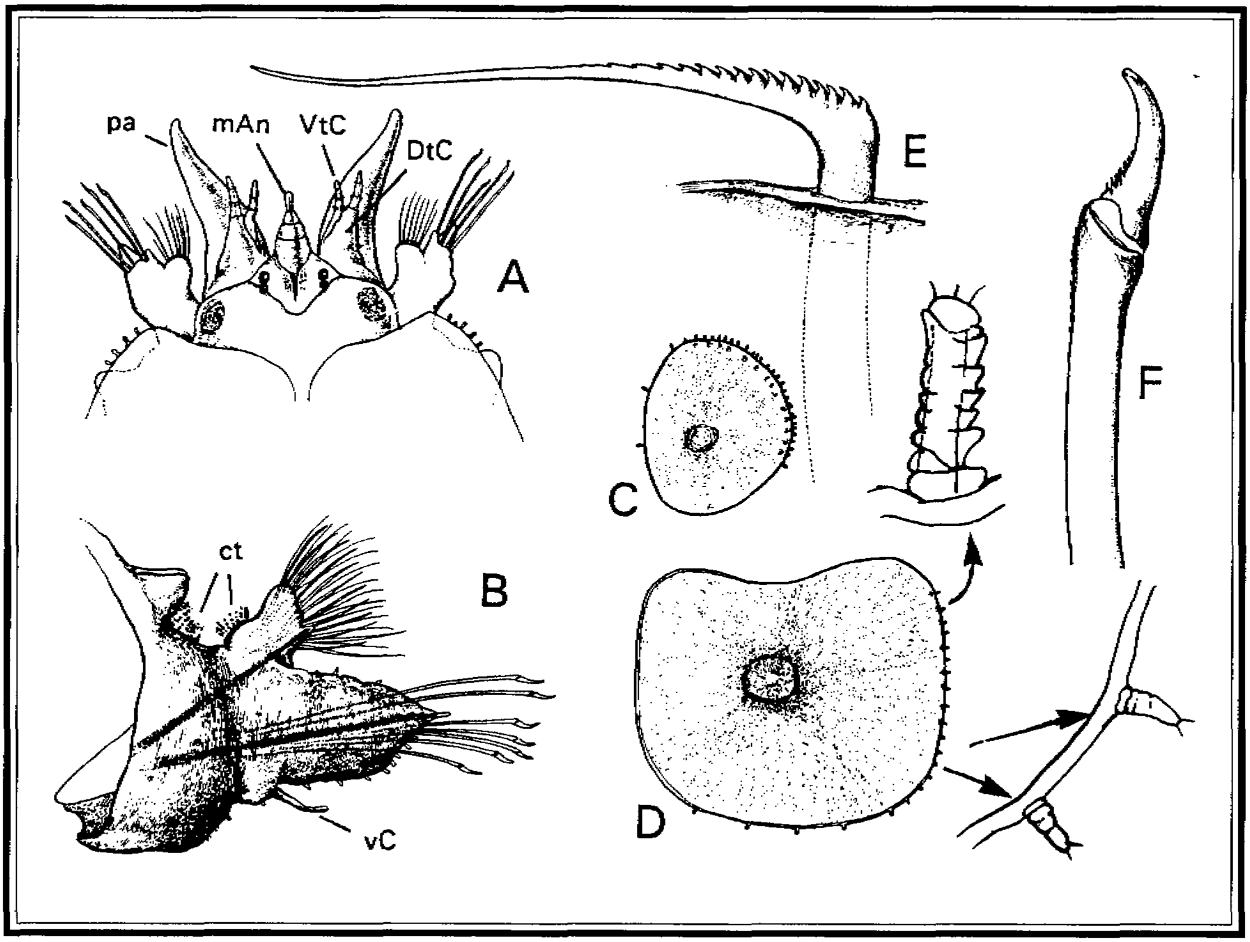

Figure 5.1. *Pholoe glabra*: A, anterior end, dorsal view; B, middle parapodium, anterior view; C, first elytron; D, middle elytron, with insets showing details of marginal papillae; E, superior notopodial seta; F, neuropodial compound falciger. (all except insets after Hartman, 1961)

Pholoe courtneyae Blake, new species

Figure 5.2

Material Examined. California, off San Francisco, Gulf of the Farallones, continental slope stations sampled as part of U.S. EPA 102-Site Disposal Designation Survey, R/V *Point Sur*, J.A. Blake, Chief Scientist: Sta. 3-1, 37°23.82'N, 123°15.55'W, 1338 m, 12 Sep 1991, 7 paratypes (USNM 169972); Sta. 3-4, 37°27.83'N, 123°11.60'W, 1040 m, 14 Sep 1991, 2 juveniles; Sta. 3-5, 37°27.39'N, 123°14.42'W, 1195 m, 14 Sep 1991, 3 paratypes (USNM 169973); Sta. 3-11, 37°25.50'N, 123°15.02'W, 1225 m, 15 Sep 1991, 1 juvenile; Sta. 3-14, 37°23.51'N, 123°21.02'W, 1880 m, 15 Sep 1991, holotype (CASIZ 103568); Sta. 3-15, 37°24.71'N, 123°12.16'W, 1010 m, 15 Sep 1991, 4 paratypes (CASIZ 103569) on slides Sta. 3-16, 37°23.20'N, 123°14.44'W, 1220 m, 15 Sep 1991, 5 small paratypes (LACM-AHF Poly 1718) Sta. 4-2, 37°15.29'N, 123°07.13'W, 995 m, 18 Sep 1991, 1 juvenile; Sta. 4-3, 37°15.13'N, 123°10.83'W, 1222 m, 18 Sep 1991, 1 specimen (JAB); Sta. 4-4, 37°16.13'N, 123°14.18'W, 1427 m, 18 Sep 1991 paratype (LACM-AHF Poly 1719); Sta. 4-8, 37°13.38'N, 123°10.46'W, 1235 m, 18 Sep 1991, 2 juveniles; Sta. C-2, 37°20.81'N, 123°02.32'W, 1025 m, 19 Sep 1991, 1 juvenile.—Santa Maria Basin, off Point Arguello, Sta. 56, 900 m (3); Sta. 63, 930 m (2).

Description. Body small, linear, depressed; holotype 7.2 mm long, 1 mm wide, with 52 setigers, other specimens up to 6 mm long, 1.2 mm wide, 42 setigers; most specimens juveniles. Dorsum completely covered by overlapping elytra (Fig. 5.2A); elytra translucent, oval anteriorly (Fig. 5.2A, B), becoming subquadrate posteriorly (Fig. 5.2C); each elytron with elongate thin, papillae, both marginal and submarginal on anterior elytra, marginal on posterior elytra; papillae of middle and posterior elytra becoming longer, sometimes up to one-fourth length of elytron; each elytral papilla simple, slender, weakly jointed, with blunt, expanded tip bearing delicate sensory cilia (Fig. 5.2B). Additional papillae on surface of body, surrounding mouth, on ventral surface, and on parapodia; parapodial papillae of several types: most short, nipplelike, but with some parapodial papillae longer, fingerlike; body papillae with terminal sensory cilium (Fig. 5.2D). Color white to light tan.

Prostomium a broadly rounded lobe from which median antenna arises; eyes absent; median antenna short, with thick, pear-shaped ceratophore, continuing distally as tapering filament; minute lateral antennae present on either side of median ceratophore (Fig. 5.2A). Palps thickened basally, directed anteriorly, tapering, more or less smooth; distal ends with sensory cilia. Facial tubercle thin, filamentous. Proboscis with 16 terminal papillae, 2-4 lateral papillae, and 2 pairs of dark jaws. Tentaculophores with dorsal and ventral tentacular cirri; dorsal tentacular cirri expanded basally, tapering to long, narrow, blunt-tipped filament, sometimes with 1 or 2 weakly developed joints; ventral tentacular cirri shorter than dorsal ones, similar in appearance, with 1-2 notches or joints.

Segment 2 (or buccal segment) first setigerous, with large ventral cirri (buccal cirri) displaced medially, broadly rounded basally, tapering apically bearing first pair of elytra. Notopodium of segment 2 and subsequent segments small, elongate, basally enlarged, distally pointed (Fig. 5.2D). Neuropodium elongate, distally pointed, with small surficial papillae continuing onto mid-ventrum of body; ventral cirrus from segment 3 long, thin, tapering with 1-2 joints or notches along length. Both podial lobes bearing thick aciculae and fascicles of setae; notosetae simple, of 3 types: (1) anterior row of about 20 short, serrated, geniculate setae beginning on posterior side of notopodium, continuing to anterior side (Fig. 5.2E); (2) about 5-8 long, thin serrated setae on either side of shorter ones (Fig. 5.2F); and (3) about 15 longer, thin, non-serrated capillaries alternating with serrated ones. Neurosetae 5-6 compound falcigers, with inconspicuous knobby denticles on blades and few fine hairlike spinelets on tip of shaft, only visible with 1000x optics, otherwise blades and shaft ending appearing smooth (Fig. 5.2G). Pygidium with pair of long, filamentous anal cirri.

Remarks. The anoculate *Pholoe courtneyae* was at first confused with *P. anoculata* Hartman, 1965 from the U.S. Atlantic continental slope. This latter species is poorly known and both the original description by Hartman (1965) and the supplementary one by Hartman and Fauchald (1971) were brief and incomplete. Types were never designated and the only figures of the species were of an elytron and two falcigers from one of the two specimens from Station Sl-4 (Hartman and Fauchald, 1971:plate 2, figs. f-h) that were cited among the original material examined by Hartman (1965). As part of the Atlantic Continental Slope and Rise Program (ACSAR) (1983-1987) numerous specimens were identified that were referred to *P. anoculata*. The species was one of the most abundant encountered from the Canadian Boundary to off the Carolinas and proved to be an important component of the slope assemblages (Blake, 1993, 1994; Blake and Grassle, 1994).

Initial comparisons of the California *Pholoe* specimens demonstrated that they were very similar to the Atlantic specimens. However, because of the inadequate nature of the published descriptions of *P. anoculata*, it was necessary to establish a morphological baseline for the Atlantic specimens in order to more carefully compare them with the California specimens. The extensive ACSAR collections were available as well as a syntype specimen of *P. minuta anoculata* obtained from the LACM (LACM-AHF 0069)[3]. When these Atlantic materials were carefully studied and then compared with California specimens from the Santa Maria Basin and off the Farallones, it became obvious that two separate, yet closely related species were involved.

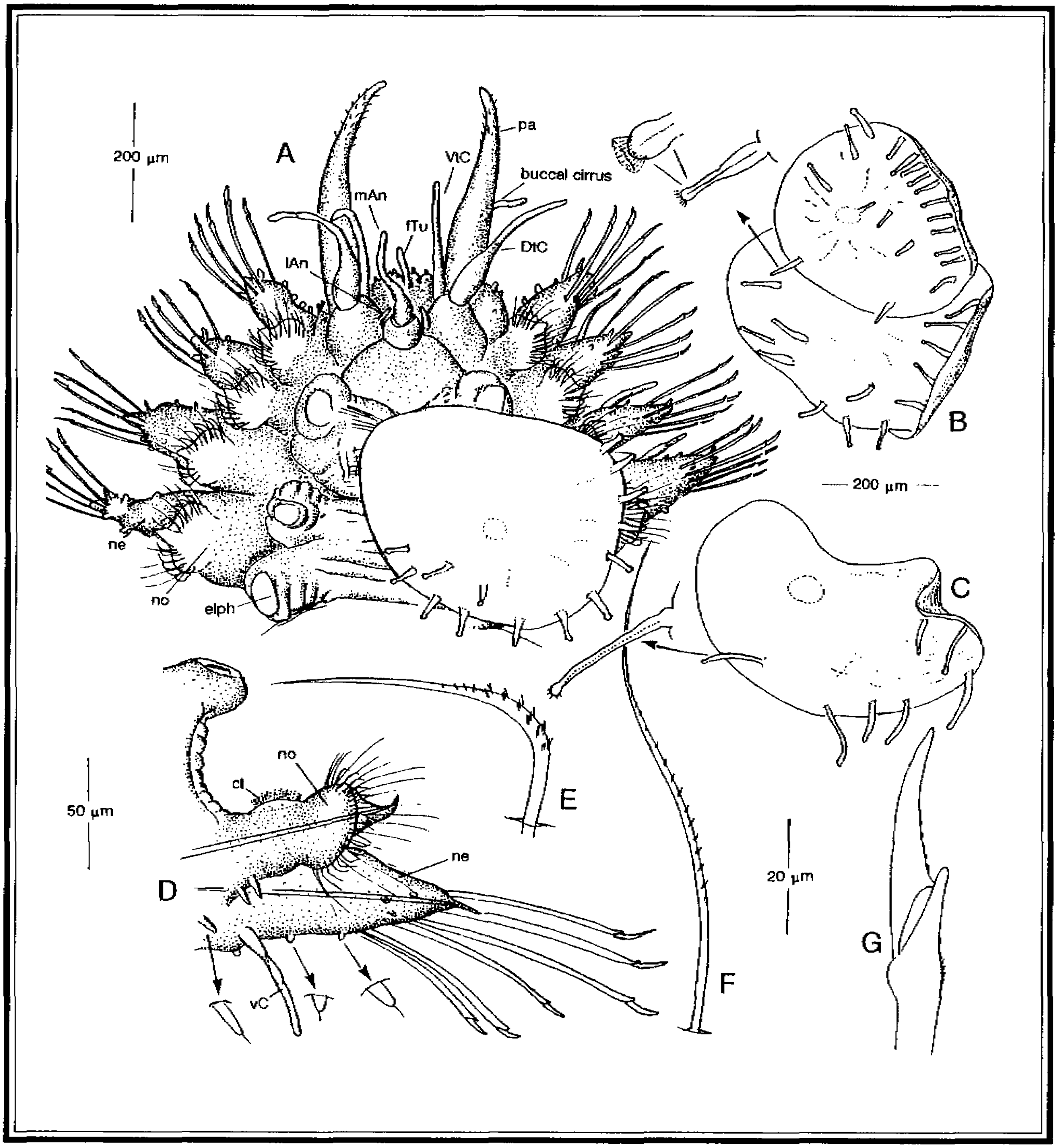

Figure 5.2. *Pholoe courtneyae* (Paratypes, Sta. 3-15, CASIZ 103569): A, anterior end, dorsal view, with only second elytron included for clarity; B, first and second elytra from right side of another paratype, with insets showing details of elytral papillae [not to scale]; C, elytron from a posterior segment; D, parapodium from setiger 10 in posterior view, with insets of different parapodial papillae [not to scale]; E, short geniculate serrated notoseta; F, long, thin serrated notoseta; G, neuropodial falciger from middle of series.

A full redescription of *Pholoe anoculata* will be published elsewhere. *Pholoe courtneyae* differs from *P. anoculata* in being larger, 7+ mm long instead of 2-3 mm long, in having relatively smooth tentacular cirri instead of ones that are knobby (especially the ventral tentacular cirri), in having elytra with papillae that are relatively smooth along their edges instead of with minute constrictions, in having smooth, forwardly directed palps instead of palps with constrictions and that are directed laterally. Furthermore, the blades and shaft endings of the neuropodial falcigers of *P. courtneyae* bear inconspicuous denticles and spinelets visible only under oil immersion, instead of larger, more conspicuous denticles and spines.

Evaluation of the collections from the Farallones has revealed the existence of two additional anoculate species of *Pholoe*. One comes from middle and lower slope depths of 1800 - 3060 m. This species is small, less than 4 mm long and very similar to Atlantic specimens of *P. anoculata*. The second species is from middle slope depths (1338-2005 m). It is large, up to 12 mm long, and differs from both *P. courtneyae* and the small California *P. anoculata*-like species in having elytral papillae that are consistently short along the entire body instead of becoming longer in posterior setigers. Both of these species will be treated in the above mentioned review of *P. anoculata*.

Etymology. *Pholoe courtneyae* is named for Dr. Catherine A. (Kitty) Courtney, Project Manager and oceanographer for several of the Farallones site selection surveys. Dr. Courtney was instrumental in assuring my participation in these deep-sea surveys of important benthic communities. She provided constant encouragement and assistance throughout the course of the program.

Biology. *Pholoe courtneyae* has only been rarely encountered in slope sediments of the eastern Pacific, probably owing to its small size and the fact that so few samples have been processed through 300 μm sieves. The species is likely an omnivore and probably similar in habitat preferences to its close relative *P. anoculata* from the Atlantic slope. Blake (1994) determined that more than 80% of the specimens of *P. anoculata* from off Cape Lookout, North Carolina occur in the upper 2 cm of the sediment.

Distribution. California continental slope, in middle slope depths, 900 - 1880 m.

Genus *Pholoides* Pruvot, 1895

Pholoides Pruvot, 1895. **Type species**: *Pholoe dorsipapillata* Marenzeller, 1893.
Peisidice Johnson, 1897. **Type species**: *Peisidice aspera* Johnson, 1897. *Fide* Pettibone, 1982.
Paraeupholoe Hartmann-Schröder, 1962. **Type species**: *Pareupholoe fimbriata* Johnson, 1897. *Fide* Pettibone, 1992.
Parapholoe Hartmann-Schröder, 1965. **Type species**: *Parapholoe tuberculata* Hartmann-Schröder, 1965. *Fide* Pettibone, 1992.

Diagnosis. Body small, linear, up to 48 segments. Middorsum not covered by elytra. Elytra on segments 2, 4, 5, 7, continuing on alternate segments to end of body; thick, subrectangular, with concentric rings and numerous, long border papillae and scattered tubercles. Prostomium and first or tentacular segment fused, ventrally forming anterior lip of mouth, without facial tubercle. Prostomium subrectangular, median

[3] The type specimen of *Pholoe minuta anoculata* Hartman, 1965 (LACM-AHF Poly 0069) that was sent to me for examination came from Sta. S1-4 (Hartman, 1965), and was labeled a paratype. I am informed that the second specimen from that station is labeled a holotype (LACM-AHF Poly 0068). However, a holotype was not designated by Hartman (1965), nor indicated subsequently by Hartman and Fauchald (1971). According to the International Code of Zoological Nomenclature (ICZN, 1985), these specimens are syntypes until a lectotype is designated. A holotype can only be designated by the original author. Consequently, the specimen I was sent must be termed a syntype not a paratype. I am unwilling to designate this specimen as a lectotype until the second specimen has been examined and confirmed as the same species. There is evidence that a second cryptic species is present among the samples examined by Hartman (1965) (M.E. Petersen, unpublished), lending further reason to be cautious in designating a lectotype.

antenna with ceratophore on anterior border, with style enlarged and papillate subdistally; lateral antennae absent; 2 pairs of eyes. Tentaculophores with notosetae and single pair of tentacular cirri similar to median antenna. Parapodia biramous, notopodium rounded, subconical; neuropodium larger, subconical. Notosetae simple, slender, capillary, finely spinose. Neurosetae stouter than notosetae, compound, with shafts smooth or spinose subdistally and blades short, falcate, smooth or faintly spinose. Ventral cirri short, subulate, papillate. Pygidium with pair of anal cirri.

Remarks. The genus *Pholoides* Pruvot, 1895 has priority over *Peisidice* Johnson, 1897. Pettibone (1992) referred the monotypic genera *Paraeupholoe* Hartmann-Schröder and *Parapholoe* Hartmann-Schröder to synonymy with *Pholoides* after examining the holotypes of their type species.

Pholoides asperus (Johnson, 1897)

Figure 5.3

Peisidice aspera Johnson, 1897:184, pl. 9, figs. 56-59, pl. 10, fig. 63.—Moore, 1908: 338; 1910: 386.—Berkeley and Berkeley, 1941:24; 1942:189; 1948:23, fig. 28.—Hartman, 1939:7; 1948:14; 1968:147, figs. 1-3.—Lie, 1968:286.—Hartmann-Schröder, 1977:81, figs. 17-18.

Paraeupholoe fimbriata Hartmann-Schröder, 1962:110, pl. 1, figs. 5, 11, pl. 2, figs. 6-7, 10, pl. 3 (figs. 8-9, 12. *Fide* Pettibone, 1992.

Parapholoe tuberculata Hartmann-Schröder, 1965, figs. 41-47. *Fide* Pettibone, 1992.

Peisidice tuberculata: Hartman and Fauchald, 1971:29.—Hartmann-Schröder, 1977:81. *Fide* Pettibone, 1992.

Pholoe minuta: Blake, 1975a:30, figs. 3A-B (descriptions of larvae). *Not P. minuta* Fabricius, 1780.

Pholoides aspera: Fauchald, 1977:67, fig. 16A-B.

Pholoides tuberculata: Carrasco and Gallardo, 1983:832.

Pholoides asperus: Pettibone, 1992:18-21, figs. 10-11 (Synonymy).

Material Examined. California, Tomales Bay, with barnacles, 15 m, (4).—Santa Maria Basin, off Point Buchon, Sta. BRA-27, 96-126 m, in rocks (31); off Purisima Point, Sta. R-4, 92 m (3, juveniles); Sta. BRC-13, 92-100 m, in rocks (24).

Description. A small species, recorded up to 11 mm long, 4 mm wide, and 48 segments; more typically, 7-8 mm long, 2-3 mm wide, for about 35 segments. Body elongate, subrectangular in outline, dorsoventrally flattened, elytra not covering dorsum (Fig. 5.3A); dorsum with globular tubercles and sand grains (Fig. 5.3B), ventrum covered with small papillae. Color in alcohol: light brown; sometimes with brown spots on elytra.

Prostomium subrectangular, fused with first tentacular segment; bearing 2 pairs of eyes, posterior pair smallest; median antenna with long ceratophore, with subdistal bulge bearing numerous thin papillae (Fig. 5.3B-C). Tentacular segment with tentaculophores bearing internal acicula, acicular lobe, 2 fascicles of long capillary notosetae, long dorsolateral tentacular cirrus similar in form to median antenna, and additional short tentacular cirrus (or long accessory papilla) present ventrally. Segment 2 with long, ventral cirrus (Fir. 5.3D). Long thick palps present ventrolateral to tentaculophores. Pharynx with 9 pairs of terminal papillae and 4 jaws.

Elytrophores bearing oval to subtriangular elytra first present on segment 2, continuing on segments 4, 5, 7, and on alternate segments to end of body. Each elytron relatively stiff, with concentric rings, thickest on medial side, with numerus long papillae on margins (Fig. 5.3G). Segments without elytra with dorsal tubercles bearing small distal papilla (Fig. 5.3E).

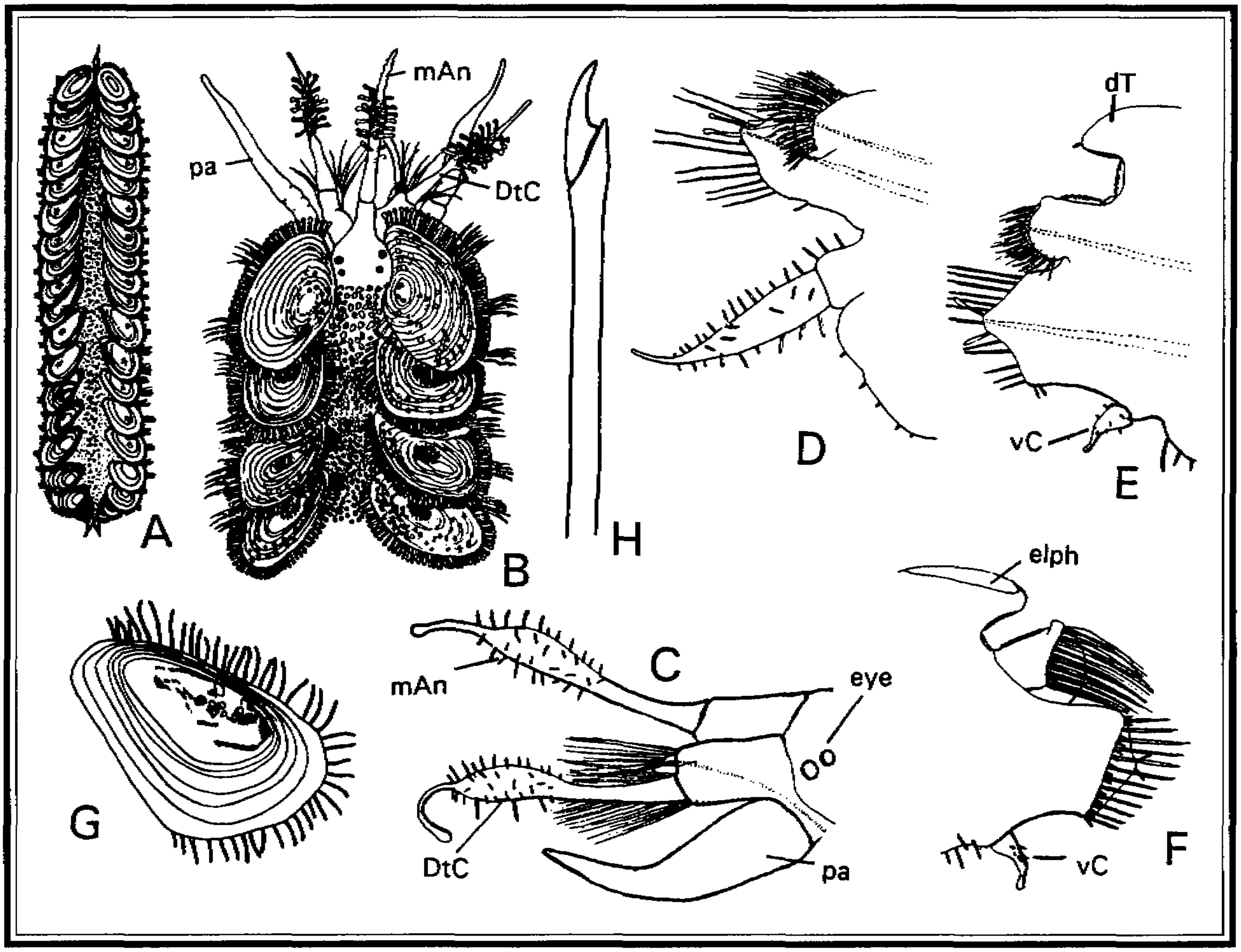

Figure 5.3. *Pholoides aspera*: A, entire animal, dorsal view; B, anterior end, dorsal view; C, dorsolateral view of prostomium and left tentaculophore, acicula dotted; D, parapodium from segment 2, anterior view; E, middle parapodium with dorsal tubercle, anterior view; F, middle elytral bearing parapodium, posterior view; G, elytron; H, neuropodial compound falciger. (A, from Pettibone, 1953; B, from Johnston, 1897; C-H, after Pettibone, 1992)

Parapodia with neuropodium longer than notopodium; notopodium rounded; neuropodium with preacicular lobe bearing 2 long papillae (Fig. 5.3E-F); ventral cirri short, tapering, with short papillae. Notosetae include numerous curved spinous capillaries; neurosetae stout, compound falcigers, with smooth or weakly spinous blades (Fig. 5.3H). Pygidium with 2 anal cirri similar in form to median antenna.

Biology. *Pholoides asperus* is widely distributed in the eastern Pacific, occurring from the low intertidal to about 350 m on rocks, in crevices, and on mixed sediment types. Pelagic larvae were collected and described by Blake (1975a: identified as *Pholoe minuta*). The nectochaete or post-larval stage clearly exhibits the papillated median antennae and tentacular cirri that are characteristic for this species. The rather sluggish nature of these larvae and the yolky appearance of the gut suggested that they were lecithotrophic.

Remarks. *Pholoides asperus* is the only species of this genus in the eastern Pacific. Because of its characteristic shape, size, papillated antenna and tentacular cirri, and form of the elytra, the species is not likely to be confused with any other scaleworm.

Distribution. Eastern Pacific: Alaska to California, Galapagos Islands, Chile; low intertidal to 350 m.

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6. Family Sigalionidae Kinberg, 1856

by

James A. Blake[1]

Introduction

The Sigalionidae includes highly active scaleworms that have a long, narrow bodies, with numerous segments and pairs of elytra. Most species are large, and they are carnivorous polychaetes that are also able to burrow rapidly into sediments. These scaleworms are widely distributed, with many species being relatively common and familiar. Sigalionids occur from the intertidal to the deep sea.

Morphology

The bodies of sigalionids are elongate and narrow, with numerous segments (up to 300). The elytra either cover the dorsum completely, or leave the middorsum uncovered. The dorsum and elytra are sometimes covered with a thick layer of sand grains. The ventral surface of the body may be smooth or thickly papillated. The prostomium is generally small, somewhat oval or pentagonal in shape, and is fused with the first tentacular segment. A pair of long, tapering ventral palps are present and there are usually 3 antennae present. The median antenna is longest and has a distinct ceratophore and sometimes diagnostic auricular lobes or ctenidia are present as well. The lateral antennae tend to be short. The prostomium may have 1 or 2 pairs of eyes, nuchal organs may be present or absent. The first segment is vestigial and bears an acicula, a bundle of notosetae, and dorsal and ventral tentacular cirri. It is called the tentaculophore and is directed forward and lies dorsal to the palps. The tentaculophores form the upper lip of the mouth and may bear a facial tubercle. The second segment is the buccal segment and bears the first pair of elytra, biramous parapodia, and the lateral lips of the mouth; the parapodia bear long ventral buccal cirri that are longer than the ventral cirri of subsequent segments. Segment 3 forms the lower lip. The pharynx is eversible, large, and muscular, with a papillated oral opening and 2 pairs of jaws.

The elytra are attached to knoblike elytrophores on segments 2, 4, 5, and 7, on alternate segments on 24 or 27, and then on every segment. The lateral margins of the elytra may bear papillae and the surface may bear microtubercles. Segments lacking elytra bear knoblike dorsal tubercles and usually lack dorsal cirri. Branchiae are cirriform, heavily ciliated, and attached to the lateral sides of the elytrophores and dorsal tubercles on all segments except a few anterior ones. Ciliated grooves occur along the dorsolateral sides of the body; these grooves contain ciliated ctenidia.

Parapodia are supported by aciculae; notopodia are generally smaller than neuropodia, generally elongate and narrow and bear papillae or stylodes and long, fanlike spreading fascicles of simple capillary setae. Neuropodia are triangular to conical and surrounded by basal bracts[2] with fringes of papillae and distal stylodes. Neurosetae are compound spinigers or falcigers, some of which may be long and multiarticulated. Ventral cirri are narrow and tapering to fine tips; sometimes they bear papillae. The pygidium bears a pair of long anal cirri.

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[1] ENSR Consulting and Engineering, 89 Water Street, Woods Hole, Massachusetts 02543

[2] Pre-and postsetal parapodial lamellae that encompass setae and sometimes bear papillae.

Taxonomic History

Approximately 15 genera of Sigalionidae may be considered as valid according to Fauchald (1977). Major revisions of some of these genera, have been published by Pettibone (1969, 1970a-c, 1971a-b, 1992a) and Mackie and Chambers (1990). Only ten species appear to have been recorded from California. Six species are described in this Atlas.

Major faunistic treatments of sigalionids may be found in Hartman (1939) for the eastern Pacific, Day (1967) for South Africa and Wolf (1984) for the Gulf of Mexico. The genera *Pholoe* and *Pholoides* have been removed from the Sigalionidae and referred to the Pholoidae. Readers are referred to Pettibone (1992b) and Blake (1995, this volume) for a review of pholoid systematics and biology. The main characteristics that differentiate the two families are summarized in Chapter 5, Table 5.1.

Biology

Sigalionids are a group of burrowing carnivores that generally live in sand or mud. They range from the intertidal zone to continental shelf and slope depths. Some species have been recorded from coarse substrates including fine gravel, coarse sand, and associated with coralline algae, shells, and bryozoans (Pettibone, 1970a). Species of *Sthenelanella* are unique among the Sigalionidae in having notopodial spinning glands that produce threads used to construct tough fibrous tubes. Species of the genus *Psammolyce* attach sand grains to their bodies and elytra producing an effective protective covering. Little is known concerning the feeding habits of sigalionids, although they are thought to feed on small invertebrates (Fauchald and Jumars, 1979).

The reproductive biology of sigalionids are poorly known, however, Pettibone (1970a) reports that large specimens of *Euthalenessa oculata* (Peters) have been observed swimming at the surface. Many species have been reported as having large, yolky eggs. Blake (unpublished) has observed planktic larvae of a species of *Sthenelais* in northern California. The trochophore, metatrochophore, nectochaete stages of *Sthenelais boa* were described by Cazaux (1968). It would appear that this species has a short, pelagic phase during its development.

Key to the Genera and Species from California

1A. Lateral antennae located on prostomium; antennae small, without ceratophores (Fig. 6.6A); elytra with bipinnately branched lateral filaments (Fig. 6.6B) .... *Sigalion spinosus*

1B. Lateral antennae, when present, fused to tentacular segment; median antenna with large ceratophore (Fig. 6.3A) 2

2A. Median antenna with basal auricles (Fig. 6.1A) 3

2B. Median antenna without auricles 9

3A. Middle body segments with notopodial spinning glands producing long, threadlike setae extending far beyond parapodia (Fig. 6.5F) .... *Sthenelanella uniformis*

3B. Notopodial spinning glands absent 4

4A. Segment 3 with long dorsal cirri .... Genus *Neoleanira*[3]

4B. Segment 3 without dorsal cirri 5

5A. Neurosetae including at least some falcigers .... Genus *Sthenelais* 6

5B. Neurosetae all spinigers .... Genus *Sthenolepis*[4]

6A. Middle group (C-shaped) of compound neurosetae include stout, short-bladed, bidentate falcigers (Fig. 6.1F); lateral antennae present or absent 7

6B Middle group (C-shaped) of compound neurosetae without short-bladed falcigers; lateral antennae absent .... *Sthenelais verruculosa*

7A. Ventral surface of body and ventral sides of parapodia densely papillated (Fig. 6.2A) .... *Sthenelais berkeleyi*

7B. Ventral surface smooth or with very few, sparse papillae (Fig. 6.2B) 7

8A. Stout compound neurosetae of middle segments numbering 5 or more; first pair of elytra unpigmented, subsequent ones pigmented in various patterns .... *Sthenelais fusca*

8B. Stout compound neurosetae of middle segments numbering only 1-2; all elytra semi-translucent, lacking pigmentation, but may be encrusted with rusty colored sediment particles .... *Sthenelais tertiaglabra*

9A. Dorsal cirri present on segment 3; elytra encrusted with sand .... Genus *Psammolyce*[5]

9B. Dorsal cirri absent on segment 3; elytra not encrusted with sand .... Genus *Leanira*[6]

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[3]*Neoleanira areolata* (McIntosh, 1885) has been recorded from the California continental slope (Pettibone, 1970c). *Leanira calcis* Hartman, 1960 is a synonym.

[4]Two species of *Sthenolepis* were recorded from California by Hartman (1968): *S. areolata* (McIntosh), subsequently referred to *Neoleanira* by Pettibone (1970c) and *S. fimbriarum* (Hartman, 1939). The latter species ranges from southern California to western Mexico from the intertidal to continental shelf depths.

[5]*Psammolyce spinosa* Hartman, 1939 has been recorded from southern California. This species is more widely distributed in shallow subtropical areas of the eastern Pacific (Hartman, 1939; 1968).

[6]*Leanira alba* Moore, 1910 is widespread in continental slope depths from Oregon to southern California (Pettibone, 1970b).

Descriptions of Species

Genus *Sthenelais* Kinberg, 1855

Type Species. *Sthenelais helenae* Kinberg, 1855, by monotypy.

Diagnosis. Body elongate, vermiform, with numerous segments; middorsal ridge on some anterior segments, bordered by few pairs of small ctenidia. Elytra on segments 2, 4, 5, 7, and alternate segments to 27, then continuing on all following segments. Elytra large, covering dorsum, with microtubercles and lateral fringes of papillae. Dorsal tubercles on segments 3, 6, 8, and alternate segments to 26. Prostomium rounded, fused to first or tentacular segment; median antenna with cylindrical ceratophore bearing lateral auricles and terminal style; lateral antennae fused to inner dorsal sides of tentacular parapodia; 4 eyes present; palps emerging ventral to tentacular parapodia; paired oval nuchal organs present. Tentacular parapodia extending anteroventral to prostomium, each with a pair of tentacular cirri, single acicula, 2 bundles of capillary setae, L-shaped inner tentacular lobe with ciliated ridge and fused to inner palpal sheath; ciliated dorsal ctenidium. Parapodia of second or buccal segment extending anteriorly, with ventral buccal cirri longer than those following; small ctenidia on lateral lips and medial to ventral cirri on some anterior segments. Third segment with dorsal tubercles fused to posterior sides of elytrophores of segment 2. Neurosetae of segments 2 and 3 compound falcigers with articulated blades and bifid tips.

Branchiae cirriform, ciliated, on external borders of all elytrophores and dorsal tubercles except for a few anterior ones. Parapodial ctenidia cup-shaped, ciliated, 3 per parapodium, from segment 2. Parapodia with accessory bracts and stylodes. Notopodia clavate, with bracts nearly encircling acicular lobes. Notosetae numerous, arranged in semicircular row and directed posterodorsally, finely spinous, and tapering to capillary tips. Neuropodia with conical acicular lobes; bilobed C-shaped posterior bracts directed anteriorly on upper and lower margins; crescent-shaped anteroventral and anterior upper bracts. Neurosetae arranged in 3 groups: (1) upper group with anterior upper bracts, (2) C-shaped group of stouter neurosetae within posterior bracts, and (3) lower arched group of more slender neurosetae within anteroventral bracts. Neurosetae simple spinous (in upper group) and compound falcigerous with some blades articulated and tips bifid; distal parts of stems smooth and spinous. Ventral cirri subulate, with outer basal knobs. Pharynx with 11 pairs of papillae and 2 pairs of jaws.

Remarks. This diagnosis follows Pettibone (1971a-b). *Sthenelais* can be distinguished by three antennae and well-defined basal auricles, no dorsal cirrus on segment 3, and neurosetae that include simple spinous capillaries and two kinds of falcigers: short, stout ones with bidentate appendages and longer, more slender ones with articulated appendages. *Sthenelais* differs from other eastern Pacific genera by the characters presented in the key. Four species are known from the eastern Pacific, all of which occur in the general vicinity of the Santa Maria Basin.

Sthenelais fusca Johnson, 1897

Figure 6.1

Sthenelais fusca Johnson, 1897:185-186, pl. 9, figs. 60-61, pl. 10, fig. 64.—Monro, 1933:16.—Berkeley and Berkeley, 1935:767; 1941:26.—MacGinitie, 1935:690.—Hartman, 1939:61, pl. 13, figs. 163-162 (in part, not fig. 60, *fide* Pettibone, 1971b).—Pettibone, 1971b:1394-1395, figs. 1-3.—Blake, 1975:177, figs. 83-84. Not Johnson, 1901:397.—Pettibone, 1953:73. (=*S. berkeleyi*, *fide* Pettibone, 1971b).

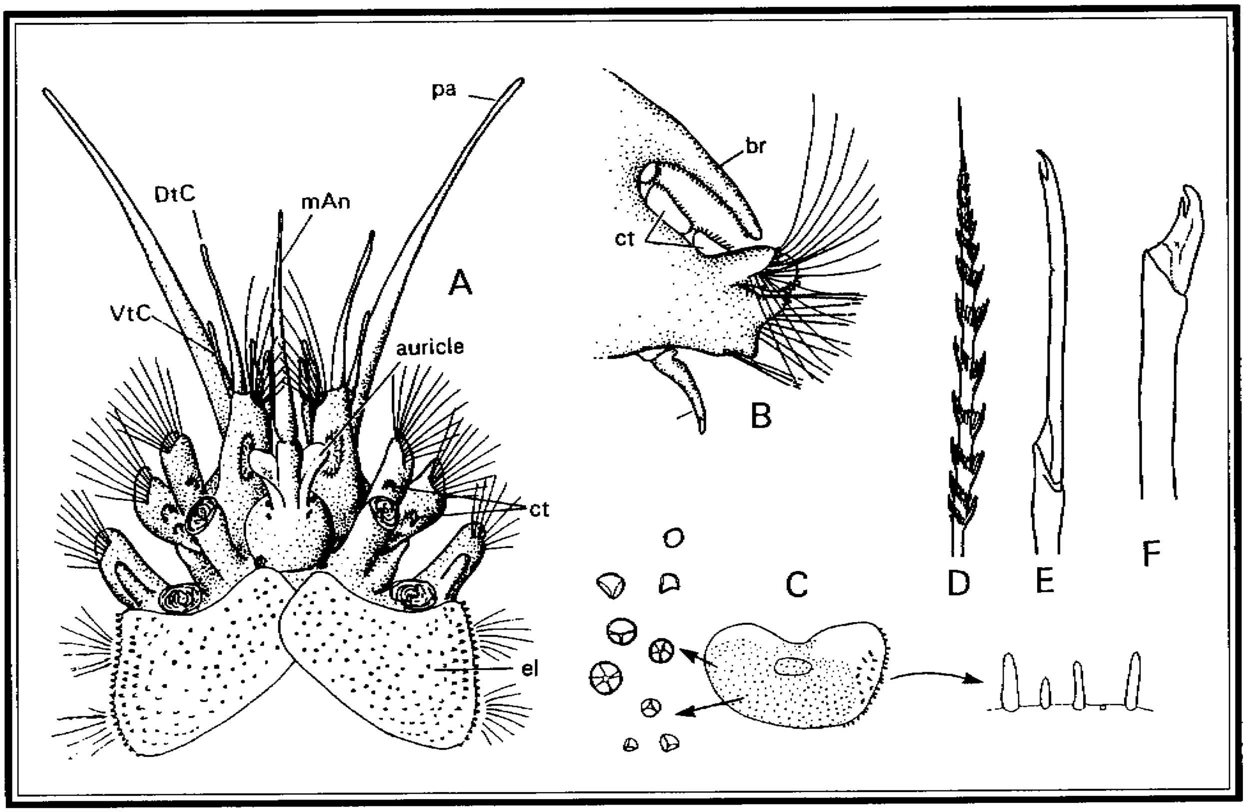

Figure 6.1. *Sthenelais fusca:* A, anterior end, dorsal view; B, anterior parapodium, posterior view; C, elytron with insets showing tubercles and papillae; D, simple neuroseta; E, superior compound neuroseta; F, stout neuropodial falciger. (A, after Blake, 1975; B-C, after Pettibone, 1971b; D-F, after Hartman, 1939)

Material Examined. California, Bodega Harbor, subtidal, coll. Nov. 1975 (2).

Description. A large species, up to 130 mm long, 5-7 mm wide, and about 200 segments. Color in alcohol: pink with elytra elegantly pigmented (see below). Ventral surface smooth. Elytra ellipsoid, concave on anterior margin (Fig. 6.1C); rusty-brown in coloration, with some considerable dark pigment forming reticulated patterns; first pair of elytra relatively unpigmented; with microtubercles uniformly distributed, but leaving lateral bare areas; microtubercles low, subconical; lateral borders with row of fringing papillae and 3-6 submarginal rows.

Prostomium with large lateral auricles (Fig. 6.1A), ciliated ventrally; lateral antennae short, cirriform; 4 eyes partially concealed by auricles, equally spaced, anterior pair larger than posterior pair; palps extending to about segment 8; nuchal organs large, located at posterior border of prostomium, at anterior border of middorsal ridge. Tentacular parapodia with dorsal tentacular cirri subequal to median antenna (Fig. 6.1A); ventral tentacular cirri about half as long as dorsal cirri; inner tentacular lobe about same length as ventral tentacular cirrus, fused to shorter, rounded inner palpal sheath; dorsal ctenidium elongate to oval.

Parapodia of segments 2 and 3 with pair of small lateral ctenidia. Compound falcigerous neurosetae with bifid tips and 3-10 articles on blade; upper and lower setae more slender than middle ones; blades longest in upper setae, shortest in lower ones.

Parapodia of anterior and middle body segments similar. Notopodial bracts papillated, with lower anterior papillae or stylodes longer than dorsoposterior ones. Neuropodial acicular lobes with stylodes only in anterior parapodia. Upper lobes of bilobed posterior bracts with several stylodes on upper anterior part, lower lobes without stylodes. Anterior upper bracts indistinct, anteroventral bracts low, not fimbriated. C-shaped group of stout neurosetae with short blades and smooth stems (Fig. 6.1F). Upper anterior group of neurosetae including simple spinous capillaries (Fig. 6.1D)and compound falcigers with blades having 3-5 articles (Fig. 6.1E) and shafts with 4-6 rows of minute spinelets. Anteroventral slender neurosetae with 1-4 articles on blades and 3-5 rows of spinelets on shaft.

Remarks. *Sthenelais fusca* is distinguished from other eastern Pacific congeners in having many heavy, non-articulated bifid falcigers in the neuropodia, while at the same time having a smooth, non-papillated ventral surface. The specimens from Bodega Harbor exhibit a rather elegant body coloration in which the unpigmented first pair of elytra contrast with the following elytra that are heavily colored with mottled brownish patterns.

Biology. An intertidal to shallow-water species, common under rocks, among algal holdfasts, and among rhizomes of *Phyllospadix*.

Distribution. Central California to Peru.

Sthenelais berkeleyi Pettibone, 1971

Figure 6.2

Sthenelais berkeleyi Pettibone, 1971b:1395-1400, figs. 4-7.—Blake, 1975:177, fig. 85.—Banse and Hobson, 1974:35, figs. 6k-m.

Material Examined. California, Santa Maria Basin, off Port San Luis, 49 m (1).

Description. A large species, up to 400 mm long, 12 mm wide, and about 270 segments (Pettibone, 1971b). Ventral surface thickly covered with small papillae, these continuing onto ventral sides of parapodia. Elytra ellipsoid, concave on anterior margin; pale to rusty-brown; microtubercles low conical, uniformly distributed, but leaving lateral bare areas, and some additional bare areas on more posterior elytra; lateral borders with row of fringing papillae and 4-7 submarginal rows (Fig. 6.2B); sometimes with additional minute sensory papillae.

Prostomium with large lateral auricles, ciliated ventrally; lateral antennae short, subulate; 4 eyes partially concealed by auricles, trapezoidally arranged, with anterior pair larger than posterior pair; palps extending to about segment 7-8; nuchal organs large, located at posterior border of prostomium, at anterior border of middorsal ridge. Tentacular parapodia with dorsal tentacular cirrus subequal to median antenna; ventral tentacular cirri about half as long as dorsal cirri; inner tentacular lobe about same length as ventral tentacular cirrus, fused to shorter, rounded inner palpal sheath; dorsal ctenidium elongate to oval.

Parapodia of segments 2 and 3 directed anteriorly. Compound falcigerous neurosetae with bifid tips and 3-11 articles on blade; upper and lower neurosetae more slender than middle ones; blades longest in upper setae, shortest in lower ones.

Parapodia of anterior and middle body segments similar. Notopodial bracts papillated (Fig. 6.2A), with lower anterior papillae longer than dorsoposterior ones. Neuropodial acicular lobes with stylodes only

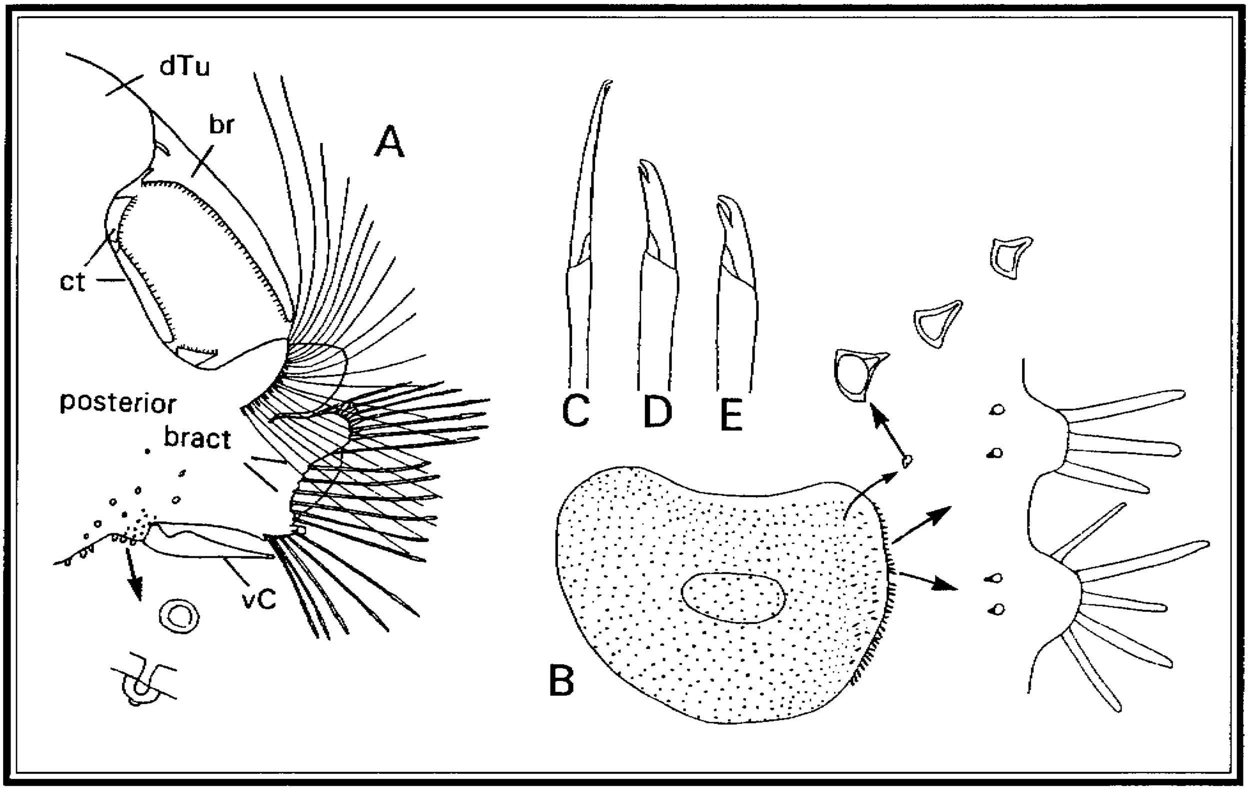

Figure 6.2. *Sthenelais berkeleyi*: A, anterior parapodium; B, elytron with insets showing tubercles and papillae; C-E, compound neurosetae from middle group as insets. (all after Pettibone, 1971b)

on anterior parapodia. Upper lobes of bilobed posterior bracts with numerous stylodes on upper and lower anterior parts. Anterior upper bracts indistinct, anteroventral bracts low, not fimbriated. C-shaped group of stout neurosetae with blades short to longer, with 1-4 articles and smooth stems (Fig. 6.2C-E). Upper anterior group of neurosetae including simple spinous capillaries and compound falcigers with blades having 7 articles and shafts with about 4 rows of minute spinelets. Anteroventral slender neurosetae with 1-4 articles on blades.

Remarks. The details that distinguish *Sthenelais berkeleyi* from the closely related *S. fusca* were defined by Pettibone (1971b), and the descriptions of the two species presented here closely follows the order presented in her paper. The two species are similar in having many heavy, uniarticulated and bifid falcigerous neurosetae. *S. berkeleyi*, however, has a thickly papillated ventral surface instead of one that is smooth. Further, the bilobed posterior bracts of the neuropodia in *S. berkeleyi* are provided with numerous stylodes on both the upper and lower parts, whereas in *S. fusca*, there are a few stylodes in the upper part and none on the lower part.

Biology. Little is known concerning the biology of this species. It has mostly been taken in shallow depths from sediments that contain gravel or include shells mixed with mud. The specimen examined here was taken from sandy silt sediments.

Distribution. British Columbia to southern California; intertidal to 110 m.

Sthenelais verruculosa Johnson, 1897

Figure 6.3

Sthenelais verruculosa Johnson, 1897: 187, pl. 9, fig. 62, pl. 10, fig. 65.—Treadwell, 1914:184.— Berkeley, 1923:216.—Berkeley and Berkeley, 1942:189.—Hartman, 1939:62-63, pl. 14, figs. 167-175; 1961:10; 1968:167-168, figs. 1-5.—Hartman and Reish, 1950:8. Not Pettibone, 1953 (=*S. tertiaglabra*). *Fide* Banse and Hobson, 1974.

Material Examined. California, Santa Maria Basin, off Point Sal, Sta. R-4 (1); off Point Arguello, Sta. 58, 99 m (1)

Description. A moderate to large species, at least up to 75 mm long, 4.5 mm wide, and with at least 150 segments; a complete specimen from Sta. R-4 is 48 mm long, 3.0 mm wide, with 118 segments. Color in alcohol: dull yellow to light tan, with elytra semi-transparent, microtubercles of posterior segments sometimes appearing as orange spots on elytra. Ventral surface smooth. Elytra suborbicular to subreniform, concave on anterior margin (Fig. 6.3B); with microtubercles more or less covering most of elytral surface; microtubercles low, conical to globular, some pointed, not surrounded by flocculent sediment as in *S. tertiaglabra*; lateral and sublateral margins with row of fringing papillae (Fig. 6.3B).

Prostomium rounded, with broad lateral auricles (Fig. 6.3A), ciliated ventrally; lateral antennae absent; 4 eyes, equally spaced, both pairs about same size; palps extending to about segment 10; nuchal organs large, located at posterior border of prostomium, at anterior border of middorsal ridge. Tentacular parapodia with dorsal tentacular cirrus subequal to median antenna; ventral tentacular cirri about one-half as long as dorsal cirri; dorsal ctenidium elongate to oval. Setae numerous, long, finely serrated capillaries.

Parapodia of segments 2 and 3 with pair of small lateral ctenidia. Compound neurosetae including (1) a few anterodorsal falcigers with elongate, narrow blades having 1-2 articles, distally bifid, and with shaft ornamented with rows of delicate spines; (2) these grading ventrally into smooth, compound falcigers with less spinose shafts, but with numerous (9-11) and more distinct articles on blades.

Parapodia of anterior and middle body segments similar (Fig. 6.3C-D). Branchiae from segment 4. Notopodial bracts bearing a row of slender papillae on anterodorsal face (Fig. 6.3D); fewer in posterior segments. Neuropodial acicular lobes with row of papillae. Neurosetae arranged in 3 groups: (1) upper anterior group of 2-3 simple spinous capillaries (Fig. 6.3E), sometimes absent; (2) main C-shaped group of compound falcigers with long, bifid-tipped blades having 9-10 articles (Fig. 6.3F); stout, short-bladed falcigers absent; (3) numerous anteroventral slender compound falcigers with long blades and slender, delicate bifid tips.

Remarks. *S. verruculosa* differs from *S. fusca, S. berkeleyi, and S. tertiaglabra* in completely lacking the stout, short-bladed, and bidentate falcigers in middle and posterior neuropodia. As an offshore species, *S. verruculosa* is most readily confused with *S. tertiaglabra*. The latter species typically has a rusty-colored floccular material surrounding the microtubercles on the elytra. This substance is lacking in *S. verruculosa*.

Biology. *Sthenelais verruculosa* is only known from subtidal depths ranging to about 100 m in sediments of mixed sand and silt. The specimen from Sta. R-4 had been collected in October 1988, and its coelom was filled with numerous small oocytes.

Distribution. Western Canada to Mexico; shallow subtidal to about 100 m.

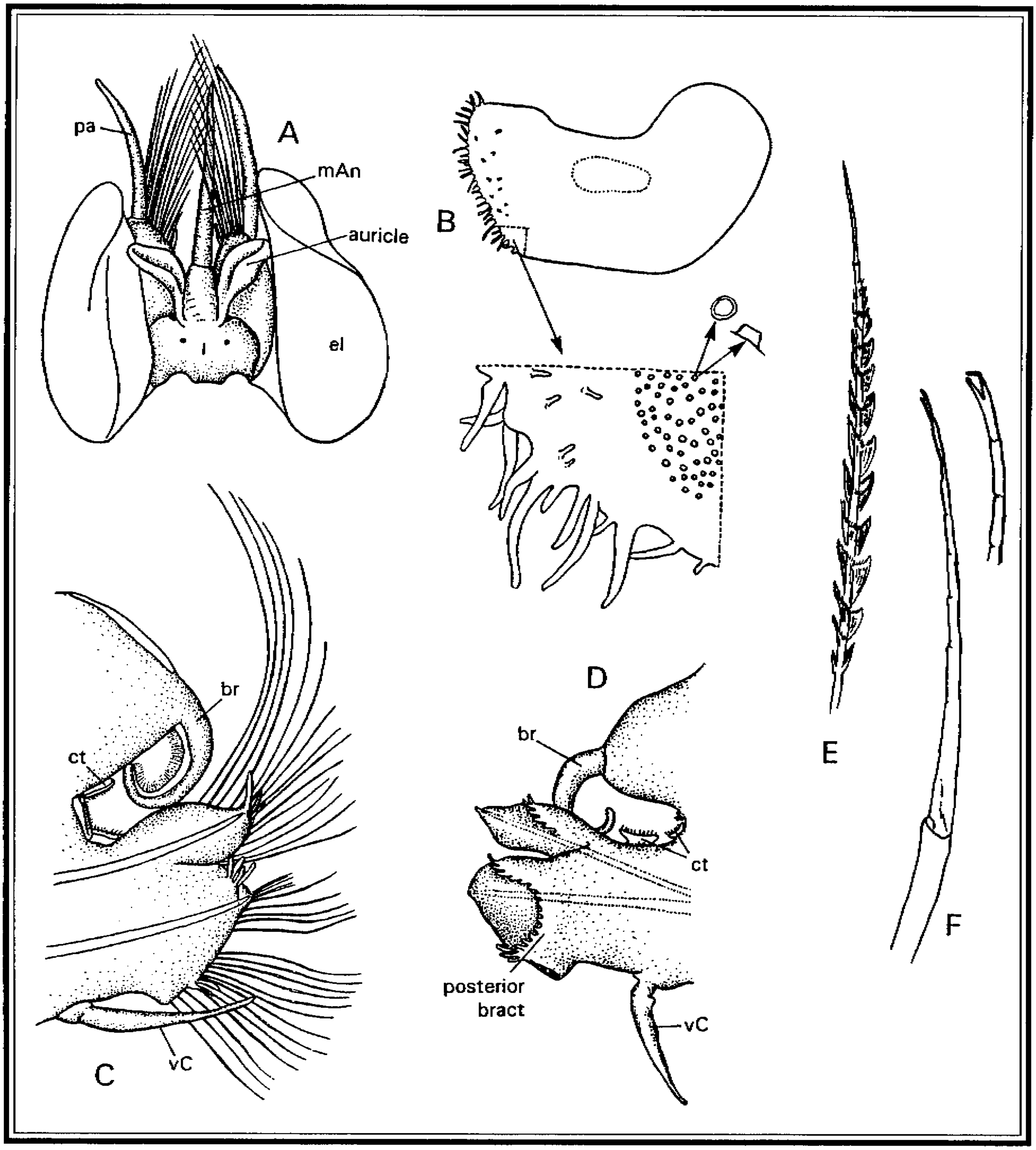

Figure 6.3. *Sthenelais verruculosa*: A, anterior end, dorsal view; B, elytron with insets showing papillae and tubercles; C, anterior parapodium in posterior view; D, middle parapodium in anterior view; E, simple neurosetae; F, compound neuroseta with 9 articulations. (all after Hartman, 1939)

Sthenelais tertiaglabra Moore, 1910

Figure 6.4

Sthenelais tertiaglabra Moore, 1910:395-398, pl. 33, figs. 113-120.—Hartman, 1961; 1968:165-166, figs. 1-6.—Banse and Hobson, 1974:35, figs.6 n-o.
Sthenelais hancocki Hartman, 1939:65-67, pl.16, 188-202.
Sthenelais verruculosa: Pettibone, 1953:75-76, pl. 38, figs. 344-354. Not Johnson, 1897. *Fide* Banse and Hobson, 1974.

Material Examined. California, off Half Moon Bay, Sta. 2-1, 37°28.18'N, 122°51.15'W, 100 m (1).—Santa Maria Basin, off Point Buchon, Sta. 12, 98 m (1); off Point Sal, Sta. PJ-3 (1, 1); Sta. PJ-7 (1, 1); Sta. PJ-10 (1); PJ-11 (1); off Purisima Point, Sta. 42 (1); off Point Arguello, Sta. 65, 107 m (1); off Point Conception, Sta. 79, 98 m (1).

Description. A moderate to large species, up to 133 mm long, 4-5 mm wide, with up to 182 segments (Pettibone, 1953 as *S. verruculosa*). Color in alcohol: dull yellow to colorless, appearing pale, with elytra semi-transparent. Ventral surface smooth. Elytra suborbicular to subreniform, concave on anterior margin; with microtubercles confined to medial halves of most elytra, but leaving anterior and lateral bare areas (Fig. 6.4B); microtubercles low, conical to globular; lateral borders with row of fringing papillae and some in marginal rows; with rust-colored flocculent material around tubercles.

Prostomium rounded, with small lateral auricles (Fig. 6.4A), ciliated ventrally; lateral antennae absent; 4 eyes, equally spaced, both pairs about same size; palps extending to about segment 8; nuchal organs large, located at posterior border of prostomium, at anterior border of middorsal ridge. Tentacular parapodia with dorsal tentacular cirri subequal to median antenna (Fig. 6.4A); ventral tentacular cirri about one-fourth as long as dorsal cirri; dorsal ctenidium elongate to oval. Setae numerous, long, finely serrated capillaries.

Parapodia of segments 2 and 3 with pair of small lateral ctenidia. Compound neurosetae including (1) a few anterodorsal falcigers with elongate, narrow blades having 1-2 articles, distally with minute bifid tips, and shaft ornamented with numerous rows of heavy and conspicuous spines (Fig. 6.4C); (2) these grading ventrally into smooth, compound falcigers with less spinose shafts, but with numerous (6-9) and more distinct articles on blades.

Parapodia of anterior and middle body segments similar. Notopodial bracts bearing 2-6 papillae on anterodorsal face. Neuropodial acicular lobes with few sparse papillae. Neurosetae arranged in 3 groups: (1) Upper anterior group of simple spinous capillaries (Fig. 6.4D); (2) main C-shaped group of compound falcigers, larger, but not stout as in *S. fusca*, including 1-3 short to moderately long bladed bifid falcigers (Fig. 6.4F), and several unidentate falcigers with articles on blades (Fig. 6.4E); (3) numerous anteroventral slender compound falcigers with slender, delicate bifid tips (Fig. 6.4G-H).

Remarks. Superficially, *S. tertiaglabra* has a less robust, and more fragile appearance than either *S. fusca* or *S. berkeleyi*. Unlike these species, *S. tertiaglabra* lacks lateral antennae; has unusual falcigers in segments 2-4 that bear heavy, almost knobbed spines on the shaft that are possibly analogous to the spinous simple setae found in subsequent segments; and has only 1-3 short, bifid falcigers in middle and posterior neuropodia. These latter setae are not as numerous, nor as stout as those found in *S. fusca* and *S. berkeleyi*. There also appears to be less development of parapodial papillae or stylodes in *S. tertiaglabra*. The rusty-colored sediment that accumulates on the elytra of some species is apparently not present in the other species of *Sthenelais* found on this coast.

Biology. A shelf species, occurring in muddy sediments.

Distribution. British Columbia and Puget Sound to southern California; in shelf depths to about 300 m.

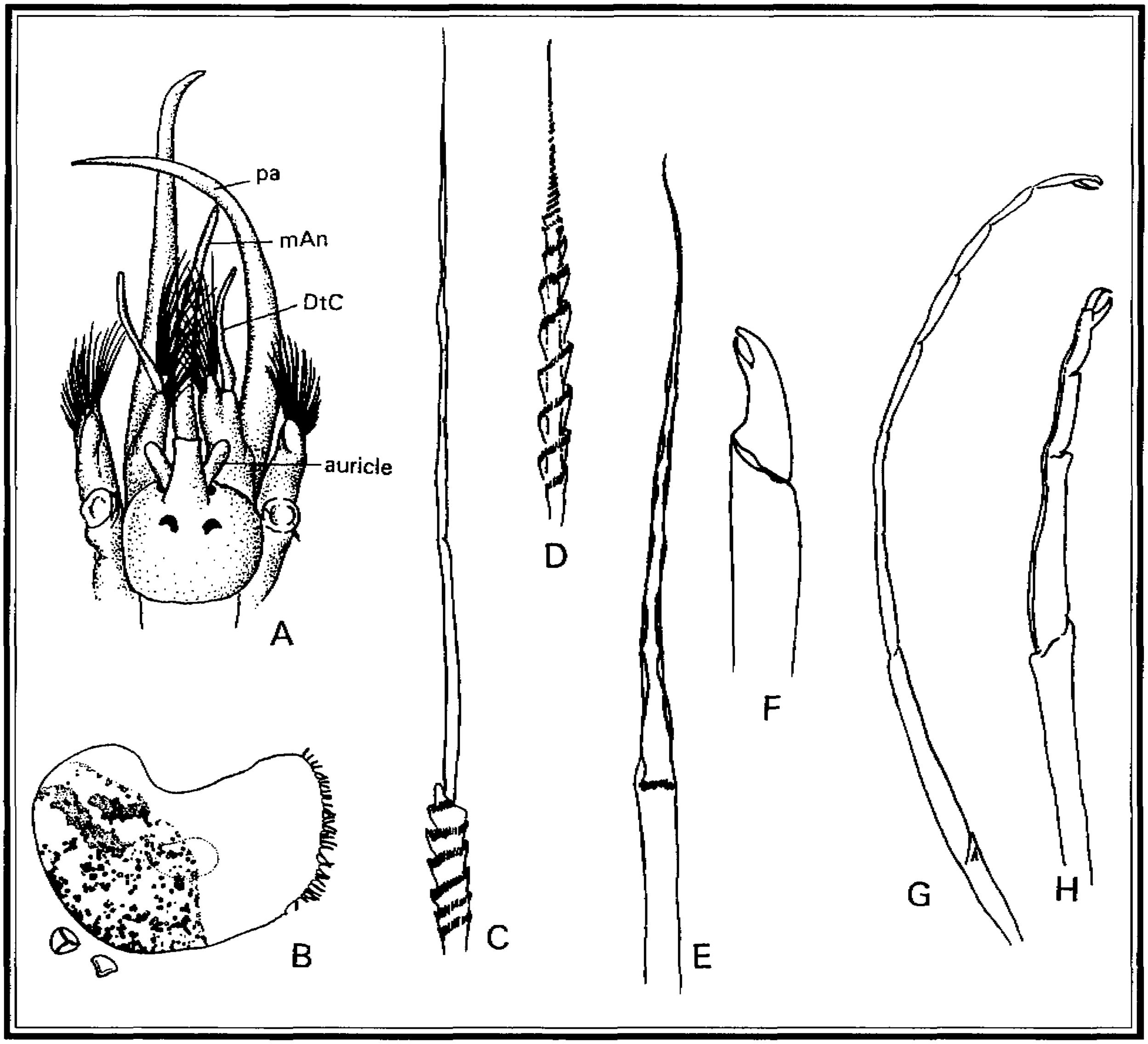

Figure 6.4. *Sthenelais tertiaglabra*: A, anterior end, dorsal view; B, elytron with details of tubercles; C, compound neuroseta from segment 2; D, simple spinose neuroseta; E, slender, unidentate neuropodial falciger; F, stout bidentate neuropodial falciger; G-H, anteroventral compound neuropodial falciger. (A-D after Moore, 1910; rest original)

Genus *Sthenelanella* Moore, 1910

Type Species. *Sthenelanella uniformis* Moore, 1910, by monotypy.
Synonym. *Euleanira* Horst, 1916.

Diagnosis. Body slender, dorsoventrally compressed, with up to 75 segments. Elytra numerous, on segments 2, 4, 5, 7, then alternating to 25 or 27, continuing on following segments to end of body. Branchiae short, conical, lateral to dorsal tubercles or elytrophores from segment 2. Without dorsal cirri. Prostomium rounded, fused with first tentacular segment; ceratophore of median antenna with lateral auricles and short style; lateral antennae very short, fused to tentacular parapodia, without sheaths; 2 pairs of eyes present on raised ocular cushions; tentacular parapodia uniramous, extending anteriorly medial to palps, each with single acicula, 2 tentacular cirri, well-developed fan-shaped fascicles of capillary setae, and medial tentacular lamella. Parapodia of segments 2-4 directed anteriorly, buccal segment (2) with ventral buccal cirri longer than following ventral cirri. Parapodia biramous, with notopodial ctenidia; without parapodial stylodes. Notopodia with conical acicular lobes and inflated rounded upper lobes; notosetae simple, spinous capillaries; notopodial spinning glands from about segment 14-16, producing long, threadlike notosetae. Neuropodia with rounded presetal and postsetal lobes. Neurosetae all compound, generally with short blades; some with spinous shafts. Ventral cirri slender, elongate. Pharynx with 13 or more pairs of distal papillae and 2 pairs of interlocking teeth. Worms inhabiting long, tough, fibrous tubes reinforced from threads of notosetae secreted by spinning glands.

Remarks. The genus *Sthenelanella* was revised by Pettibone (1969) to include two species. The type species, *S. uniformis* Moore, 1910 is an eastern Pacific species, originally described form off California. Species of *Sthenelanella* are unique among the sigalionids by having notopodial spinning glands that produce long, silky threadlike strands of setae.

Sthenelanella uniformis Moore, 1910

Figure 6.5

Sthenelanella uniformis Moore, 1910:391, pl. 33, figs. 105-112.—Hartman, 1939:69, pl. 18, figs. 226-231; 1961:54; 1968:169, figs. 1-6.—Reish, 1968:72.—Pettibone, 1969:431-434, figs. 1-3.
Sthenelanella atypica Berkeley and Berkeley, 1941:26, pl. 5, figs. 1-3. *Fide* Pettibone, 1969.

Material Examined. California, Santa Maria Basin, off Point Sal, Sta. R-8 (1); Western Santa Barbara Channel, Sta. 79, 98 m (1); Sta. 85, 113 m (1).

Description. Specimen from Sta. R-8 complete, 23 mm long, 2 mm wide, for 75 segments; recorded up to 26 mm long and 2-3 mm wide (Pettibone, 1969). Color in alcohol: light tan, with mottled, rust-colored pigment on some anterior elytra. Elytra delicate, transparent; first pair round, with fringe of short, crowded papillae on anterior margin (Fig. 6.5C); subsequent elytra subreniform (Fig. 6.5D) to oval, smooth or with scattered sensory papillae on lateral margin.

Prostomium recessed into segment 2; median antenna with lateral auricles in middle of ceratophore (Fig. 6.5A); with 2 pairs of eyes, anterior pair larger than posterior pair (Fig. 6.5A-B). Dorsal tentacular cirri subequal to median antenna; ventral tentacular cirri shorter, subequal in length to ventral buccal cirri of segment 2; lateral antennae short, subulate, on inner dorsal bases of tentacular parapodia. Capillary setae of tentacular parapodia finely spinous or smooth; with elongate tentacular lamellae medial to setal bundles (Fig. 6.5B). Neurosetae of segments 2-4 compound, with rows of minute spines on shaft and elongate, slender and slightly hooked blades (Fig. 6.5G).

Notopodia forming conical acicular lobes and inflated rounded upper lobes with ciliated ctenidia; 2 additional ctenidia between notopodia and branchiae. Notosetae all spinous capillaries, arranged in spreading fascicles. Notopodial spinning glands from about segment 14; slender threads extending far beyond body (Fig. 6.5F). Neurosetae with short blades (Fig. 6.5H), upper ones rod-shaped, rest conical and pointed. Ventral cirri short, with bulbous base, tapering apically. Pharynx with 2 pairs of chitinous teeth and 13 or more pairs of papillae.

Remarks. *Sthenelanella uniformis* is readily identified by the mottled red spots on the anterior pairs of elytra and by the long, silky thread-like notosetae emerging from the notopodial spinning glands.

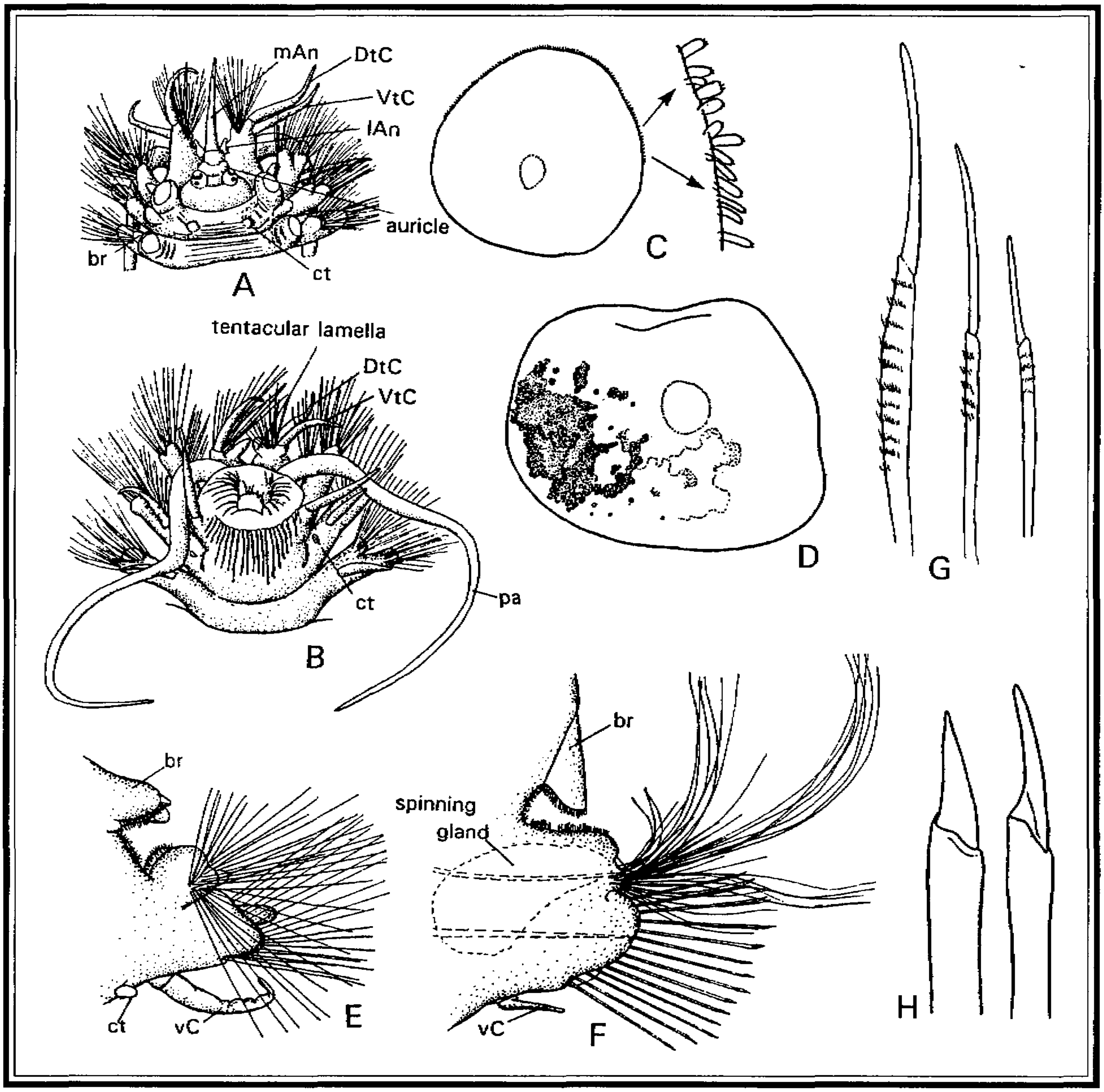

Figure 6.5. *Sthenelanella uniformis*: A, anterior end, dorsal view; B, anterior end, ventral view; C, first elytron with inset showing marginal papillae; D, fifth elytron; E, third parapodium, anterior view; F, middle parapodium, anterior view; G, neurosetae from segment 2; H, neuropodial falcigers from middle parapodium. (A-C, E-G, after Pettibone, 1969; D, H, after Hartman, 1939)

Biology. *S. uniformis* inhabits long tubes that have thickened walls, that are covered with mud or sand and reinforced by the long felt or setal threads produced from the spinning glands.

Distribution. Central California to Ecuador; intertidal to 113 m.

Genus *Sigalion* Audouin and Milne Edwards, in Cuvier 1830

Sigalion Audouin and Milne Edwards, in Cuvier 1830:207. **Type species**: *Sigalion mathildae* Audouin and Milne Edwards, in Cuvier 1830:207, designated by Hartman, 1959.
Thalenessa Baird, 1866:34. **Type species**: *Sigalion edwardsi* Kinberg, 1856:387, by original designation. *Fide* Mackie and Chambers, 1990.
Eusigalion Augener, 1918:112-113. **Type species**: *Eusigalion vazensis* Augener, 1918:113-118, fig. 3, pl. 14, figs. 44-46, by monotypy. *Fide* Mackie and Chambers, 1990.

Diagnosis. Body elongate with numerous segments. Elytra on segments 2, 4, 5, 7, and alternating segments to 27, then continuing on all following segments. Elytra with lateral fringe of bipinnate papillae. Dorsal tubercles on segments 6, 8, and alternate segments to 26. Prostomium subrectangular to subpentagonal, situated dorsally on segments 1 and 2; with 3 small antennae lacking ceratophores; lateral antennae arising from anterior margin; median antenna arising from dorsal surface of prostomium; 4 small subdermal eyes present; palps long, tapering, arising ventral to tentacular parapodia. Pharynx with a pair of jaws, 2 pairs of oblique muscular ridges, and up to 2 middorsal papillae. Tentacular parapodia anteriorly directed, each bearing a pair of short tentacular cirri, 2 aciculae, and 2 groups of long, thin, bifid simple setae. Pair of nuchal organs present between prostomium and elytrophores of segment 2. Facial tubercle present or absent. Segment 3 partially or entirely reduced dorsally, with single pair of laterally directed dorsal cirri.

Branchiae cirriform, from segment 4-7, sometimes absent from segments with dorsal tubercles. Parapodia biramous from segment 2, with each ramus bearing a single acicula. Notopodia lacking bracts, with a single presetal stylode. Neuropodia lacking bracts, with a single presetal tubercle and up to 2 postsetal lobes; superior postsetal lobe cirriform, inferior postsetal lobe rudimentary; with long, tapering ventral cirri. Three large ctenidia between notopodia and elytrophores/ dorsal tubercles. Additional ctenidia may variously occur ventral to neuropodia, dorsal to elytrophores and dorsal tubercles, and elsewhere on parapodia. Notosetae all simple with bifid tips. Neurosetae include simple spinous setae, compound falcigers with blades ranging from long and multiarticulate to short with a single article. Pygidium with 2 filiform anal cirri.

Remarks. Following an examination of the type species of *Sigalion, Thalenessa*, and *Eusigalion*, Mackie and Chambers (1990) determined that the two latter genera were junior synonyms of the first. *Sigalion* has usually been distinguished as lacking a median antenna, but the type species was determined to have one. A single species, *Sigalion spinosus* (=*Thalenessa spinosum*) has been found in collections examined as part of this study. Specimens labeled as *Sigalion* sp. A in the Phase I collections proved to be *Sigalion spinosus* that had lost the median antenna.

Sigalion spinosus (Hartman, 1939)

Figure 6.6

Eusigalion spinosum Hartman, 1939:57-59, pl. 11, figs. 134-144, pl. 12, figs. 146-147.
Thalenessa spinosa: Hartman, 1968:177, figs. 1-5.
Thalenessa cf. *spinosa:* Wolf, 1984:25-17, fig. 25-13, 25-14a-o.
Sigalion spinosus: Mackie and Chambers, 1990:52.

Material Examined. California, off Half Moon Bay, Sta. 2-1, 37°30.23'N, 122°45.95'W, 77 m, coll. 23 Sep. 1991 (1); Sta. 2-2, 37°28.18'N, 122°51.15'W, 100 m, coll. 23 Sep. 1991 (1).—Santa Maria Basin, off Port San Luis, Sta. 21, 49 m (1, 2); off Point Sal, Sta. R-8 (1).

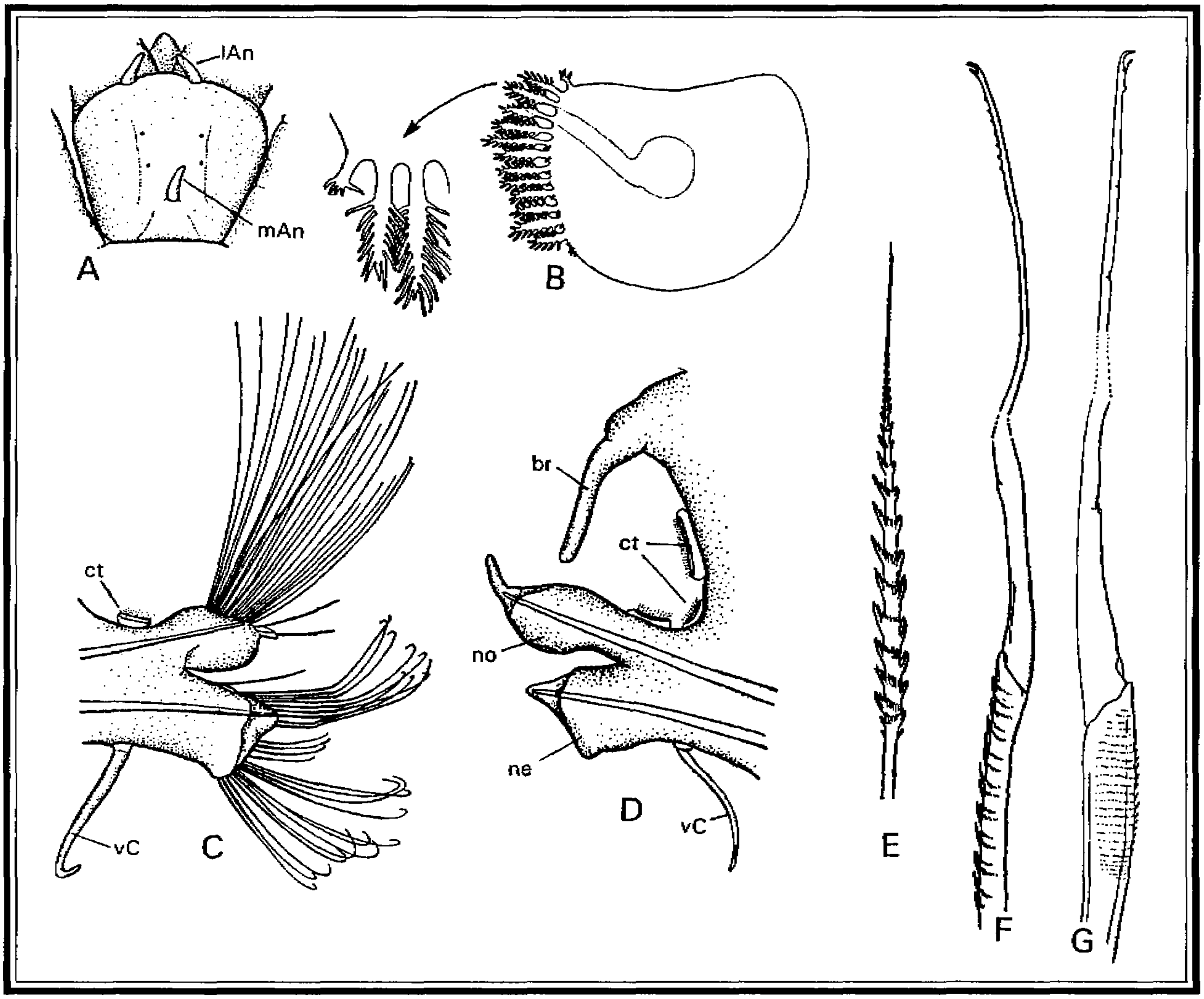

Figure 6.6. *Sigalion spinosus*: A, prostomium, dorsal view; B, elytron with inset showing detail of marginal papillae; C, anterior parapodium; D, middle parapodium; E, simple neuroseta; F-G, compound multiarticulated neuroseta. (all after Hartman, 1939)

Description. A large species, up to 100 mm long, 5.0 mm wide for about 115 segments; present specimens smaller, largest (Sta. 2-2), 33 mm long, 2.5 mm wide for about 150 segments. Color in alcohol: light tan, pink, or opaque white. Elytra translucent, more or less covering dorsum. Body compressed, subrectangular in cross section, widest at about segments 8-10; posterior segments narrow. Pygidium with 2 long cirri.

Prostomium trapezoidal, about as wide as long, widest anteriorly; with 2 short lateral antennae on frontal margin and a short median antenna in posterior half of prostomium (Fig. 6.6A), all 3 antennae subequal, digitiform; 4 small, circular eye present, arranged in a square anterior to median antenna. Facial tubercle present. Palps long, slender, tapering apically, extending posteriorly to about segment 7. Tentacular segment with ventral tentacular cirrus slightly longer than dorsal one; with 2 bundles of slender capillary notosetae. Proboscis with 13 dorsal and 13 ventral papillae on anterior margin in addition to a single, larger, subterminal papilla on ventral side; with two copper-colored teeth or jaws on dorsal and ventral sides.

Elytra pale or white, translucent, smooth, slightly concave on anterior margin, with row of elegant, bipinnately branched filaments on lateral margin (Fig. 6.6B); without tubercles.

Parapodia elongate throughout, with notopodia initially shorter than neuropodia (Fig. 6.6C), then notopodia gradually increasing in length, becoming longer than neuropodia by middle of body (Fig. 6.6D). Notopodia slightly inflated, terminating in short cirrus. Neuropodia obliquely truncate, terminating in triangular lobe bearing acicula; ventral cirri cirriform, thin, about as long as neuropodium. Branchiae from segment 4, each long, thick (Fig. 6.6D).

Notosetae long, simple capillaries with finely serrated edge. Neurosetae arranged into supracicular and subacicular fascicles; supracicular fascicle consisting of an anterior group of 7-10 fine compound falcigers and 6-9 spinose simple setae (Fig. 6.6E), and a posterior group of 12-15 heavier, bifid compound falcigers with blades ranging from short to long. Subacicular fascicle with 3-5 heavy, stout compound falcigers with short blades and 40 or more long, multiarticulated compound falcigers (Fig. 6.6F-G).

Remarks. *Sigalion spinosus* has been reported as *Eusigalion spinosum* or *Thalenessa spinosa* from collections ranging from central California south to central America and the Galapagos Islands. The species was recently reported from the Gulf of Mexico by Wolf (1984). The present collections include material from off Half Moon Bay, extending the northern range slightly north of Monterey Bay. In some specimens the median antenna has been lost, confirming the deciduous nature of this structure in species of *Sigalion*.

Biology. The species is found in continental shelf depths to about 100 m in sediments consisting of mixed sand and silt. According to Hartman (1939), there were no tubes associated with the species when it was collected and she assumed it was a burrower.

Distribution. Northern California to Central America; Galapagos Islands; Gulf of Mexico; 18-119 m.

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7. Family Amphinomidae Lamarck, 1818

by

Jerry D. Kudenov[1]

Introduction

The amphinomids, along with other members of the Order Amphinomida *sensu* Fauchald, 1977a, are strongly isolated in the Class Polychaeta (Clark, 1969). Certain species such as *Eurythoe complanata*, the so-called "fireworm," can be dangerous to humans. They produce an acidic neurotoxin that is transmitted to unwary humans or erstwhile predators through detachable, and highly brittle, calcareous harpoon notosetae. Only those amphinomids that produce setal associated neurotoxins can rightly be called fireworms; many amphinomids apparently do not. Generally speaking, most members of this family tend to be much smaller than *Amphinome*, *Eurythoe* or *Hermodice*, which can approach lengths of 500 mm and widths in excess of 15 mm, excluding setae.

Morphology

Members of this family are brilliantly pigmented, and sometimes have characteristic color patterns, which is particularly true for both *Chloeia* and *Notopygos*. The bodies of such amphinomids as the *Chloeia-Notopygos* species complex (Kudenov, 1991) tend to be grublike and oval in cross-section for a limited number of segments, whereas *Amphinome*, *Eurythoe*, *Hermodice*, *Pareurythoe*, and similar forms are elongate and subrectangular in cross section and have many more segments. The prostomium is represented by anterior and posterior lobes and tends to be tightly surrounded by anterior setigers and dense fascicles of notosetae. The anterior lobe is rounded to slightly incised anteriorly, rounded dorsally, has a pair each of palpal and lateral antennae, and a pair of eyes. The posterior lobe is wider than long, with a median antenna, another pair of eyes, and a median caruncle that generally extends posteriorly in configurations such as: (1) a flat unadorned plate in *Paramphinome*, (2) a sinuous lobe in *Pareurythoe*, (3) a median keel with a pair of lateral ridges in *Eurythoe*, or (4) a median keel with complexly folded margins as in the *Chloeia-Notopygos* species complex and *Pherecardia*. *Hipponoa* lacks a caruncle (Kudenov, 1977, 1994). The pharynx is unarmed, highly muscular, and has an extensive series of characteristic transverse ridges. A peristomial segment is apparently absent. Parapodia are biramous, and the notopodial and neuropodial rami are widely separated. Notopodia have setae arrayed in radiating circular whorls, with one or two dorsal cirri. Branchiae may be present on some notopodia as in *Paramphinome* or *Linopherus*, or on most as in *Branchamphinome* and *Pareurythoe*, and are usually absent from the first few setigers. They are generally dendritic in most genera, and can be bipinnate in *Chloeia* and related taxa, or palmate in *Branchamphinome* (Kudenov, 1993). Neuropodia also have setae arrayed in radiating circular whorls and bear one ventral cirrus. All setae are simple, calcareous and brittle. Notosetae include bifurcate and harpoon setae, unadorned or spurred spines, and spurred and nonspurred capillaries. Neurosetae may include recurved hooks as in *Hipponoa* and *Amphinome*, bifurcate setae, unadorned or spurred spines, and spurred or nonspurred capillaries. Aciculae are generally blunt distally, club-shaped and located in a narrow arc just anterior to the dorsal cirri in the notopodia and in a

[1] Department of Biological Sciences, University of Alaska Anchorage, 3211 Providence Drive, Anchorage, Alaska 99508

narrow superior arc in the neuropodia. The pygidium is either dorsal with unpaired midventral anal papilla in such genera as *Amphinome* and *Eurythoe*, or terminal with a pair of anal cirri, as in the *Chloeia-Notopygos* species complex (Kudenov, 1991).

Amphinomids and other members of the Order Amphinomida are unusual, compared to other polychaetes, in having such features as calcareous setae, two pairs of longitudinal nerve cords including an additional lateral tract, and a series of ventral epidermal pigment canals that parallel the nervous system (Gustafson, 1930; Kudenov, 1974). All other known modern day polychaetes reported to date lack these features, although a few interstitial forms may have two pairs of nerve cords.

Specific characters having taxonomic importance include the morphology of the prostomium, development of prostomial appendages, eyes, caruncle, setiger 1, parapodia of middle body segments, the kinds of noto- and neurosetae, development and numbers of noto- and neuroaciculae, distribution and placement of branchiae and parapodial cirri, and development and kinds of anal cirri.

Taxonomic History

The first four amphinomids ever to be described in western literature were assigned to the genus *Aphrodita* by Pallas (1766). The family Amphinomidae was later formally recognized by Lamarck (1818), as noted by Pettibone (1982), and not Savigny (1818) as reported by Hartman (1959:128; for comments see Kudenov, 1992). The primary systematic study for amphinomids is that of Gustafson (1930:305-471) who focused on comparative anatomy. Other important references for this group have been summarized by Kudenov (1974, 1992).

This family is not well understood systematically. The Order Amphinomida to which it is assigned is clearly monophyletic (Fauchald, 1974, 1977a) and not closely related to any other extant Order in the Class (Clark, 1969). Only recently has the Order Amphinomida been restricted to include the families Amphinomidae and Euphrosinidae by Fauchald, 1977a (see also Pettibone, 1982); the spintherids were removed and placed into a separate Order. Prior to 1977, the Order Amphinomida embraced amphinomids and euphrosinids either as the family Amphinomidae containing two subfamilies, or as two separate families which applies here. Historically, spintherids were included because of their superficial resemblance to the other taxa (Manton, 1967). Kudenov (1991) has since established the Archinomidae, a new family in this Order from the Galapagos hydrothermal vents, based upon a single, unusual species, *Archinome rosea* (Blake). Kudenov (1991) provides a brief historical overview of the Amphinomida.

In all, 19 genera and around 130 species of amphinomids generally considered valid have been described (Hartman, 1959, 1965; Fauchald, 1977a). This will undoubtedly change as each genus is revised based on type specimens. For example, the only generic revisions performed to date on amphinomids are those of Bindra (1927) who worked on the genus *Eurythoe*, and Fauchald (1977b) who proposed *Linopherus* as the senior synonym of *Pseudeurythoe*. Both were based on the literature. *Eurythoe* is complex in that its extreme morphological variation may be the result of its reproductive behavior (at least in *Eurythoe complanata*, see Kudenov, 1974); it is also fraught with numerous synonymies, some of which seem to be highly dubious (Kudenov, unpublished data). Pettibone (*in litt.*) did not agree with Fauchald, and severely questioned his proposal to treat *Pseudeurythoe* as the junior synonym of *Linopherus*.

Biology

Amphinomids are most commonly distributed in shallow tropical and subtropical waters; a number have also been reported from abyssal depths and polar habitats. Most amphinomids tend to be small and cryptic, especially in intertidal and shallow subtidal habitats where they are associated on rocks, in or under dead coral or other hard surfaces inhabited by other organisms. Other taxa such as *Amphinome* live on driftwood, and *Hipponoa* is an inquilinistic commensal inhabiting the mantle cavity of *Lepas* (Kudenov, 1977). Other amphinomids, some of which may be strongly reduced, live in sediments (Kudenov and Blake, 1985).

Most amphinomids are slow moving carnivores that feed on soft sessile taxa such as sponges, anemones, hydroids and ascidians, although *Pherecardia* preys upon injured crown-of-thorn starfish in the Caribbean (Glynn, 1984). When disturbed, most assume a defensive posture by arching their bodies dorsally to display expansive fascicles of notosetae. Some taxa such as *Chloeia* and *Notopygos* are relatively active predators while others such as *Eurythoe* and *Pareurythoe* are omnivorous with decided preferences for animal remains. Some larger and rather conspicuous taxa such as *Hermodice* can be observed feeding on coral polyps during daylight hours, in contrast to *Eurythoe complanata* which exhibits an aversion to light and may be nocturnal or crepuscular in its feeding habits. The feeding habits of this family are poorly known, and summarized by Fauchald and Jumars (1979).

Relatively little is known about the reproductive biology of amphinomids. The literature was summarized by Kudenov (1974) and Schroeder and Hermans (1975). *Eurythoe complanata* exhibits an annual cycle of architomic scissiparity in the spring followed by a release of gametes later in the summer. Some species are known to swim using natatory setae (Fauvel, 1951; Hartman, 1951) and are attracted to night lights (Fauvel, 1951). The rostraria larva is attributed to amphinomids, although the complete larval cycle has not been described for this group to date.

Description of Species

Genus *Chloeia* Lamarck, 1818

Type Species. *Aphrodita flava* Pallas, 1766

Diagnosis. Body ovate, oval in cross section, with around 30 segments. Prostomium with anterior and posterior lobes. Anterior lobe with pair of palpal antennae; posterior lobe with 2 pairs of eyes, pair of lateral antennae, and an unpaired median antenna. Caruncle well developed, with high median keel and pleated lateral folds. Branchiae first present from setigers 4-5, bipinnate. Dorsal cirri numbering one or two per anterior segment. Notosetae including thick bifurcate setae, heavy spines with minute spurs and slender bifurcate capillaries. Neurosetae including bifurcate setae and heavy spines with minute spurs.

Chloeia pinnata Moore, 1911

Figures 7.1, 7.2

Chloeia pinnata Moore, 1911:239-243, pl. 15, figs. 1-6; —Hartman, 1940:206-207, pl. 31, figs. 10-13; 1968:193-194, figs. 1-4; —Banse and Hobson, 1974:37 (key only).

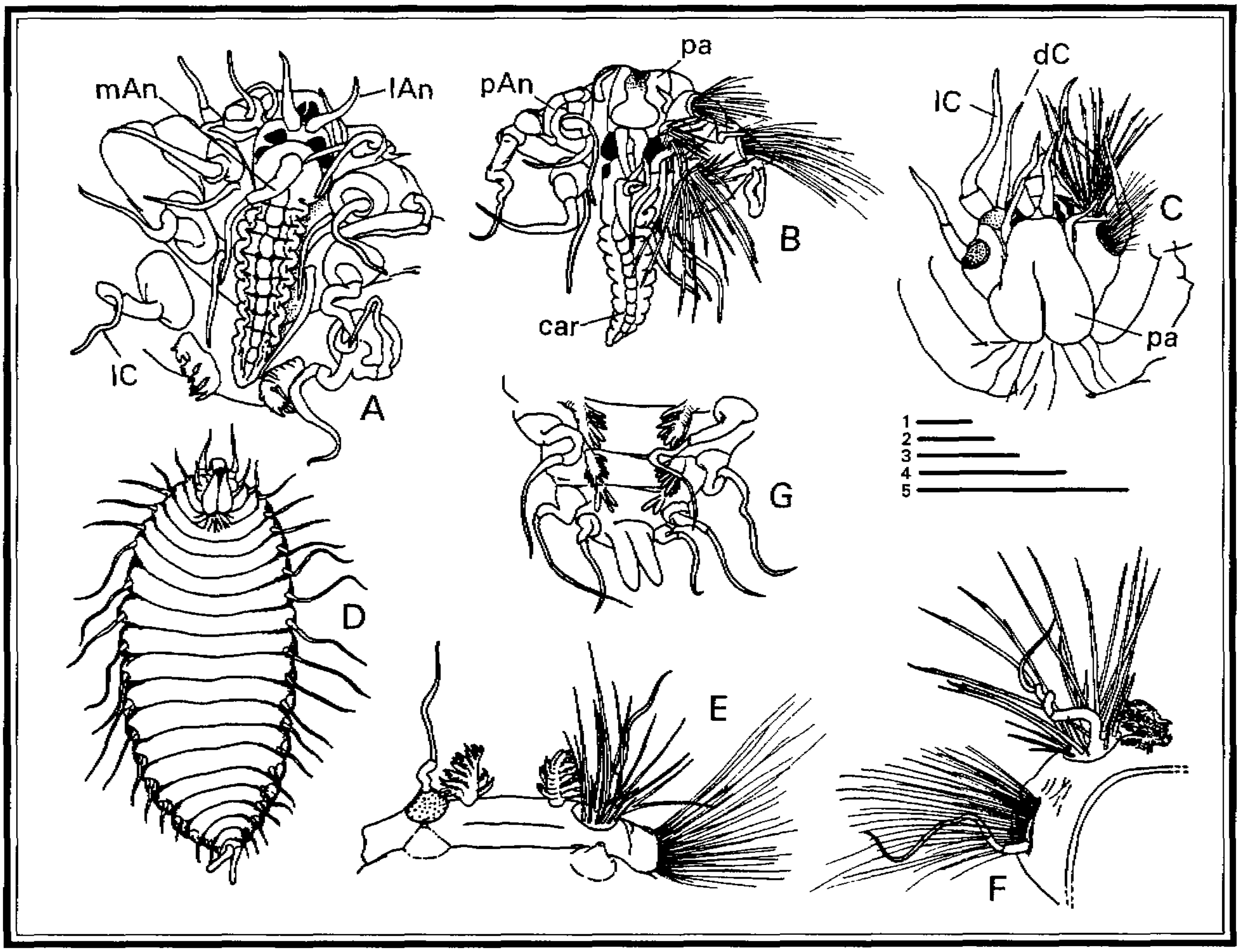

Figure 7.1. *Chloeia pinnata*: A, anterior end, dorsal view; B, same, anterodorsal view; C, same, anteroventral view; D, entire worm, ventral view; E, setiger 10, anterodorsal view; F, left setiger 12, posterior view; G, posterior end, dorsal view. Setae omitted for clarity. All scales = 1 mm. Scale 1, D; 2, E; 3, F; 4, A-C; 5, G.

Material Examined. California: Santa Maria Basin, off Point Estero, Sta. 3, 291 m, (90, USNM); off Port San Luis, Sta. R-2, 161 m, (7, USNM); off Point Arguello, Sta. 53, 196 m, (100, SBMNH).

Description. Present materials measuring up to 13 mm long, 5 mm wide excluding setae, for 24 segments. Species reported up to 30 mm long, 7 mm wide without setae, for 17-28 segments. Body generally pale pink-orange in alcohol, without pigmented bands or pattern; with purple pigment on prostomium anterior to paired lateral antennae, ceratophores of all dorsal cirri from setiger 4, dorsal cirri from setigers 4-6, and on medial and paired lateral ridges of caruncle.

Prostomium with anterior lobe rounded anteriorly, with paired palpal antennae long, slender, cirriform; posterior lobe smaller, with paired lateral antennae, cirriform, longer than palpal antennae, arising from anterior margin, two pairs of pronounced purple eyes of which anterior pair largest, and median antenna arising from anterior margin of caruncle, 2x longer than lateral antennae, 0.6x length of caruncle (Fig. 7.1A-C). Caruncle as described for the genus, extending posteriorly to middle of setiger 4 (Fig. 7.1A, B); fused to dorsum of setigers 1-2, free thereafter. Palps fused, converging midventrally into longitudinal groove leading to mouth (Fig. 7.1C). Mouth located between palps and posterior lip formed by setiger 3 (Fig. 7.1C, D).

Parapodia well developed with widely separated rami in all segments (Fig. 7.1E, F). Notopodia set off from body wall by incised groove, elliptical in cross section, conical, terminating in long cirrophores for dorsal cirri; neuropodia set off from body wall by low narrow rim, circular in cross section, pad-shaped (Fig. 7.1C). Setiger 1 strongly reduced, both noto- and neuropodia directed dorsally (Fig. 7.1C); setiger 2 reduced, notopodia directed dorsally, neuropodia laterally; setiger 3 completely developed.

All setae hollow. Notosetae yellow, thicker, less numerous than neurosetae, tips distally ensheathed or capped by a clear matrix (Fig. 7.2A', L-O), of three kinds including: (1) long bifurcate setae, most numerous, having long prongs straight and smooth in all fascicles of anterior half of body, ratio of long to short prongs ranging from 7.1-28.6:1 (Fig. 7.2A, B, F-K); (2) bifurcate harpoon setae in all fascicles of posterior half of body, with barbs offset from small prong, not 180° apart (angle of line running from harpoon barbs to center of seta and base of small prong approximately 150° when viewed in cross-section), ratio of long to short prongs ranging from 8.1-8.8:1 (Fig. 7.2C-E); and (3) spinous notosetae, short, thinner than bifurcate notosetae, smooth, numbering around 15 per fascicle, arrayed as outermost whorl along notopodial border (Fig. 7.2L-M). Notoaciculae spinose, entire, numbering 3-4 per notopodial fascicle, arrayed directly in front of notopodial cirrus (Fig. 7.2O). All notosetae with regular pattern of minute, file-like teeth set in alternating spiral rows, best developed on all surfaces proximal to small prong, generally absent distal to small prong (Fig. 7.2B').

Neurosetae paler yellow, considerably thinner, and much more numerous than notosetae, all bifurcate, including an outer ring of relatively heavier neurosetae (Fig. 7.2P-S, X, Y, AB) surrounding dense tufts of long spurred capillaries (Fig. 7.2T-W, Z, AA), of which superior ones longest, thinnest (Fig. 7.2Z). All neurosetal fascicles especially dense in posterior half of body. Neuroaciculae spinose, not as heavy as notoaciculae, numbering 10-12 per fascicle, arrayed along dorsal superior region of fascicle (Fig. 7.2AC). All neurosetae with regular pattern of rasp-like teeth set in alternating spiral rows, best developed on all surfaces proximal to small prong, generally reduced distal to small prong (Fig. 7.2X-AB).

All setigers with parapodial cirri. Setigers 1-3 with relatively thick cirri, including true dorsal, lateral and ventral cirri (Fig. 7.1A). Dorsal cirri arising medial to lateral cirri, lacking cirrophores. Lateral cirri (called dorsal cirri on first branchial parapodia) associated with notopodia, long, length of cirrophores about equal to length of segment; cirrostyle slender, cirriform, about 3.5x longer than cirrophores. Ventral cirri with cirrophore conspicuous, about 0.5x length of dorsal cirrophores in midbody segments; cirrostyle gradually increasing in length to about 0.5x body width of midbody segments, longer than dorsal cirri (Fig. 7.1D).

Branchiae bipinnate, present from setiger 4 to end of body, with 8 alternating branches arising from primary axis, each terminating in smaller branches of fine, digitiform pinnae or terminal filaments on posterior surfaces only; anterior surface lacking pinnae (Fig. 7.1E, F). Branchiae best developed in anterior and middle segments, decreasing in size and development thereafter.

Pygidium terminal, opening between pair of thick, cylindically appressed anal cirri (Fig. 7.1G).

Biology. *Chloeia pinnata* is one of the most abundant amphinomids known off the coast of southern and central California where it inhabits green and gray muds, and poorly sorted fine to coarse sands with shell fragments, cobbles and rocks (Jones & Thompson, 1988).

Remarks. *Chloeia pinnata* was adequately described but poorly illustrated by Moore (1911). Few additional details and illustrations were provided by Hartman (1940, 1968) and other subsequent workers. The most noteworthy finding in this study is the presence of unusual bifurcate notosetae from posterior segments with a row of harpoon barbs on the long prong separated by an angle of approximately 150° from the small prong; they are not separated by an angle of 180°. This is the very feature that Hartman (1940, 1968), Banse and Hobson (1974) and others have used to distinguish *Chloeia entypa* Chamberlin, 1919, which has this seemingly unusual kind of notoseta, from *C. pinnata*. Given this and other traits, it appears that *Chloeia pinnata* may be the senior synonym of *C. entypa*. However, there are other apparent differences between these two species, and their treatment will be discussed elsewhere once the type of *C. entypa* can be examined.

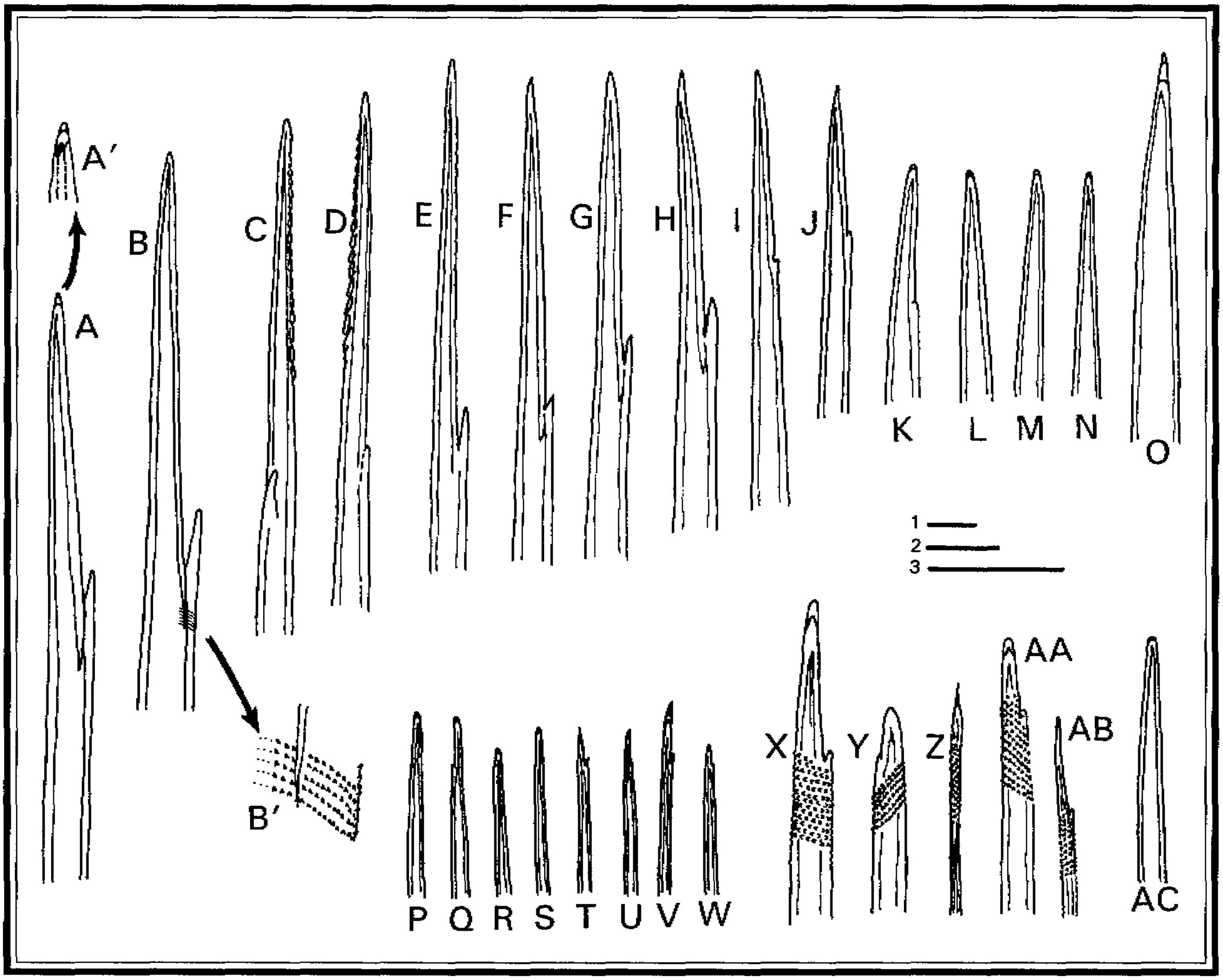

Figure 7.2. *Chloeia pinnata*: A, notoseta, from superior of fascicle, with A' showing detail of tip; B, same, with B' showing detail of surface; C-E, bifurcate harpoon notosetae; F-K, spurred notoseta from inner setal field: F, center of fascicle; G, superior of fascicle; H, anterior of fascicle; I-J, inferior of fascicle; K, superior of fascicle; L-N, spinose notosetae, from outermost whorl: L, superior of fascicle; M, anterior of fascicle; N, inferior of fascicle; O, notoacicula; P-S, spurred neurosetae from outer field of fascicle: P, superior neuroseta; Q, anterior neuroseta; R, inferior neuroseta; S, posterior neuroseta; T-W, spurred neurosetal capillaries from inner setal field: T, superior neuroseta; U, anterior neuroseta; V-W, inferior neurosetae; X-AB, surface details of neurosetae: X, Y, AA, spurred neurosetae from outer field of fascicle; X, superior neuroseta; Y, posterior neuroseta; AA, anterior neuroseta; Z, AB, spurred neurosetal capillaries from inner field of fascicle: Z, longest capillary from center of fascicle; AB, shorter capillary from inferior of fascicle; AC, neuroacicula. Scales: 1 = .001 mm, X-AB; 2 = .001 mm, B'; 3 = .01 mm, A-W, AC and .005 mm, A'.

Chloeia pinnata can thus be characterized as a relatively small *Chloeia* species, lacking any apparent color patterns on the dorsum when in alcohol, although purple pigment is present on the prostomium anterior to the paired lateral antennae, notopodial cirri from setiger 4, and anal cirri. Black pigment specks noted by Hartman (1940) on the dorsum were not noted in any of the nearly 200 specimens examined in this study. The caruncle extends posteriorly to setiger 4. Two dorsal cirri (actually the true dorsal and lateral cirri; see Gustafson, 1930; Kudenov, 1987, 1991) are present on setigers 1-3. Branchiae are bipinnate and occur from setiger 4 to the end of the body. Notosetae of three kinds including: (1) bifurcate setae with long smooth prongs in the anterior half of the body, (2) bifurcate harpoon notosetae in the posterior half, and (3) spinous notosetae that are smooth and short, present in an outer whorl around the periphery of notopodial fascicles. Neurosetae are all bifurcate and include relatively short slender spines arrayed around the periphery of neuropodial fascicles, and an inner tuft of very long capillaries which are best developed in the posterior one-half of the body. All setae are hollow, with characteristic file- or rasp-like teeth arranged in alternating spiral rows on nearly all surfaces, and are either distally ensheathed or are tipped with hyaline-like caps. The second trait was referred to by Moore as being granular.

Note that Moore (1911) assumed the peristomium to be entirely fused with the prostomium, and counts segments in both the amphinomids and euphrosinids accordingly. There is no evidence supporting his assumption (Gustafson, 1930).

Distribution. Southern California, in shelf and slope habitats to depths of 567 m.

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8. Family Euphrosinidae Williams, 1851

by

Jerry D. Kudenov[1]

Introduction

Euphrosinids, like their amphinomid relatives, represent another family in the Order Amphinomida *sensu* Fauchald (1977), which is strongly isolated in the Class Polychaeta (Clark, 1969). Euphrosinids differ from amphinomids in lacking harpoon notosetae, or any kind of notoseta that readily detaches. They apparently do not produce associated setal neurotoxins, and are therefore not called fireworms. Generally speaking, most members of this family tend to be less than 40 mm long, 10 mm wide, and have fewer than 50 segments.

Morphology

Members of the Euphrosinidae tend to be pigmented a brilliant orange, but characteristic color patterns are apparently absent. Bodies are somewhat semi-circular in cross-section and elliptical in outline; the dorsum is arched and the ventrum is flat.

The prostomium is an elongate, narrow ridge extending over the anterior end from the dorsum to ventrum, tightly wedged between anterior setigers and highly obscured by dense fascicles of notosetae. The dorsal part of the prostomium bears a pair of large eyes located lateral to the median antenna. The caruncle is fused to the dorsum in *Euphrosine*, and generally free in both *Euphrosinella* and *Euphrosinopsis*; a median keel and three pairs of lateral ciliated ridges are present on a variable number of anterior segments. A pair of small palpal antennae arise lateral to the smaller pair of eyes; all are placed anteriorly to a pair of elliptical, medial palps which, in turn, are anterior to the mouth. The mouth is surrounded by the first four setigers. The pharynx is unarmed, highly muscular, and has an extensive series of characteristic transverse ridges.

Parapodia are biramous, with rami projecting only slightly above the body surface; notopodial and neuropodial rami are separated. Notopodia are present as transverse ridges with several tiers of bifurcate notosetae arrayed in transverse rows. Branchiae occur either singly or with up to 13 in a transverse row posterior to the dorsal and lateral cirri. Neuropodia are circular in outline, with setae arrayed in radiating circular whorls. A ventral cirrus is present.

Branchiae are generally present from setiger 1, either as a single cirriform filament, as several filaments arising directly from the body wall, or as dichotomously branching, arborescent processes; or they may be absent (Kudenov, 1993).

All setae are simple, calcareous and brittle. Notosetae include bifurcate and ringent setae. Neurosetae include bifurcate setae, and delicate spurred capillaries in some sexually mature specimens. Aciculae are generally bifurcate, and apparently located in a transverse tier just anterior to dorsal and lateral cirri in the notopodia, and in a narrow superior arc in the neuropodia. All bifurcate noto- and neurosetae vary consistently both within fascicles and along the body in two species of *Euphrosine* (Vogt and Kudenov, 1994).

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[1]Department of Biological Sciences, University of Alaska Anchorage, 3211 Providence Drive, Anchorage, Alaska 99508

The pygidium is terminal with a pair of short, cushion- to cup-shaped anal cirri surrounded by posterior setigers.

Euphrosinids and other members of the Order Amphinomida are unusual compared to other polychaetes in having such features as calcareous setae, two pairs of longitudinal nerve cords including an additional lateral tract, and a series of ventral epidermal pigment canals that parallel the nervous system (Gustafson, 1930; Kudenov, 1974). All other known modern day polychaetes reported to date lack these features, although a few interstitial forms may also have two pairs of nerve cords.

Specific characteristics having taxonomic importance include the number of body segments; morphology of the prostomium; development of prostomial appendages; eyes; caruncle; palps; setiger 1; parapodia of middle body segments; the distribution, development and placement of branchiae, especially in relation to lateral parapodial cirri; the number of setal tiers in the notopodia; the notosetae from superior and inferior regions of each tier; the neurosetae from various aspects of the neuropodia; development and numbers of noto- and neuroaciculae; and the development and kinds of anal cirri.

Taxonomic History

The first two euphrosinids to be described in western literature were assigned to the genus *Euphrosine* by Savigny from the Red Sea (Egypt) in a manuscript that was published by Lamarck (1818). A type for the genus was not designated until Hartman (1959) cited *E. myrtosa* Savigny, 1818. The correct authority is Lamarck, 1818, as noted by Pettibone (1963) and Kudenov (1992). The primary systematic study for euphrosinids is that of Gustafson (1930:305-471) who focused on comparative anatomy. Other important references for this group have been summarized by Kudenov (1987, 1992).

As is true for the amphinomids (Chapter 7, this volume), euphrosinids are not well understood systematically. The Order Amphinomida to which the euphrosinids are assigned is clearly monophyletic (Fauchald, 1974, 1977) and not closely related to any other extant Order of the Polychaeta (Clark, 1969). Only recently has the Order Amphinomida been restricted to include the families Amphinomidae and Euphrosinidae by Fauchald, 1977 (see also Pettibone, 1982); the spintherids were removed and placed into a separate Order. Prior to 1977, the Order Amphinomida embraced amphinomids and euphrosinids either as the family Amphinomidae containing two subfamilies, or as two separate families which applies here. Historically, spintherids were included because of their superficial resemblance to the other taxa (Manton, 1967). Kudenov (1991) added a new family, Archinomidae, to the Amphinomida, based on a single, unusual deep-sea species, *Archinome rosea* (Blake, 1985), from the Galapagos Rift hydrothermal vents. Kudenov (1991) provides a brief historical overview of the Amphinomida.

In all, three genera (*Euphrosine*, *Euphrosinella* and *Euphrosinopsis*) and over 55 species of euphrosinids generally considered to be valid have been described (Hartman, 1959, 1965; Fauchald, 1977; *Palmyreuphrosine* Fauvel is here excluded from the above account of morphology and taxonomic history. Its affinities are quite uncertain and will be reported on elsewhere). These numbers will change as each genus is revised, based on type specimens and new collections. For example, Kudenov (1992) includes descriptions of one new genus and eight new species of euphrosinids from Antarctica.

Biology

Euphrosinids seem to be most commonly distributed in cold shelf to abyssal habitats and polar seas; a number have also been reported from shallow-water tropical and subtropical habitats. Most euphrosinids tend to be small and cryptic, especially in intertidal and shallow subtidal habitats where they are associated with sponges, corals, barnacles, kelp holdfasts or found in rock crevices. Otherwise they tend to be associated with sandy, shelly or silty-muddy sediments in considerable depths. Their unusual body shape and that of the anal cirri, strongly suggests that some species may be epibiotic or ectoparasitic, although this needs to be confirmed.

Most euphrosinids are considered to move somewhat faster than amphinomids and all are thought to be carnivorous (Fauchald and Jumars, 1979), feeding on sponges, corals, and hydrozoans. Deep-water species from both the Atlantic and Antarctic Oceans also feed on foraminifera. The feeding habits of euphrosinids, however, are poorly known (Fauchald and Jumars, 1979).

When disturbed, most species assume a defensive posture by rolling their bodies into a coil, displaying expansive fascicles of noto- and neurosetae, and looking very much like a hedgehog or porcupine.

Relatively little is known about the reproductive biology of euphrosinids. Specimens containing gametes and having delicate spurred capillary neurosetae are occasionally noted in the literature (Kudenov, 1992). The rostraria larva may be attributable to euphrosinids, although neither the complete reproductive or larval cycle has been described for any species of this family to date.

Key to the Species of Euphrosinidae

1A. Prostomium with 3 antennae (Fig. 8.1B); caruncle generally attached to dorsal body wall (Figs. 8.1A, 8.3A) .... *Euphrosine* 2

1B. Prostomium with 5 antennae; caruncle generally not attached to dorsal body wall .... *Euphrosinella paucibranchiata*[2]

2A. Branchiae sessile, numbering 6-7 pairs per segment where best developed in midbody segments, each usually terminating in 2, sometimes 1 or 3, cirriform filaments (Figs. 8.3D, E) .... *Euphrosine bicirrata*

2B. Branchiae arborescent, dichotomous (Fig. 8.1D), numbering 5 pairs per segment where best developed in midbody segments, each terminating in 4-5 distal branches, each branch having 8-10 subdistally expanded sugar beet-like tips (Fig. 8.1E) .... *Euphrosine arctia*

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[2] Although *Euphrosinella paucibranchiata* (Hartman) was not found in the present material, it was originally described from submarine canyons off southern California, and is included in the key. It will be redescribed elsewhere.

Description of Species

The Euphrosinidae is a relatively small and seldom encountered family. The fauna of Santa Maria Basin and Western Santa Barbara Channel includes two species:

Euphrosine arctia Johnson, 1897
Euphrosine bicirrata Moore, 1905

Specimens originally identified as *Euphrosine* species A are juvenile specimens of *E. bicirrata*. Measurements and counts of segment numbers of the present materials are cited in closed parentheses in the descriptions that follow.

***Euphrosine arctia* Johnson, 1897**

Figures 8.1, 8.2

Euphrosyne arctia Johnson, 1897:159, pl. 5, figs. 5-7.
Euphrosine arctia: Hartman, 1940:208-209; 1968:207-208, figs. 1-4.—Banse and Hobson, 1974:37, Fig. 7.
Not *Euphrosine arctia*: Monro, 1930:34-36, fig. 4a-e; 1936:79; 1939:93-94.—Hartman, 1964:45, pl. 14, figs. 1, 2. [=*E. monroi* Kudenov, 1993].

Material Examined. California, Santa Maria Basin, off Purisima Point, Sta. BRA-20, 90-130.5 m, from rocks, (1, USNM).—Western Santa Barbara Channel, off Point Conception, Sta. BRC-2, 110-126 m, from a rock (1, SBMNH).

Description. Reported less than 20 mm long (7mm); width of present specimens 2.2 mm, 3 mm without setae; segments numbering 22 (23). Body light tan in alcohol, lacking pigmentation pattern; color in life ochraceous, with broad red middorsal stripe about 0.25x body width.

Prostomium well developed, with two pairs of eyes (Fig. 8.1A-C); dorsal pair largest, each eye present lateral and basal to ceratophore of median antenna; ventral pair about one-tenth size of dorsal pair, located between and dorsal to palpal antennae, at extreme anteroventral prostomium. Median antenna short, about 0.2x length of caruncle, ceratophore tapering, about 2x longer than basal width, distal style cirriform, about 0.5x length of ceratophore (Fig. 8.1B). Palpal antennae long, cirriform, about as long as style of median antenna (Fig. 8.1C). Caruncle appearing bilobed dorsoventrally, lobes attached to one another through middle of setiger 5, free from one another thereafter; dorsal lobe with median keel, 3 pairs of lateral ridges, each with single rows of 12-13 ciliated tufts, extending to middle of setiger 6; ventral lobe to anterior margin setiger 6 (Fig. 8.1B). Palps large, elliptical, paired, separated by midventral groove leading directly to mouth (Fig. 8.1C). Mouth ventral, opening between setigers 2-3, latter forming posterior lip of mouth (Fig. 8.1C).

Parapodia biramous, with spreading notosetal and whorl-like neurosetal fascicles separated by interramal gap occupied by the fifth branchia; all with dorsal, lateral and ventral cirri from setiger 1 to end of body (Fig. 8.1D, E). Notopodia not raised above dorsum. Neuropodia resembling distally round, circular pads (Fig. 8.1D).

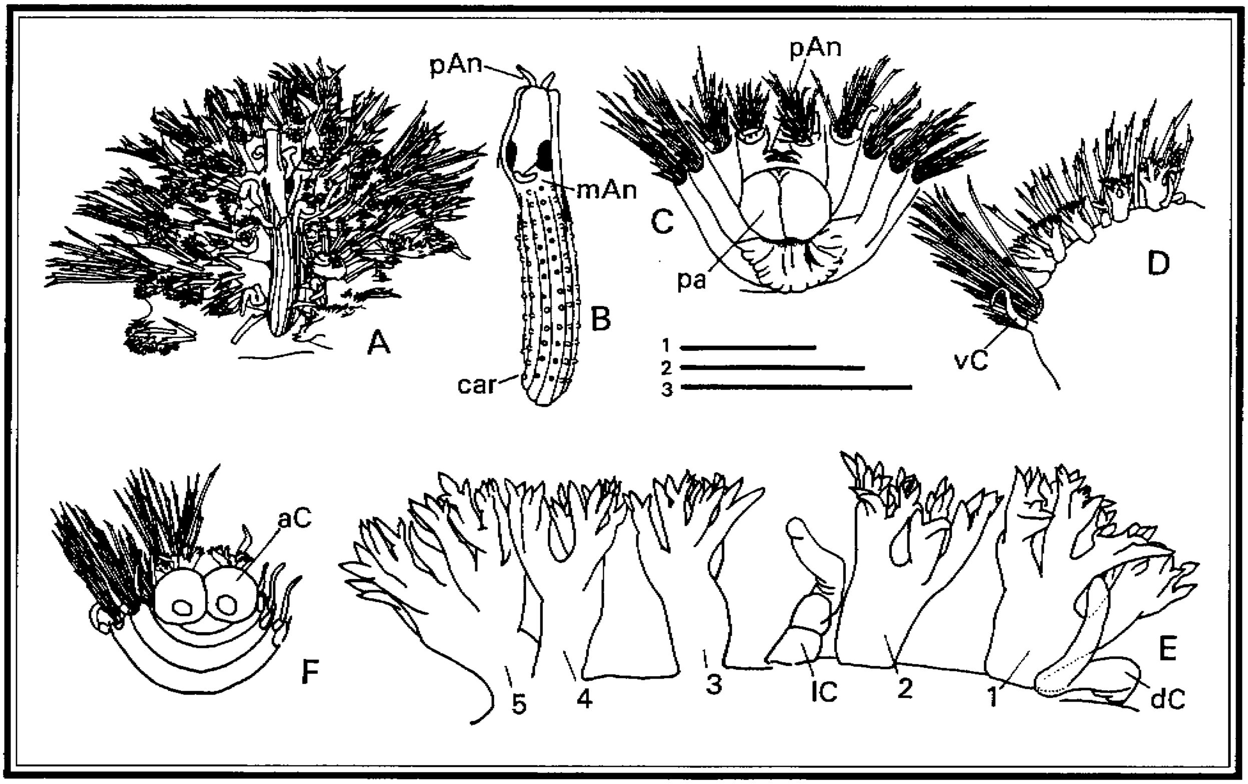

Figure 8.1. *Euphrosine arctia*: A, anterior end, dorsal view; B, prostomium, dorsal view; C, anterior end, anteroventral view; D, left setiger 13, posterior view; E, Branchiae Nos. 1-5, depicting dorsal and lateral cirri, posterior view; F, pygidium, posteroventral view. All scales = 1 mm. Scale 1, A, C, D, F; 2, E; 3, B.

Notosetae all orderly, short, uniform in appearance, hollow, arrayed in a continuous outer whorl surrounding inner tier, of 2 basic kinds: bifurcate and ringent notosetae. Bifurcate notosetae present (Figs. 8.2A-D) in outer whorl (tiers 1, 3), all short, of uniform length, clear, glass-like in appearance, with long prongs straight, stout, distally blunt, having smooth cutting surfaces; short prongs relatively short, stout, all distally entire (Figs. 8.2A-D); with regular spiral pattern of rectangular file-like teeth on shaft of tier 3 notosetae (Fig. 8.2E), absent from tier 1 notosetae; ratio of long to short prongs decreasing within a fascicle, ranging from 4.1:1 superiorly to 3.9:1 inferiorly in tier 1, and increasing slightly from 3.9:1 to 4.1:1 in tier 3.

Ringent notosetae in tier 2, all category IIA, of 2 different lengths and shapes: long, heavy forms (Fig. 8.2F), similar in general appearance to bifurcate notosetae (Fig. 8.2A-D), numbering 4 per tier, arising from superiormost part of tier 2; short, light forms (Fig. 8.2G, H), characteristic of category IIA ringent notosetae (Kudenov, 1987), present throughout remainder of tier 2, alternating with long, heavy ringent setae superiorly; all with regular spiral pattern of minute, scale-like teeth on shaft (Fig. 8.2I); b:a ratios (Kudenov, 1987:184, Fig. 2) varying slightly within a fascicle, ranging from .68 superiorly to .66 inferiorly.

Neurosetae of one kind, all bifurcate, hollow, longest in superior half of neurofascicle, these longer than notosetae, becoming shorter inferiorly (Fig. 8.2J-S); long prongs smooth, characteristically narrow and curved, appearing sword-shaped, those along posterior outer margins distally bidentate (Fig. 8.2S); with regular spiral pattern of poorly defined rectangular file-like teeth on some superior neurosetae (Fig. 8.2T); ratio of long to smooth prongs changing within a fascicle, ranging from 4.9:1 superiorly to 5.4:1 centrally to

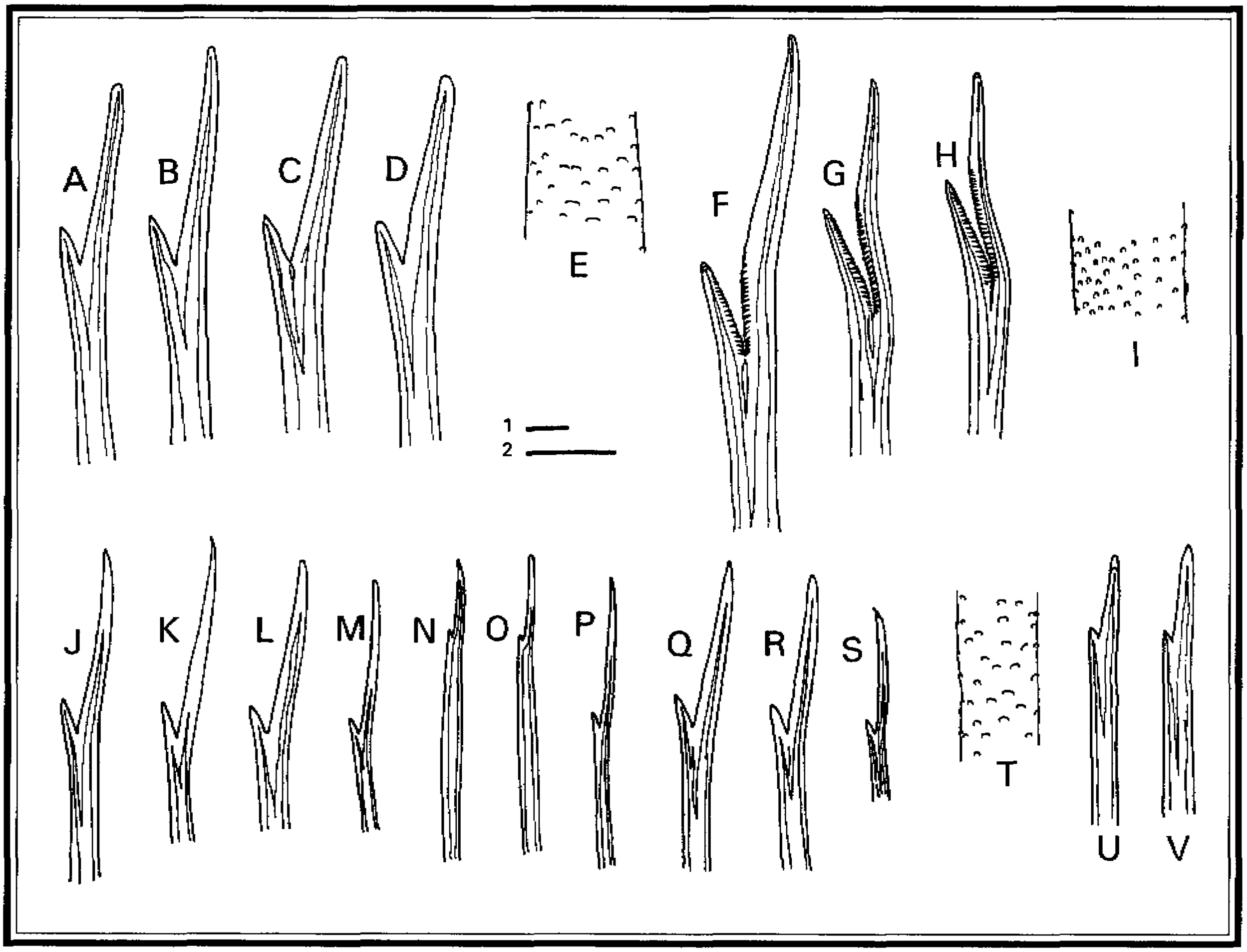

Figure 8.2. *Euphrosine arctia*: A, superior notoseta, tier 1; B, inferior notoseta, tier 1; C, superior notoseta, tier 3; D, inferior notoseta, tier 3; E, middle notoseta, detail of shaft, tier 3; F, long superior ringent notoseta, tier 2; G, short superior ringent notoseta, tier 2; H, short inferior ringent notoseta, tier 2; I, ringent notoseta, detail of shaft, tier 2; J, long superior neuroseta; K, long neuroseta from center of fascicle; L, long inferior neuroseta; M, short inferior neuroseta; N, subinferiormost neuroseta; O, inferiormost neuroseta; P, short anterior neuroseta; Q, long anterior neuroseta; R, long posterior neuroseta; S, short posterior neuroseta; T, superior neuroseta, detail of shaft; U, anterior acicula; V, superior acicula. Scales: 1 = .001 mm, E, I, T; 2 = .005 mm, A-D, F-H, J-S, U-V.

14.4:1 inferiorly (Fig. 8.2J-O), and from 8.5-4.8:1 anteriorly to 5.4:1 centrally to 4.8-7.4:1 posteriorly (Fig. 8.2K, P-S). Neuroaciculae bifurcate, numbering 5-6 per fascicle, present in anterosuperior row, prong ratios ranging from 6.6-6.8:1 (Fig. 8.2U,V).

Branchiae present from setiger 1 to end of body, numbering 5 per segment where best developed in midbody segments, slightly less than 0.5× length of notosetae, 0.67 to 0.75× length of dorsal, lateral cirri; dichotomously branching 2 to 2.5×, trunks and branches stout, short, terminating in characteristically thick distally pointed and subterminally enlarged sugar beet-shaped lobes (Fig. 8.1A,D,E) Lateral cirri arising between gills 2-3.

Paired anal cirri terminal, inflated, with ventral cup-shaped depression in each cirrus, about as wide as long; anus terminal (Fig. 8.1F).

Biology. Relatively little is known about the biology of *Euphrosine arctia*. It was originally obtained from fish traps set at 100 and 55 m in Monterey Bay. The specimens from the Santa Maria Basin were collected from rocks at depths of 69-135 m.

Remarks. Type specimens of *Euphrosine arctia* Johnson, 1897 are apparently no longer available. The above description must therefore temporarily characterize *E. arctia* until adequate materials from the type locality of Monterey Bay can be obtained. However, the Santa Maria Basin is adjacent to Monterey Bay, and the specimens on which this description is based generally agree well with Johnson's description.

Johnson's original description of *Euphrosine arctia* is generally accurate as far is it goes, but is quite incomplete. For example, his description did not include the prostomium, parapodia and setal fascicles, and the branchia he illustrated has led to confusion in the literature (Kudenov, 1992).

Perhaps the most glaring discrepancy between Johnson's description and the present specimens is that Johnson described and illustrated one kind of ringent notoseta for *E. arctia*. In fact, there are two variants of the category IIA ringent notoseta: a few long, heavy forms reminiscent of bifurcate notosetae of *E. abyssalis* Kudenov, 1992, confined to superior notofascicles that alternate with the more numerous short, light forms that are present throughout the tier. Johnson illustrated the latter. Given this highly characteristic feature, *E. arctia* can be readily identified.

This species is further characterized by having a bilobed caruncle (K-1) extending to midsetiger 6, a very short median antenna, and 5 pairs of arborescent branchiae per midbody segment where the gills are best developed. Branchial trunks and branches are stout, branching dichotomously 2 to 2.5×, terminating in stout, subdistally enlarged, sugar beet-shaped lobes. Johnson's branchial illustration is similar to those presented above in general form; his portrayal of the distal branchial lobes is exactly what one would expect to see if the gill were compressed on a slide by coverglass.

Euphrosine arctia is assigned to Group II (Kudenov, 1987:187, 189), which is characterized by *Euphrosine* species having ringent notosetae (category IIA) and dorsoventrally bilobed caruncles (category K-1), and is similar to five other species in having dichotomously branching branchiae with subterminally expanded tips. These five species include: *E. armadillo* Sars; *E. capensis* Kinberg; *E. dumosa* Moore; *E. maorica* Augener; and *E. monroi* Kudenov.

Euphrosine arctia is an example of how a poor or incomplete description can become convoluted (Kudenov, 1993). Briefly, Monro (1930, 1936, 1939) identified *E. arctia* as a species from Antarctica primarily on branchial and ringent notosetal traits. Monro also suggested that *E. armadilloides* was the senior synonym of *E. arctia*, but deferred synonymizing the two, which Hartman did in 1964. Orensanz (1972) later suspected that Monro's citations actually represented another species, which was confirmed by Kudenov (1993).

Distribution. California.

Euphrosine bicirrata Moore, 1905

Figures 8.3-8.4

Euphrosyne bicirrata Moore, 1905:532-534, pl. 34, figs. 8-12; 1908:339; 1911:234.—Berkeley, 1923:211.—Hartman, 1940:208, 209, 210-211, pl. 32, figs. 21-23.
Euphrosine bicirrata: Hartman, 1968:211-212, figs. 1-4.—Banse and Hobson, 1974:37, Fig. 7g;

Material Examined. California, Santa Maria Basin, off Purisima Point, Sta. BRA-13 A/B, 92-100 m, from a rock (1, USNM); Sta. BRA-14, 96-105 m, from a rock (1, SBMNH); Sta. BRC-14, 96-105 m, from a rock (1, SBMNH); Sta. BRA-20, 90-130.5 m, from a rock (1, USNM).

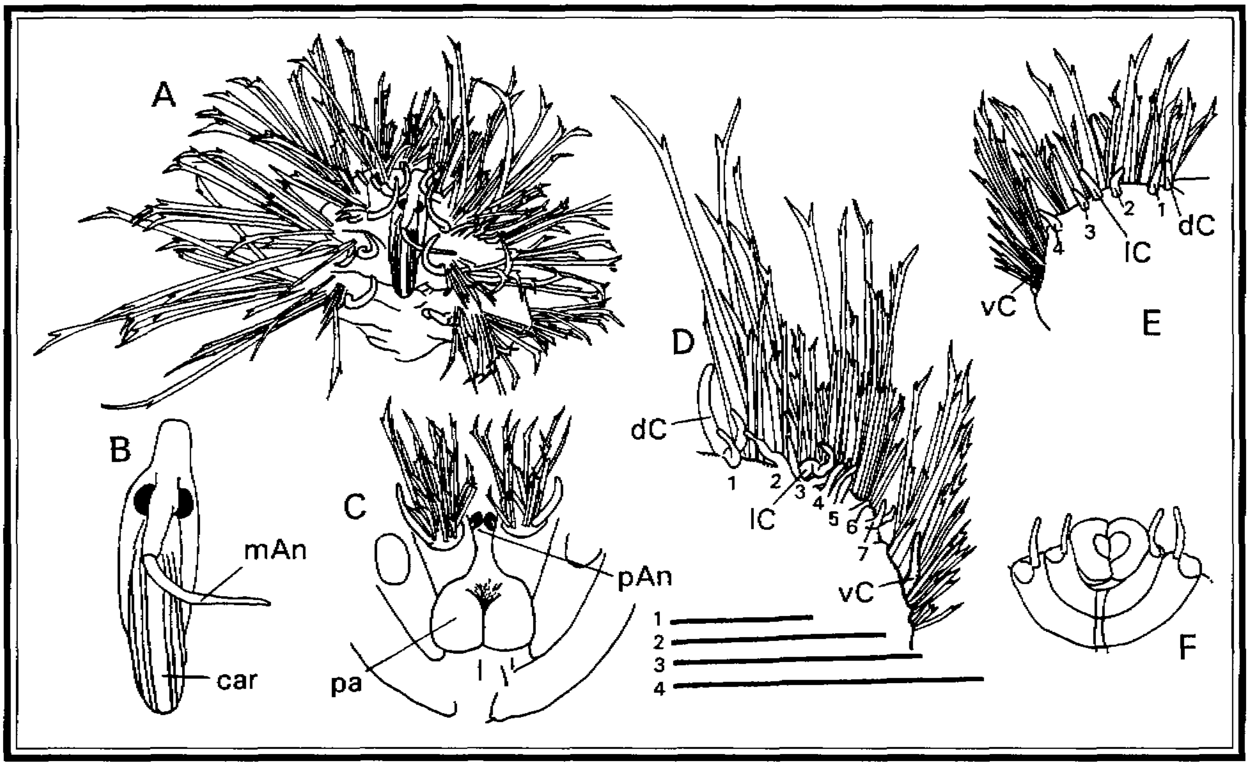

Figure 8.3. *Euphrosine bicirrata*: A, anterior end, dorsal view; B, prostomium, dorsal view; C, anterior end, anteroventral view; D, right segment 9, posterior view; E, left setiger 12, posterior view; F, pygidium, posteroventral view. All scales = 1 mm. Scale 1, A; 2, D-E; 3, C-F; 4, B.

Description: Reported up to 20 mm long (4.5 mm), 6.5 mm wide (2 mm) without setae, for 23-25 (19) segments. Body light tan in alcohol, lacking pigmentation pattern, usually coiled, resembling bristly balls.

Prostomium well developed, with 2 pairs of eyes (Fig. 8.3A-C); dorsal pair largest, lateral and basal to ceratophore of median antenna (Figs. 8.3A, B); ventral pair about half as large, between, dorsal to palpal antennae (Fig. 8.3C). Median antenna nearly as long as caruncle, ceratophore 2x longer than basal width, distal style cirriform, 2.5x longer than ceratophore (Fig. 8.3B). Palpal antennae short, stout, distally pointed (Fig. 8.3C). Caruncle appearing bilobed dorsoventrally, both lobes totally attached to one another from setigers 2 to the middle of setiger 4; dorsal lobe with median keel and 3 pairs of lateral ridges, extending to anterior third of setiger 5 (setiger 4), ventral lobe to posterior one-third of setiger 4 (mid-setiger 3) (Fig. 8.3A,B). Palps paired, each ovoid, separated by midventral groove leading directly to mouth (Fig. 8.3C). Mouth ventral, opening between setigers 2-3, forming posterior lip of mouth (Fig. 8.3C).

Parapodia biramous, with spreading notosetal and whorl-like neurosetal fascicles separated by narrow interramal gap occupied by gill 7 (Fig. 8.3D); all with dorsal, lateral and ventral cirri from setiger 1 to end of body. Notopodia not raised above dorsum (Fig. 8.3D,E). Neuropodia resembling flat circular pad (Fig. 8.3D,E).

Notosetae exceedingly long, much longer than neurosetae, radiating in various directions from fascicle, all hollow, arrayed in continuous outer whorl surrounding 2 inner tiers (Fig. 8.3D,E), of 2 basic kinds: bifurcate and ringent notosetae.

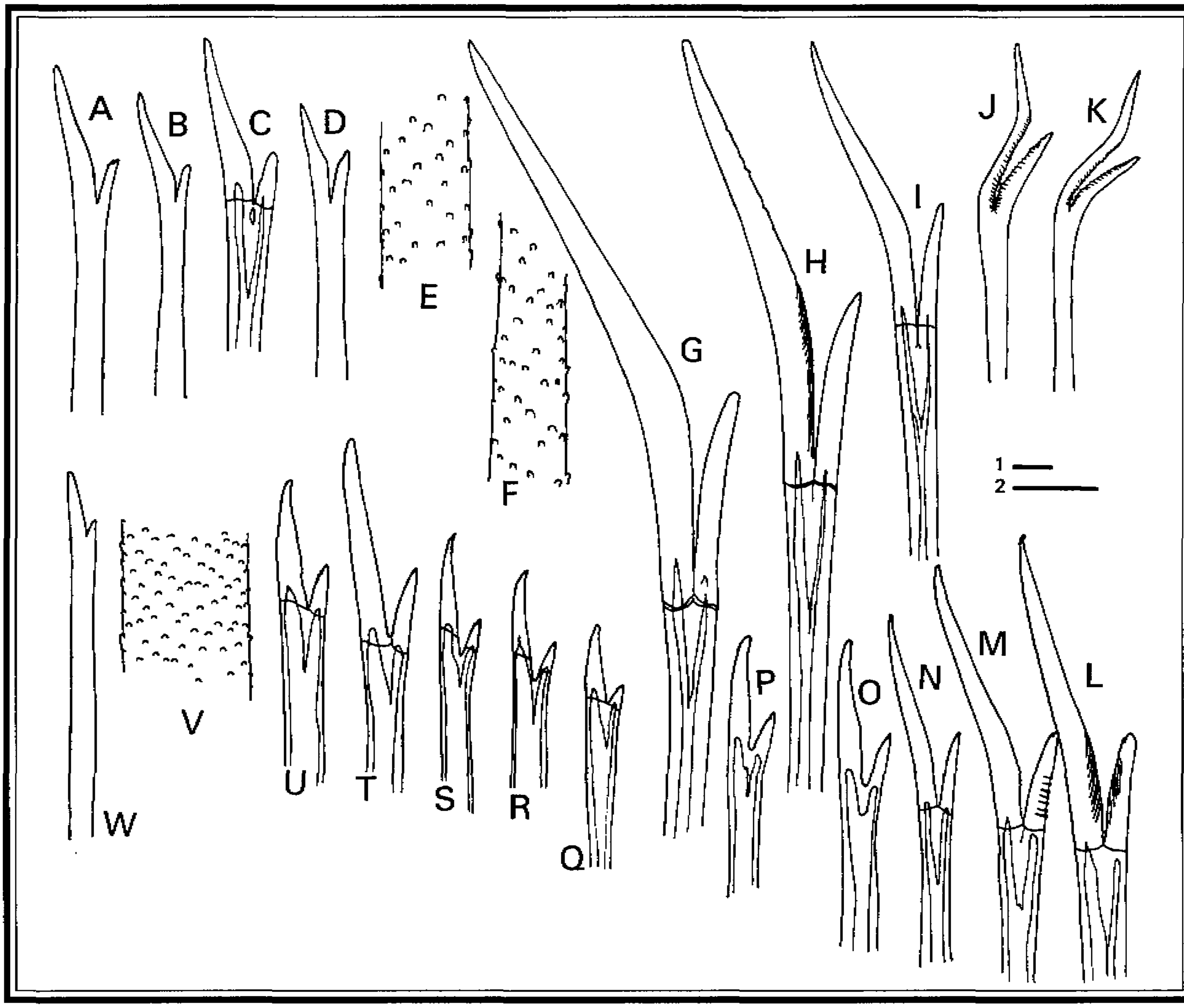

Figure 8.4. *Euphrosine bicirrata*: A, superior notoseta, tier 1; B. inferior notoseta, tier 1; C, superior notoseta, tier 4; D, inferior notoseta, tier 4; E, superior notoseta, detail of shaft, tier 4; F, inferior notoseta, detail of shaft, tier 4; G, superiormost notoseta, tier 2; H, superior notoseta, tier 2; I, inferior notoseta, tier 2; J, superior ringent notoseta, tier 3; K, inferior ringent notoseta, tier 3; L, largest superiormost neuroseta; M, superior neuroseta; N, long neuroseta from center of fascicle; O, same, from point below center of fascicle; P, subinferiormost neuroseta; Q, inferiormost neuroseta; R, short anterior neuroseta; S, long anterior neuroseta; T, long posterior neuroseta; U, short posterior neuroseta; V, superior neuroseta, detail of shaft; W, anterior acicula. Scales: 1 = .001 mm, E, F, V; 2= .005 mm, A-D, G-U, W.

Bifurcate notosetae present in outer whorl (tiers 1, 4) and anteriormost inner tier (tier 2); all opaque white proximal to prongs, latter clear, glass-like, heavily calcified (Fig. 8.4A-D); notosetae of tiers 1 and 4 half as long as those of tier 2, with long prongs having characteristic change in curvature at a point about equal to length of short prong from base of cleft (Fig. 8.4A-D); short prongs relatively well developed, generally entire except bidentate in 1-3 superiormost setae of tier 1 (Fig. 8.4A); with regular spiral pattern of square file-like teeth on shaft of tiers 1, 4 notosetae (Fig. 8.4E,F); ratio of long to short prongs increasing slightly within a fascicle, ranging from 3:1 superiorly to 3.1:1 inferiorly in tier 1 (Fig. 8.4A,B), and decreasing from 3.2:1 to 1.9:1 in tier 4 (Fig. 8.4C,D). Notosetae of tier 2 longest, best developed (Fig. 8.4G,H), generally longer than body width, interfacing with similar notosetae of same and neighboring segments; long prongs distally smooth, sometimes subtly dentate, having characteristic change in curvature similar to those of tiers 1, 4, proximally striated (Fig. 8.4C); short prongs very well developed; file-like teeth not present on shafts; ratio of long to short prongs decreasing within a fascicle, ranging from 3.2:1 superiorly (Fig. 8.4G,H) to 2.3:1 inferiorly within tier 2 (Fig. 8.4I).

Ringent notosetae (category IIB) present in tier 3 (Fig. 8.4J,K), decreasing in size inferiorly within a fascicle; b:a ratios (Kudenov, 1987:184, Fig. 2) constant at .97:1 for both superior and inferior ringent notosetae of tier 3.

Neurosetae longest superiorly, becoming abruptly short in middle and inferior regions of fascicle, all hollow, arrayed in tuft-like whorl; all of one kind, bifurcate, generally having characteristic appearance similar to bifurcate notosetae with opaque white bands proximal to clear, heavily calcified prongs (Fig. 8.4L-V); nearly all with short prong distinctly bidentate; some neurosetae unusual in having ringent-like dentitia on inner surface of long and outer surface of short prongs (Fig. 8.4L); with regular spiral pattern of minute file-like teeth well developed on all neurosetae in superior half of fascicle (Fig. 8.4V); ratios of long to short prongs changing within a fascicle, ranging from 2.8:1 superiorly to 2.5:1 centrally to 2.6-3.3:1 inferiorly (Fig. 8.4L-Q), and from 2.5-2.8:1 anteriorly to 2.5:1 centrally to 2.7:1 posteriorly (Fig. 8.4N,O,R-U). Neuroacicula bifurcate, numbering 4-5 per fascicle, present in anterosuperior row, prong ratios around 3.4:1 (Fig. 8.4W).

Branchiae present from setiger 1 to end of body, numbering 6-7 pairs per segment where best developed in midbody segments, around 0.1× length of longest notosetae, 0.5× length of dorsal and lateral cirri; having 2 cirriform filaments per gill, occasionally one, sometimes three in adults, only single filaments in juveniles. Branchiae unevenly spaced from one another, with large gap present between gills 1-2 especially conspicuous in juveniles. Lateral cirri arising between gills 2-3, all closely associated.

Paired anal cirri terminal, cup-shaped, about as long as wide; anus terminal (Fig. 8.3F).

Biology. Relatively little is known about the biology of *Euphrosine bicirrata.* It has been collected from depths of 18-369 fms in green mud, and coarse sand-shells-rock. Prong lengths and ratios of bifurcate notosetae in *E. bicirrata* vary systematically along both the body axis and within setal fascicles in relation to body size, based upon univariate and multivariate analysis of covariance (Vogt and Kudenov, 1994).

Remarks. *Euphrosine bicirrata* is a highly characteristic species which can be readily identified by the presence of bifurcate notosetae that tend to: (1) be longer than the width of the body; (2) interface with one another to completely conceal branchiae, cirri, prostomium, caruncle and dorsum; (3) have very well developed short prongs; (4) have fine parallel striae on the proximal cutting surface of the long prong; (5) be calcified over both distal prongs; (6) have a deep cleft between both prongs; and (7) have a characteristic shape.

Its neurosetae are, perhaps, even more characteristic in having (1) the short prong of most setae distally bidentate; and (2) some of the larger neurosetae with ringent-like teeth on the inner surface of the long prong, and outer surface of the short prong. The short neurosetal prong in most described species of *Euphrosine* is entire; *E. setosissima* may be the only other congener suspected of having the short neurosetal prongs distally bidentate (Kudenov, 1993). In addition, no other described *Euphrosine* species is known to have neurosetae with the ringent-like notosetal dentitia described above for *E. bicirrata* (Kudenov, 1987; 1993). It may eventually be demonstrated that this kind of neuroseta represents a second category of euphrosinid neurosetae; until then, it is here considered to be a bifurcate neuroseta.

Branchial features of adult *E. bicirrata* are easily distinguishable from those of other eastern Pacific *Euphrosine* species. However, the branchiae of juvenile *E. bicirrata* are present as single, cirriform filaments, and highly reminiscent of such species as *E. armata* Kudenov and *E. setosissima* Ehlers. Several obvious features allow ready identification of such juvenile *E. bicirrata*: characteristic setal morphology; the relatively large spacing between gills 1-2; and the tight association between gills 2-3 and the lateral cirri.

Euphrosine bicirrata is assigned to Group II (Kudenov, 1987:187, 189), which is characterized by having ringent notosetae (category IIA) and dorsoventrally bilobed caruncles (category K-1), and is similar to seven other species in having dichotomously branching branchiae having cirriform filaments that lack subdistally expanded tips. These seven species include: *E. abyssalis* Kudenov; *E. borealis* Örsted; *E. echidna* Kudenov; *E. heterobranchia* Johnson; *E. notialis* Ehlers; *E. orientalis* Gustafson; and *E. superba* Marenzeller.

Distribution. Northeast Pacific: Alaska, British Columbia, Washington, Oregon, California, and Mexico (Gulf of California).

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9. Family Onuphidae Kinberg, 1865

by

Brigitte Hilbig[1]

Introduction

Onuphids are midsized to large worms with dorsoventrally flattened bodies and a distinctive array of prostomial appendages, including five occipital antennae, two frontal palps, and two labial palps. This arrangement of antennae and palps is consistent in all onuphids, in contrast to the morphologically similar eunicids where the number of antennae varies from one to five. The first few segments, particularly the parapodia, are often specialized and, in combination with the head appendages, make the Onuphidae the most spectacular and morphologically diverse family among the Eunicida. The largest onuphids are the Australian beachworms (*Australonuphis*), living representatives of which have been known to reach a length of 300 cm with more than 1000 segments.

Morphology

The prostomium is usually round to pentagonal and, because of its relatively small size, is often obstructed by the ceratophores of the occipital antennae (Fig. 9.1A). The antennae are arranged in a crescent that may be closed to a circle by the small, simple frontal palps (also called frontal antennae) that arise from the frontal margin of the prostomium. The ceratophores of the occipital antennae are of varying length and usually ringed (rarely smooth); the number of rings is often important for species discrimination, and the length of the ceratophores relative to the prostomial length is used to distinguish genera. Another pair of simple, short appendages are the ventrally situated labial palps (Fig. 9.1C). Eyes are often present, one pair near the bases of the frontal antennae and one pair between the bases of the outer (anterior) and inner (posterior) lateral antennae. The posterior pair is usually the larger, and may be lensed in a few taxa. A pair of crescentic to straight nuchal grooves is located near the posterior margin (Fig. 9.1B). The peristomium consist of a single apodous ring that may or may not bear a pair of tentacular cirri, usually on the anterior margin.

The eversible and muscular pharynx is armed with mandibles and five maxillae. The mandibles consist of two elongate shafts that bear a roughly crescentic, often dentate, calcified cutting plate (Fig. 9.1D); the remains of the juvenile mandibles can often be seen as black, L-shaped structures in the cutting plate of the adult ones. The maxillae are asymmetrical; they typically have short and wide, often square carriers linked to falcate MI enveloping a pair of triangular MII with serrated cutting edge and a left MIII of similar shape and dentition (the right MIII are absent). Anterior to MI-MIII, a pair of rounded MIV with serrated cutting edges and a pair of small, usually unidentate or smooth MV are located. The right MIV is often larger than the left one, bears more teeth, and extends further back than the latter (Fig. 9.1E). A pair of small MVI is present in a few genera. As in the other eunicemorph families, the morphological details of the maxillary apparatus are among the most important taxonomic characters for species discrimination.

[1] ENSR Consulting and Engineering, 89 Water Street, Woods Hole, Massachusetts 02543

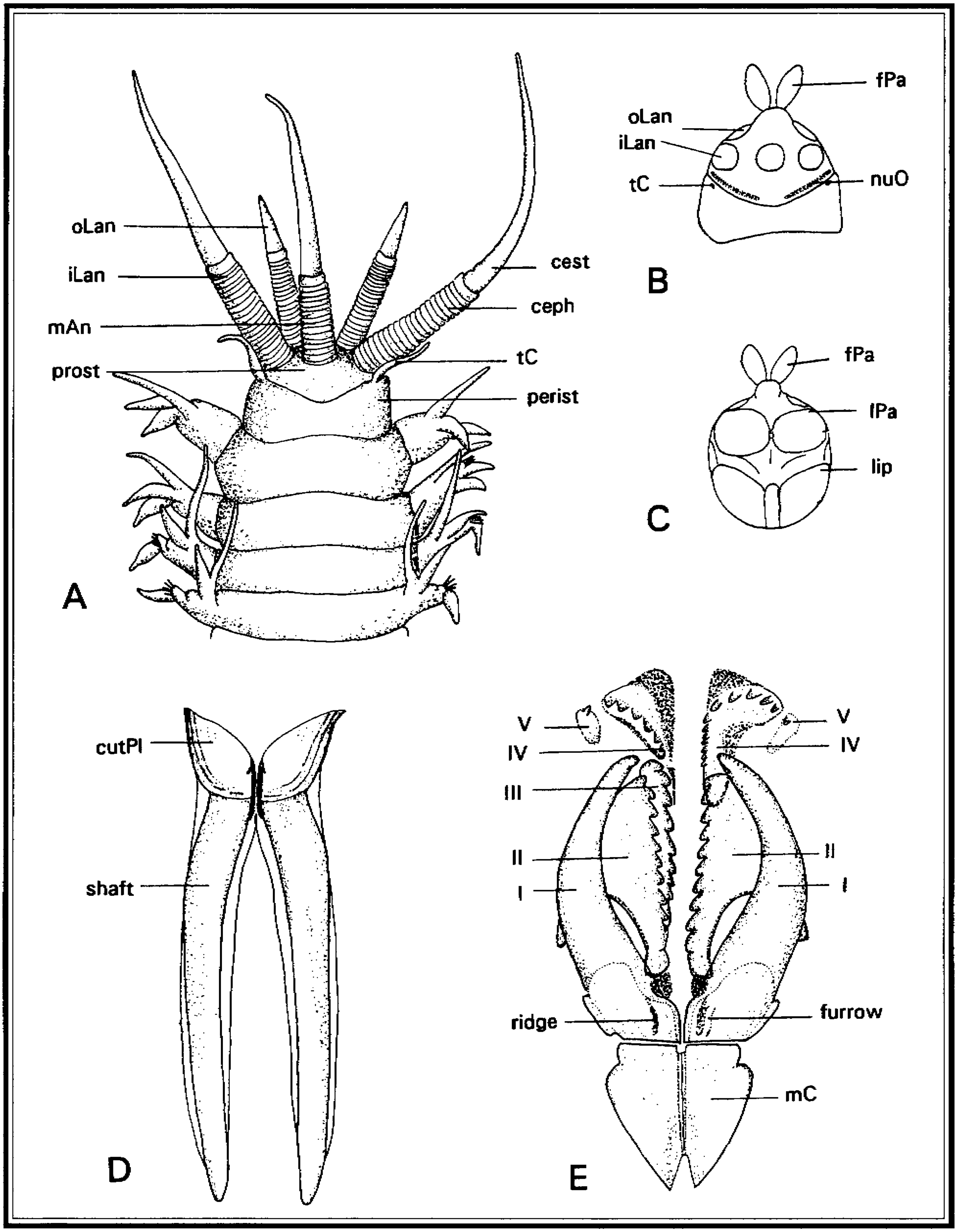

Figure 9.1. Morphological features of onuphids: prostomial and peristomial appendages and jaws. A, anterior end, dorsal view; B, C, schematic dorsal and ventral views of prostomium; D, mandibles; E, maxillae. (all from Paxton, 1986a).

The anterior 1-8 setigers usually bear modified parapodia that are directed forward rather than to the sides, and often displaced dorsally (*Hirsutonuphis*) or ventrally (*Americonuphis*). In some genera, the first few parapodia are extremely prolonged and project well beyond the prostomium (*Longibrachium*), while in others they extend about as far as the frontal palps and differ from unmodified parapodia only slightly in the relative length of dorsal and ventral cirri and postsetal lobes. The genus *Nothria* is characterized by bluntly rounded, fleshy, auricular presetal lobes on the modified parapodia (Fig. 9.2A). Ventral cirri are generally present in a small number of anterior segments and replaced by glandular pads in subsequent setigers. The position of the first parapodium with padlike ventral cirri is used for species discrimination. Dorsal cirri are present throughout, although they are largest in anterior setigers. The bases of the dorsal cirri are the only remainders of the notopodia, supported by a bundle of fine notoaciculae that extends into the proximal part of the dorsal cirrus (Fig. 9.2B). There are no notosetae. Branchiae are usually present and may be simple, pectinate, or spiraled (*Diopatra*) (Fig. 9.2C).

The setae include a wide variety of simple and compound limbate (Fig. 9.2F), and pectinate setae (Fig. 9.2D, E) and compound, pseudocompound, and simple hooded hooks (Fig. 9.2G-K). Their distribution along the body and morphological details, such as number of teeth, are of great taxonomic importance for genus and species discrimination. The division of the onuphids into two subfamilies, the Onuphinae and Hyalinoecinae, is based on the presence of a lower fascicle of simple limbate setae throughout (Hyalinoecinae) or up to the first setiger with subacicular hooks (Onuphinae). In the first case, the subacicular hooks are positioned in the middle of the fascicle ("intrafascicular hooks" of Fauchald (1982)), in the second case these hooks occupy the ventralmost position of each fascicle.

The presence of so many countable morphological features makes the establishment of species discriminating characters very simple; however, some of these characters are growth- or size-dependent (see below), and individual variability has to be kept in mind when following keys or descriptions.

Taxonomic History

Due to their generally large size and richness of morphological features, onuphid species have largely been valid since the majority were described about 100 to 150 years ago. In contrast, generic concepts have been changed several times, and the establishment of monophyletic taxa with clearly defined character sets was not achieved until the early 1980's when Fauchald (1982a) and Paxton (1986a, b) published their invaluable revisions of the family. The onuphids now include 22 genera and about 220 species. For more details, the reader is referred to the excellent accounts by Fauchald (1982a) and Paxton (1986a, b).

Distribution and Biological Notes

Onuphids are distributed worldwide and in can be found from the intertidal to abyssal depths. Fauchald (1982a) provided a comprehensive overlook over distributional patterns of some onuphid genera, and it appears that the eastern Pacific Ocean is a center of radiation for this family. All onuphids are tubicolous, although not necessarily sessile; Orensanz (1990) defined three different ecotypes, including (1) species that live partially buried in the sediment and produce permanent tubes with a more or less elastic inner layer and an outer layer consisting of sediment or shell particles (many genera); (2) species that can move around on the sediment and carry their tubes with them; these tubes are quill-like (*Hyalinoecia*) or flat, two-layered, with a cover of flat shell or rock particles (*Nothria*); and (3) species that are epibenthic scavengers on sandy beaches and produce delicate, elastic, temporary tubes (*Australonuphis*). The tubes are often much longer than the animal.

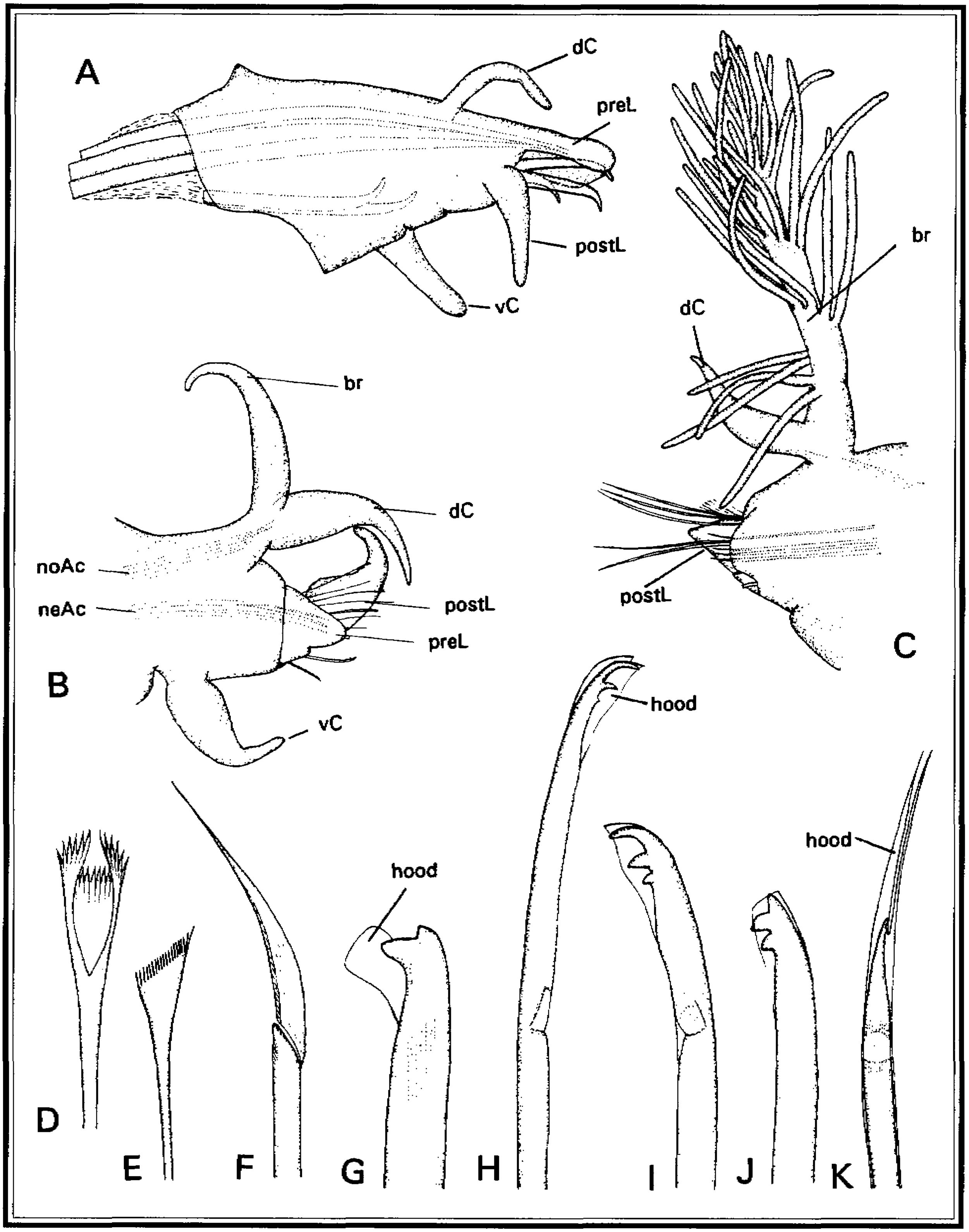

Figure 9.2. Morphological features of onuphids: parapodia and setae. A, first parapodium, *Nothria*; B, anterior parapodium, *Onuphis*; C, middle parapodium, *Diopatra*; D, E, scoop-shaped and flat pectinate setae; F, compound spiniger (*Mooreonuphis*); G, subacicular hook; H, I, pseudocompound hooks; J, simple hooded hook ("large median hook"); K, pseudocompound hook (*Paradiopatra*). (all from Paxton, 1986a).

Feeding habits of onuphids were summarized by Fauchald and Jumars (1979). From the often contradictory accounts in the literature, they concluded that most onuphids are probably ominvorous scavengers that may specialize in a certain food item if it is the only one available. Dayton and Hessler (1972) observed opportunistic behavior in *Hyalinoecia* spp.; several hundred specimens were seen to aggregate around a fish cadaver. At least some populations of *Diopatra ornata* seem to feed exclusively on kelp (Fauchald and Jumars, 1979).

The reproductive biology of onuphids is not well known; sexes are generally separate, and no asexual reproduction is known. According to the few existing investigations, eggs are generally large and yolky, and brood protection in the maternal tube seems to be common (Hsieh and Simon, 1987). Larvae are often non-pelagic, and the juveniles may stay in the parent's tube until they are about 17 to 20 setigers long; direct development is known for *Hyalinoecia araucana* (Carrasco, 1983). Many taxonomically important characters, such as the setae, jaws, parapodial cirri, and branchiae, differ in larvae and adults (Blake, 1975b; Paxton, 1986a; Hsieh and Simon, 1987); a synopsis of larval morphology of onuphids was compiled by Bhaud and Cazaux (1987). From these and other studies, it is clear that some characters used for species discrimination are only valid in adults; for example, gills are always first present on setigers 6-8, and the setiger of their first occurrence may move to a more anterior or posterior position during postlarval development; ventral cirri and postsetal lobes are cirriform and prominent in a smaller number of anterior parapodia in younger specimens. Pseudocompound hooks may occur in a greater number of anterior setigers with increasing body length, and special larval setae, reminiscent of eunicid compound setae, are present in very young individuals; subacicular hooks may start on a more anterior setiger in younger specimens. Fauchald (1982a, b) was the first to draw the attention of systematists to these growth dependent changes by providing tables and graphics depicting ranges of many key taxonomic characters. Some larval characters, such as the distribution of larval setae, may be species specific (Hsieh and Simon, 1987).

Key to the Onuphidae

1A. First three setigers greatly modified, with very long, slender, distally recurved hooks, with setal sacs extending back to setiger 50, at least through setiger 25; antennae no longer than first 2-3 setigers . ... *Rhamphobrachium longisetosum*

1B. Anterior setigers modified, but carrying pseudocompound or simple hooded hooks; at least inner lateral antennae longer than first 2-3 setigers 2

2A. Branchiae spiraled (Fig. 9.2C) .... genus *Diopatra*[2]

2B. Branchiae simple, pectinate, or absent 3

3A. First parapodia with prominent, auricular presetal lobes in addition to subulate postsetal lobes (Fig. 9.2A); pectinate setae scoop-shaped (Fig. 9.2D); second parapodia with foliaceous, prominent presetal lobes; hooks in setiger 1 simple, in setigers 2 and 3 pseudocompound; branchiae from setiger 8 .... *Nothria occidentalis*

3B. Presetal lobes inconspicuous throughout; pectinate setae flat (Fig. 9.2E) 4

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[2] Not found in present material, but common in shallower water.

4A. Ceratophores of occipital antennae distinctly longer than prostomium; styles of outer lateral antennae shorter than ceratophores .... genus *Onuphis* 5

4B. Ceratophores of occipital antennae as long as prostomium or shorter; styles of outer lateral antennae longer than ceratophores 9

5A. Branchiae present from setiger 3-6 6

5B. Branchiae present from setiger 1 (2 or 3 in smaller specimens) 7

6A. Pseudocompound hooks in setigers 1-3 .... *Onuphis geophiliformis*

6B. Pseudocompound hooks in setigers 1-4 .... *Onuphis affinis*

7A. Branchiae in middle setigers winged, distinctly wider and thicker than in preceding and subsequent segments; pseudocompound hooks in setigers 1-4, subacicular hooks from setiger 8 or 9 .... *Onuphis elegans*

7B. Branchiae slender throughout, not winged 8

8A. Subacicular hooks first present in setiger 12 or 13 .... *Onuphis iridescens*

8B. Subacicular hooks first present in setiger 8 or 9 .... *Onuphis* intermediates

9A. Hoods of pseudocompound hooks projecting well beyond apical tooth, acutely pointed (Fig. 9.2K); branchiae pectinate, from setiger 2-4 through about 30, maximally 7 filaments .... *Paradiopatra parva*

9B. Hoods of pseudocompound hooks not prolonged, oblique or bluntly rounded 10

10A. Lower fascicle of limbate setae compound (Fig. 9.2F) .... genus *Mooreonuphis* 11

10B. Lower fascicle of limbate setae simple; branchiae pectinate, first present between setigers 2 and 4, with maximally 10 filaments; pseudocompound hooks in 7 or 8 setigers, subacicular hooks from setiger 18-25 .... *Kinbergonuphis vexillaria*

11A. Tridentate pseudocompound hooks in 8 setigers, median ones often simple in last 3 or 4 parapodia; compound spinigers present from setiger 7 to 19, then replaced by subacicular hooks .... *Mooreonuphis nebulosa*

11B. Pseudocompound hooks in 4 setigers 12

12A. Branchiae simple, first occurring between setigers 11 and 20 .... *Mooreonuphis exigua*

12B. Branchiae pectinate, first occurring between setigers 7 and 15, with maximally 5 filaments .... *Mooreonuphis segmentispadix*

Description of Species

The onuphid fauna in the Santa Maria Basin and Western Santa Barbara Channel is fairly diverse with ten or 11 species in six genera; two species were found that are new to science. The only genus common to the eastern Pacific, but not represented in the Phase I and II collections, is *Diopatra*. The following species are described:

Kinbergonuphis vexillaria (Moore, 1911)
Mooreonuphis exigua (Shisko, 1981)
Mooreonuphis nebulosa (Moore, 1911)
Mooreonuphis segmentispadix (Shisko, 1981)
Nothria occidentalis Fauchald, 1968
***Onuphis affinis* Hilbig, new species**
Onuphis elegans (Johnson, 1901)
Onuphis geophiliformis (Moore, 1903)
Onuphis iridescens (Johnson, 1901)
Onuphis sp. intermediates *sensu* Hobson, 1971
Paradiopatra parva (Moore, 1911)
Rhamphobrachium longisetosum Berkeley and Berkeley, 1938

Genus *Kinbergonuphis* Fauchald, 1982

Type Species. *Onuphis tenuis* Hansen, 1882

Diagnosis. Ceratophores of occipital antennae short, usually no longer than prostomium, with 3 to 10 rings; outer (anterior) styles at least as long as their ceratophores. Pseudocompound hooks with short, blunt hoods, usually tridentate; median ones often becoming simple after setiger 4 ("large median hooks" of Fauchald, 1982). Compound spinigers absent. Modified parapodia slightly or not at all prolonged. Branchiae usually pectinate, rarely simple or absent; first occurring on setiger 6, rarely before or after. Body size generally small, length rarely surpassing 100 mm, width typically to 2 mm.

Remarks. The generic definition is taken from Paxton (1986) and includes her minor revisions of Fauchald's (1982) original diagnosis. *Kinbergonuphis* is a large genus with more than 30 species, with its main distribution in shelf depths off both coasts of the Americas. While the majority of Pacific species occur off Central and South America, only three species have been described from off California, the poorly known *K. paradiopatra* (Hartman, 1944) from intertidal depths, and the slope species *K. proalopus* (Chamberlin, 1919) and *K. vexillaria* (Moore, 1911). Only the latter was found in the Phase I and II material, and the Santa Maria Basin may be the northern boundary of its distribution.

***Kinbergonuphis vexillaria* (Moore, 1911)**

Figure 9.3

Onuphis vexillaria Moore, 1911:266-269, pl. 17, figs. 69-76.—Fauchald, 1982:54-55.
Kinbergonuphis vexillaria: Paxton, 1986a:54.
Kinbergonuphis sp. A Steinhauer and Imamura, 1990:F-1.
Onuphis sp. A Lissner *et al.*, 1986:D-11.
Onuphis sp. B Lissner *et al.*, 1986:D-11.

Material Examined. California, Santa Maria Basin, off Point San Luis, Sta. 27 (1); off Point Sal, Sta. 35 (1), Sta. R-7 (1); off Point Arguello, Sta. 77 (2).

Description. All specimens incomplete; length to 159 mm, width to 4 mm (measured behind pharyngeal region, parapodia excluded), setigers to 242. Body wide and dorsally flattened, with crowded segments, except for pharyngeal region encompassing first 10 setigers. Color in alcohol pale with iridescent cuticle.

Prostomium small, rounded, almost concealed by bases of occipital antennae. Frontal antennae ovoid, shorter than prostomium; ceratophores of occipital antennae shorter than prostomium, each with 5-8 rings; outer (anterior) lateral antennae as long as peristomium and first 2-3 setigers, styles much longer than their ceratophores; inner (posterior) lateral antennae as long as peristomium and first 8-14 setigers; median antenna as long as peristomium and first 5-10 setigers; all styles gently tapering toward long, filiform distal portion (Fig. 9.3A). Eyes and nuchal organs not observed. Peristomium shorter than following setigers, with very long, slender tentacular cirri projecting just beyond frontal margin of prostomium.

Maxillae hard, calcified, with dark teeth; maxillary carriers very short, only 1.5 times as long as wide; MI gently curved, about 3 times as long as carriers; MII 5-6+7-9, MIII 7-8+0, MIV 6-8+6-8, MV very small, delicate, squarish plates without teeth (with single tooth according to Moore, 1911) (Fig. 9.3B).

First 4 parapodia modified, slightly enlarged, pointing forward, with long, slender, tapered dorsal and ventral cirri and postsetal lobes (Fig. 9.3C); ventral cirri replaced by pads in setiger 9 or 10, last ventral cirrus sometimes spherical rather than subulate; postsetal lobes subulate through setiger 16-30, then gradually shortening and turning conical; dorsal cirri always as long as longest branchial filament, becoming filiform in middle and posterior setigers. Branchiae present from setiger 2-4, simple at first, quickly becoming pectinate (Fig. 9.3D, E), with up to 12 filaments arising from thick stem, diminishing toward posterior end, in one specimen simple from setiger 70. Pseudocompound hooks tridentate, with short, oblique hoods (Fig. 9.3F), present in setigers 1-7 or 8, median one sometimes turning into large median hook in last 2 or 3 setigers; simple limbate and pectinate setae present from setiger 2; limbate setae densely covered with surficial spines (Fig. 9.3G); pectinate setae oblique, with about 10 long, slender teeth, terminal tooth on one side much longer than others in anterior setigers, all teeth equal in posterior setigers (Fig. 9.3H, I). Subacicular hooks present from setiger 18-25 (Fig. 9.3J). Neuropodia supported by 2-4 neuroaciculae, number declining toward posterior end; base of dorsal cirri with dense fascicle of about 12-15 delicate, transparent notoaciculae.

Pygidium unknown.

Remarks. *Kinbergonuphis vexillaria* differs from all its congeners by the presence of gills on setigers 2-4; it is related to *K. vermillionensis* (Fauchald, 1968), *K. nannognathus* (Chamberlin, 1919), and *K. proalopus* (Chamberlin, 1919) that all occur slightly to the south of the type locality of *K. vexillaria* and are characterized by pectinate branchiae. Aside from the first occurrence of gills, *K. vexillaria* differs from *K. vermillionensis* by the distribution of subacicular hooks (present from setiger 12 in *K. vermillionensis*, not before setiger 18 in *K. vexillaria*) and the number of maxillary teeth (MII 14+12 in *K. vermillionensis*, maximally 6+9 in *K. vexillaria*). *K. nannognathus* and *K. proalopus* both have pseudocompound hooks in 6-7, rather than 7-8 setigers.

Type Locality and Type Specimens. Pacific Ocean off California, Soledad Hill, Point La Jolla, *Albatross* Sta. 4326: holotype (USNM 19061).

Habitat. Moore (1911) found *K. vexillaria* in soft green mud; the Phase 1 and 2 specimens occurred in fine sediments with at least 75% silt and clay.

Distribution. Southern and central California, 442 - 611 m.

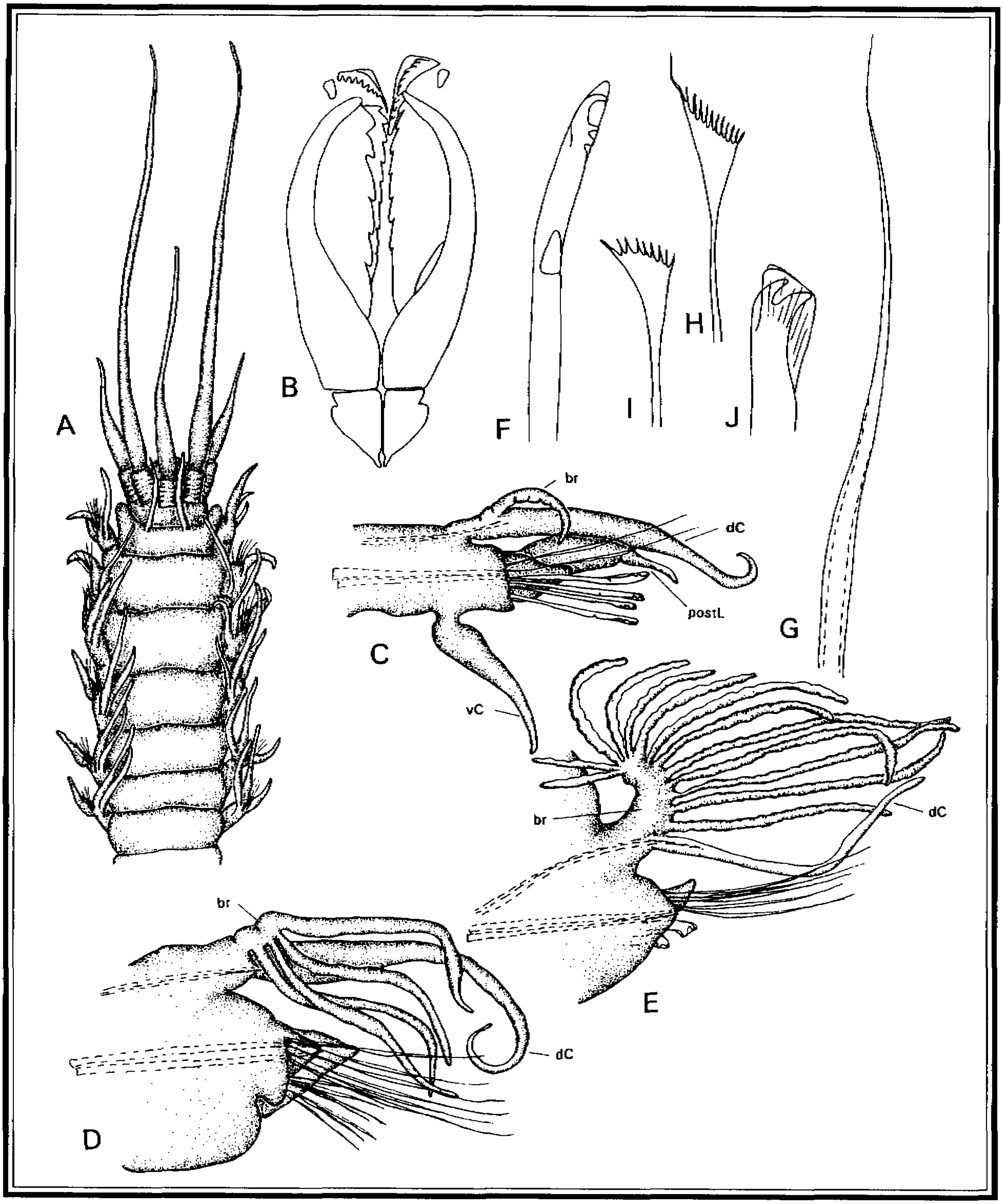

Figure 9.3. *Kinbergonuphis vexillaria*: A, anterior end, dorsal view; B, maxillae; C, parapodium 2, anterior view; D, middle parapodium, anterior view; E, posterior parapodium, anterior view; F, pseudocompound seta; G, simple seta; H, pectinate seta, setiger 2; I, same, setiger 10; J, subacicular hook.

Genus *Mooreonuphis* Fauchald, 1982

Type Species. *Onuphis nebulosa* Moore, 1911

Diagnosis. Ceratophores of occipital antennae short, no longer than prostomium, with maximally 5 rings; outer (anterior) styles at least as long as their ceratophores. Pseudocompound hooks bi- to tridentate, with short, blunt hoods; median ones sometimes becoming simple ("large median hooks" of Fauchald, 1982). Lower setae compound spinigers in segments between last one with pseudocompound hooks and first one with subacicular hooks. Modified parapodia not prolonged. Branchiae simple, rarely pectinate, usually present after setiger 17, rarely from 6 or 7. Body size small, length less than 100 mm, width up to 2 mm.

Remarks. To distinguish this genus from the similar *Kinbergonuphis*, several parapodia should be examined carefully for the presence of compound spinigers. These setae may be difficult to observe especially in small individuals. Differences in the development of branchiae are also helpful; they are usually pectinate and present from setiger 6 in *Kinbergonuphis*, usually simple and present after setiger 17 in *Mooreonuphis*. The distribution of *Mooreonuphis* is somewhat similar to that of *Kinbergonuphis*, with the majority of species being found along the Atlantic and Pacific coasts of the Americas. Four species are known from California, and all but one (*M. veleronis* (Fauchald, 1980)) are present in the Santa Maria Basin.

Mooreonuphis exigua (Shisko, 1981)

Figure 9.4

Nothria exigua Shisko, 1981:973-976, fig. 3.
Mooreonuphis exigua: Paxton, 1986:56.—Steinhauer and Imamura, 1990:F-1.

Material Examined. California: Santa Maria Basin, off Purisima Point, Sta. R5 (1).

Description. Length to 24 mm, width to 1 mm, segments to 100. Body slender, flattened; Peristomium and first 20 segments with wide reddish brown dorsal pigment bands; first setiger light colored, subsequent segments gradually darkening.

Prostomium relatively large, rounded, bearing globular frontal antennae and occipital antennae arranged in a crescent. Ceratophores of lateral antennae with 3-4 rings, ceratophore of median antenna smooth; outer (anterior) lateral antennae as long as peristomium and first 1 or 2 setigers, inner (posterior) lateral antennae as long as peristomium and first 10 setigers, median antenna as long as peristomium and first 8 or 9 setigers. Two pairs of eyes, located behind and in front of inner lateral antennae (Figure 9.4A). Peristomium about half as long as first setiger; tentacular cirri reaching bases of inner lateral antennae.

Jaws poorly sclerotized; larval mandibles distinctly visible as black feature on weakly calcified cutting plate; maxillae transparent with dark teeth. Maxillary formula: MI 1+1, strongly falcate; MII 6+6, MIII 7+0, MIV 7+8, MV oval plates without dentition.

Anterior parapodia only slightly modified (Fig. 9.4B); first 2 pairs directed anterolaterally. Postsetal lobes digitiform through setiger 8, papilliform after a few transitory setigers; ventral cirri replaced by pads on setiger 5. Branchiae simple, first present on setiger 11 in examined specimen (range 11-20). Simple limbate setae present throughout, winged part finely serrated and covered with surficial spines (Fig. 9.4C); pectinate setae present on most setigers, with few teeth. Slender and stout pseudocompound hooks present in setigers 1-4, tridentate, with proximal tooth in slender hooks minute and easily overlooked (Fig. 9.4D, E). Compound spinigers present on setigers 5-16 (range 4-5 to 11-16); end of shaft and blade densely covered with surficial spines (Fig. 9.4F); subacicular hooded hooks starting on first setiger without compound spinigers.

Tubes not observed, thin and transparent according to Shisko (1981).

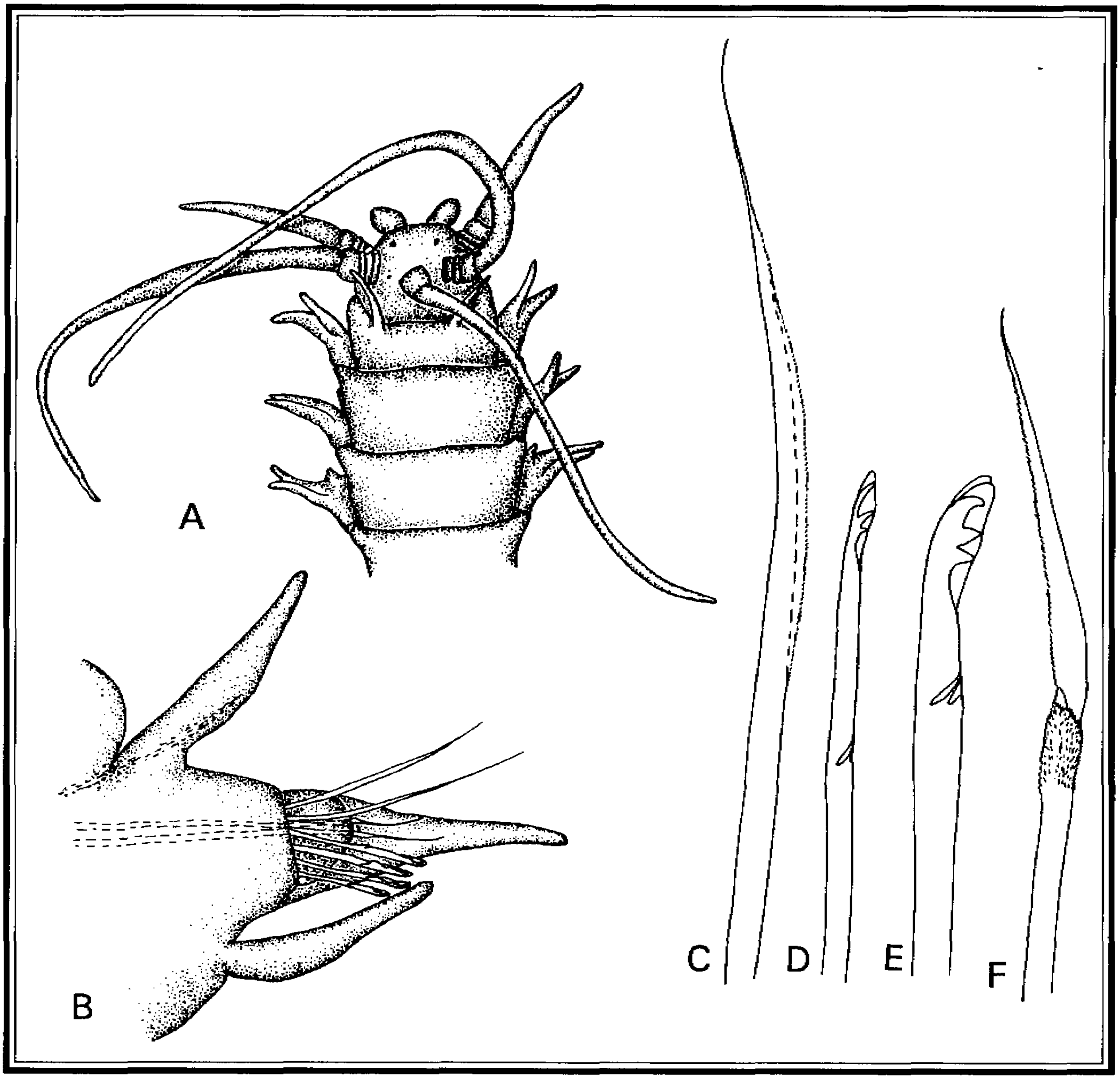

Figure 9.4. *Mooreonuphis exigua*: A, anterior end, dorsal view (after Shisko, 1981); B, anterior parapodium, anterior view; C, simple seta; D, slender pseudocompound hook; E, stout pseudocompound hook; F, compound spiniger.

Remarks. This species is somewhat similar to *M. nebulosa* (see below), especially with regard to pigmentation, and may be mistaken for its juvenile. The two species differ mainly in the distribution of pseudocompound hooks (setigers 1-4 in *M. exigua*, 1-8 in *M. nebulosa*) and the first appearance and shape of the gills (present from setiger 11-20, all simple in *M. exigua*, 6-8, with up to 6 branches in *M. nebulosa*).

Type Locality and Type Specimens. Southern California Bight: holotype (USNM 63081) and 4 paratypes (USNM 63082-63085).

Habitat. *M. exigua* prefers sandy sediments, but was also found in silt and clay.

Distribution. Southern and central California, 65 - 319 m.

Mooreonuphis nebulosa (Moore, 1911)

Figure 9.5

Onuphis nebulosa Moore, 1911:269-273, pl. 17, figs. 58-68.—Hartman, 1944:75-78, pl. 4, figs. 76-85.
Mooreonuphis nebulosa: Fauchald, 1982:56-57, fig. 17a.—Lissner *et al.*, 1986:D-11.
Mooreonuphis nr. *nebulosa*: Steinhauer and Imamura, 1990:F-1
Mooreonuphis cf. *nebulosa*: Gathof, 1984:39-23, figs. 39-19, 39-20a-i.

Material Examined. California: Santa Maria Basin, off Purisima Point, Sta. R5 (1); off Point Arguello, Sta. 64 (1); Western Santa Barbara Channel, Sta. 85 (rock) (1), Sta. 94 (1).

Description. Length to 125 mm, width to 2.0 mm, segments to 175. Body slender, linear, dorsoventrally flattened behind pharyngeal region, tapering toward pygidium within last 5 setigers (Fig. 9.5A, B). Peristomium and first 15-25 setigers with wide, brownish transverse pigment bands across dorsum; darkly pigmented peristomium sometimes contrasting against relatively pale first setiger.

Prostomium rounded, without eyes. Ceratophores of occipital antennae short, crowded, with 3 or 4 rings; outer (anterior) lateral antennae as long as peristomium and first 1 or 2 setigers, inner (posterior) lateral ones as long as peristomium and first 6 or 7 setigers, median one as long as peristomium and first 5 or 6 setigers; frontal antennae short and tapered. Peristomium only about 1/4 as long as first setiger and about as wide, bearing two relatively short tentacular cirri.

Maxillae poorly sclerotized; with short, squarish carriers about half as long as MI; MII 7-10+8-10, MIII 8-10+0, similar in size to MII; MIV 6+8, crescent-shaped plates; MV unidentate or smooth, roughly triangular, small plates (Fig. 9.5C). Mandibles about as long as maxillae, with cutting plate deeply incised medially and irregularly serrated (Fig. 9.5D).

First 7 or 8 parapodia slender, about as long as segmental width, supported by 2 notoaciculae projecting into base of dorsal cirri and 2-3 neuroaciculae with long, geniculate free tips (Fig. 9.5E), with digitiform postsetal lobes and clavate dorsal and ventral cirri projecting about as far as postsetal lobes; slightly displaced ventrally and directed forward on first two setigers, gradually moving to lateral position within following few setigers. Ventral cirri usually clavate to conical through setiger 10 (range 7-10), replaced by rounded pads from setiger 11 (range 8-11); postsetal lobes digitiform through first 20 setigers, then gradually diminishing in size and papilliform from about setiger 50; dorsal cirri present throughout, markedly decreasing in width within branchial region but of almost equal length throughout (Fig. 9.5F, G). Gills present from setiger 7 (range 6-8), starting as single filaments, with 4 branches where best developed, absent from posterior region.

Tridentate pseudocompound hooks present in first 8 setigers, of two kinds: (1) slender, with long shaft and blade, with terminal tooth much larger than proximal ones (Fig. 9.5H), (2) stout, short-bladed, terminal tooth smallest; some or all stout pseudocompound hooks replaced by simple hooks ("large hooks" of Fauchald) from setiger 4 or 5 on (Fig. 9.5I, J). Simple limbate capillaries present throughout (Fig. 9.5K), pectinate setae starting on anterior setiger and continuing to almost end of body; with about 10 short, fine teeth (Fig. 9.5L); compound spinigers present on setigers 7 to maximally 19, usually to setiger 13 or 15. Subacicular hooded hooks present from setiger behind last one bearing compound spinigers; two per fascicle, stout, amber colored, present to end of body (Fig. 9.5M).

Tube flattened, consisting of relatively stiff mucous lining, covered with often quite large sand and shell particles.

Remarks. This species is readily distinguished from its congeners by the large number of segments bearing modified parapodia. None of the species specific characters of the single specimen originally called *Mooreonuphis* nr. *nebulosa* were found to be outside the variability documented in the literature. The specimens from the Gulf of Mexico (Gathof, 1984) were reported to have longer parapodia than the Californian ones and

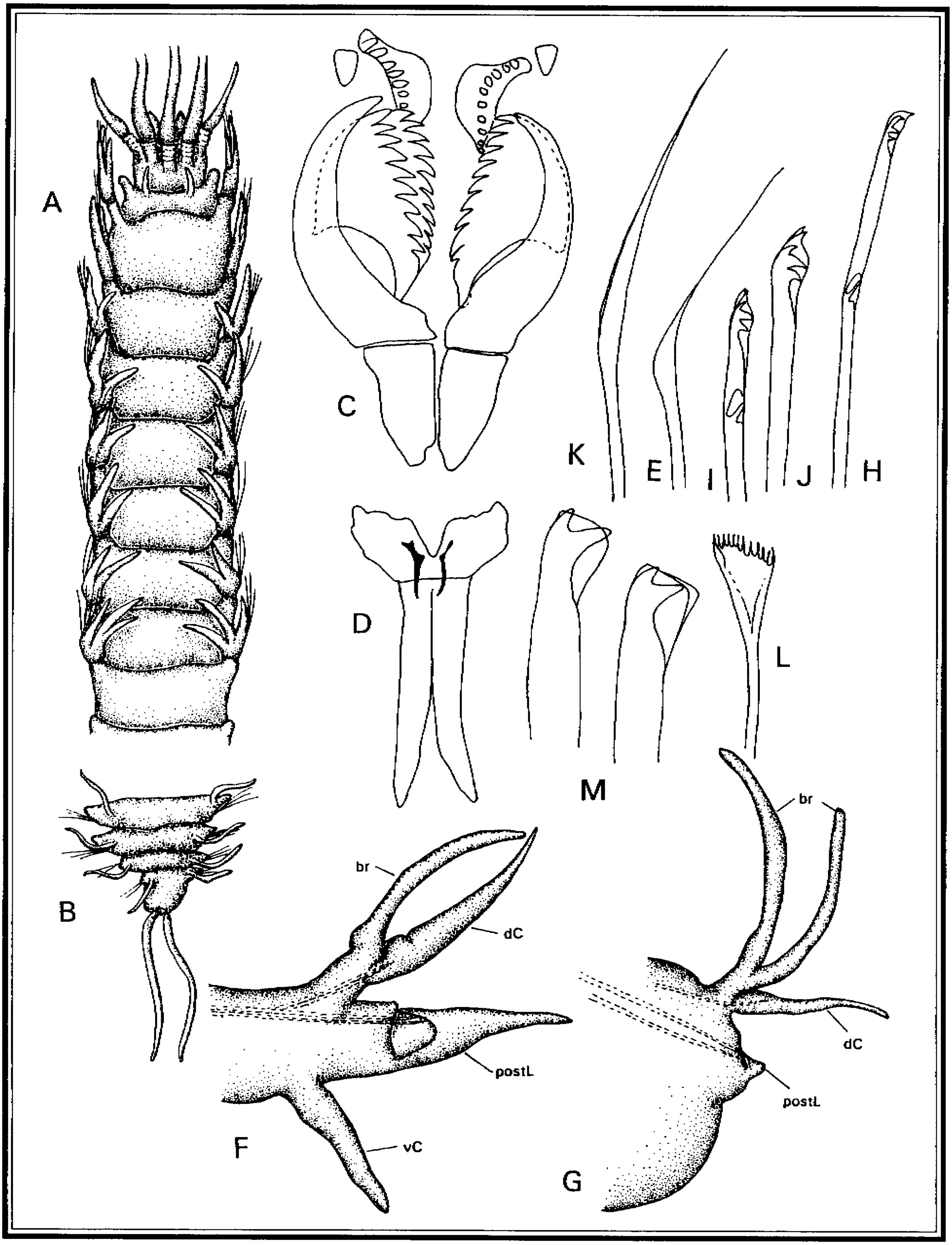

Figure 9.5. *Mooreonuphis nebulosa*: A, anterior end, dorsal view; B, posterior end, dorsal view; C, maxillae; D, mandibles; E, free end of acicula; F, anterior parapodium, anterior view; G, middle parapodium, anterior view; H, slender pseudocompound hook; I, stout pseudocompound hook; J, large hook; K, limbate seta; L, pectinate seta; M, subacicular hooks. (C after Moore, 1911; F, G after Gathof, 1984).

were therefore described as *M.* cf. *nebulosa.* However, a comparison of Moore's (1911) original illustration and that of Gathof (1984) does not reveal any readily visible differences in the proportions of the parapodia.

Type Locality and Type Specimens. Monterey Bay, off Point Piños Lighthouse: holotype (USNM 16881) and 2 paratypes (USNM 17062).

Habitat. *M. nebulosa* is found in various sediments ranging from clayey silt to sand and gravel; the examined specimens were collected in sediment consisting of approximately 70 to 80% sand and only 3 to 5% clay.

Distribution. California; Gulf of Mexico; 19 - 142 m.

Mooreonuphis segmentispadix (Shisko, 1981)

Figure 9.6

Onuphis segmentispadix Shisko, 1981:978-981.
Mooreonuphis segmentispadix: Paxton, 1986:56.—Lissner *et al.*, 1986:D-11.
Mooreonuphis sp. B Lissner *et al.*, 1986:D-11.

Material Examined. California: Santa Maria Basin, off Point Sal, Sta. 36 (2), Sta. 108 (4); off Purisima Point, Sta. 46 (3).

Description. Length at least 28 mm, width to 2 mm, segments over 100. Body flattened except for pharyngeal region, with crowded segments, 2 to 3 times as wide as long anteriorly, at least 4 times as wide as long after first 5 setigers. Dorsum with wide transverse bars of reddish brown pigment through setiger 20 to 30; pigmentation gradually fading in subsequent setigers, middle and posterior part of body pale.

Prostomium rounded, with globular, slightly tapering frontal antennae; eyes not observed in California specimens, two pairs present according to Shisko (1981). Ceratophores of occipital antennae with 3 to 4 rings. Outer (anterior) lateral antennae as long as peristomium and first 2 setigers, inner (posterior) lateral antennae as long as peristomium and first 14 setigers, median antenna as long as peristomium and first 11 setigers. Posterior prostomial margin with dark transverse pigment band delineating nuchal organs (Fig. 9.6A). Peristomium short, bearing long cirri projecting beyond antennal bases.

Maxillae with slender, triangular carriers and strongly falcate MI; MII 8-9+8, MIII 9+0, MIV 8-10+10-14, arching over MII and MIII; MV rounded plates with smooth edges (Fig. 9.6B). All maxillae poorly sclerotized and calcified, transparent with dark teeth.

First 3 parapodia elongate (Fig. 9.6C), slightly displaced ventrally and pointing forward; subsequent parapodia inserted laterally and pointing to the sides and upward. Postsetal lobes conical through setiger 14 to 17, ventral cirri padlike from setiger 5 or 6; gills typically first present on setiger 7 or 8 (range 7-15), simple at first, pectinate where best developed, with 4-5 branches (Fig. 9.6D, E). Pseudocompound hooks tridentate, present in setigers 1 to 4, no large hooks (Fig. 9.6F); compound spinigers in ventralmost position of fascicle in setigers 5 to 15, distal end of shaft and entire blade covered with surficial spines (Fig. 9.6G); subacicular hooks from setiger 16 (Fig. 9.6H); simple limbate setae present throughout, covered with surficial spines, widest and shortest in ventral part of fascicle (Fig. 9.6I, J); pectinate setae in median and posterior setigers, with about 10 subequal teeth and one outer tooth about 4 times as long (Fig. 9.6K). Notopodia with 6 fine aciculae in anterior setigers, reduced to 3 in posterior setigers; neuroaciculae 4 to 2 from anterior to posterior, with very long tips resembling short limbate setae (Fig. 9.6L).

Remarks. Several specimens originally designated *Mooreonuphis* sp. B in the MMS Phase 1 material were identified as *M. segmentispadix* here because no differences could be detected; the original voucher sheet was obviously prepared from a juvenile specimen.

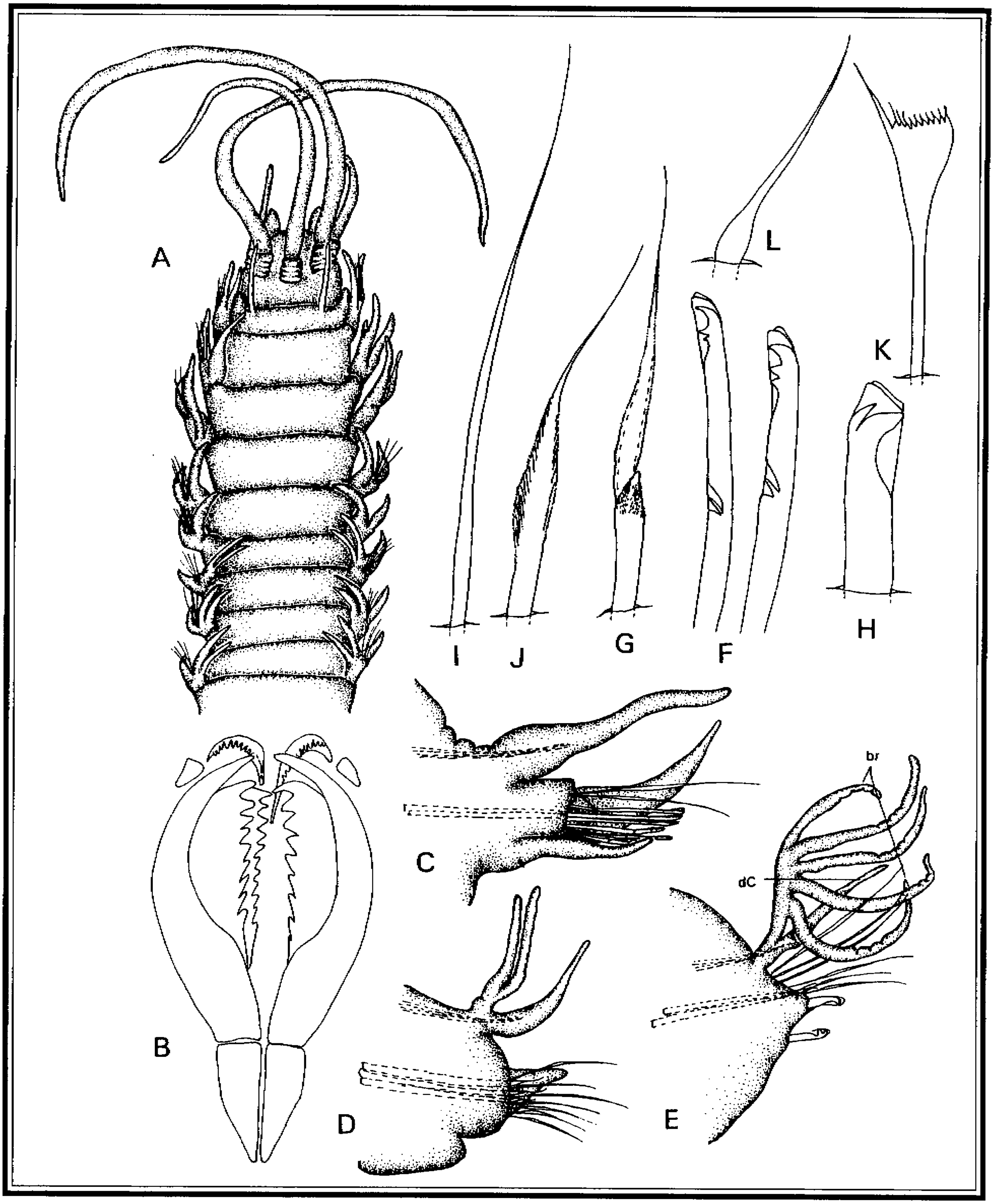

Figure 9.6. *Mooreonuphis segmentispadix*: A, anterior end, dorsal view; B, maxillae; C, parapodium 1, anterior view; D, prebranchial parapodium, anterior view; E, parapodium 12, anterior view; E, far posterior parapodium, anterior view; F, slender and stout (left) pseudocompound hook; G, compound spiniger; H, subacicular hook; I, upper simple seta; J, lower simple seta; K, pectinate seta; L, free tip of acicula.

Type Locality and Type Specimens. Southern California: holotype (USNM 63074) and 6 paratypes (USNM 63075-63080).

Habitat. *M. segmentispadix* lives in a wide variety of sediments from silt to sand and gravel, but seems to prefer sandy substrata.

Distribution. Southern and central California, 63 - 670 m.

Genus *Nothria* Malmgren, 1866

Type Species. *Onuphis conchylega* Sars, 1835

Diagnosis. Ceratophores of occipital antennae barely longer than wide, smooth or with 3-5 rings. Anterior 2 to 3 parapodia modified, first parapodium prolonged; presetal lobes large, auricular in setiger 1, rounded to conical in subsequent setigers, gradually diminishing; postsetal lobes subulate in some anterior setigers; ventral cirri subulate in 2 to 3 setigers, followed by 1 or 2 transitory parapodia with spherical ventral cirri, replaced by pads after that. Branchiae simple if present, first occurring on between setigers 8 and 13. Simple to pseudocompound hooded hooks in 2 or 3 setigers, uni- to bidentate; pectinate ans limbate setae present from setiger 2; pectinate setae scoop-shaped, forming often dense fascicles; limbate setae geniculate with broad wings, resembling lumbrinerid setae. Subacicular hooks first present between setigers 8 and 14, usually with long shafts and relatively small heads.

***Nothria occidentalis* Fauchald, 1968**

Figure 9.7

Nothria conchylega occidentalis Fauchald, 1968:20-21, pl. 5, figs. a-n.
Nothria occidentalis: Fauchald, 1982a:95, fig. 27d.
Paranorthia sp. A Steinhauer and Imamura, 1990:F-1.

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

Description. Length more than 14 mm, width to 2 mm, segments more than 30. Body slender, linear, slightly flattened; color in alcohol pale.

Prostomium rounded, with antennae inserted along outer margin; two large posterior eyes and two smaller anterior ones. Frontal palps small, conical; ceratophores of occipital antennae as long as wide, with 3-4 very short rings; outer (anterior) lateral antennae as long as peristomium and first 2 setigers, inner (posterior) lateral antennae as long as peristomium and first 8-9 setigers median antenna as long as peristomium and first 3-8 setigers (Fig. 9.7A). Peristomium short, about one-third as long as prostomium, with slender, tapering tentacular cirri extending to frontal margin of prostomium. Maxillary formula unknown.

First setiger twice as long as following ones, with broad, muscular parapodial bases; parapodia elongate, pointing forward, anterior side facing body; with large, auricular presetal lobe, subulate postsetal lobe and long, tapering dorsal and ventral cirri (Fig. 9.7B). Second setiger slightly longer than following ones, parapodia somewhat prolonged and pointing forward, with rounded presetal lobe; postsetal lobe and cirri resembling those of first parapodium (Fig. 9.7C). Presetal lobes of subsequent setigers short, conical; postsetal lobes subulate to about setiger 15, then low and rounded; ventral cirri in setigers 3 and 4 spherical, replaced by pads after that; dorsal cirri long and tapering to setiger 15, then shortening and narrowing. Branchiae starting on setiger 8, smaller than dorsal cirri at first, after setiger 15 surpassing them in width and length, broadly foliaceous (Fig. 9.7D).

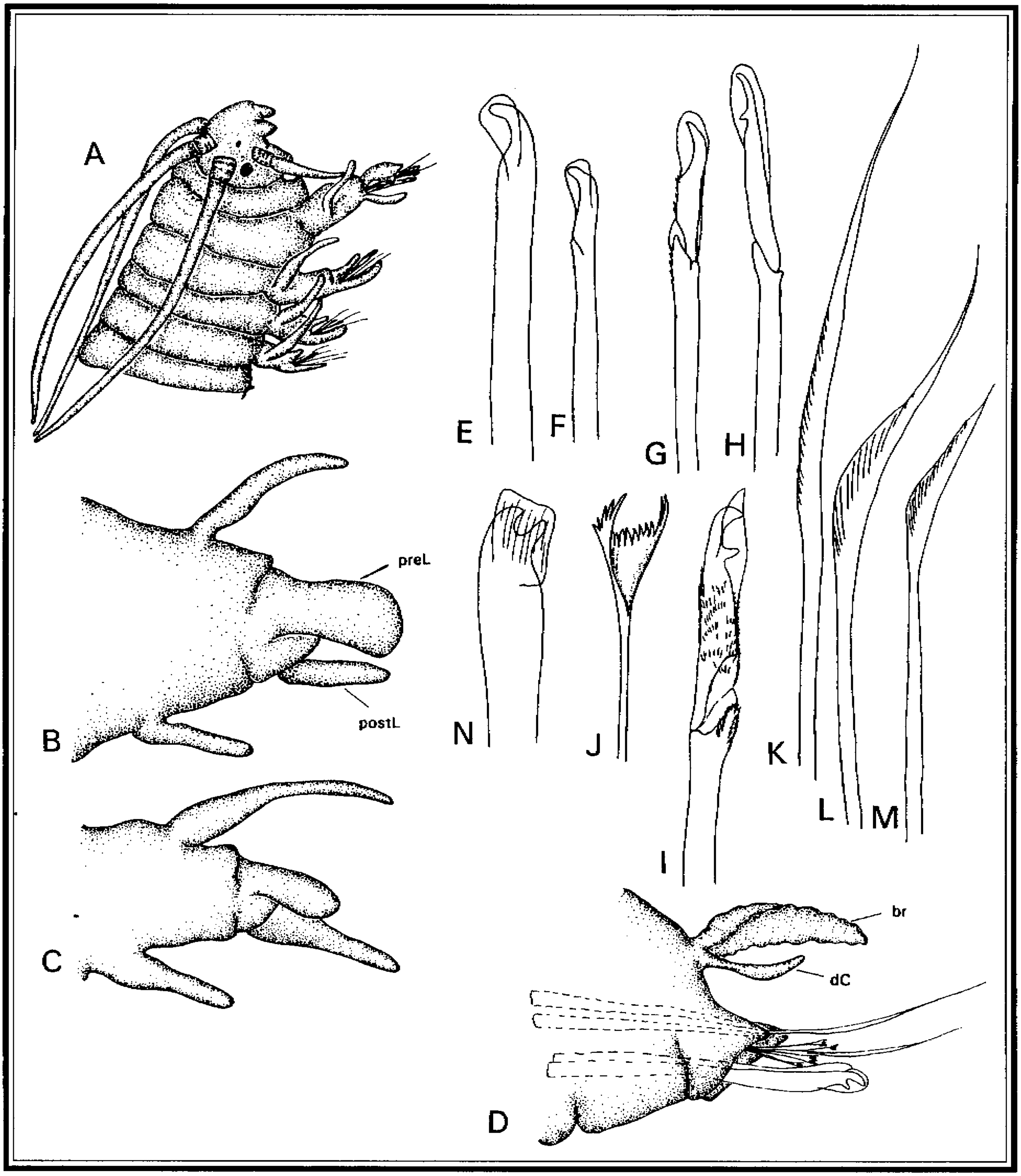

Figure 9.7. *Nothria occidentalis*: A, anterior end, dorsolateral view; B, parapodium 1, anterior view; C, parapodium 2, anterior view; D, middle parapodium, anterior view; E-F, simple and pseudocompound hook, setiger 1; G-H, uni- and bidentate pseudocompound hooks, setiger 2; I, nearly compound hook, setiger 3; J, Pectinate seta; K-M, anterior, middle, and posterior simple setae.

Unidentate spines with hooked tips and short, oblique hoods in setiger 1 (Fig. 9.7E, F); pseudocompound to compound uni- and bidentate hooks with long, spinose hoods in setigers 2 and 3 (Fig. 9.7G-I); scoop-shaped pectinate setae with 10-15 long, equal teeth from setiger 2, often forming dense fascicles (Fig. 9.7J); limbate setae present from setiger 2, geniculate, with broad wings; in posterior setigers geniculate part becoming shorter in relation to shaft (Fig. 9.7K-M). Subacicular hooks long and slender, with relatively small heads and short, oblique hoods; present singly from setiger 9 or 10, in pairs from setiger 13 (Fig. 9.7N).

Tubes flat, with tough inner lining and outer cover of shell hash.

Remarks. The auricular presetal lobes of the first parapodia clearly mark this specimen as a *Nothria*. The genus *Paranorthia* has been recognized as a synonym of *Rhamphobrachium* by Paxton (1986) and represents juveniles of the latter.

Habitat. Found in sand mixed with shells and mud.

Distribution. Central California to Colombia, 80 to 200 m.

Genus *Onuphis* Audouin and Milne Edwards, 1833

Type Species. *Onuphis eremita* Audouin and Milne Edwards, 1833

Diagnosis. Ceratophores of occipital antennae distinctly longer than prostomium, usually with 10 to 25 rings; styles of outer (anterior) lateral antennae shorter than their ceratophores. Pseudocompound hooks bi- to tridentate, rarely quadridentate, with short, blunt hoods; large median hooks and compound spinigers absent. Modified parapodia prolonged, at least in anteriormost setigers. Branchiae simple to pectinate, most often present from setigers 4 to 6, sometimes from setiger 1, rarely absent. Body size moderate to small, length to 300 mm, width to 4 mm.

Remarks. *Onuphis* is a typical part of the fauna of the Eastern and Western Pacific oceans. The genus is easily recognized by the long ceratophores of the occipital antennae. Seven previously described species have been reported off California; three of those, and an additional species new to science were found the Santa Maria Basin.

Onuphis affinis Hilbig, new species

Figure 9.8

Onuphis pallida Lissner *et al.*, 1986:D-11.—*Not* Moore, 1911.
Onuphis sp. 1 SAIC, 1992:A-7

Material Examined. California, R/V *Point Sur*, off the Farallon Islands, north of Pioneer Canyon, Sta. 3-10, 37°26.00'N, 123°10.83'W, 985 m, 16 September, 1991: holotype (CASIZ 099239) and 3 paratypes (USNM 170423); Sta. 3-4, 37°27.83'N, 123°11.60'W, 1040 m, 14 September, 1991: 4 paratypes (LACM-AHF Poly 1657); Santa Maria Basin, off Point Arguello, Sta. 63, 34°26.29'N, 120°58.08'W, 930 m: 1 paratype (USNM 170422); Sta. 69, 34°22.88'N, 120°54.20'W, 927 m: 1 paratype (SBNMH 142695); additional specimens: off the Farallon Islands, north of Pioneer Canyon (9), axis of Pioneer Canyon (1), south of Pioneer Canyon (10).

Description. Holotype complete, 100 mm long, 2 mm wide excluding parapodia (measured behind pharyngeal region) for 247 setigers; longest incomplete specimen 135 mm long, 2 mm wide for about 225 setigers; other specimens 20 to 91 mm long, 1 to 3 mm wide for 38 to 176 setigers. Body slender, flattened, rigid, with crowded segments behind pharynx, tapering toward pygidium within last 20 setigers or so. Color in alcohol pale or dusky because of very fine transverse dark brown lines running across dorsal and ventral surface; cuticle highly iridescent.

Prostomium small, bluntly triangular, bearing oval to clavate frontal antennae about as long as prostomium; ceratophores of occipital antennae crowded, arranged in semicircle; eyes not observed; nuchal organs in pigmented specimens delineated by blackish lines along posterior prostomial margin separated by small median gap. Outer (anterior) occipital antennae as long as peristomium and first 1-2 setigers, ceratophores with 10-15 rings, distinctly longer than ceratostyles; inner (posterior) lateral antennae as long as peristomium and first 13-18 setigers (8-9 in small individuals), ceratophores with 12-16 rings, always longer than those of outer lateral antennae; median antenna as long as peristomium and first 6-9 setigers (rarely 14; 4 in small individuals), ceratophores with 6-10 rings, usually about half as long as those of inner lateral antennae. Palps massive, about as long and twice as wide as frontal antennae. Peristomium about half as long as first setiger, bearing two very slender and long tentacular cirri extending to anterior prostomial margin (Fig. 9.8A).

Maxillae weakly sclerotized, but calcified and hard, with darkened outer margins and teeth; carriers short, triangular, laterally incised, less than half as long as MI; MII 7-9+8-10, MIII 9+0, MIV 7-8+11, arching over first 3 maxillae, very hard and massive; MV small, delicate, triangular plates without dentition (Fig. 9.8B). Mandibles about as long as maxillae, with slender, sclerotized shafts bearing calcified, deeply incised and irregularly serrated cutting plate (Fig. 9.8C).

First two setigers about as long as wide, bearing modified parapodia with long dorsal and ventral cirri and postsetal lobes; parapodia 1-4 slightly displaced ventrally and pointing forward (Fig. 9.8D, E). Subsequent setigers quickly becoming wider and shorter, only as long as width of parapodial stem throughout. Ventral cirri cirriform through setiger 5 or 6, sometimes followed by transitory cirrus, replaced by pad in setigers 6-8. Postsetal lobes elongate conical through setiger 11-13 (9-10 in small individuals), gradually turning papilliform in middle and posterior setigers (Fig. 9.8F, G). Dorsal cirri present throughout, very long and prominent in modified setigers, gradually diminishing and very short and slender through most of body. Gills simple, first present in setiger 4 (rarely 3 or 5), as long as corresponding dorsal cirri at first, quickly surpassing dorsal cirri and reaching at least half body width; absent from last 20 or 30 setigers.

Tridentate pseudocompound hooks present in setigers 1-4, stout and short-bladed or slender and long-bladed, with slightly pointed hoods (Fig. 9.8H); subacicular hooks present from setiger 12, (occasionally 10 or 11 in small specimens, rarely 13), with short, squarish hood (Fig. 9.8I); simple limbate capillaries with very narrow wings present throughout, pectinate setae present in most setigers, bearing about 10-12 equal teeth (Fig. 9.8J, K).

Pygidium very small, bearing 2 pairs of ventrally inserted anal cirri, upper pair longer than lower pair.

Remarks. The new species shows similarities with several co-occurring species that seem to form a cluster of closely related forms similar to that including *O. elegans*, *O. iridescens*, *O. opalina* and the "intermediates" described by Hobson (1971). *O. affinis* resembles *O. pallida* and *O. similis* in the number of setigers with pseudocompound hooks, but is most similar in the occurrence of subacicular hooks to *O. geophiliformis*, a species with only 3 segments bearing pseudocompound setae. *O. affinis* and *O. pallida* differ in the first occurrence of the subacicular hooks (setiger 16 for *O. pallida*, 11-13 for *O. affinis*) and most likely also the number of maxillary teeth, especially MII (6+9 for *O. pallida*, 7-9+8-10 for *O. affinis*) and MIV (6-7+8 for *O. pallida*, 7-8+11 for *O. affinis*). *O. affinis* differs from *O. similis* in those same two characters (subacicular hooks present from setiger 8-9, MII 5+7, MIV 5+8) and in addition in the first occurrence of the branchiae (nearly always setiger 4 for *O. affinis*, setiger 6 for *O. similis*).

Etymology. The species name is the Latin word for close or related and refers to the morphological resemblance to several related species.

Distribution. Central California, 800 - 2755 m, in silt and sand mixed with silt.

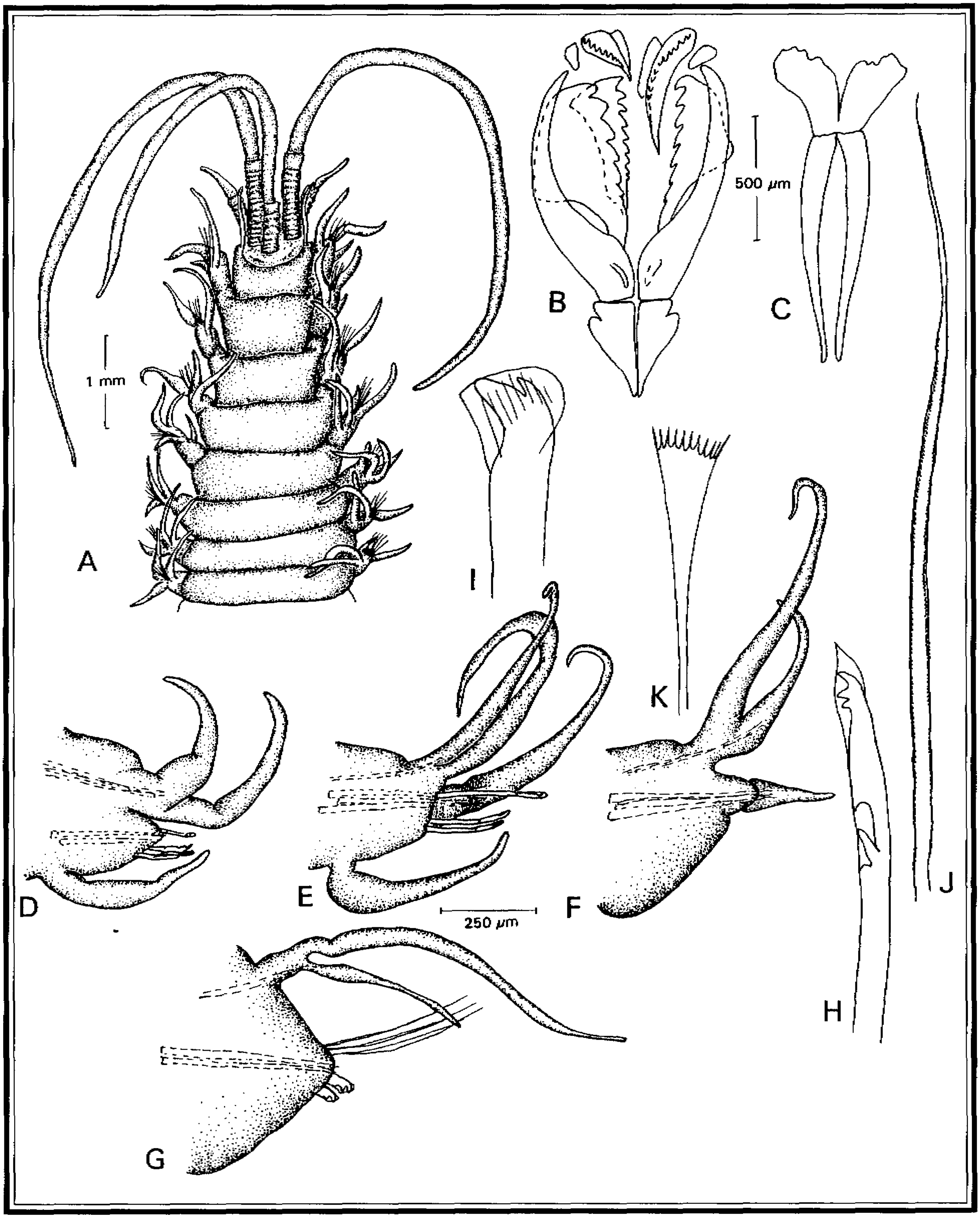

Figure 9.8. ***Onuphis affinis* Hilbig, new species**: A, anterior end, dorsal view; B, maxillae; C, mandibles; D-E, parapodium 1 and 4, anterior view; F-G, middle and posterior parapodium, anterior view; H, pseudocompound hook; I, subacicular hook; J, simple seta; K, pectinate seta. (all from non-type specimens).

Onuphis elegans (Johnson, 1901)

Figure 9.9

Northia elegans Johnson, 1901:406-407, pl. 8, figs. 77-85.
Nothria elegans: Hartman, 1968: 675 (in part).—Blake, 1975a:201, figs. 172-175; 1975b:43-61.
Onuphis elegans: Hobson, 1971:529-531, fig. 1.—Fauchald, 1982:45.

Material Examined. California: Dillon Beach, Lawson's Flat, coll. 13 July, 1973 (1); Bodega Lagoon, coll. 11 June, 1952 (2).

Description. Length to 160 mm, width to 6 mm, segments to about 250. Body cylindrical through first 4 or 5 setigers, then dorsoventrally flattened and linear, tapering gently toward pygidium within last 25 setigers. Color in alcohol pale or, in anterior setigers, with brown dorsolateral spots located at posterior margin of each segment, sometimes forming a transverse line.

Prostomium small, rounded, almost concealed by crowded bases of occipital antennae, bearing 2 pairs of eyes in front of and beside insertion of inner (posterior) lateral antennae. Frontal antennae ovoid, almost as long as prostomium; ceratophores of outer (anterior) lateral antennae much longer than styles, with 10 rings, antennae as long as peristomium and first setiger; ceratophores of inner (posterior) lateral antennae with 11 rings, antennae as long as peristomium and first 7 setigers (range 3-11); ceratophore of median antenna shortest, with 5 rings, antenna as long as peristomium and first 2 setigers (Fig. 9.9A).

Maxillary formula, according to Fauchald (1982): MI 1+1, MII 6-7+5-7, MIII 7-10+0, MIV 6-7+5-8, MV 1+1.

First 4 or 5 parapodia modified, with long cirri and postsetal lobes, directed forward and slightly displaced ventrally, gradually inserting more dorsallly and pointing to the side. Gills present from first setiger, simple and straplike throughout, between setigers 10 and 60-80 markedly wider and thicker than preceding and subsequent gills, typically appearing to be winged on one side (Fig. 9.9B). Ventral cirri replaced by pads from setiger 6, rarely 7; postsetal lobes cirriform through setiger 12 or 13. Slender and stout pseudocompound hooks present in first 4 setigers, usually tridentate (Fig. 9.9C), rarely bi- or quadridentate; subacicular hooks first present in setiger 8 or 9 (Fig. 9.9D); simple limbate and pectinate setae present throughout, the latter distally oblique, with about 14 teeth.

Remarks. The description of *O. elegans* is added here although the main distribution of this species seems to be Puget Sound and further north to Canada and its depth range is shallower than any Phase I and II station. Most of the individuals from California identified as *O. elegans* based on the first occurrence of the subacicular hooks seem to actually belong to the "intermediates" described by Hobson (1971), which in turn do not occur in Washington and Canada. If the anterior branchiae in an individual do not match Johnson's (1901) very accurate illustration, but subacicular hooks are present in setiger 9 (rather than 10-12 as in *O. iridescens*), it should be assigned to the intermediates. Specimens of less than 0.6 mm body width should be identified to species with caution because the first occurrence of subacicular hooks is growth-dependent (see Hobson, 1971); in adults of greater body width, however, this character seems to be sufficiently consistent for species discrimination.

Type location and type specimens. Washington, Puget Sound, Port Townsend region: 2 syntypes (LACM-AHF Poly 740 and MCZ 1895).

Biology. Larvae were reported to be most abundant between January and April, and postlarval juveniles were found between February and October in California waters (Blake, 1975b). A 60-setiger stage, the smallest adult size, is reached within 120 days of fertilization. *O. elegans* seems to prefer sandy sediments and can be hand collected on beaches.

Distribution. British Columbia to southern California, intertidal to 23 m.

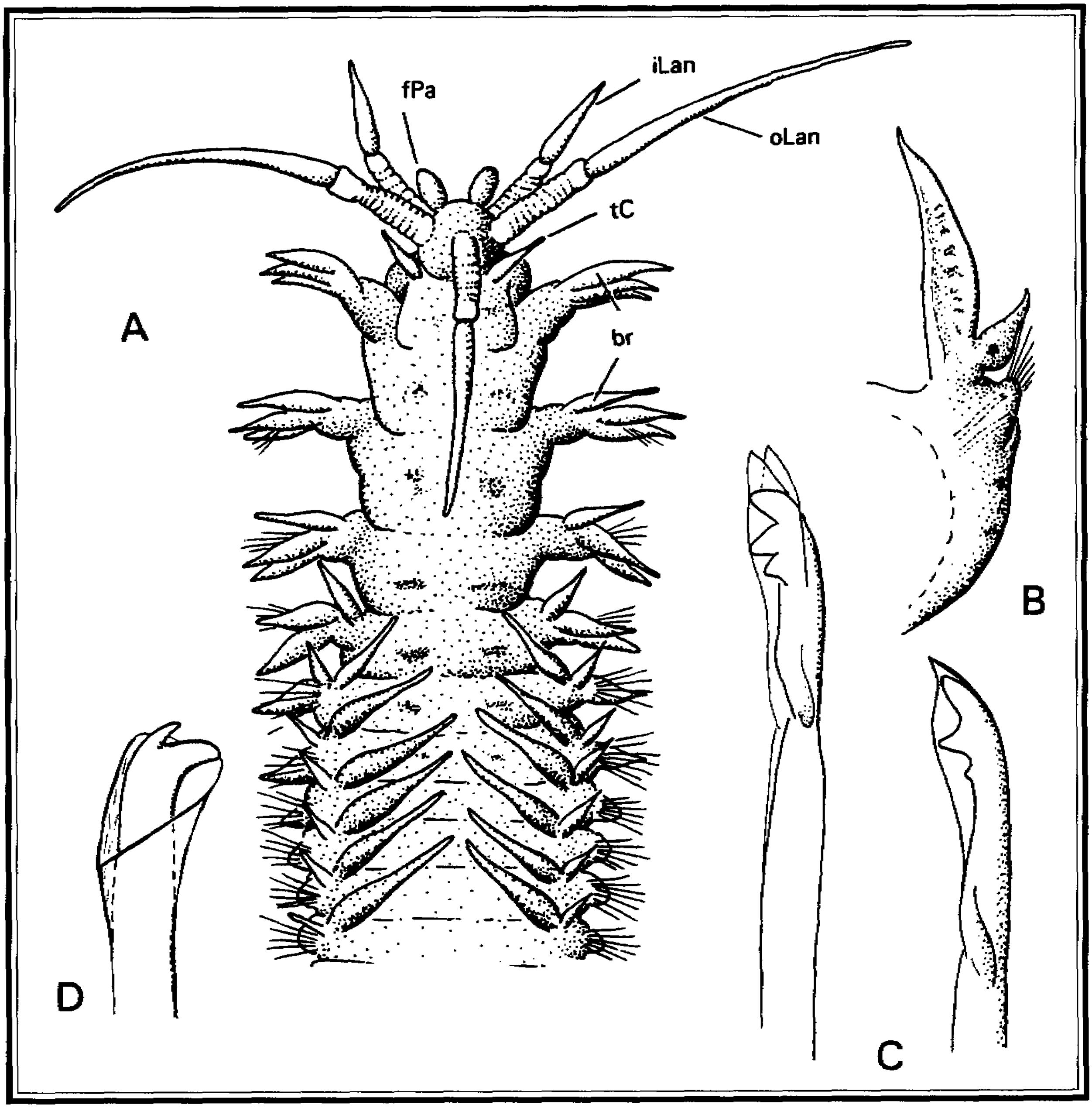

Figure 9.9. *Onuphis elegans*: A, anterior end, dorsal view; B, middle parapodium with wide gill; C, pseudocompound hooks, setiger 2; D, subacicular hook. (all from Blake, 1975a).

Onuphis geophiliformis (Moore, 1903)

Figure 9.10

Northia geophiliformis Moore, 1903:445-448, pl. XXV, figs. 57-59.
Nothria geophiliformis: Fauchald, 1968:22.—Hartman, 1968:677.
Onuphis geophiliformis: Fauchald, 1982:47-48, fig. 13a, tab. 14.—Maekawa and Hayashi, 1989:72-74, fig. 7a-j.

Material Examined. California: Santa Maria Basin, off Point San Luis, Sta. R2 (7).

Description. Length to 10 mm, width to 1 mm excluding parapodia, segments more than 100. Body slender, gracile, flattened except for pharyngeal region, tapering toward pygidium within last 10 segments or so; pigmentation consisting of wide brown bands across dorsum in anterior segments, alternating with pale intersegmental furrows; cuticle vividly iridescent.

Prostomium small, bluntly triangular, with crowded antennal bases. Frontal antennae oval, relatively slender; occipital antennae with long ceratophores divided into 10 to 15 rings, those of outer lateral antennae distinctly longer than ceratostyles. Outer (anterior) lateral antennae as long as peristomium and first 1-4 setigers, inner (posterior) lateral antennae as long as peristomium and first 6-11 setigers, median antenna as long as peristomium and first 5-8 setigers. Eyes usually absent (Fig. 9.10A).

Maxillae with triangular, laterally slightly incised carriers about half as long as MI; MII 7+6, MIII 7-8+0, MIV 8+9, MV 1+1 (Fig. 9.10B).

First 4 parapodia elongate, displaced ventrally and pointing forward, subsequent parapodia inserted laterally and pointing to the sides, dorsal cirri, gills and postsetal lobes arched across dorsum. Postsetal lobes elongate triangular to setiger 10-12, ventral cirri padlike from setiger 5 or 6; gills first present on setiger 3-6, simple and straplike throughout, much larger than dorsal cirri, absent from last 20 to 30 setigers (Fig. 9.10C-E). Pseudocompound hooded hooks present in setigers 1-3, tridentate, with pointed hoods (Fig. 9.10F); subacicular hooks first present on setiger 10-12 (Fig. 9.10G); simple limbate capillaries present throughout, pectinate setae ("paddle-shaped setae" in Moore's original description) with 10-15 subequal teeth, one outer tooth longer than others, present after setiger 10 (Fig. 9.10H).

Pygidium small, bearing 2 pairs of ventrally inserted anal cirri, outer pair twice as long as inner pair; anus dorsal (Fig. 9.10I).

Remarks. The species is easily recognized by its gills that are simple and start on setigers 3-6 rather than 1; it differs from *O. similis* (Fauchald, 1968), a species occurring off Baja California, by the number of setigers with pseudocompound hooks (3 for *O. geophiliformis*, 4 for *O. similis*).

Type Locality and Type Specimens. Japan, north of Sendai Bay: holotype (USNM 15711), 7 paratypes (USNM 5362), 11 paratypes (ANSP 971).

Habitat. Found in mud and sand; the examined specimens were collected from sediments with more than 80% silt.

Distribution. Japan; Alaska to southern California, 100 - 295 m.

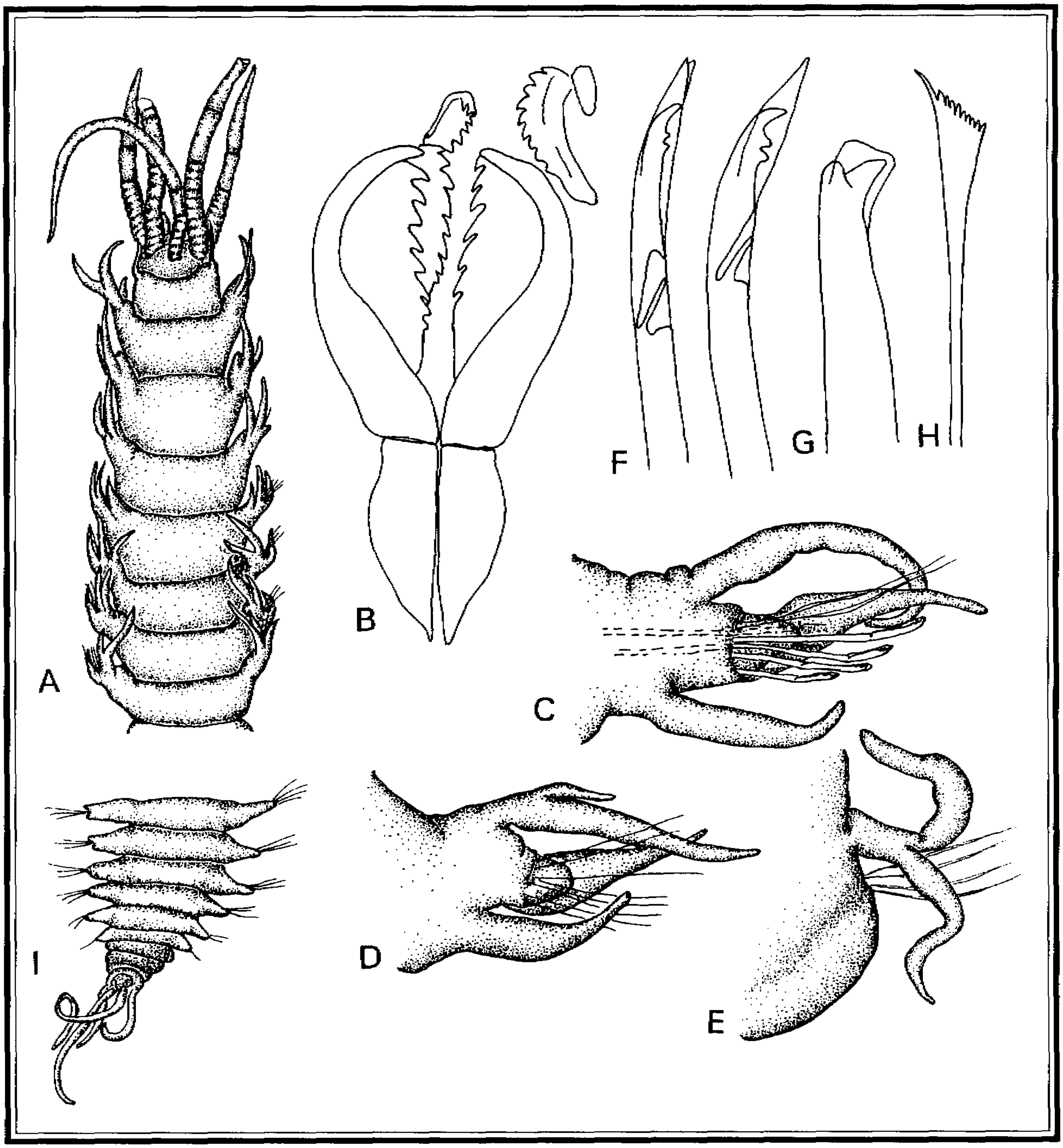

Figure 9.10. *Onuphis geophiliformis*: A, anterior end, dorsal view; B, maxillae; C, first parapodium, anterior view; D, fourth parapodium, anterior view; E, middle parapodium, anterior view; F, pseudocompound hooks; G, subacicular hook; H, pectinate seta; I, posterior end, dorsal view. (A-H after Maekawa and Hayashi, 1989).

Onuphis iridescens (Johnson, 1901)

Figure 9.11

Northia iridescens Johnson, 1901:408, pl. 8, figs. 86-87, pl. 9, figs. 88-92.
Nothria iridescens: Hartman, 1944:87-88, pl. 5, figs. 99-104 (in part); 1968:681.
Onuphis iridescens: Hobson, 1971:533-535, figs. 3a-d, 4a-c.—Fauchald, 1982:49, fig. 14a.—Lissner *et al.*, 1986:D-11 (in part).—Steinhauer and Imamura, 1990:F-1.

Material Examined. California: Santa Maria Basin, off Point San Luis, Sta. 23 (1), Sta. R-3 (2).

Description. Length more than 30 mm, width to 3 mm excluding parapodia, segments more than 50. Body linear, stout, flattened behind pharyngeal region; color in alcohol pale, anterior segments brownish transverse bar across posterior part of each segment (Fig. 9.11A); cuticle highly iridescent.

Prostomium rounded, wider than long, nearly concealed by bases of occipital antennae; outer (anterior) lateral antennae as long as peristomium and first 2 or 3 setigers, ceratophores distinctly longer than styles, with 8-14 rings; inner (posterior) lateral antennae as long as peristomium and first 14 setigers (range 7-25), ceratophores with 9-14 rings; median antenna as long as peristomium and first 10 setigers, ceratophore with 9 rings, only half as long as those of inner lateral antennae. Frontal antennae ovate, shorter than prostomium. Peristomium shorter than first setiger, bearing relatively short tentacular cirri projecting about as far as bases of inner lateral antennae.

Maxillae with slender, together urn-shaped carriers and slender, gently curved first maxillae. Maxillary formula: MI 1+1, MII 7+7-8, MIII 7-8+0, MIV 5+10, arching over MI-MIII; MV squarish, delicate plates with no teeth (Fig. 9.11B). Mandibles about as long as maxillary apparatus, with slender shafts bearing deeply incised, scalloped, calcified cutting plate (Fig. 9.11C).

First 3 or 4 parapodia enlarged, with long cirri and postsetal lobes, slightly displaced ventrally, pointing forward (Fig. 9.11D); subsequent parapodia gradually moving into lateral position and pointing to the sides. Ventral cirri replaced by pads in setiger 6 (rarely 7 or 8; 4 or 5 in juveniles), postsetal lobes cirriform through setiger 12-16 (8 in juveniles). Gills simple and slender throughout, present from setiger 1; smaller than corresponding dorsal cirri at first, but quickly surpassing the latter after the first 3 or 4 setigers (Fig. 9.11E, F); arched over dorsum, reaching dorsomedian line where best developed. Slender and stout tridentate pseudocompounds present in setigers 1-4 (Fig. 9.11G, H); hooded subacicular hooks present from setiger 12 or 13 (8-10 in small individuals) (Fig. 9.11I); limbate setae with very narrow wings in all setigers (Fig. 9.11J); pectinate setae in most setigers, distally slightly oblique with about 15 teeth.

Tube parchment-like, white, with outer layer of sand grains.

Remarks. *Onuphis iridescens* is very similar to two co-occurring forms, *O. elegans* and the *Onuphis* intermediates of Hobson (1971). As the characters that separate those forms are growth dependent and seem to stabilize when the individuals are about 60 setigers long and about 0.6 mm wide, specimens smaller than that should not be identified to species.

Type Locality and Type Specimens. British Columbia, Victoria: holotype (MCZ 1887).

Habitat. The examined specimens were found in silty mud, but generally occur in various types of mixed sediments.

Distribution. British Columbia to Mexico; Sea of Okhotsk; South Atlantic; intertidal to 2400 m.

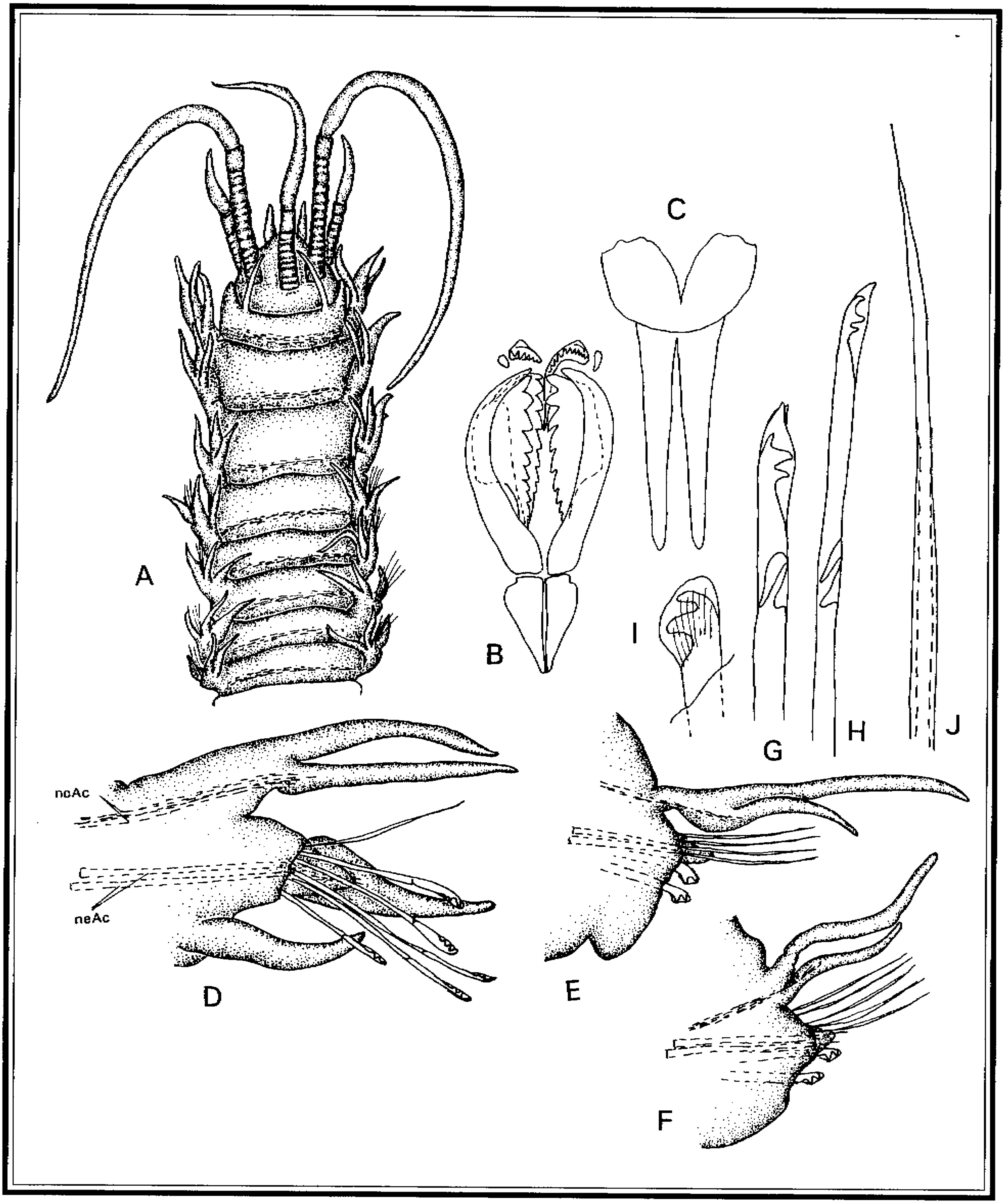

Figure 9.11. *Onuphis iridescens*: A, anterior end, dorsal view; dashes: pigment pattern; B, maxillae; C, mandible; D-E, parapodia 2 and 15, anterior view; F, middle parapodium, anterior view; G-H, stout and slender pseudocompound setae; I, subacicular hook; J, simple seta.

Onuphis sp. "intermediates"

Figure 9.12

Onuphis sp. "intermediates" Hobson, 1971:535-537.
Onuphis elegans: Lissner *et al.*, 1986:D-11.
Onuphis iridescens: Hartman, 1944:87-88, pl. 5, figs. 99-104 (in part).—Lissner *et al.*, 1986:D-11 (in part).

Material Examined. California: Santa Maria Basin, off Point San Luis, Sta. 21 (3). Tomales Bay, PMS 180240, 180242 (2).

Description. Length more than 92 mm, width to 1.5 mm, segments more than 260. Body slender, linear, flattened after first few setigers, in posterior region becoming softer and almost cylindrical; color in alcohol pale, occasionally anterior segments with transverse dorsal stripes of brown pigment across posterior half; cuticle strikingly iridescent.

Prostomium bluntly triangular, about as long as wide; frontal antennae ovate, slightly shorter than prostomium; lateral occipital antennae with very long ceratophores and short styles; outer (anterior) lateral antennae as long as peristomium and first 2 or 3 setigers, ceratophores 2-3 times as long as styles, with 13-15 rings; inner (posterior) lateral antennae as long as peristomium and first 7 or 8 setigers, ceratophores as long as entire outer lateral antennae, with about 16 rings; median antenna about as long as peristomium and first 4 setigers, ceratophore short and slender, with 8 rings. Eyes not observed. Peristomium widest posteriorly, laterally continuous with prostomium, with slender tentacular cirri projecting to middle of prostomium (Fig. 9.12A).

Maxillary formula MI 1+1, MII 7+7, MIII 8+0, MIV 6+8, MV squarish plates with no dentition.

First 4 parapodia enlarged, with elongate cirri and postsetal lobes, inserted slightly ventrally and pointing forward (Fig. 9.12B). Vental cirri replaced by pads in setiger 6 or 7, postsetal lobes cirriform through setiger 8 or 9; gills present from setiger 1, slender and thin throughout, exceeding dorsal cirri after first few setigers. Pseudocompound hooks present in setigers 1-4, tridentate, sometimes with rudimentary (or broken?) terminal tooth, in anteriormost setigers of 3 or 4 kinds, stout to very slender with large to delicate teeth (Fig. 9.12C-F), of 2 kinds in subsequent setigers. Subacicular hooks present from setiger 8 or 9, dark amber colored, projecting further in more posterior setigers than in anterior ones (Fig. 9.12G). Simple limbate setae present throughout, with very narrow wings; pectinate setae in most setigers, distally oblique, with about 15 teeth (Fig. 9.12H). Dorsal cirri with fascicles of 3 delicate notoaciculae, neuropodia with 2-3 neuroaciculae with geniculate free tips.

Remarks. Hobson (1971) hypothesized that these intermediates with characters reminiscent of *O. elegans* (start of subacicular hooks) and *O. iridescens* (slender shape of branchiae) may be offspring of interbreeding individuals of these two species. Although this hypothesis has not been proven through experiments in the laboratory, it is favoured here over the possibility of a new species (also suggested by Hobson). It appears likely that the two established species and the intermediates are still in the process of speciation, and they may be isolated more strongly by biological characters, such as depth range or reproductive behaviour, than their respective genetic makeups.

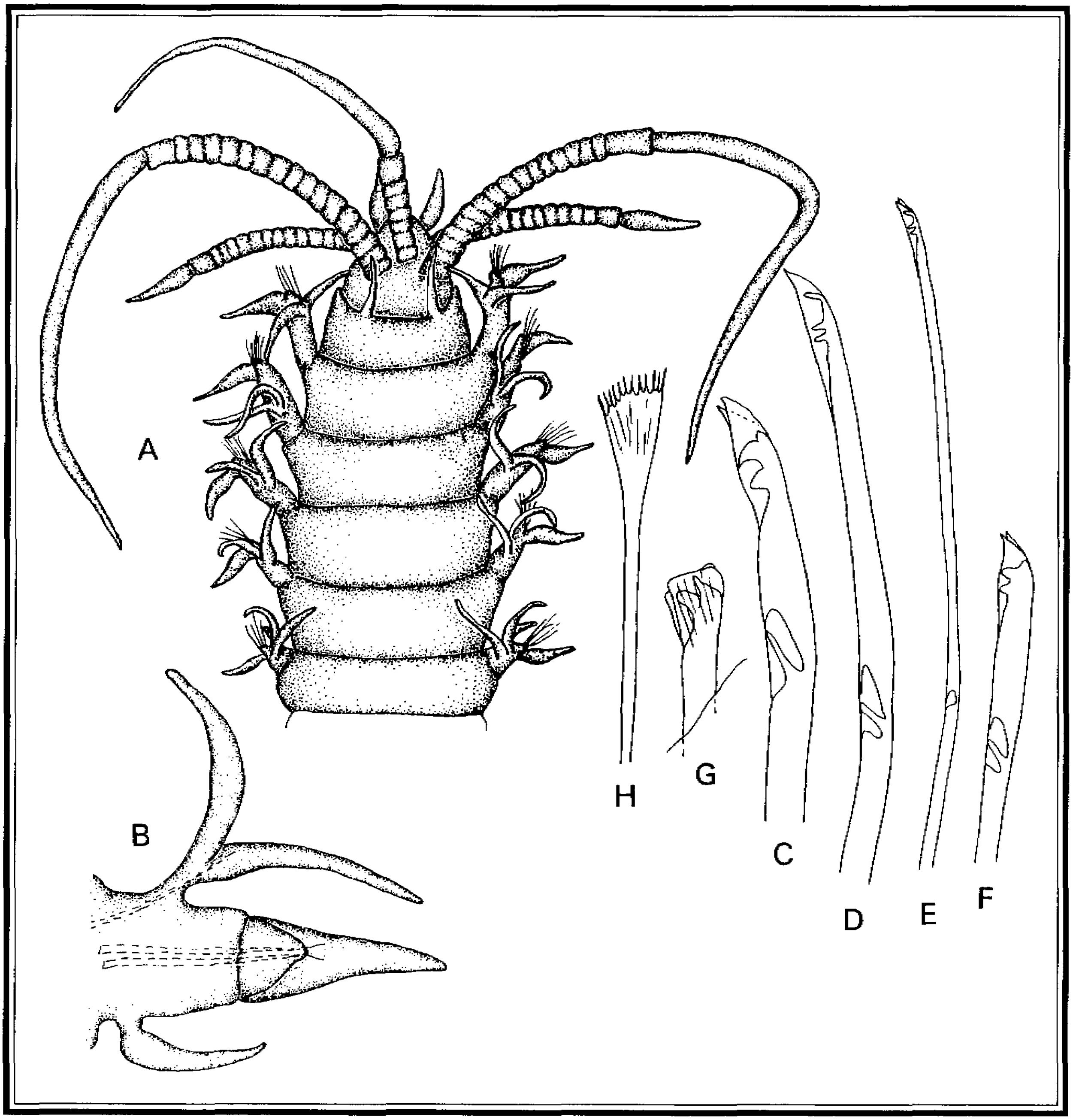

Figure 9.12. *Onuphis* sp. "intermediates", specimen indentified and dissected by Hobson: A, anterior end, dorsal view; B, parapodium 2 or 3, anterior view; C-F, pseudocompound hooks from same, dosal to ventral; G, subacicular hook; H, pectinate seta.

Genus *Paradiopatra* Ehlers, 1887

Type Species. *Paradiopatra fragosa* Ehlers, 1887

Diagnosis. Ceratophores of occipital antennae short, no longer than prostomium; styles of outer (anterior) lateral antennae distinctly longer than their ceratophores. Pseudocompound hooks uni- to tridentate, most often bidentate, with long, slender, acutely pointed hoods; large median hooks and compound spinigers absent. Modified parapodia not prolonged. Branchiae pectinate, often restricted to short anterior part of body between setigers 2-18 and 30-50, rarely absent. Body size generally small, length to 100 mm, width to 2 mm.

Remarks. The genus *Paradiopatra* was revised by Paxton (1986) and now includes all species formerly assigned to *Sarsonuphis* Fauchald, 1982, a genus recognized as junior synonym of *Paradiopatra* by Paxton (1986a). The pointed hoods of the pseudocompound hooks, often visible without dissection of the parapodia, readily distinguish *Paradiopatra* from *Kinbergonuphis* and *Mooreonuphis* who also have short ceratophores. The distribution of *Paradiopatra* is worldwide, but most species are typical deep-water forms. Only two species are known from California, one of which was present in the Phase I and II material.

Paradiopatra parva (Moore, 1911)

Figure 9.13

Onuphis parva Moore, 1911:263-266, pl. 17, figs. 51-57, pl. 18, figs. 98-99.—Fauchald, 1968:37, pl. 9, figs. a-e.
Sarsonuphis parva: Fauchald, 1982:76-77, fig. 20f.—Lissner *et al*., 1986: D-11.—Steinhauer and Imamura, 1990:F-1.
Paradiopatra parva: Paxton, 1986a:38.

Material Examined. California: Santa Maria Basin, off Point San Luis, Sta. R-2 (2); off Purisima Point, Sta. 48 (1); off Point Arguello, Sta. 65 (1).

Description. Length to 45 mm, width to 1 mm, segments to about 100. Body slender, gracile, linear, only slightly flattened, tapering toward pygidium within last 5-8 setigers; color in alcohol pale.

Prostomium rounded, about as long as wide, with clusters of 3-6 small lateral eyespots just outside inner lateral and behind outer lateral antennae; 2 additional single eyes (rarely 3) on frontal margin. Ceratophores of occipital antennae short, with 4-5 rings, arising from crescentic line across middle of prostomium (Fig. 9.13A). Outer (anterior) lateral antennae as long as peristomium and first setiger, styles much longer than ceratophores; inner (posterior) lateral antennae as long as peristomium and first 4-7 setigers; median antenna as long as peristomium and first 5 setigers. Peristomium shorter than prostomium, about as long as subsequent setigers; tentacular cirri slender, extending to antennal bases.

Jaws delicate, transparent; maxillary carriers together urn-shaped, shorter than MI; MII 8-9+9, MIII 7+0, MIV 5-6+7-8, arched over MI; MV small rounded plates without teeth (Fig. 9.13B). Mandibles with slender shafts and poorly mineralized cutting plate.

All setigers of similar width and length except for last 6-8 prepygidial ones; first 2-3 parapodia slightly modified, with somewhat elongate cirri and postsetal lobes (Fig. 9.13C); ventral cirri replaced by pads in setiger 4 (rarely 3 or 5), postsetal lobes cirriform through setiger 9-12; branchiae first present on setiger 3 (rarely 2 or 4), simple at first, then quickly becoming pectinate with up to 8 filaments, arched over dorsum, about one-fourth as long as segmental width, longer than dorsal cirri (Fig. 9.13D); last branchia on setiger 37-45. Pseudocompound hooks bidentate, sometimes unidentate or with tiny subdistal tooth, hoods very long and pointed, present in setigers 1-3 (Fig. 9.13E); subacicular hooks first present in setiger 9, short and very stout at first, gradually projecting further out and becoming more slender with teeth pointing almost straight up rather than forming right angle with shaft (Fig. 9.13F, G); slender, narrowly limbate setae present throughout, least numerous in posterior parapodia; pectinate setae present from anterior setigers, wide with about 15 short teeth anteriorly, gradually narrowing, with 10 long teeth in far posterior segments (Fig. 9.13H, I).

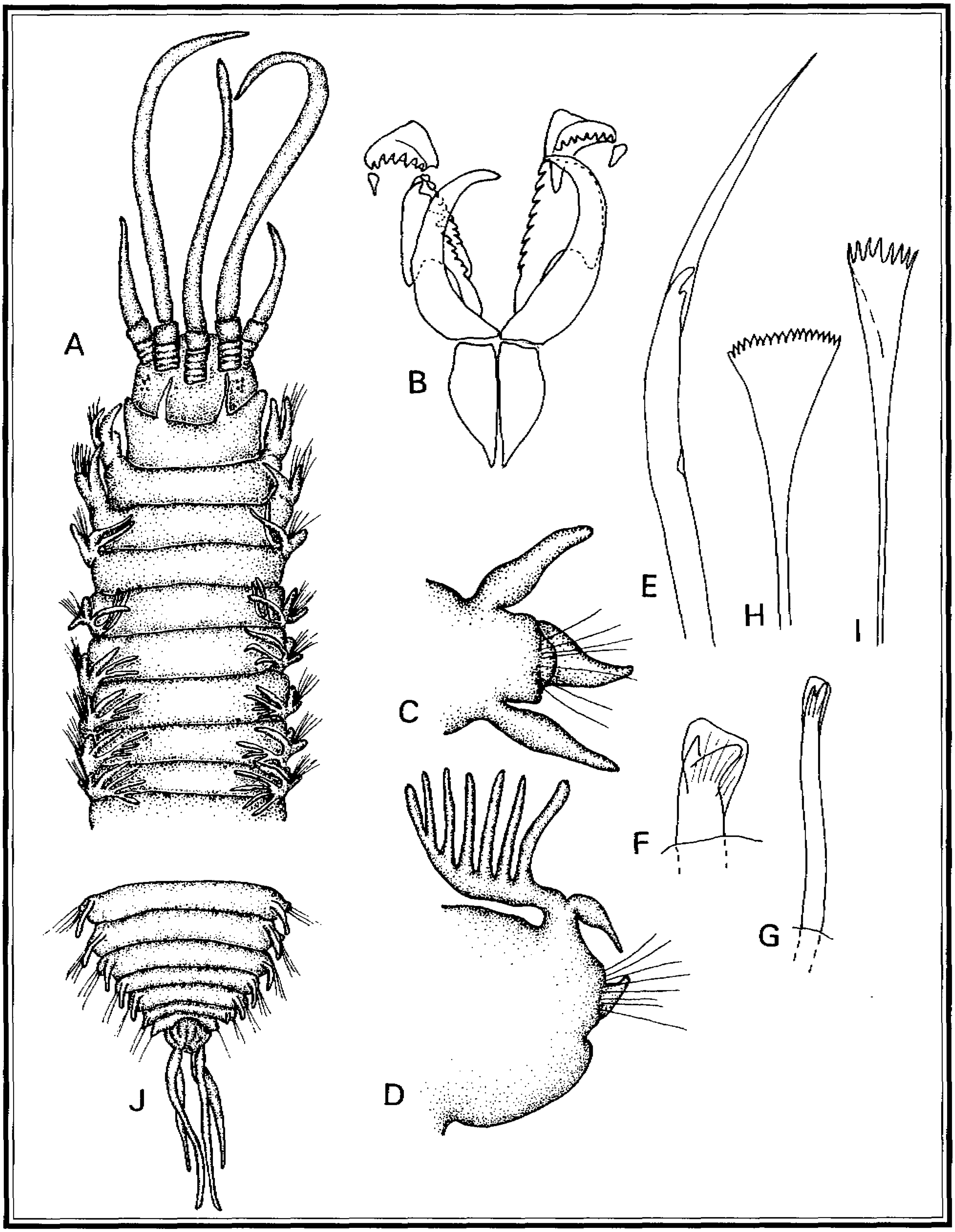

Figure 9.13. *Paradiopatra parva*: A, anterior end, dorsal view; B, maxillae; C-D, parapodia 1 and 7, anterior views (after Fauchald, 1968); E, pseudocompound seta (after Fauchald, 1968); F-G, subacicular hooks, anterior and far posterior setiger; H-I, pectinate setae, anterior and far posterior setiger; J, posterior end, dorsal view.

Pygidium with dorsal anus and 2 pairs of anal cirri, shorter pair as long as last 6 setigers, longer pair as long as last 8 setigers (Fig. 9.13J).

Remarks. *Paradiopatra parva* is easily recognized by the presence of gills before setiger 10; the only other known species with this character is *P. furcasetosa* (Monro, 1937) which occurs in the Indian Ocean. The co-occurring *P. hiadentata* (Moore, 1911) differs most conspicuously from *P. parva* in the branchiae; they are simple rather than pectinate and start on setiger 12 rather than 3.

Type Locality and Type Specimens. California, Monterey Bay, off Point Piños Lighthouse: holotype (USNM 17356) and 9 paratypes (USNM 17359).

Biology. Moore (1911) reported that this species can be found in great abundances, mostly in mud, but also in sandy sediments. The examined specimens were collected in sediments with about 80% silt.

Distribution. Southern and central California; Baja California; 10 - 300 m.

Genus *Rhamphobrachium* Ehlers, 1887

Type Species. *Rhamphobrachium agassizi* Ehlers, 1887

Diagnosis. First three setigers highly modified, bearing elongate parapodia with very long, delicate setae with spiny shafts and hooked tips, setal sacs extending back to setigers 30-60. Ceratophores of occipital antennae short, with 2-5 rings; all styles short, no longer than peristomium and first 2-5 setigers. Branchiae from setiger 6-17, simple or pectinate. Body size moderate, length to more than 190 mm, width to 7 mm. Distribution worldwide, all species rare.

Remarks. *Rhamphobrachium* and related genera were revised by Paxton (1986b), who erected the subgenera *R. (Rhamphobrachium)* and *R. (Spinigerium)*, the latter differing from the former by the presence of compound spinigers in some anterior segments and a sixth pair of maxillae.

Rhamphobrachium longisetosum Berkeley and Berkeley, 1938

Figure 9.14

Rhamphobrachium longisetosum Berkeley and Berkeley, 1938:428-435, figs. 1-8.—Hartman, 1944:48-49, pl. 1, figs. 1-8.—Paxton, 1986:88-89, figs. 7a-g.—Lissner *et al.*, 1986:D-11.—Steinhauer and Imamura, 1990:F-1.

Material Examined. California: Santa Maria Basin, off Point Estero, Sta. 2 (1); off Point Sal, Sta. R-8 (1).

Description. Length more than 84 mm, width to 5 mm, setigers more than 127. Body linear, somewhat flattened, with highly modified anterior setigers; color in alcohol uniformly pale, or prostomium, peristomium and first few setigers with brownish dorsal pigment bands.

Prostomium small, rounded, with short appendages; frontal antennae spherical; ceratophores of occipital antennae shorter than prostomium, with 4 short (range 3-6) rings and longer terminal ring; outer (anterior) lateral antennae as long as peristomium and first 1 or 2 setigers, inner (posterior) lateral antennae as long as peristomium and first 3-5 setigers, median antenna as long as peristomium and first 4 setigers. Two pairs of eyes, usually faded in alcohol. Peristomium short, bearing fairly long, tapered tentacular cirri, almost reaching palps (Fig. 9.14A).

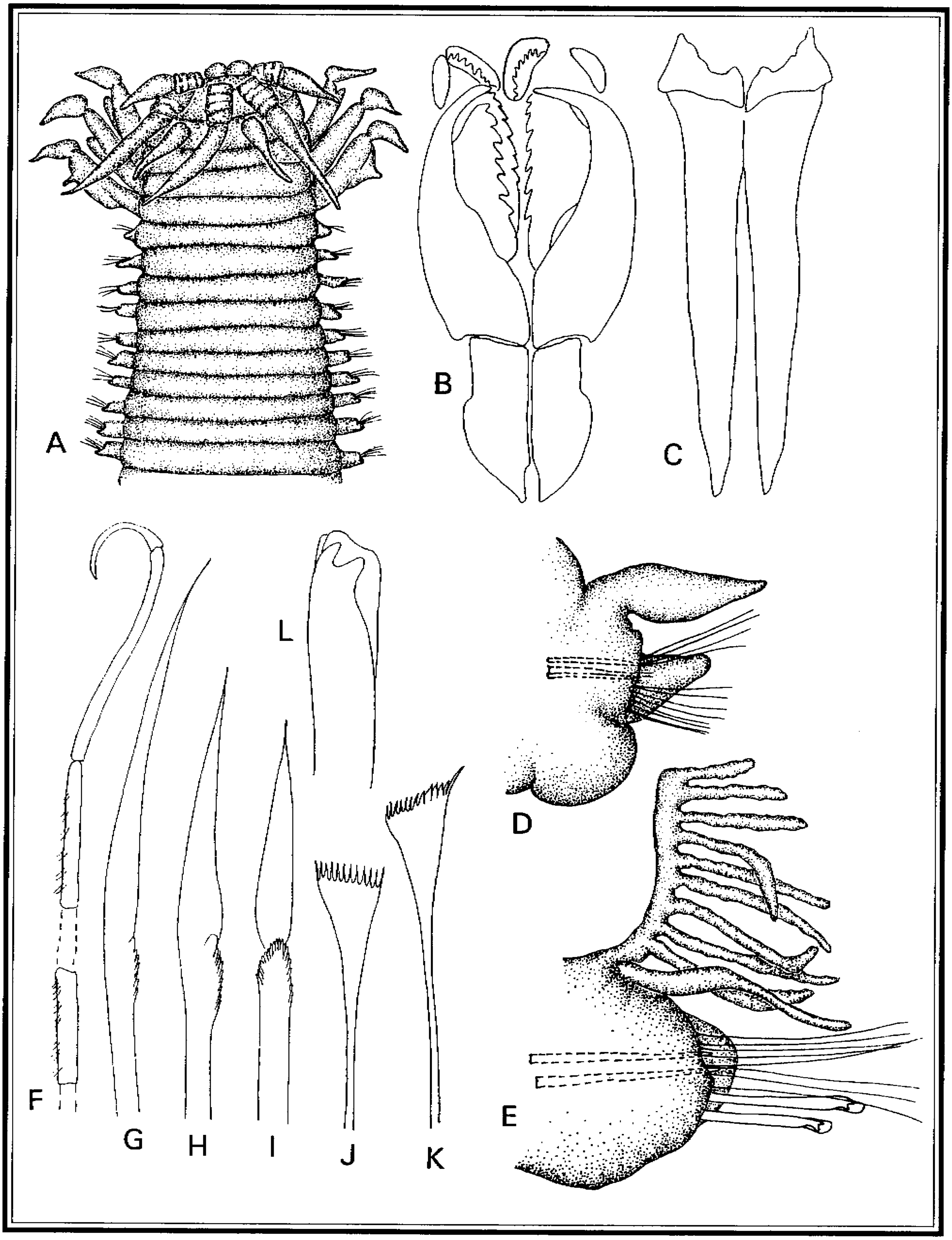

Figure 9.14. *Rhamphobrachium longisetosum*: A, anterior end, dorsal view; B, maxillae; C, mandibles; D, parapodium 4, anterior view; E, far posterior parapodium, anterior view; F, recurved hook; G-I, pseudocompound setae; J-K, pectinate setae; L, subacicular hook. (A, F after Berkeley and Berkeley, 1938; B, C after Hartman, 1944; D, G-I after Paxton, 1986b).

Mandibles calcified, with long, slender shafts bearing crescentic cutting plate with large tooth on either side of median cleft. Maxillae hard and calcified, with large, squarish carriers and wide, strongly falcate MI. MII6-7+7, MIII 7-8+0, MIV 7-8+9-11, MV flat plates with no teeth (Fig. 9.14B, C).

First 3 parapodia strongly modified, progressively longer from anterior to posterior, pointing forward, with anterior sides facing body wall, with long subulate postsetal lobes and 3 short, papilliform lobes surrounding each seta; dorsal and ventral cirri subulate. Postsetal lobes present through setigers 15-20, much reduced in size after setiger 5; ventral cirri subulate through setiger 3, spherical in setiger 4 (Fig. 9.14D), replaced by pads after that. Branchiae from setiger 8 or 9, pectinate, with maximally 8-10 short filaments (Fig. 9.14E), simple in first few setigers. Modified parapodia each with 3 very long, slender recurved hooks, shafts with two longitudinal rows of spines, setal sacs extending to about setiger 50 (Fig. 9.14F). Pseudocompound setae present in setigers 4 to about 15, in lower part of setal fascicles (Fig. 9.14G-I); simple limbate setae and pectinate setae with 12-20 teeth present from setiger 4, in upper part of setal fascicles (Fig. 9.14J, K); subacicular hooks present singly from setiger 12-14, in pairs from setigers 15-17 (Fig. 9.14L).

Tubes with tough, parchment-like inner layer and sandy outer layer.

Remarks. *Rhamphobrachium longisetosum* is the only species of this genus known to occur in the northeastern Pacific; the strongly modified first three segments bearing prolonged parapodia make this species unmistakeable even if the rather fragile hooks have broken off. The specimen from Point Estero appears to be the largest one reported and may also represent a range extension.

Type Locality and Type Specimens. California, off mouth of Santa Ana River: syntype (USNM 32865); off Balboa: syntype (USNM 32866).

Habitat. Found in sandy sediments; the examined specimens were collected at stations with about 75% sand.

Distribution. Central California to Mexico; Galapagos Islands; 20 - 730 m.

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10. Family Eunicidae Savigny, 1818

by

Brigitte Hilbig[1]

Introduction

The eunicids are among the more spectacular polychaetes because of their considerable size and vivid coloration. They are not only one of the largest polychaete families in terms of number of species, but also one of the very few with a fossil record which reaches back to the Cretaceous period (fossils are also known from most other eunicemorph families, although more scattered than for the eunicids). The largest known polychaete, reported by Fauvel (1923) as being about three meters long, is a species of *Eunice*. The only polychaetes eaten regularly by people are swarming species caught in regions of the South Pacific (genus *Palola*). The family is important ecologically because they break down coral rock. Eunicids are most closely related to the Onuphidae, but can be distinguished from the latter by the presence of five antennae (sometimes only one or three) arising from very short, cylindrical ceratophores; in contrast, onuphids always have seven prostomial appendages, including five antennae that arise from long, usually annulated ceratophores, and two frontal appendages referred to as frontal antennae or frontal palps. Eunicids are not quite as iridescent as onuphids, but often more colorful, and typically have larger, more delicate gills than onuphids. In addition, eunicids build fragile, parchmentlike tubes if any, whereas many onuphids are known for their hard, quill-like or very tough fibrous tubes.

Morphology

The prostomium is typically bilobed with deep median dorsal and ventral folds, but it may also be rounded. In most genera, it bears five occipital antennae: a pair of outer and inner lateral antennae (also referred to as A-I and A-II) and a single median antenna (also called A-III). There are only two exceptions to this pattern; *Nematonereis* has only one antenna, *Lysidice* has three antennae. The ceratophores are inconspicuous and short; the ceratostyles may be as long as about 10 to 15 setigers, and they may be smooth, wrinkled, or articulated, with the articles being cylindrical, moniliform, or drop-shaped. Characters of the antennae, such as their relative lengths, are often important for species discrimination. Many species have two or four eyes. The pharynx is developed into an eversible proboscis with very massive muscle layers and a jaw apparatus consisting of ventral mandibles and several pairs of maxillary plates as is typical for the order Eunicida. The maxillae are asymmetrical; the left side consists of five to six plates, the right side only of four to five (the third maxilla is absent on the right side). All jaw elements are more or less sclerotized and often calcified with aragonite, the same mineral that is found in onuphid jaws.

The peristomium consists of two apodous and asetigerous rings, the anterior one usually much longer than the posterior, which may or may not bear a pair of tentacular cirri. The presence of tentacular cirri is used as a diagnostic character at the generic level; proportions and the presence of articulations or wrinkles can sometimes be used for identification to species.

[1] ENSR Consulting and Engineering, 89 Water Street, Woods Hole, Massachusetts 02543

Parapodia are subbiramous with the notopodia reduced to the base of the dorsal cirri; a fascicle of fine notoaciculae extends into the cirri that may be smooth, wrinkled, or articulated. The articles are typically cylindrical and separated by very thin folds, so that in preserved specimens they are easily overlooked. The neuropodia are well developed and bear large setal fascicles. Setae include simple capillaries, furcate setae, hooded compound spinigers (*Marphysa* and *Euniphysa*) and falcigers, and simple, uni- to tridentate, hooded subacicular hooks (subacicular hooks are absent in the genus *Palola*). The color and dentition of the subacicular hooks is used to divide the genus into four major groups, at least some of which are natural (Fauchald, pers. comm.). Branchiae are often present and typically consist of several branches arising from a more or less well-defined stem in a palmate or pectinate arrangement. The branchial region may be restricted to a small number of anterior segments or encompass most of the length of the animal; the number of branchiae, the arrangement and number of filaments, and the distribution of simple and branched gills along the body are important characters for species discrimination.

Taxonomic History

The first eunicids, including the type species of *Eunice*, *E. aphroditois*, were described by Linné, Pallas, and Müller in the years between 1767 and 1788 as a species of *Nereis*, which at that time was a genus used to accommodate almost all polychaetes that were not scaleworms. The wealth of eunicid species known today, however, was described during the second half of the 19th century, during a period of numerous expeditions by European countries that had colonies in tropical and subtropical locations. In recent years, the focus in the literature has shifted from taxonomy to the systematics of this family and its relationship to other eunicemorphs (Fauchald, 1970, 1992; Orensanz, 1990), and the definition of eunicid genera is still in flux (Fauchald, pers. comm.). Orensanz (1990) provides an excellent account on the phylogeny of the eunicemorph families, including fossil ones. A very extensive account of the history of the genus *Eunice* can be found in Fauchald (1992). Currently, the Eunicidae contain about 275 species in 8 genera, with 205 species alone in the genus *Eunice*.

Distribution and Biological Notes

Although eunicids are distributed worldwide and in depths ranging from the intertidal to the continental slope, they are typical tropical, shallow-water organisms, often associated with coral reefs. Some species are known to build thin, sometimes branched, parchment-like tubes, including *Eunice americana* Hartman, 1944, a species common in central California. Most species, however, bore into corals and sponges, burrow into the sediment, live among algal holdfasts, or dwell in fissures and cracks among rocks. Winsnes (1989) reported that some Scandinavian species of *Eunice* are found inside of cold-water corals where they may secrete a thin tube. Eunicids are typically very active and thought to be mostly carnivorous (Pettibone, 1982; Fauchald and Jumars, 1979), feeding on nemerteans (Winsnes, 1989), annelids, small crustaceans and bivalves, chaetognaths, and diatoms (Gathof, 1984). Some species of *Marphysa* are believed to be herbivorous or omnivorous. Gathof (1984) describes in some detail how reef-dwelling eunicids feed on small organisms attached to coral rock. The maxillae are used to hold on to the substratum, while the mandibles function as a rasp to break down the coral. Some species leave their tube or shelter to feed, while others just extend their anterior end. When food is abundant, they may store food in the tube (Winsnes, 1989).

When disturbed, eunicids fragment readily and are able to regenerate both ends. Hofmann (1969) investigated regeneration in *Eunice siciliensis* under laboratory conditions and found that (1) results were better the more anterior the fragment was, and (2) regenerated heads had fully developed sense organs, appendages, and brain including neurosecretory glands, but no mouth and pharynx. Apparently regeneration of the prostomium ensures completion of one reproductive cycle even though the animals are not able to resume feeding.

Sexes are separate, and several modes of reproduction are known (Åkesson, 1967; Hofmann, 1972, 1974). The most widely known and extensively studied reproductive behavior is epitoky and swarming influenced by lunar cycles. Swarming during full moon nights has been described for several species of *Palola*, *Eunice*, and *Lysidice*. Either the entire animals or the shedded posterior ends filled with gametes ascend to the surface en masse and release eggs and sperm while swarming; since posterior ends are easily regenerated, both groups of species can reproduce more than once in their lifetime. Some species, such as *Eunice valens* (as *E. kobiensis* in Åkesson, 1967), do not become epitokous and reproduce on the sea floor. Bhaud and Cazaux (1987) summarized two studies on larval development of eunicids, one on *Eunice harassii* by Herpin (1925) and the other on *Marphysa borradailei* by Pillai (1958). The pelagic stage of *E. harassii* lasts for about 8 to 10 days; the settling larva has 3 setigers. About 3 days later, the jaws and the median antenna are visible; inner lateral antennae appear after 8 months when the juvenile has 13 setigers, and outer lateral antennae and tentacular cirri appear even later. Species of *Marphysa* do not swarm, but form gelatinous egg masses. After a very short pelagic period, the larvae settle. A median antenna was observed in *M. borradailei* at the 11-setiger stage, and gills first appeared at the 12-setiger stage. As in *E. harassii*, the lateral antennae and tentacular cirri form very late, so that specimens with less than 80 setigers cannot even be identified to genus.

Key to the Eunicidae

1A. Peristomium without tentacular cirri; compound setae with spinigerous or falcigerous blades, sometimes occurring together .... genus *Marphysa* 2

1B. Peristomium with tentacular cirri; compound setae falcigerous, subacicular hooks present .... genus *Eunice* 3

2A. Subacicular hooks and aciculae yellow; branchiae large, pectinate, up to 7 filaments, present on only 10 segments; all compound setae falcigerous .... *Marphysa conferta*

2B. Subacicular hooks and aciculae dark brown to black; branchiae simple throughout, present from setiger 5-7 to nearly end of body; all compound setae falcigerous .... *Marphysa stylobranchiata*[2]

3A. Subacicular hooks and aciculae black; MIII short, arching over MI and MII .... *Eunice multipectinata*

3B. Subacicular hooks and aciculae yellow; MIII long, located alongside MI and MII 4

4A. Compound setae with pointed hoods; branchiae with up to 23 filaments, on setigers 3 through about 38 .... *Eunice americana*

4B. Compound setae with blunt hoods; branchiae with maximally 10 filaments 5

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[2] Not found in the Phase I and II material, but likely to occur on hard bottom in the area.

5A. Antennae thick, with club-shaped articles; branchial region encompassing less than half of entire body length; peristomial cirri reaching to middle or posterior margin of prostomium .... *Eunice multicylindri*

5B. Antennae slender, with cylindrical articles; branchial region encompassing more than half of entire body length; peristomial cirri reaching tip of prostomium .... *Eunice vittatopsis*

Description of Species

Eunicids are typical inhabitants of subtropical to tropical, shallow-water, hard-substratum habitats, and consequently only few members of this family were found during Phases I and II. The following species are treated in this chapter:

Eunice americana Hartman, 1944
Eunice multicylindri Shisko, 1981
Eunice multipectinata Moore, 1911
Eunice vittatopsis Fauchald, 1970
Marphysa conferta Moore, 1911

Genus *Eunice* Cuvier, 1817

Type Species. *Nereis aphroditois* Pallas, 1788

Diagnosis. Prostomium bilobed or anteriorly entire, bearing 5 antennae with short, smooth ceratophores and smooth or annulated styles; 1 or 2 pairs of eyes usually present. Maxillary apparatus with falcate MI, paired MII, left MIII, asymmetrical MIV with the right one being longer and bearing more teeth than the left one, small edentate or unidentate MV, and occasionally small MVI resembling MV. Mandibles flat, about as large as maxillae, with elongate shafts bearing crescentic, medially cleft cutting plate. Peristomium consisting of 2 apodous rings; posterior ring with a pair of tentacular cirri arising from anterior margin. Setae including hooded compound falcigers, simple limbate capillary and pectinate setae, and bi- to tridentate, hooded subacicular hooks. Branchiae rarely absent, often pectinate, starting between setigers 5 and 10, usually present in all but last few prepygidial segments.

Remarks. The shape of the anterior prostomial margin is usually included in a species description, but it may not be of much taxonomic value. For the most part, the degree to which a prostomium is notched anteriorly depends on the orientation of the prostomium. If it points anteriorly, the notch is always visible in dorsal view; if it points slightly downward, the anterior margin appears smoothly rounded because the actual margin cannot be seen from above.

Eunice americana Hartman, 1944

Figure 10.1

Eunice americana Hartman, 1944:118-121, pl. 8, figs. 164-174, 189; 1968:727.—Fauchald, 1970:19, pl. 1, figs. d-e; 1992:51, fig. 8, tab. 42, 43.—Lissner *et al.*, 1986:D-11.—Steinhauer and Imamura, 1990:F-1.

Material Examined. California, western Santa Barbara Channel, off Point Conception, Sta. 81 (1), Sta. 101 (3); Santa Maria Basin, off Purisima Point, Sta. R4 (1).

Description. Length to 105 mm, width to 4 mm, segments to 133. Body robust, dorsoventrally flattened, with delicate, conspicuous branchiae arched over dorsum of anterior segments. Color in alcohol pale.

Prostomium incised anteriorly, with two pairs of large eyes (occasionally only one pair visible in preserved specimens) between bases of inner and outer lateral antennae. Antennae with indistinct cylindrical articles; outer lateral antennae shortest, as long as peristomium and first setiger; inner lateral antennae up to 5 times longer, usually as long as peristomium and first 4 to 8 setigers; median antenna as long as inner laterals or only about half as long. Tentacular cirri slender, tapering, projecting to tip of prostomium or slightly beyond (Fig. 10.1A).

Maxillary formula: MI 1+1, MII 8-9+8-9, MIII 9-10+0, MIV 8+10, MV 1+1, large cones; MVI small, edentate plates or absent (Fig. 10.1B).

Parapodia with simple, basally inflated ventral cirri and indistinctly articulated, medially inflated dorsal cirri; pre- and postsetal lobes low, rounded folds, acicular lobes conical throughout. Branchiae present in short anterior body part, occurring from setiger 3 through setiger 34 or 35 (range 33-38); with 2 or 3 filaments in first two setigers, then quickly becoming pectinate, stems distinctly longer than dorsal cirri and not much wider than filaments, with up to 23 filaments where best developed, usually on setigers 10-15 (Fig. 10.1C). Last 2 branchiae simple. Setae numerous, in dense, bushy fascicles; limbate setae longest, finely serrated; compound hooded hooks with long, slender blades bearing two small, widely diverging teeth, appearing almost unidentate when worn; hoods with distinct mucrons (Fig. 10.1D). Pectinate setae short, with about 15 teeth, the outermost ones longest, of equal or subequal length (Fig. 10.1E). Subacicular hooks yellow, first present from setiger 23-25 (setiger 29 in one specimen), tridentate, usually occurring singly, occasionally 3 or 4 hooks present including replacement hooks (Fig. 10.1F). Aciculae yellow, 2 per parapodium, with slightly curved and tapered tips projecting through parapodial wall (Fig. 10.1G).

Remarks. *E. americana* is one of the most common eunicids off the California coast. The species is easily recognized by the pointed hoods of the compound setae and the numerous filaments of the gills.

Type Locality and Type Specimens. California, off Redondo Beach, 256-309 m: holotype (LACM-AHF Poly 0725).

Habitat. Living in branched, parchment-like tubes in sandy and silty sediments.

Distribution. Central California to western Mexico, 27 - 357 m.

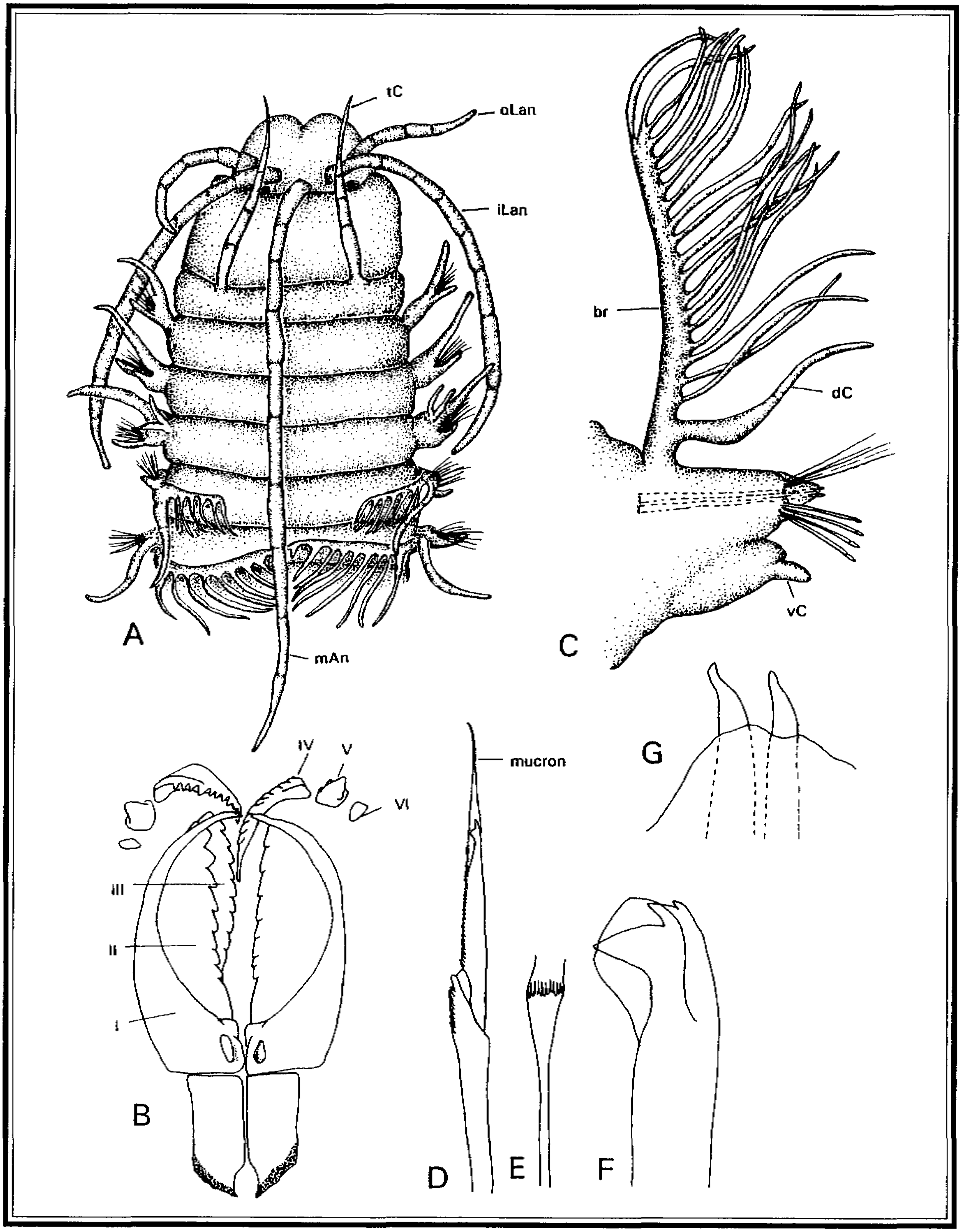

Figure 10.1. *Eunice americana*: A, anterior end, dorsal view; B, maxillae; C, parapodium from branchial region, anterior view; D, compound falciger; E, pectinate seta; F, subacicular hook; G, tips of aciculae. (D-G after Fauchald, 1992).

Eunice multicylindri Shisko, 1981

Figure 10.2

Eunice multicylindri Shisko, 1981:971-973, fig. 2, tab. 1.—Lissner *et al.*, 1986: D-11.—Fauchald, 1992:227-228, fig. 75f-i, tab. 10, 41, 42.
Eunice vittatopsis: Lissner *et al.*, 1986: D-11 (in part).

Material Examined. California: Santa Maria Basin, off Point Estero, Sta. 6 (1); off Point Buchon, Sta. 16 (2); off Point San Luis, Sta. 27 (1)

Description. Length to 45 mm, width to 1 mm, segments to 132. Body slender, cylindrical, uniformly pale in alcohol.

Prostomium rounded, with 2 large, dark eyes behind bases of inner lateral antennae. Antennae with 3-6 club-shaped articles, relatively thick compared to overall body size. Peristomial cirri indistinctly articulated, articles cylindrical; reaching to posterior margin or middle of prostomium (Fig. 10.2A).

Jaws weakly sclerotized and not calcified. Maxillary formula: MI 1+1, MII 8+8, MIII 8+0, MIV 7+10, MV 1+1, according to Fauchald (1992); MVI absent.

Parapodia with low, truncated pre- and postsetal lobes and conical acicular lobes from which tips of aciculae are emerging (Fig. 10.2B, C). Dorsal and ventral cirri smooth, ventral cirri slender in first 5 to 6 setigers. Branchiae first present from setiger 3 or 4, simple in first 2 to 7 setigers, then becoming pectinate with maximally 6 (usually 4) filaments; last 10 to 15 branchiae simple. Branchial region extending through 20 to 40 setigers, representing less than half of body length. Compound falcigers with moderately long blades bearing blunt hoods; subdistal tooth much larger than distal one (Fig. 10.2D). Pectinate setae with about 12 teeth, outermost ones longest, subequal (Fig. 10.2E). Subacicular hooks yellow, tridentate, with distal tooth much smaller than subdistal one (Fig. 10.2F); hooks occurring singly, first present in setiger 13 (young specimens) to about 30. Aciculae yellow, tapering, with free filamentous tips.

Remarks. This species is very similar to *E. vittatopsis* Fauchald, 1970 and can best be separated from the latter by the relatively thick antennae and the shorter branchial region; the absolute number of gills overlaps between the two species.

Type Locality and Type Specimens. Southern California: holotype (USNM 63066) and 5 paratypes (USNM 63068-63970).

Habitat. In coarse sand or on rocky bottom; tubes with outer lining of relatively coarse sand grains.

Distribution. Central and southern California, 70 to 611 m.

Eunice multipectinata Moore, 1911

Figure 10.3

Eunice multipectinata Moore, 1911:248-251, pl. 15, figs. 20-23.—Hartman, 1944:112-113.—Fauchald, 1970:36-37, pl. 3, figs. h-i; 1992:228-229, fig. 76a-i, tab. 27, 32.—Lissner *et al.*, 1986: D-11.

Material Examined. California: Santa Maria Basin, off Point Estero, Sta. 6 (2).

Description. Length to 205 mm, width to 11 mm, segments to 181. Body robust, nearly cylindrical with slightly flattened ventrum; widest in pharyngeal region, gently tapering toward pygidium. Color in alcohol pale, in life variously pigmented, with pearl-colored to orange-brown or yellow dorsum, banded, mottled, or with scattered irregular red blotches in most anterior setigers.

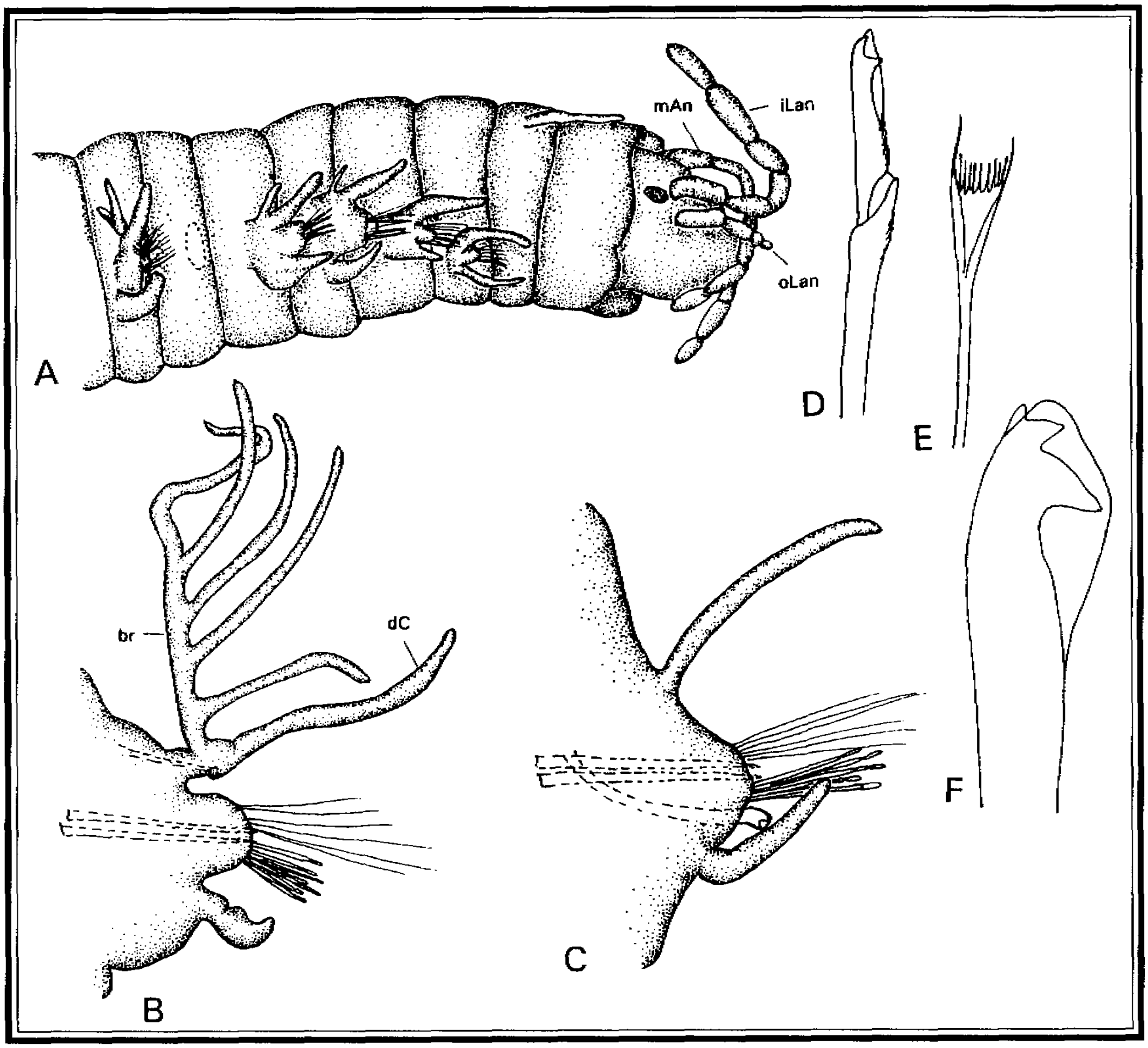

Figure 10.2. *Eunice multicylindri*: A, anterior end, lateral view; B-C, parapodia from branchial and postbranchial region, anterior vierw; D, compound falciger; E, pectinate seta; F, subacicular hook. (A, D-F after Fauchald, 1992).

Prostomium deeply notched anteriorly, withdrawn into anterior peristomial ring to antennal bases, less than half as deep as peristomium. Antennae irregularly articulated, median one (A-III) longest, reaching to setiger 7-11, with 7-12 articles; inner lateral antennae (A-II) reaching to setiger 4-8, with 5-11 articles; outer lateral antennae (A-I) much shorter, reaching setiger 1-3, with 4-7 articles. Eyes conspicuous, dark, but easily overlooked when head is withdrawn into peristomium. Anterior peristomial ring about 5 times as long as posterior one; peristomial cirri slender, tapered, with 5-6 articles, reaching posterior margin of prostomium or front of anterior peristomial ring (Fig. 10.3A).

Jaws very hard, strongly calcified and sclerotized (dark brown) in adults, less sclerotized (white to light brown) in younger specimens. Maxillary formula: MI 1+1, MII 5-8+5-8, MIII 6-9+0, MIV 4-7+10-11, MV 1+1, MVI 1+1. Teeth on MII very coarse and offset to close tightly when withdrawn; MIII short, arched over MI and MII; teeth on MV very large and conical, those on MVI minute. Mandibles with dark shafts and very hard, white cutting plate with smooth anterior edge, with about 3 large, irregular teeth in juveniles.

Parapodia with articulated dorsal cirri, at least in anterior setigers; ventral cirri digitiform in first 5 setigers, basally inflated in middle setigers (Fig. 10.3B), long and slender in far posterior setigers. Branchiae present from setiger 7, with 7 filaments in holotype, 3 in largest examined specimen; number of branchial filaments quickly increasing to maximum number (5 in largest examined specimen, 11 in holotype); decreasing after about 20 setigers, only last one with single filament. Branchial region extending to end of body except for last 2 or 3 setigers. Limbate setae with narrow, very finely serrated wings; pectinate setae slightly furled, with about 10 to 15 teeth, one outer tooth much longer than others (Fig. 10.3C). Compound falcigers with ends of shafts finely and very regularly serrated; blades moderately long, bearing sharply oblique, short hoods with serrations similar to shaft (Fig. 10.3D). Subacicular hooks dark brown to jet black, first present from setiger 32-45, occurring singly; with large main fang and smaller distal tooth above (Fig. 10.3E). Aciculae large, dark, tapering, straight or slightly bent, especially in posterior setigers, protruding from dorsal tip of acicular lobes (Fig. 10.3F).

Pygidium small, ring-shaped, surrounding dorsal anus and bearing 2 pairs of anal cirri, both inserted ventrolaterally; larger pair thick, as long as last 7-11 setigers; smaller pair much thinner and only as long as last 1-2 setigers (Fig. 10.3G).

Remarks. There appear to be two oversights in Fauchald's (1992) review of the eunicids considering this species, both related to the branchiae. Both in the key and the description of *E. multipectinata*, the branchiae are said to be distinctly longer than the dorsal cirri, but later in the text the branchiae are described as being "shorter than notopodial cirri except in setigers 15-30", which agrees with the illustrations. Fauchald also describes the branchiae as having "single filaments in first 8-10 branchiated setigers", which clearly differs from the illustration and also from Moore's (1911) description of the branchiae as being "strictly unilateral pectinate throughout". The examined specimens, both not fully grown, are more similar to Moore's description in that the branchiae are shorter than the dorsal cirri and pectinate throughout except for the last few setigers.

Type Locality and Type Specimens. Southern California, off Point Loma Lighthouse: holotype (USNM 16919).

Habitat. *E. multipectinata* is found in sand mixed with mud or rocks.

Distribution. Central California to western Mexico (Baja California), 43 - 270 m.

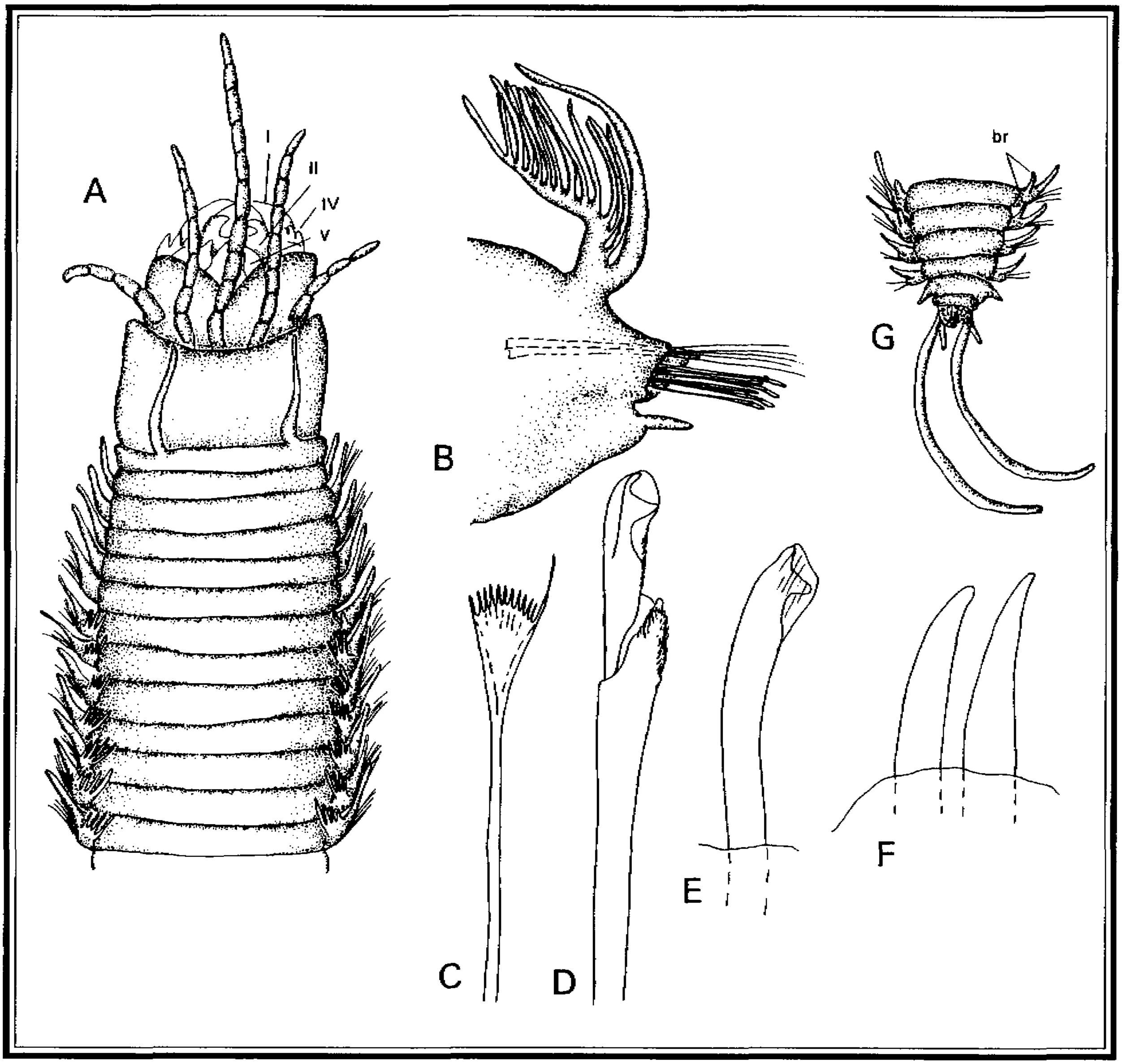

Figure 10.3. *Eunice multipectinata*: A, anterior end, dorsal view, proboscis partly everted; B, middle parapodium, anterior view (after Fauchald, 1992); C, pectinate seta; D, compound falciger; E, subacicular hook; F, tips of aciculae; G, posterior end, dorsal view.

Eunice vittatopsis Fauchald, 1970

Figure 10.4

Eunice vittatopsis Fauchald, 1970:50-52, pl. 7, figs. a-d.—1992:340, fig. 115 j-s, tab. 41, 43.—Lissner *et al.*, 1986: D-11 (in part).

Material Examined. California: Santa Maria Basin, off Purisima Point, Sta. BRA-16 (1).

Description. Length to 40 mm, width to 2.5 mm, segments to 115. Body slender, oval in cross-section; color in alcohol pale, often strongly iridescent.

Prostomium deeply incised anteriorly, bearing slender, tapered, articulated antennae; eyes absent. Outer lateral antennae shortest, with about 6 cylindrical articles, as long as peristomium and first 1 to 4 setigers; inner lateral and median antennae subequal, as long as peristomium and first 6 or 7 setigers, with 5 to 9 cylindrical articles. Peristomial cirri reaching to or beyond anterior prostomial margin, slender, with 4 to 6 cylindrical articles (Fig. 10.4A).

Jaws well sclerotized; maxillary formula: MI 1+1, MII 8+9, MIII 9+0, MIV 6+13, MV 1+1; MVI absent.

Parapodia with articulated dorsal cirri, smooth ventral cirri, and low, rounded pre- and postsetal lobes throughout; acicular lobes bluntly conical, barely projecting beyond pre- and postsetal lobes. Ventral cirri digitiform through setiger 4, basally inflated with filiform tips through setiger 60, more slender and digitiform to end of body (Fig. 10.4B-D). Branchiae present from setiger 3, pectinate except for first 2 setigers, with up to 10 filaments about as long as dorsal cirri (Fig. 10.4C, D). Branchial region encompassing most of body length; last branchia of holotype on setiger 85. Simple setae with long, slender serrations along one margin (Fig. 10.4E), appearing broadly limbate under low magnification; pectinate setae narrow, with 6 to 8 teeth, one outer one much longer than others (Fig. 10.4F); compound falcigers with moderately long blades; shafts distally slightly inflated, smooth or finely serrated; blades with 2 fairly large teeth and smooth or finely serrated hood (Fig. 10.4G). Subacicular hooks present from setiger 39, tridentate with very small distal tooth (Fig. 10.4H), occurring singly; aciculae usually 2 per parapodium, straight with tapered tips; subacicular hooks and aciculae yellow.

Remarks. *E. vittatopsis* is similar to *E. multicylindri* Shisko, 1986; it can best be distinguished by the shape of the antennae, which are more slender in *E. vittatopsis* and composed of cylindrical rather than drop-shaped articles.

Type Locality and Type Specimens. Mexico, Baja California, Ensenada de San Francisco: holotype (LACM-AHF Poly 0337).

Habitat. Found on hard substrata.

Distribution. Central California to western Mexico (Baja California), intertidal to 92 m.

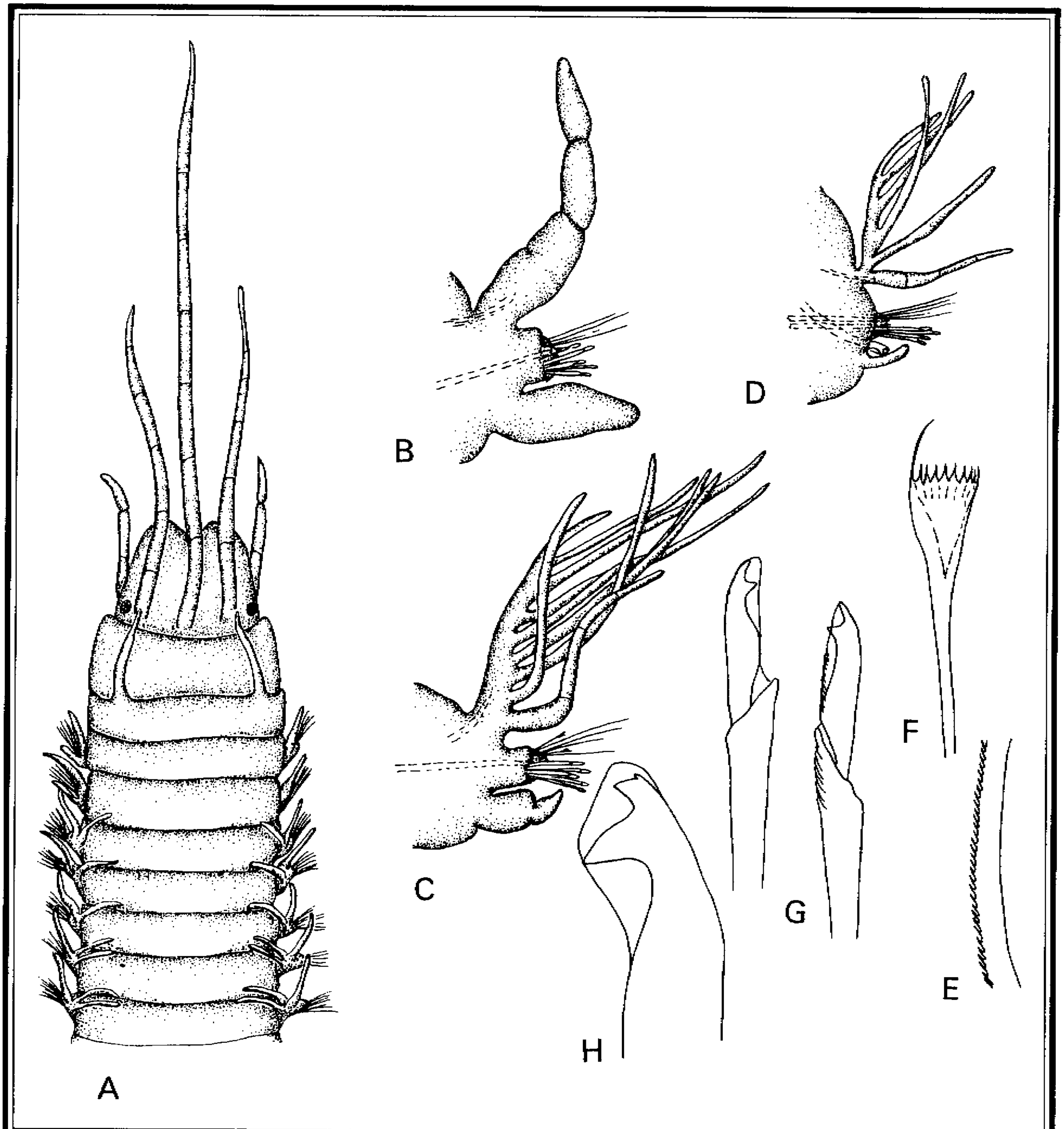

Figure 10.4. *Eunice vittatopsis*: A, anterior end, dorsal view; B-D, anterior, middle, and posterior parapodia, anterior view; E, detail of limbate seta; F, pectinate seta; G, anterior (left) and posterior compound falciger; H, subacicular hook. (B-D, G, H after Fauchald, 1992).

Genus *Marphysa* Quatrefages, 1865

Type Species. *Nereis sanguinea* Montagu, 1815

Diagnosis. Prostomium rounded or bilobed, with 5 occipital antennae arising directly from prostomium, not divided into ceratophores and styles; tentacular cirri absent; setae include hooded compound spinigers and falcigers, limbate and pectinate setae, and hooded subacicular hooks. Branchiae usually present, often pectinate, distributed along short length of body.

Remarks. The genus is currently being revised by Fauchald; it differs from *Eunice* mainly in the absence of tentacular cirri and the presence of both spinigerous and falcigerous compound setae. Additionally, the branchial region tends to be shorter in *Marphysa* than in *Eunice*. Hartman (1968) lists six species for California; only one was found during Phase I and is treated in this chapter.

Marphysa conferta Moore, 1911

Figure 10.5

Marphysa conferta Moore, 1911:252-254, pl. 16, figs. 29-34.—Hartman, 1944:129; 1961:83; 1968:727.—Fauchald, 1970:59-60.—Lissner *et al.*, 1986:D-11.

Material Examined. California: Santa Maria Basin, off Point Estero, Sta. 6 (1).

Description. Length to 33 mm, width to 2 mm including parapodia, segments to 69. Body slender, dorsoventrally flattened except for pharyngeal region. Color in alcohol pale to light orange.

Prostomium wider than long, anteriorly rounded or very slightly incised, depending on whether proboscis is extended or not. Two large eyes present; all antennae articulated, short, about as long as peristomium, outer lateral antennae shortest. Anterior peristomial ring about 1.5 times longer than posterior one (Fig. 10.5A).

Parapodia with low presetal lobe, conical acicular lobe, and conical postsetal lobe in prebranchial and branchial segments; all parapodial lobes gradually reduced to very low folds in postbranchial setigers. Branchiae first present on setiger 7 (range 6-9), only about 11 pairs (range 7-13); first branchia with up to 5 filaments, may be simple; larger than dorsal cirri, with up to 7 filaments on remaining segments, meeting middorsally where best developed. Dorsal cirri digitiform, tapering, longer than parapodia; ventral cirri short, basally inflated (Fig. 10.5B). Setae in dense fascicles, particularly in anterior setigers; simple setae long and delicate; pectinate setae with about 16 teeth, outer ones prolonged (Fig. 10.5C); all compound setae with falcigerous blades, teeth large and widely separated; hoods and distal portion of shafts covered with surficial spines, appearing serrated in side view (Fig. 10.5D). Subacicular hooks first present in setiger 28, yellow to amber, bidentate, with short, truncate hoods (Fig. 10.5E). Aciculae yellow, 1 or 2 per parapodium, with straight, tapering free ends; notoaciculae very fine, difficult to see (reported as absent by Moore).

Pygidium unknown except for regenerating posterior end of holotype.

Remarks. The combination of very few gills and the absence of compound spinigers is so unmistakable that this species is not likely to be misidentified; however, there is some confusion in the literature concerning the first branchial segment. The branchial region was reported by Moore (1911) to extend from X through XVIII. This has been misinterpreted as setiger 10 through 18 (e.g., Gathof (1984) in the description of *M.* cf. *conferta*), when indeed Moore refers to what he calls "somites", which includes the two peristomial rings. Somite X is therefore setiger 8. Hartman (1944) recorded *M. conferta* off southern California in depths ranging from shallow intertidal to 76 m; however, she does not refer to these records in 1961, but only mentions that the species was found in "slope depths" (although the depth range is indicated to be to "76-200

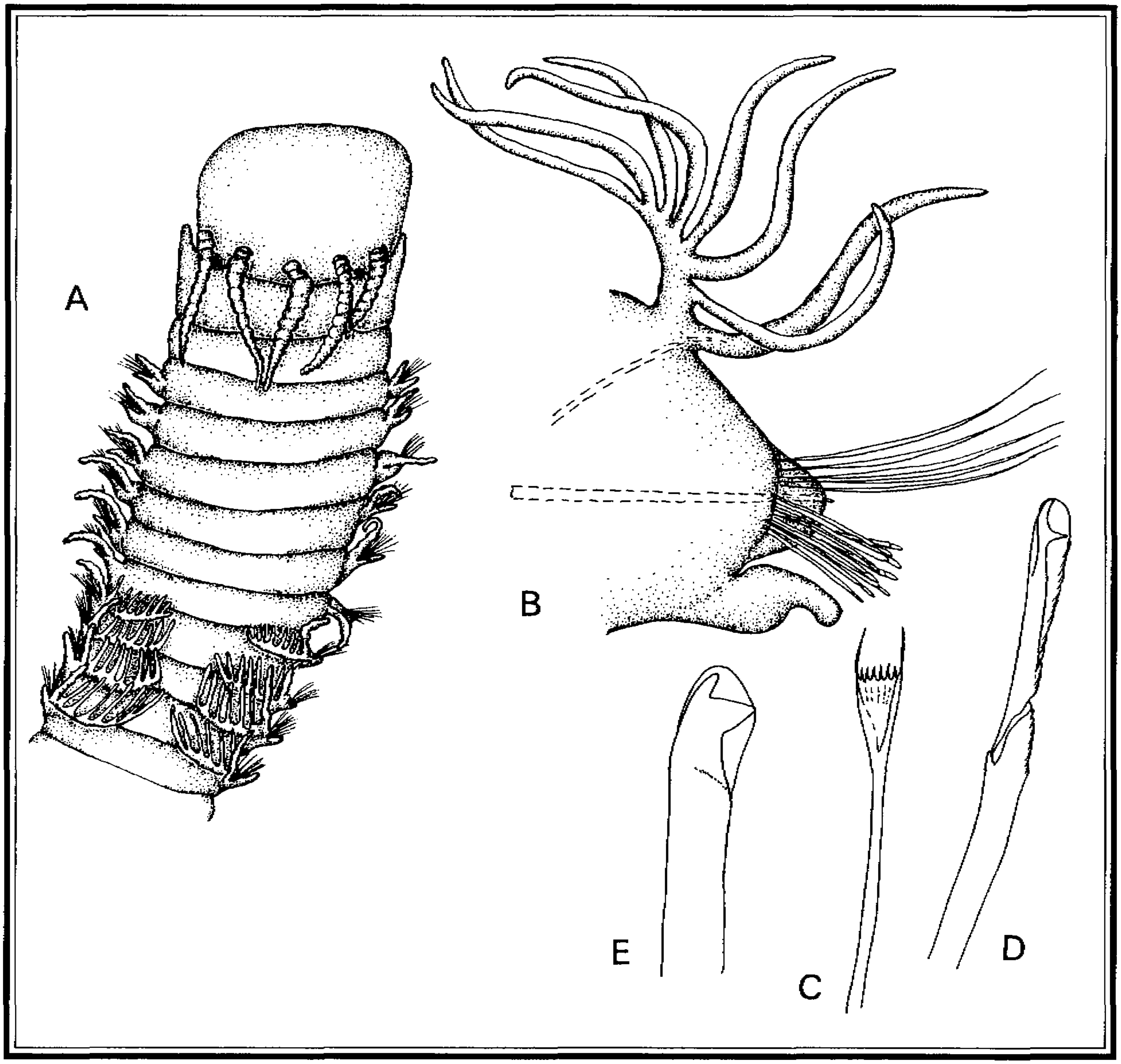

Figure 10.5. *Marphysa conferta*: A, anterior end, dorsal view; B, middle parapodium, anterior view; C, pectinate seta; D, compound falciger; E, subacicular hook.

meters"); the first gill is described as occurring on setiger 7. In the Atlas of Polychaetous Annelids, Hartman (1968) cited the records from 1961, but erroneously described the gills as starting on setiger 4. It is possible that she saw some specimens with gills from setiger 4 in the material she described in Hartman (1944), which she may later have found to be a different species because they are not cited in subsequent publications.

Type Locality and Type Specimens. California, Santa Rosa Island, off Brockway Point: holotype (USNM 17328, ANSP slide 6.22).

Habitat. In sand mixed with mud and rocks.

Distribution. Central California to Baja California, intertidal to 200 m.

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11. FAMILY LUMBRINERIDAE MALMGREN, 1867, EMENDED ORENSANZ, 1990

by

Brigitte Hilbig[1]

Introduction

Lumbrinerids are long, cylindrical, burrowing worms that can reach considerable size, especially tropical species belonging to the genus *Lysarete* that attain lengths of more than 60 cm. Despite the relatively featureless morphology, a remarkably large number of species have been described. The genus *Lumbrineris* s.l. alone contains about 200 species, and many others still await description. Lumbrinerids can be distinguished from the similar looking Oenonidae by the shape of the prostomium; it is always rounded in side view in lumbrinerids and dorsoventrally flattened in oenonids. Dissection of the pharynx will also reveal that the two families have very different jaw structures.

Morphology

The prostomium is conical to globular and usually about as long as wide except in the genera *Lumbrinerides* and *Lumbrineriopsis* where the elongate prostomia may be up to seven times longer than wide. Antennae, palps, and eyes are usually absent except for *Lysarete* and *Kuwaita* where three antennae and two pairs of eyes are present (nuchal papillae, occasionally seen everted from a groove at the posterior margin, are not homologous to antennae). The eversible pharynx is armed with five pairs of maxillary plates (referred to as MI through MV) and paired mandibles embedded in thick muscle pads. The first maxillae are generally forceps-shaped and usually unidentate; *Lysarete* and *Lumbrinerides* possess bi- or tridentate MI. Basally the first maxillae are attached to roughly triangular, often laterally incised maxillary carriers. On the outside of each MI, a slender support piece is attached ("bridles" of Orensanz, 1990). The second maxillae are located ventral of the MI, usually about the same size (except for the genus *Eranno* where they are much smaller) and armed with 3 to 8 teeth with internal canals. The first and second maxillae are basally connected by thin, threadlike ligaments; in the genus *Eranno*, a wide, ribbonlike, sclerotized ligament or additional jaw piece forms the connection between MI and MII. The third, fourth, and fifth maxillae are located in front of MI and MII and considerably smaller. MIII and MIV are usually rounded plates with a thick, hard cutting edge that may form a few teeth devoid of internal canals. *Ninoe* and *Lumbrineriopsis* have MIV (sometimes also MIII) with multidentate cutting edges; *Augeneria* possesses large MIV with a white center and dark rim. The fifth maxillae are not present in all species, and they may be completely fused to MIV (*Abyssoninoe*). In the literature they are generally referred to as lateral supports. The mandibles consist of two shafts bearing a hard, more or less crescent-shaped plate with a smooth cutting edge that may bear a few large, irregular teeth. The shafts are usually fused, at least partially, and running parallel when free from each other, except for *Augeneria* where the shafts are divergent so that the mandibles are roughly X-shaped. All jaw pieces are formed by folds of the inner pharyngeal lining.

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[1] ENSR Consulting and Engineering, 89 Water Street, Woods Hole, Massachusetts 02543

The peristomium consists of two apodous and achaetous rings (not true segments) that dorsally resemble the following setigers. Ventrally the peristomium is developed into a pair of buccal cushions and the posterior margin to the mouth. Except for some slight tapering toward the prostomium and the pygidium, the setigers are very similar. Small species reach their greatest body width in the pharyngeal region, but large individuals are of uniform width along the entire length of the body. Parapodia are subbiramous, with the notopodium usually reduced to a small bundle of fine notoaciculae; large individuals may show an externally visible notopodial rudiment. The neuropodia have presetal lobes that are usually short and rounded and postsetal lobes that are longer than the presetal lobes. Only *Kuwaita* and *Lysarete* possess dorsal and ventral cirri; palmate branchiae emerge from the back of the postsetal lobes of *Ninoe*. Vascularized postsetal lobes, functioning as gills, are found in anterior setigers of *Paraninoe* and in middle and posterior setigers of *Lumbrineris, Eranno*, and *Scoletoma* (*Lumbrineris* s.l.). Neuroaciculae are conspicuous, yellow to black, often occurring in bundles of two to about six in a parapodium. Setae include simple limbate capillaries (*Lumbricalus* has compound limbate setae in addition) and hooded hooks that are either bidentate or bear a crest of small teeth above a main fang; they may be compound in some anterior setigers. Hooded hooks are absent in *Arabellonereis*.

The pygidium bears one or two pairs of short anal cirri and a terminal anus; some species lack anal cirri, and the anus is dorsal.

Taxonomic History

The morphological homogeneity of the lumbrinerids and the paucity of external features has made generic definitions difficult ever since the first lumbrinerids were described. Most of the lumbrinerid species were erected in the 19th century by Kinberg, Grube, McIntosh, Ehlers, and others, and while the majority of the species are still valid, the genus has been changed more than once for many of them. The oldest species is *Scoletoma fragilis* (O.F. Müller, 1776) described as *Lumbricus fragilis*. Blainville (1828) erected *Scoletoma* for this species. The genus was subsequently synonymized with *Lumbrineris* by Audouin and Milne-Edwards (1833), but was recently resurrected by Frame (1992) to include species formerly assigned to *Lumbrineris* that are characterized by the presence of simple hooded hooks only. *Eranno*, erected in 1865 by Kinberg, has a similar history. Kinberg considered the everted nuchal organ of *E. bifrons*, the type species, as a diagnostic character; this proved to be invalid, and *Eranno* was synonymized with *Lumbrineris* by Hartman (1949). Orensanz (1990) resurrected the genus with a different set of diagnostic characters, including details of the jaw apparatus. Similarly, *Augeneria* Monro, 1930 was defined by the presence of an everted nuchal organ, but later emended by Orensanz (1973) based on characters of the mandible and maxillae. The emphasis in lumbrinerid systematics has thus shifted in the last 25 years from the often rather ill-defined differences in external morphology to more reliable, although less readily accessible characters of the jaws, a trend that can be observed in the systematics of all euniceform polychaetes. The generic revisions by Orensanz (1990) and Frame (1992) mark the end point of about 30 years of aiming toward integration of fossil and extant records of euniceform polychaetes to develop a more natural system for these families. Important milestones include publications by Kielan-Jaworowska (1966, 1968) on fossils and Hartman (1944) and Fauchald (1970) on extant *Lumbrineris*.

Distribution and Biological Notes

Most lumbrinerids live in soft bottoms on the continental shelf, but some species are found within a large depth range between the intertidal and abyssal zone. They are generally free living burrowers, although some species construct temporary mucus tubes (Fauchald, 1977; Petch, 1986). Some species live on hard substratum such as reefs. Lumbrinerids have been variously reported to be carnivores, scavengers, detritus feeders, and deposit feeders. The strong musculature and the large, heavily sclerotized jaw apparatus suggest that food is picked up by a grasping and sucking motion of the eversible pharynx. Petch (1986) observed feeding habits of two Australian populations of *Lumbrineris* cf. *latreilli* and concluded that this species, at least in the study area, is a selective deposit feeder. The animals construct mucus-lined tubes down to about 11 cm into the sediment; from this main tube, they burrow horizontal side tunnels in which they feed.

There is little information on the reproduction of lumbrinerids; a summary can be found in Bhaud and Cazaux (1987). The few studies available indicate that the eggs are deposited in gelatinous ribbons or masses from which large lecithotrophic larvae with at least four setigers eventually emerge. The pelagic stage is very short, and lumbrinerid larvae are seldomly found in plankton samples. The first setae appear at the 2- to 3-setiger stage; they are very broadly limbate and can still be seen in juveniles with about ten setigers (personal observation), but are later replaced by limbate capillaries with moderate to narrow wings and long, fine tips. The jaw apparatus is visible at the 4-setiger stage (Bhaud and Cazaux, 1987).

Key to the Lumbrineridae

The key follows the generic concepts established by Orensanz (1990) and Frame (1992). All known genera are included because the newly established genera may not yet be widely known. Genera that are not represented in the Santa Maria Basin and Santa Barbara Channel are marked with a footnote. *Paraninoe* and *Abyssoninoe* may be synonyms of *Scoletoma*.

1A. Parapodia with notopodial rudiments and dorsal cirri; prostomium with 3 antennae 2

1B. Dorsal cirri absent; notopodia usually reduced to small bundle of thin notoaciculae, not visible externally; antennae absent 3

2A. MI bifid .... *Lysarete*[2]

2B. MI falcate, unidentate .... *Kuwaita*[2]

3A. All setae simple limbate capillaries; hooded hooks absent .... *Arabellonereis*[2]

3B. Hooded hooks present on at least middle and posterior parapodia 4

4A. Prostomium much longer than wide, acutely pointed; hooded hooks bifid 5

4B. Prostomium conical to rounded, about as long as wide; hooded hooks multidentate (worn hooks on small species may look bidentate) 6

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[2] Genus not known from California.

5A. Mandibles fused entirely; MI bi- or tridentate, MIV with smooth cutting edge (also referred to as unidentate), maxillary carriers very large and wide .... *Lumbrinerides*[3]

5B. Mandibles free along posterior part; MI falcate, unidentate; MIV multidentate; maxillary carriers long and slender .... *Lumbrineriopsis*[2]

6A. Setae including simple limbate capillaries, limbate compound setae, and simple and compound hooded hooks .... *Lumbricalus*[2]

6B. Setae including simple limbate capillaries and simple hooded hooks, sometimes also compound hooded hooks in anterior setigers 7

7A. Anterior notopodia with palmate gills; MIII and MIV, or MIV only, with multidentate cutting edge: genus .... genus *Ninoe* 8

7B. Gills absent or represented by vascularized postsetal lobes of anterior parapodia 12

8A. Hooded hooks present from setiger 1 to 3 9

8B. Hooded hooks first present on or after setiger 7 11

9A. Gills present in setigers 2 to 17, with maximally 6 filaments; hoods of anteriormost hooks short and rounded; MII with 4 teeth, MIII and MIV multidentate .... *Ninoe* sp. C

9B. Last gill present between setigers 30 and 50; hoods of anteriormost hooks long and slender 10

10A. Gills first present on setiger 2, with maximally 5 filaments; MII with 6 teeth, MIV multidentate .... *Ninoe palmata*

10B. Gills first present on setiger 5 or 6, with maximally 4 filaments; MII with 8 teeth, MIII and MIV multidentate .... *Ninoe gemmea*

11A. Gills first present on setiger 1 or 2, with maximally 10 filaments; MII with 4 to 5 teeth, MIII and MIV multidentate (?) .... *Ninoe* sp. D

11B. Gills first present on setiger 2 or 3, with maximally 11 filaments; MII with 8 teeth, MIII tridentate, MIV multidentate .... *Ninoe tridentata*

12A. Postsetal lobes of anterior parapodia vascularized; aciculae black; prostomium with two longitudinal slits .... *Paraninoe*[2]

12B. Vascularized lobes, if present, on posterior parapodia; aciculae yellow or black; prostomium without dorsal slits 13

13A. Setae including simple limbate capillaries and simple hooded hooks (may be absent or transitional in anteriormost setigers) 14

13B. Setae including simple limbate capillaries and simple and compound hooded hooks 17

14A. MV (also referred to as lateral supports) fused with MIV; aciculae yellow .... *Abyssoninoe*[2]

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[3] *L. acutus* occurs in California, but is not included in this Atlas. See Hartman (1968).

14B. MV free or partially fused with MIV; aciculae yellow or black 15

15A. MV free from MIV; MIII with smooth cutting edge or 1 to 3 teeth; MI and MII of subequal length, connected by thin, threadlike basal ligament; aciculae yellow; posterior parapodia with elongate, conical postsetal lobes; MIII bidentate; hooks present from setiger 1, in middle and posterior setigers with numerous small teeth and slightly larger main fang .... *Scoletoma tetraura*

15B. MV partially fused to MIV; MIII with smooth cutting edge; MII to ½ as long as MI, connected to MI by wide, ribbonlike, sclerotized ligament or additional jaw piece .... genus *Eranno* 16

16A. Aciculae black, 3 to 6 per parapodium; pre-and postsetal lobes of posterior parapodia elongate, digitiform, about as long as setae .... *Eranno bicirrata*

16B. Aciculae yellow to amber, 1 per parapodium; pre-and postsetal lobes of posterior parapodia elongate, digitiform, projecting about twice as far as setae .... *Eranno lagunae*

17A. Mandible only slightly longer than wide, roughly X-shaped; MIV large, with white center and dark rim; MV absent .... *Augeneria*[2]

17B. Mandible much longer than wide, roughly Y-shaped; MIV uniformly dark; MV present in most species, free from MIV .... genus *Lumbrineris* ... 18

18A. Aciculae yellow 19

18B. Aciculae dark brown or black 22

19A. At least postsetal lobes of posterior parapodia elongate 20

19B. Pre- and postsetal lobes short and rounded throughout 21

20A. Pre-and postsetal lobes of posterior parapodia elongate and digitiform; blades of compound hooks short; hoods of shaft inflated and short, hoods of simple hooks of the same shape ....
.... *Lumbrineris cruzensis*

20B. Only postsetal lobes of posterior parapodia elongate; blades of compound hooks about 4-5 times as long as wide, all hoods slender .... *Lumbrineris limicola*

21A. Prostomium conical; MIII with 2 teeth, MIV unidentate; compound hooks with slender blades, 6-7 times as long as wide .... *Lumbrineris latreilli*

21B. Prostomium globular; MIII with 3-5 teeth, MIV bidentate; compound hooks with short blades, about 3-5 times as long as wide .... *Lumbrineris inflata*

22A. At least postsetal lobes of posterior parapodia elongate 23

22B. Pre- and postsetal lobes short and rounded throughout; MIII bidentate .... *Lumbrineris japonica*

23A. Pre- and postsetal lobes of posterior parapodia digitiform and elongate; MIII unidentate, maxillary carriers slender, about 3 times as long as wide .... *Lumbrineris californiensis*

23B. Only postsetal lobes of posterior parapodia elongate, conical; presetal lobes short and rounded throughout; MIII bidentate, maxillary carriers less than twice as long as wide, very broad ....
.... *Lumbrineris index*

Description of Species

Two species of *Eranno*, one species of *Scoletoma*, seven species of *Lumbrineris* s. str., and five species of *Ninoe* were found in the Santa Maria Basin and Western Santa Barbara Channel. One species, *Ninoe tridentata*, is new to science. The following species are treated in this account:

Eranno bicirrata (Treadwell, 1929)
Eranno lagunae (Fauchald, 1970)
Lumbrineris californiensis Hartman, 1944
Lumbrineris cruzensis Hartman, 1944
Lumbrineris index (Moore, 1911)
Lumbrineris inflata Moore, 1911
Lumbrineris japonica (Marenzeller, 1879)
Lumbrineris latreilli (Audouin & Milne-Edwards, 1834)
Lumbrineris limicola Hartman, 1944
Ninoe gemmea Moore, 1911
Ninoe palmata Moore, 1903
***Ninoe tridentata* Hilbig, new species**
Ninoe sp. C
Ninoe sp. D
Scoletoma tetraura (Moore, 1911)

Genus *Eranno* Kinberg, 1865, emended Orensanz, 1990

Type Species. *Eranno bifrons* Kinberg, 1865

Diagnosis. Setae including limbate capillaries and simple hooded hooks that may be very slender in anterior setigers. MII only about half as long as MI, connected to MI with wide, sclerotized ligament or additional jaw piece. MV present, partially fused to MIV or free.

Remarks. Orensanz (1990) provided the taxonomic history of this genus and emended it to encompass a number of species previously assigned to *Lumbrineris*. His generic definition is followed here and slightly modified to include species with free, rather than partially fused, MV.

Eranno bicirrata (Treadwell, 1929), new combination

Figure 11.1

Lumbrinereis bicirrata Treadwell, 1929:1-3, figs.1-7.
Lumbrineris bicirrata: Hartman, 1944:156-158, pl.9, figs. 207-212; 1968:745.—Fauchald, 1970:77-78, pl. 10, figs. e-g.—Lissner *et al.*, 1986:D-11.—Hyland and Neff, 1988:A-2.—Hyland *et al.*, 1990:F-1.
Lumbrineris nr. *bicirrata*: Lissner *et al.*, 1986:D-12.

Material Examined. California: Santa Maria Basin, off Point San Luis, Sta. R-1 (1); off Point Arguello, Sta. 58 (2), Sta. 67 (1); Western Santa Barbara Channel, Sta. 85 (1).

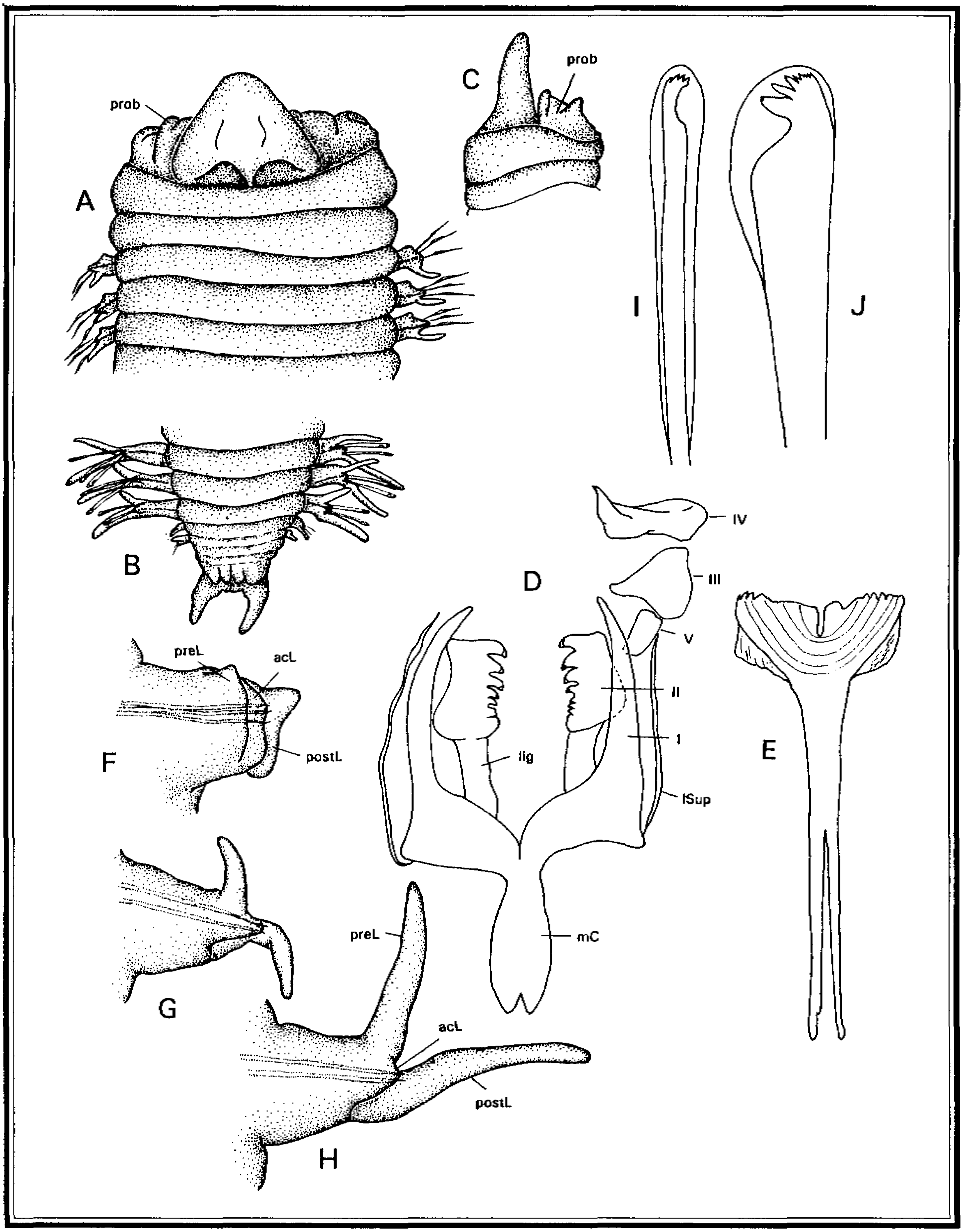

Figure 11.1. *Eranno bicirrata*: A, anterior end, dorsal view, peristomium slightly distorted because of everted proboscis; B, posterior end, dorsal view; C, prostomium and partly extended proboscis, lateral view; D, maxillae, dorsal view, left MIII - MV omitted, right MIII - MV slightly displaced for better visibility; E, mandibles; F-H, anterior, median, and posterior parapodium, anterior view; I, hooded hook, setiger 15; J, same, setiger 120 (from Fauchald, 1970).

Description. Length to 200 mm, width to 7 mm, setigers to about 300. Body long, of equal width along greatest portion, widest in pharyngeal region, tapering toward pygidium within last 20 to 30 segments (Fig. 11.1A, B). Color in alcohol pale.

Prostomium conical, about as long as wide, distinctly narrower than first segments, slightly depressed dorsoventrally (Fig. 11.1A, C). Maxillae: MI large, pointed, with squarish, flared base, distally very slender; MII much smaller, only about one-third as long as MI, with 4 major teeth and 2 to 3 additional small ones proximally, often developed as barely visible ridges; major teeth with white calcified tips. MIII elongate, very hard, with prominent conical tooth; MIV large soft plate, tapering to single tooth; MV square, weakly sclerotized plates. Maxillary carriers rounded, fused along distal half, darkly sclerotized but soft. MII attached to carriers by very broad sclerotized ligament. Pharyngeal wall alongside MI sclerotized, forming elongate, soft lateral support pieces (Fig. 11.1D). Mandibles slightly longer than maxillae, light-colored but very hard; handles fused along distal half, bearing flared cutting edge with concentric lines and several irregular teeth, very dark except for middle ones that are white and very hard (Fig. 11.1E).

Parapodia bluntly rounded in anterior segments, with low presetal lobe, slightly longer acicular lobe, and asymmetrical, bluntly triangular postsetal lobe surpassing acicular lobe (Fig. 11.1F). By about setiger 75, postsetal lobes becoming more pointed, gradually developing into digitiform structure and increasing in length; presetal lobes with papilliform projection directed upward, gradually developing into digitiform lobe matching postsetal lobes; both lobes longer than setae where best developed, reaching about one-half body width (Fig. 11.1G, H). All setae simple, including limbate setae in anterior third of body and hooded hooks starting from setiger 1 (young individuals) to about 20; hoods long and slender in anterior segments, gradually shortening and widening; hooks with small heads bearing few very fine teeth in anterior setigers, much stouter and with main fang surmounted by several smaller teeth thereafter (Fig. 11.1I, J). Aciculae numerous, up to 6 in anterior parapodia, 3 or 4 in middle and posterior parapodia; setae dark amber at bases, distally colorless.

Pygidium small, with two ventral cirri and two shorter dorsal ones.

Remarks. *Lumbrineris bicirrata* was not included in Orensanz's list, but agrees with his generic definition and is therefore referred to *Eranno*.

Type Locality and Type Specimens. Friday Harbor, Washington; holotype: AMNH 1692.

Habitat. *Eranno bicirrata* lives in sand, silt, and mixed sediments.

Distribution. Puget Sound, Washington to western Mexico, shallow subtidal to 2500 m.

Eranno lagunae (Fauchald, 1970)

Figure 11.2

Lumbrineris lagunae Fauchald, 1970:92-94, pl. 15, figs. a-e.—Lissner *et al.*, 1986:D-12.—Hyland *et al.*, 1990:F-1.
Lumbrineris bifilaris: Hartman, 1944:153-155, pl. 9, figs. 196-206. *Not* Ehlers, 1901.
Lumbrineris sp. A Lissner *et al.*, 1986:D-12.
Eranno lagunae: Orensanz, 1990:78.—Frame, 1992:195.

Material Examined. California: Santa Maria Basin, off Point Buchon, Sta. 12 (1); off Point Conception, Sta. 73 (1); off Point San Luis, Sta. R-1 (1).

Description. Length at least 85 mm, width to 3 mm, segments more than 150. Body robust, almost cylindrical, with parapodia inserted ventrolaterally; body widest behind pharynx, around setiger 20. Color in alcohol pale, cuticle iridescent.

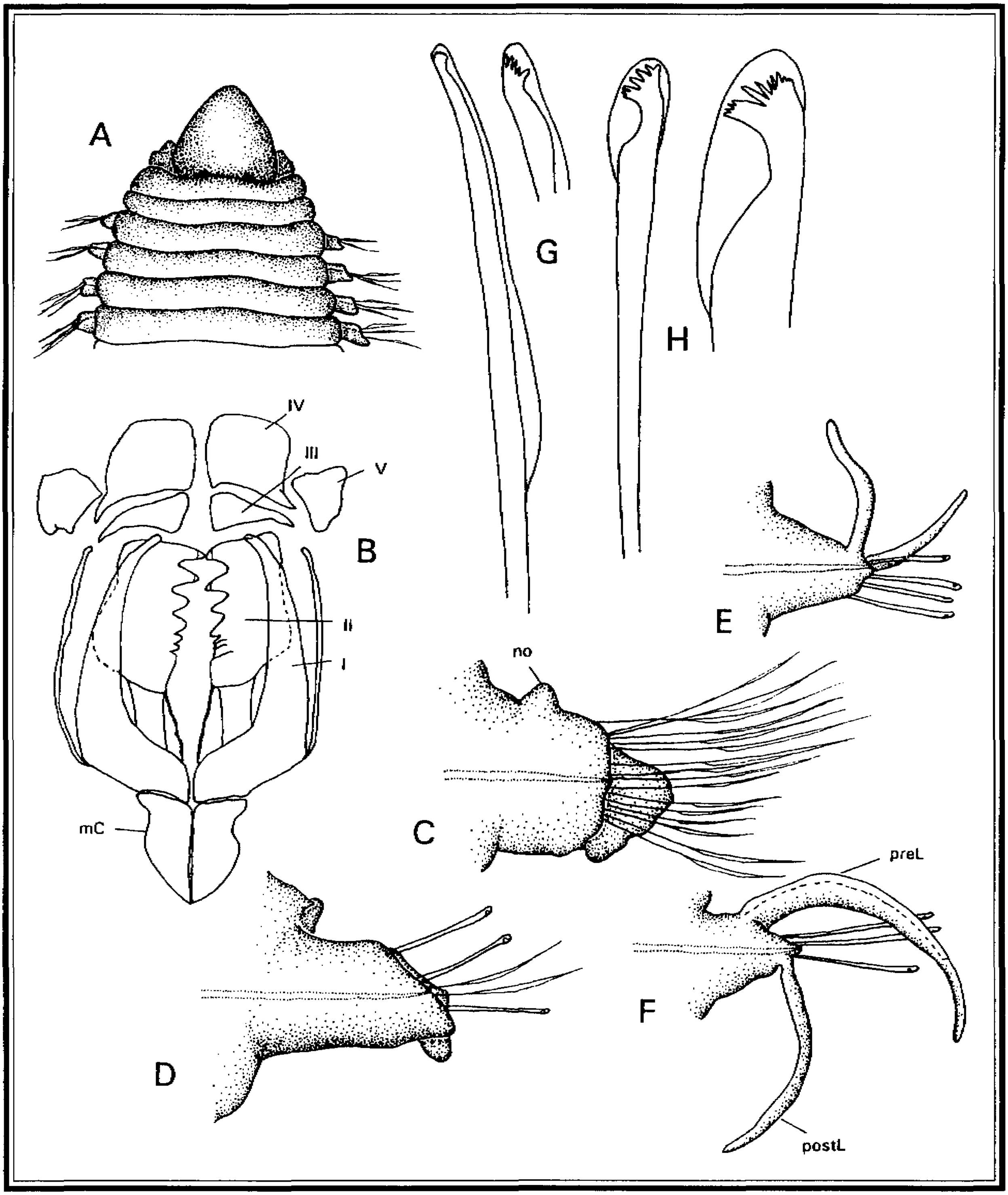

Figure 11.2. *Eranno lagunae*: A, anterior end, dorsal view; B, maxillae, dorsal view, *in situ*; C-F, anterior, median, posterior, and far posterior parapodium, anterior view; G, hooded hook, anterior setiger, with detail of crest; H, same, posterior setiger.

Prostomium conical, about as long as wide (Fig. 11.2A). Maxillae with short, oval, laterally incised carriers and large, basally almost rectangular forceps; MII only half as long as MI, with 4 large and 0 to 2 much smaller teeth, large teeth with white calcified tips; MIII elongate, hard plates with single tooth, MIV large, rounded, soft plates with single tooth; MV large, roughly triangular, soft plates. MII attached to carriers with long, broad ligaments and also thin ones; lateral supports long and slender (Fig. 11.2B).

Parapodia short in anterior setigers, with obliquely truncate pre- and postsetal lobes and distinct notopodial rudiment (Fig. 11.2C); in middle setigers parapodial lobes reduced, with postsetal lobes only as long as presetal lobes (Fig. 11.2D); posterior to about setiger 70 both lobes increasing and becoming digitiform, about twice as long as parapodial stem and surpassing setal fascicles in far posterior setigers (Fig. 11.2E, F). Limbate setae present in anterior setigers; hooded hooks simple throughout, very slender and long-hooded in anterior setigers, with hoods gradually shortening in middle setigers. Anterior hooks with very small crest bearing 7 to 8 fine teeth (Fig. 11.2G), middle and posterior hooks with main fang surmounted by 10 to 14 irregular teeth (Fig. 11.2H). Aciculae single in each parapodium, yellow to amber, darkest in posterior parapodia of large specimens.

Remarks. *E. lagunae* is most easily distinguished from the co-ocurring *E. bicirrata* by the color of the aciculae (yellow in *E. lagunae*, black in *E. bicirrata*) and the proportions of the parapodia along the body.

Type Locality and Type Specimens. Laguna Beach, California; holotype: LACM-AHF Poly 000340.

Habitat. Sand mixed with silt.

Distribution. Western Canada to western Mexico, shallow subtidal to 110 m.

Genus *Lumbrineris* Blainville, 1828

Type Species. *Lumbrineris latreilli* Audouin and Milne Edwards, 1834

Diagnosis. Setae including simple limbate capillaries, simple hooded hooks, and compound hooded hooks. MII about as long as MI, connected to MI with short, thin basal ligament, with aliform lateral expansions; MIII and MIV with aliform expansions; MV present, free from MIV.

Remarks. Frame (1992) provides an account of the taxonomic history of *Lumbrineris* and discusses the problem of a missing type species of the restricted genus.

Lumbrineris californiensis Hartman, 1944

Figure 11.3

Lumbrineris californiensis Hartman, 1944:163-165, pl.12, figs. 257-262; 1968:749.—Fauchald, 1970:78-80, pl. 10, figs. a-d.—Lissner *et al.*, 1986:D-12.—Hyland and Neff, 1988:A-2.—Hyland *et al.*, 1990:F-1.

Material Examined. California: Santa Maria Basin, off Point San Luis, Sta. 21 (1); off Point Sal, Sta. R-8 (1); Tomales Bay, coll. 1957 (1), coll. 1958 (1).

Description. Length to 130 mm, width to 3 mm, segments to 200. Body robust, cylindrical to slightly depressed, segments longest and widest in pharyngeal region, much shorter in posterior region (Fig. 11.3A, B), body tapering toward pygidium within last 20 or so segments. Color pale to purplish, with iridescent cuticle.

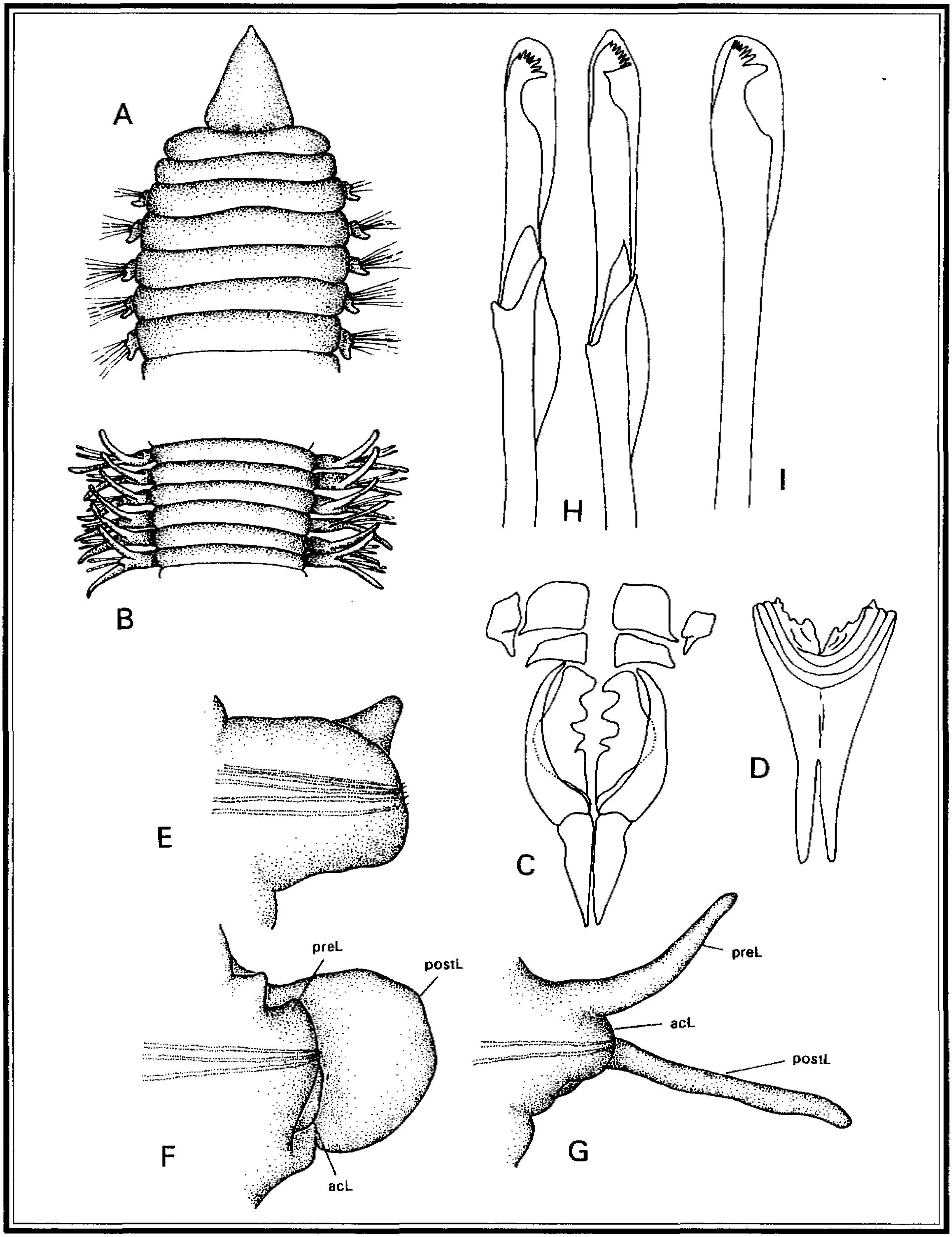

Figure 11.3. *Lumbrineris californiensis*: A, anterior end, dorsal view; B, some posterior segments, dorsal view; C, maxillae, dorsal view, *in situ*; D, mandibles (after Hartman, 1968); E, anterior parapodium, posterior view; F, same, anterior view; G, posterior parapodium, anterior view; H, compound hooded hooks, same fascicle, setiger 7; I, simple hooded hook (F, G, I after Fauchald, 1970).

Prostomium conical, slightly longer than wide, much narrower than first segment. Maxillae : MI short, rounded, falcate; MII as large as MI, with 3 or 4 very coarse teeth bearing white tips in large specimens; MIII elongate, tapering to single tooth; MIV large, soft rectangular plates bearing single tooth; MV weakly sclerotized, squarish plates. Maxillary carriers shorter than forceps (MI), slightly incised laterally. MII attached to carriers by short, thin ligaments. Weakly sclerotized lateral supports along MI (Fig. 11.3C). Mandibles fused through most of their length, handles free in proximal third; cutting edge flared, with concentric rings and irregularly dentated anterior margin (Fig. 11.3D).

Parapodia minute in first 5 to 15 setigers, gradually increasing to about one-third body width; anterior parapodia broadly rounded, with short presetal and acicular lobes and somewhat longer postsetal lobe; notopodial rudiment conspicuous (Fig. 11.3E, F). Pre- and postsetal lobes gradually lengthening until about setiger 70 to 100, then becoming digitiform and projecting beyond setal fascicles (Fig. 11.3G). Up to 5 aciculae, dark amber to black; setae yellow at base, clear and colorless distally. Anterior 20 to 30 setigers with composite hooded hooks; blades about 4 times as long as wide, with 6 to 8 apical teeth of equal or subequal size, with the largest tooth in proximal position (Fig. 11.3H). In further posterior setigers hooks becoming simple, more stout than composite hooks, with short hood and several progressingly smaller teeth above main fang (Fig. 11.3I). Limbate setae present throughout anterior half of body, in superior and inferior position of fascicle.

Pygidium with two lateral anal cirri; anus terminal.

Remarks. In her description of *L. californiensis*, Hartman (1944) stated that the aciculae were yellow, although in the key this species is among those that have black aciculae. The same discrepancy can be found in the Atlas of Polychaetous Annelids (Hartman, 1968). However, a specimen confirmed by Hartman (Tomales Bay) was examined here and was found to clearly possess black aciculae. Fauchald (1970) also states that *L. californiensis* has black aciculae. Hartman's statement is therefore regarded as erroneous.

Type Locality and Type Specimens. San Nicolas Island, California; holotype: LACM-AHF Poly 50.

Habitat. *L. californiensis* is found in sandy and muddy sediments.

Distribution. Washington to western Mexico, in 10 - 1200 m.

Lumbrineris cruzensis Hartman, 1944

Figure 11.4

Lumbrineris cruzensis Hartman, 1944:165-166, pl. 12, figs. 263-269; 1968:751.—Fauchald, 1970:83-84, pl. 12, figs. g-j.—Lissner *et al.*, 1986:D-12.—Hyland and Neff, 1988:A-2.—Hyland *et al.*, 1990:F-1.
Lumbriconereis cruzensis: Uschakov and Wu, 1965:81, figs. 22A-F.
Lumbrinereis crucensis [sic]: Rioja, 1962:180.

Material Examined. California: Santa Maria Basin, off Point San Luis, Sta. 21 (2); off Point Sal, Sta. PJ-2 (2), Sta. R-8 (2); Western Santa Barbara Channel, Sta. 79 (4).

Description. Length to 55 mm, width to 1 mm, segments to 200. Body slender, gracile, with segments only about as wide as prostomium (Fig. 11.4A); color in alcohol very pale with iridescent cuticle.

Prostomium about as wide as long, bluntly conical. Maxillae: forceps (MI) short, rounded, falcate; MII at least as long as forceps, with 4 large teeth. MIII hard, elongate plates with one tooth; MIV large, soft plates tapering to single tooth. Maxillary carriers about as long as forceps, incised laterally, tapering to fine tip proximally. MII attached to carriers with short, thin ligaments (Fig. 11.4B). Mandibles fused through about two-thirds of their length, bearing crescent-shaped plate with irregularly dentate cutting edge (Fig. 11.4C).

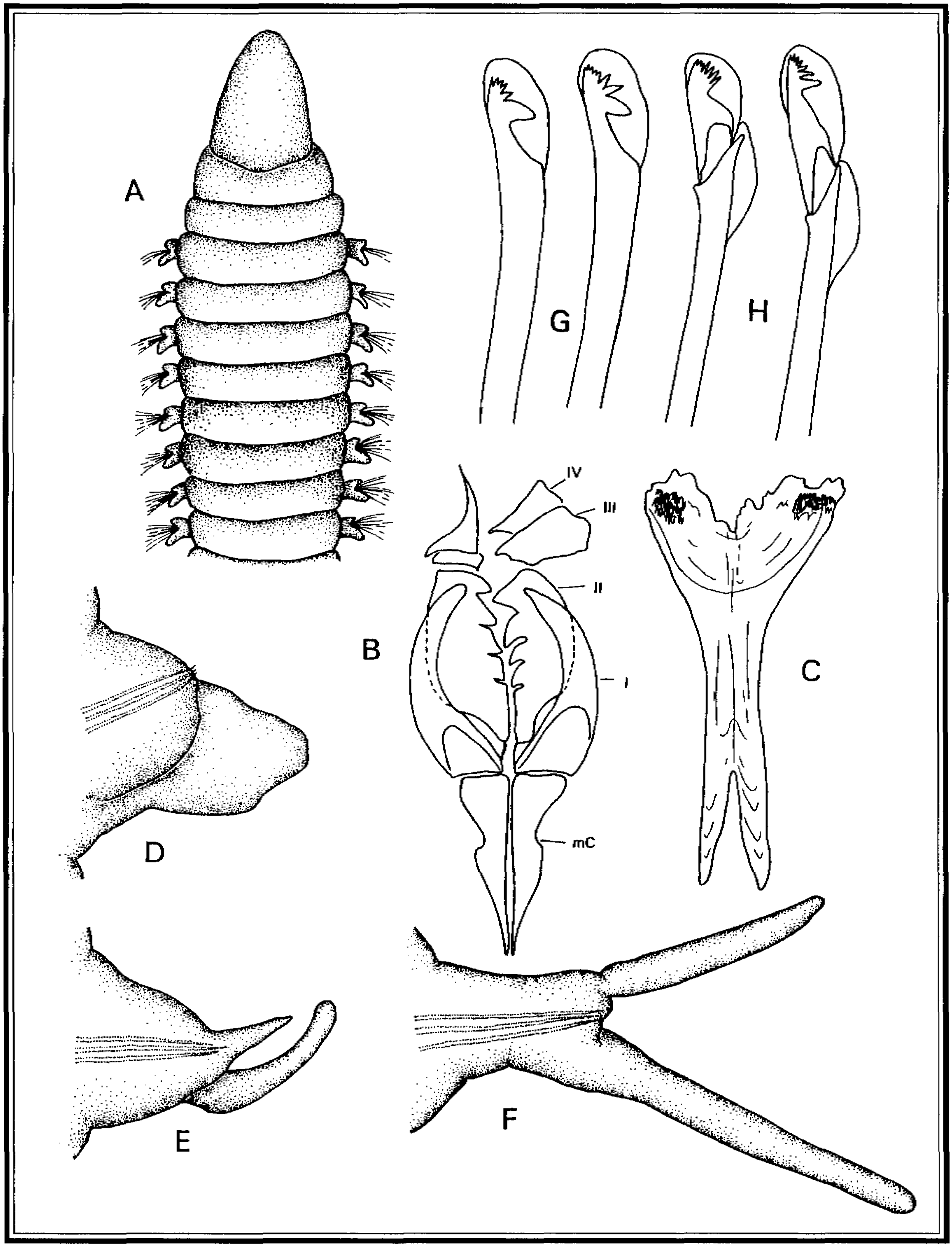

Figure 11.4. *Lumbrineris cruzensis*: A, anterior end, dorsal view (after Day, 1973); B, maxillae, dorsal view, *in situ*, right MIII and MIV after Hartman, 1944; C, mandibles; D-F, anterior, median, and posterior parapodium, anterior view; G, simple hooded hooks, setiger 20; H, compound hooded hooks, setiger 10 (C-F after Hartman, 1944).

Parapodia in anterior segments with bluntly rounded, short presetal and acicular lobes and longer, rounded postsetal lobes (Fig. 11.4D); from setiger 60 to 100 pre-and postsetal lobes increasing in length and gradually turning digitiform, surpassing setal fascicles in posterior setigers (Fig. 11.4E, F). Setae of 3 kinds: (1) in anterior 12 to 21 setigers compound hooded hooks with short blades, about 2 to 3 times longer than wide, and apex bearing either 6 to 8 subequal teeth or main fang surmounted by about 6 increasingly smaller teeth (Fig. 11.4G); both types found in same fascicle; (2) simple hooded hooks, first appearing around setiger 15, with short hoods and apex bearing main fang, 1 to 2 coarse teeth and several much smaller ones (Fig. 11.4H); (3) limbate capillaries, present in anterior half of body. Usually 2 to 4 aciculae present; all setae transparent and colorless, aciculae in juveniles clear, in older specimens yellow.

Pygidium with 2 anal cirri.

Remarks. The prolonged pre- and postsetal lobes in posterior setigers combined with yellow or clear setae and aciculae make this species readily recognizable if whole specimens or anterior ends of at least 100 setigers are present; short anterior fragments encompassing only parapodia with short pre-and postsetal lobes may be confused with *L. limicola* (see below) and should be identified with caution. Examination of the compound hooded hooks may be helpful because the blades are short and bear relatively large teeth in *L. cruzensis*, but of moderate length with a crest of many equal, slender teeth in *L. limicola*.

Type Locality and Type Specimens. Santa Cruz Island, California; holotype: LACM-AHF Poly 51.

Biology. The species lives in silt and silt mixed with sand, shells, and rocks. In the Yellow Sea, gravid females were found from June through August (Uschakov and Wu, 1965).

Distribution. British Columbia to western Mexico; Yellow Sea; 4 - 200 m.

Lumbrineris index (Moore, 1911)

Figure 11.5

Lumbrineris japonica index Moore, 1911:288-289, pl. 19, figs. 119-127.
Lumbrineris index: Hartman, 1944:162-163, pl. 12, figs. 254-256; 1968:755.—Lissner *et al.*, 1968:D-12.—Hyland *et al.*, 1990:F-1.

Material Examined. California: Santa Maria Basin, off Point Buchon, Sta. 13 (1); off Point Sal, Sta. 36 (1); off Purisima Point, Sta. R-4 (1).

Description. Length to 109 mm, width to 4 mm, segments over 200. Body robust, depressed, with prominent parapodia throughout. Color in alcohol tan with iridescent cuticle.

Prostomium bluntly conical, depressed, slightly longer than wide. Peristomium and subsequent setigers not much wider than prostomial base, body width gradually increasing within pharyngeal region, greatest width around setiger 15 (Fig. 11.5A), tapering toward pygidium within last 20 segments or so (Fig. 11.5B). Maxillae with large, broadly rounded, weakly incised carriers and slender forceps; MII with 4 white-tipped teeth, the distal two much larger than the proximal two; MIII elongate, hard plates with 2 distinct teeth, MIV large, soft plates with single large tooth. MII attached to carriers with short, thin ligaments (Fig. 11.5C). Mandibles in adults almost completely fused, roughly rectangular, with crescentic cutting edge bearing several irregular calcified teeth (Fig. 11.5D); mandibles in juveniles with much slenderer shafts, fused along distal two-thirds, triangular, with cutting edge bearing about 7 to 8 regular, small black teeth (Fig. 11.5E); the latter visible in adult mandibles as fine subdistal line.

Parapodia with short presetal lobes and conspicuous postsetal lobes throughout; postsetal lobes broadly triangular and vascularized (Fig. 11.5F, bv) in anterior setigers, narrowing around setiger 15, becoming digitiform by setiger 30, pointing laterally and slightly upward, slightly surpassing length of parapodial stem

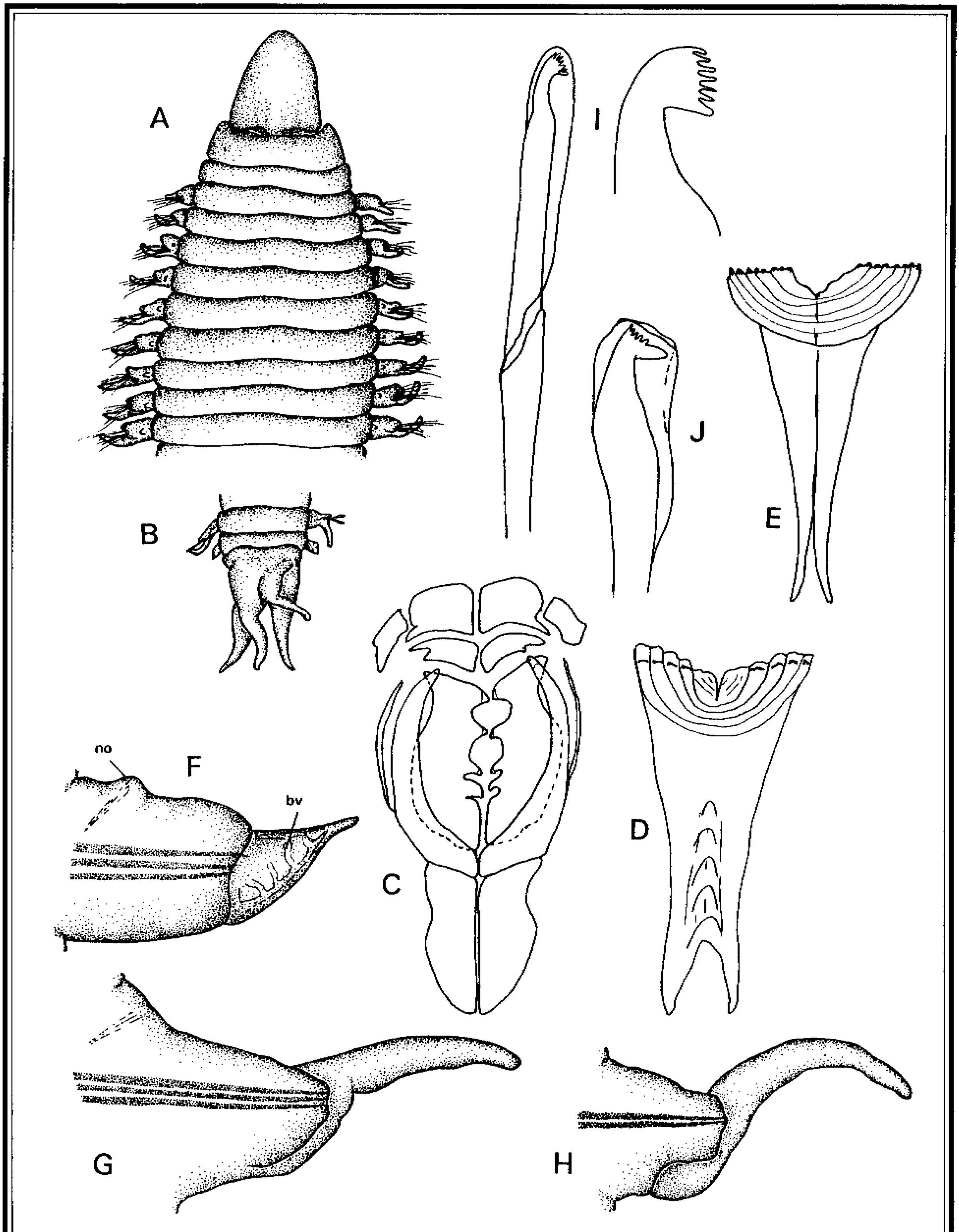

Figure 11.5. *Lumbrineris index*: A, anterior end, dorsal view; B, posterior end, dorsal view; C, maxillae, dorsal view, *in situ*; D, mandibles, adult specimen; E, same, juvenile specimen; F-H, anterior, posterior, and far posterior parapodium, anterior view; I, compound hooded hook, with detail of crest; J, simple hooded hook (G, H after Moore, 1911).

where best developed (Fig. 11.5F-H). Notopodial rudiment present throughout, supported by fascicle of several thin, translucent aciculae. Setae very numerous in anterior parapodia, fascicles consisting of about 12 limbate setae and 16 hooks. Hooded hooks in anterior 25 to 33 setigers composite, with long, slender blades and small apex carrying about 7 teeth of subequal size (Fig. 11.5I). Hood of shaft short, narrow. Simple hooks with moderately long hood and main fang surmounted by about 4 small teeth (Fig. 11.5J). Limbate setae present through setiger 50 to 70, sometimes single fine limbate seta present throughout entire body. Aciculae black, in fascicles of about 3 in anterior parapodia, single in posterior parapodia.

Pygidium short, with four subequal anal cirri.

Remarks. Among species with black aciculae and compound hooded hooks, *L. index* is easily recognized by the postsetal lobes that are prominent throughout and digitiform in middle and posterior parapodia. The dense setal fascicles in anterior setigers are also characteristic. Anterior ends can further be distinguished from the co-occurring *L. californiensis* by the number of teeth on MIII (2 for *L. index*, 1 for *L. californiensis*).

Type Locality and Type Specimens. California, Monterey Bay, off Point Piños Lighthouse: holotype (USNM 17201); off Santa Catalina Island: paratype (ANSP AD1991).

Habitat. The species lives in silt and green mud in depths between 30 and 1400 m.

Distribution. Off Southern and central California.

Lumbrineris inflata Moore, 1911

Figure 11.6

Lumbrineris inflata Moore, 1911:289-291, pl. 19, figs. 128-132, pl. 20, figs. 133-134.—Hartman, 1944:160; 1968:757.—Fauchald, 1970:89-91, pl. 14, figs. a-d.—Imajima and Higuchi, 1975:20-22, figs. 7a-l.—Uebelacker, 1984:41-37, figs. 41-33, 41-34a-g.
Lumbriconereis inflata: Uschakov and Wu, 1965:82-83.
Lumbrineris cervicalis Treadwell, 1922:176.—Uschakov, 1955:239, figs. 79A-D. *Fide* Hartman, 1959.
Lumbrineris cingulata Treadwell, 1917:263, pl. 2, figs. 7-12. *Fide* Hartman, 1959.

Material Examined. California: Santa Maria Basin, off Point Estero, Sta. 6 (1); off Point San Luis, Sta. 27 (2).

Description. Length to 68 mm, width to 3 mm, segments at least 130. Body long, linear, tapering toward pygidium (Fig. 11.6A, B). Color in alcohol pale with iridescent cuticle.

Prostomium about as wide as long, usually globular, sometimes oval, but not depressed. Maxillae with strongly incised carriers and long, slender forceps; MII with 4 to 5 teeth, often asymmetrical; MIII with 3 to 5 teeth, MIV with 2 teeth (Fig. 11.6C, D). Mandibles fused along distal half, with crescentic cutting edge bearing 2 irregular teeth on each side of median notch (Fig. 11.6E).

Parapodia similar throughout, with short, rounded presetal lobe and moderately long postsetal lobes, pointing lateral in anterior parapodia and slightly upward in middle and posterior parapodia (Fig. 11.6F-H). Limbate setae present in first 30 to 40 segments; hooded hooks in first 22 to 26 parapodia compound, with short blades bearing small main fang and 4 to 8 teeth decreasing in size; hood of blade continuous with that of shaft (Fig. 11.6I). Middle and posterior parapodia bearing simple hooks with main fang surmounted by 6 to 11 fine teeth; hood short, inflated (Fig. 11.6J). Aciculae yellow to amber, usually 2 or 3 per parapodium.

Pygidium small, with four short, equal, conical anal cirri (Fig. 11.6B).

Remarks. Although *L. inflata* is most readily recognized by the globular shape of its prostomium, young specimens of this species are easily misidentified because their prostomium is often bluntly conical rather than spherical. However, even very small individuals possess more than one tooth on both MIII and MIV.

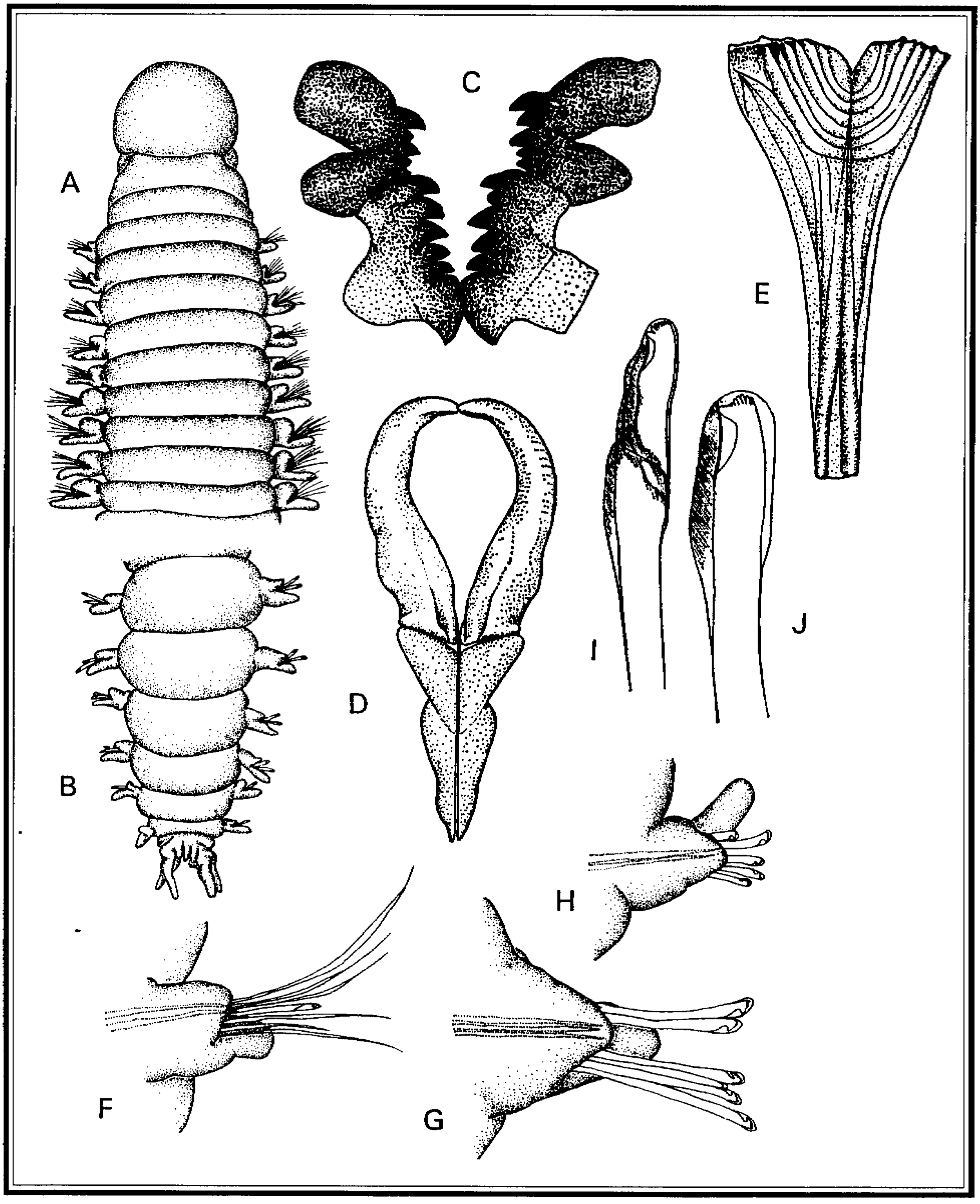

Figure 11.6. *Lumbrineris inflata*: A, anterior end, dorsal view; B, posterior end, dorsal view; C, MII, MIII, and MIV, dorsal view; D, MI and maxillary carriers, dorsal view; E, mandibles; F-H, first, median, and posterior parapodium, anterior view; I, compound hooded hook, setiger 6; J, simple hooded hook (A, B, F-H after Imajima and Higuchi, 1975; C-E, I, J from Imajima and Higuchi, 1975).

Type Locality and Type Specimens. Monterey Bay, California, off Santa Cruz Lighthouse: syntypes (USNM 16840, USNM 17205).

Habitat. *L. inflata* lives in mixed, gravelly, sandy, shelly or rocky sediments.

Distribution. British Columbia to western Mexico; Gulf of Mexico; Bering Sea; Yellow Sea; Japan; South Africa; intertidal to 130 m.

Lumbrineris japonica (Marenzeller, 1879)

Figure 11.7

Lumbriconereis japonica Marenzeller, 1879:137-138, pl. 5, fig. 3-3D.—Izuka, 1912:139-140, pl. 14, figs. 17-18.
Lumbriconereis latreilli: Uschakov and Wu, 1962:65-66; 1965:83. *Not* Audouin and Milne Edwards, 1834.
Lumbrineris latreilli japonica: Hartman, 1944:159-160.
Lumbrineris japonica: Imajima and Hartman, 1964:263-264.—Hartman, 1968:759.—Fauchald, 1970:91-92, pl. 14, figs. e-f.—Lissner *et al.*, 1986:D-11.

Material Examined. California: Santa Maria Basin, off Point Buchon, Sta. 13 (1); Tomales Bay, coll. 1959 (2).

Description. Length to 130 mm, width to 6 mm, segments at least 115. Body long, slender, linear, almost cylindrical, gently tapering at both ends (Fig. 11.7A, B); segments appearing weakly biannulate due to whitish ring of epidermal cells, perhaps glandular. Color in alcohol pale to tan, iridescent.

Prostomium bluntly conical, somewhat depressed, almost as wide as long. Maxillae with laterally incised carriers and long, sharply falcate forceps. MII with 4 to 6 teeth, MIII elongate plates with 2 teeth (sometimes only a boss on lower edge), MIV large plates with one tooth (Fig. 11.7C, D). MII attached to carriers with short, thin ligaments. Mandibles fused for almost entire length, with crescentic cutting edge bearing a calcified tooth on either side (Fig. 11.7E).

Parapodia similar throughout, with short presetal and somewhat elongate postsetal lobes (Fig. 11.7F, G). Limbate setae present in first 40 to 50 setigers, few per fascicle (Fig. 11.7H); hooks in first 15 to 33 setigers compound, with medium long blades (length/width ratio about 3) bearing 8 to 9 fine teeth above main fang; hoods of blades clearly separated from those of shafts (Fig. 11.7I). In subsequent setigers hooks becoming simple, with short hoods and large main fang surmounted by crest of 4 to 8 small teeth (Fig. 11.7J). Aciculae dark amber to black, in fascicles of 2 to 4 in anterior parapodia, single in posterior parapodia.

Remarks. This species is characterized by having black aciculae and parapodia of similar shape throughout the entire body; the postsetal lobes are somewhat elongate and nearly reach the length of the parapodial stem. Anterior ends can be distinguished from co-occurring *L. californiensis* by the number of teeth on MIII (2 for *L. japonica*, 1 for *L. californiensis*.)

Type Locality. Eno-Sima, Japan.

Biology. Gravid females were found between May and October in the Yellow Sea (Uschakov and Wu, 1965). The species lives in mixed sediments including sand, shells, rocks, and eelgrass roots.

Distribution. Japan; Indopacific; western Canada to western Mexico; Yellow Sea; intertidal to 75 m.

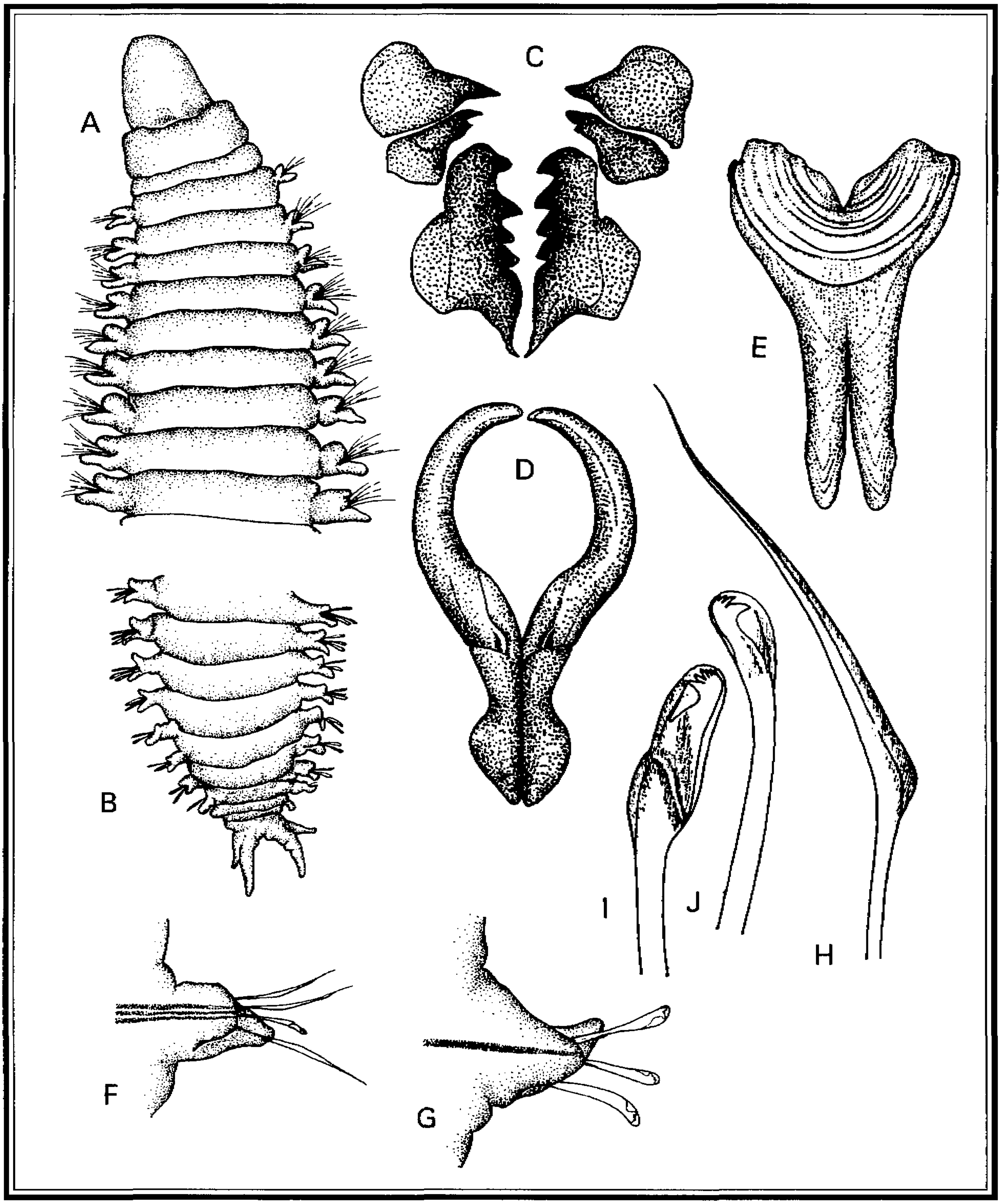

Figure 11.7. *Lumbrineris japonica*: A, anterior end, dorsal view; B, posterior end, dorsal view; C, MII, MIII, and MIV, dorsal view; D, MI and maxillary carriers, dorsal view; E, mandibles; F, first parapodium, anterior view; G, posterior parapodium, anterior view; H, limbate capillary seta, setiger 5; I, compound hooded hook, setiger 1; J, simple hooded hook, setiger 60 (A, B, F, G after Imajima and Higuchi, 1975; C-E, H-J from Imajima and Higuchi, 1975).

Lumbrineris latreilli Audouin and Milne-Edwards, 1834

Figure 11.8

Lumbrineris latreilli Audouin and Milne Edwards, 1834:168, pl. 38, figs. 13-15.—Hartman, 1944:158-159, pl. 9, figs. 213-216; 1968:761.—Pettibone, 1963:258-260, figs. 67 a-c.—Fauchald, 1970:94-97, pl. 15, figs. f-h.—Orensanz, 1973:359-361, pl. 6.—Imajima and Higuchi, 1975:32-36, fig. 13.—Ramos, 1976:121-124, figs. 16-18.

Lumbrinconereis latreilli: Fauvel, 1923:431, figs. 171 m-r; 1953:266, figs. 134 m-r.—Okuda, 1946:120, pls. 12-13.

Lumbrinereis latreilli: Berkeley and Berkeley, 1948:98, figs. 154-156.

Description. Length to 300 mm, width to 5 mm, segments at least 120. Body robust; color in alcohol pale to brown with iridescent cuticle.

Prostomium conical, slightly longer than wide, depressed (Fig. 11.8A). Maxillae with broad, laterally incised carriers and strong forceps; MII with 4 to 6 teeth, often asymmetrical, MIII with 2 teeth, MIV with single tooth (Fig. 11.8B, C). Mandibles large, roughly rectangular, fused except for small proximal part, with crescentic cutting edge (Fig. 11.8D).

Parapodia similar throughout, with low presetal lobes and conical postsetal lobes, in posterior setigers directed slightly upward (Fig. 11.8E-G). Limbate setae present in anterior and middle segments, sometimes singly in posterior segments (Fig. 11.8H); hooded hooks in first 11 to 24 segments composite, with blades about 5 times as long as wide, bearing small main fang surmounted by 6 to 9 fine teeth; hood of blade separate from that of shaft (Fig. 11.8I). Hooded hooks in subsequent setigers simple, much stouter than compound hooks, with large main fang and 9 to 10 smaller teeth, hoods short (Fig. 11.8J). Aciculae yellow to amber, in fascicles of 3 anteriorly, only 2 in posterior segments; aciculae occasionally occurring singly in a parapodium.

Pygidium with 4 equal, short anal cirri (Fig. 11.8K).

Remarks. Within the genus *Lumbrineris*, *L. latreilli* appears to be one of the most variable species. Ramos (1976) explored the ranges of variability for several characters, such as the number of teeth on MII and the length of the blades of composite hooks relative to the blade width and the length of the shaft. She compared two collections from the Catalonian coast (Mediterranean Sea) and concluded that the species could not be split into two even though slight differences between the two populations were found.

Type Locality. France.

Biology. Hartman (1944) found gravid females tightly packed with salmon colored eggs about 220 ìm in diameter present in all segments but the first and last 20 to 30. Eggs are laid in gelatinous masses and attached to macroalgae. Development is direct; larvae leave the egg masses at the 4- to 7-setiger stage (Pettibone, 1963). *L. latreilli* occurs in mud and sand, among eelgrass roots, and under rocks.

Distribution. Cosmopolitan; Greenland to France; Mediterranean Sea; eastern Canada to North Carolina; western Canada to California; Mexico, Peru; Galapagos Islands; Gulf of Mexico to Panama; Japan; Indian Ocean, Red Sea, Persian Gulf; West and South Africa; intertidal to 2300 m.

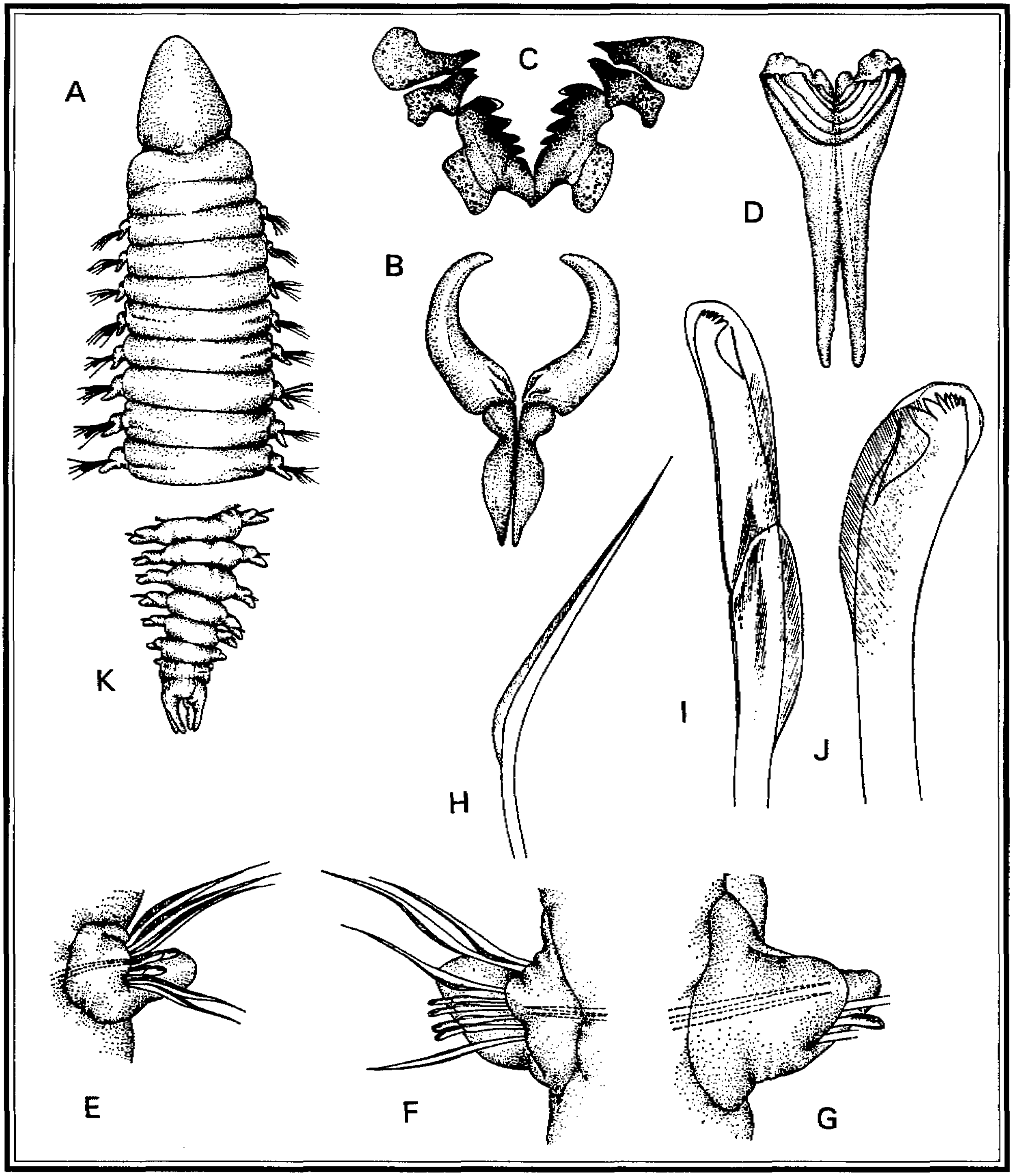

Figure 11.8. *Lumbrineris latreilli*: A, anterior end, dorsal view; B, MI and maxillary carriers, dorsal view; C, MII, MIII, and MIV, dorsal view; D, mandibles; E-G, first, 10th, and posterior parapodium, anterior view; H, limbate capillary seta, setiger 1; I, compound hooded hook, setiger 10; J, simple hooded hook, posterior setiger (all from Imajima and Higuchi, 1975).

Lumbrineris limicola Hartman, 1944

Figure 11.9

Lumbrineris limicola Hartman, 1944:161-162, pl. 11, figs. 230-237; 1968:765.—Fauchald, 1970:97-98, pl. 16, figs. a-d.—Hyland *et al.*, 1990:F-1.

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

Description. Length to 84 mm, width to 6 mm, segments to 81. Body robust; color in alcohol pale with iridescent cuticle.

Prostomium bluntly conical, as long as wide, depressed (Fig. 11.9A). Maxillae with large, laterally incised maxillary carriers about as long as MI; MII with 4 teeth, MIII unidentate, sometimes with small boss on cutting edge resembling a reduced second tooth; MIV with single heavy tooth (Fig. 11.9B). Mandibles fused along anterior half, shafts posteriorly diverging, wide, approaching shape typical for *Augeneria* (Fig. 11.9C).

Parapodia conspicuous from setiger 1, with notopodial rudiments; presetal lobes low, rounded throughout, postsetal lobes becoming elongate and pointing dorsad in posterior setigers (Fig. 11.9D-F). Compound hooded hooks and simple limbate setae present through 25-40 setigers in adult specimens; shafts of hooks 3-4 times as long as wide, with crest of about 8 subequal teeth (Fig. 11.9G). Simple hooks stouter than composite ones, with main fang surmounted by about 8 small teeth (Fig. 11.9H). Aciculae pale yellow.

Remarks. This species may be much more common than suggested by the small number of records off California. It is likely that anterior ends have been misidentified as *L. latreilli*, a "cosmopolitan" species with few unmistakable diagnostic characters. It is suggested that only specimens with a distinctly bidentate MIII be assigned to *L. latreilli*, whereas individuals with a unidentate or indistinctly bidentate MIII should be identified as *L. limicola*.

Type Locality and Type Specimens. California, off Point Fermin, California: holotype (LACM-AHF Poly 49).

Habitat. Mud and silt.

Distribution. Central California to western Mexico, shallow subtidal to about 190 m.

Genus *Ninoe* Kinberg, 1865

Type Species. *Ninoe chilensis* Kinberg, 1865

Diagnosis. Prostomium conical, usually with longitudinal slits or folds. Parapodia with branchiae arising from postsetal lobe, with 2 to about 15 digitiform lobes. Setae including simple limbate capillaries and simple hooded, multidentate hooks. Aciculae dark amber to jetblack, setae usually with dark bases and amber-colored to clear tips. MIV and often also MIII with 1 to 3 teeth and serrated cutting edge; MV absent.

Remarks. Kinberg (1865) established the genus (and a family Ninoidea) to accommodate eunicemorph forms with no prostomial appendages or tentacular cirri, but with branchiae arising from the postsetal lobes of a limited number of anterior parapodia. He included three new species from off Chile and Brazil: *N. chilensis*, *N. brasiliensis*, and *N. oculata.* Fauchald (1970) emended the genus to include not only species with gills on postsetal lobes of anterior parapodia, but also those with gills on posterior parapodia and the adjacent body wall. This emendation was rejected by Orensanz (1973, 1990) because these different branchial structures are not considered homologous. The definition of *Ninoe*, as originally stated by Kinberg, is followed here. The presence of serrations on the cutting edges of MIV, and often MIII, is an additional reliable character for discrimination of this genus.

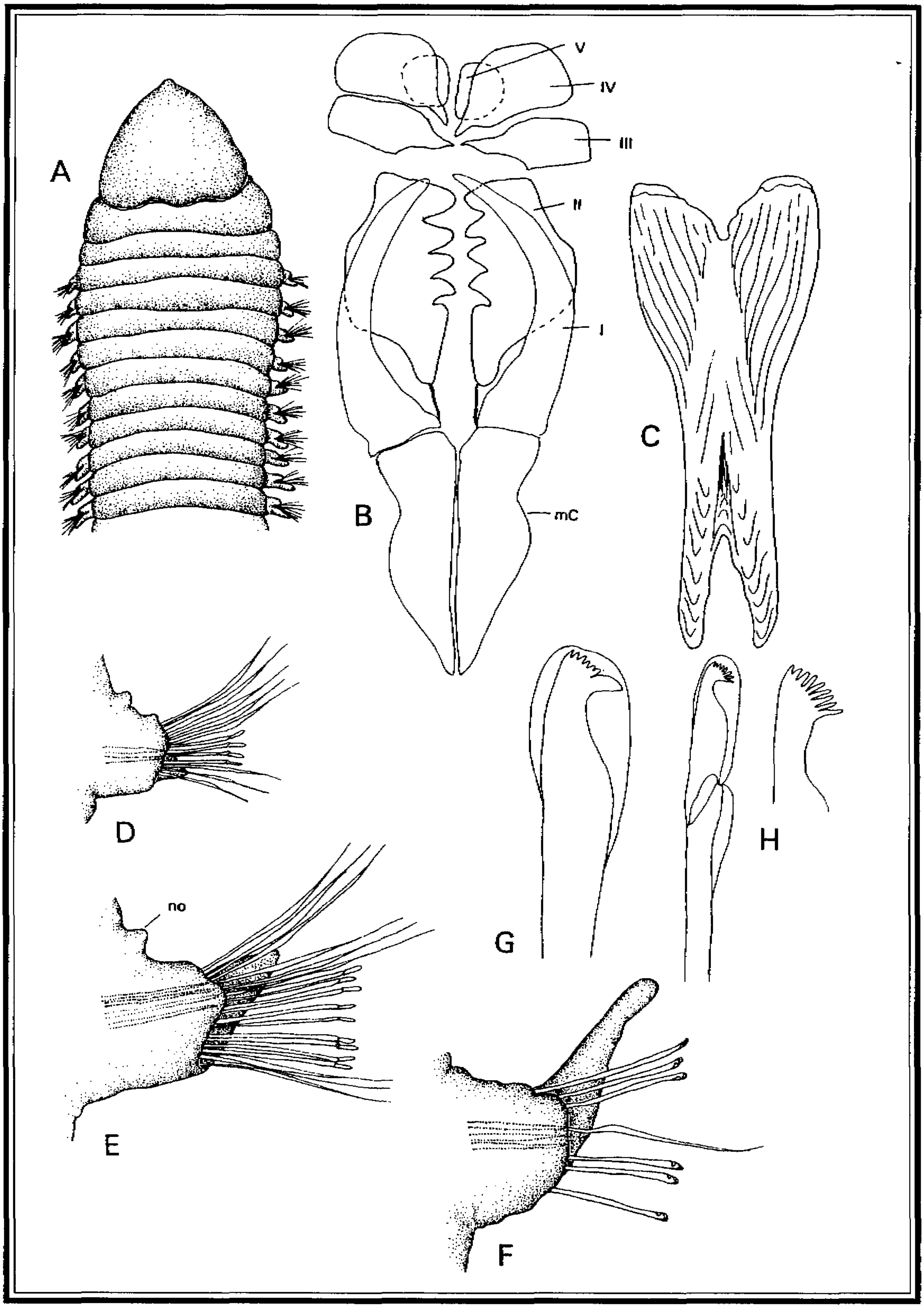

Figure 11.9. *Lumbrineris limicola*: A, anterior end, dorsal view; B, maxillae, dorsal view, *in situ*; C, mandibles; D-F, anterior, median, and posterior parapodium, anterior view; G, simple hooded hook; H, compound hooded hook, with detail of crest (C-F after Hartman, 1944; G from Fauchald, 1970).

Ninoe gemmea Moore, 1911

Figure 11.10

Ninoe gemmea Moore, 1911:283-285, pl. 19, figs. 101-109.—Lissner *et al.*, 1986:D-12.

Material Examined. California: Monterey Bay, Sta. 4450 (holotype); Santa Maria Basin, off Point Sal, Sta. 38 (1); off Purisima Point, Sta. 42 (1).

Description. Length to 104 mm, width to 2.5 mm excluding parapodia, segments to 146. Body slender, linear, slightly wider in branchial region than in postbranchial region. Color in alcohol tan to dark grey, with highly iridescent cuticle.

Prostomium slightly longer than wide, conical, somewhat depressed dorsoventrally, with 2 distinct nuchal organs at posterior margin (Fig. 11.10A); dorsal surface smooth, ventral side with 2 longitudinal furrows stretching from the insertion of the large palps to nearly tip of prostomium. Two peristomial rings developed dorsally, partly fused ventrally to form crenulated lower lip (Fig. 11.10B). Maxillae with slender, laterally incised carriers about as long as MI; MII with 8 teeth, MIII and MIV unidentate with serrated cutting edges (Fig. 11.10C). Mandibles slender, proximally fused, with irregularly serrated cutting edge (Fig. 11.10D).

Parapodia small in first five setigers, then increasing; presetal lobe obliquely truncate, postsetal lobe much longer, conical to foliaceous (Fig. 11.10E-G). Gills first present on setigers 4 (holotype) to 6, starting as 2 nearly equal halves of the postsetal lobe (Fig. 11.10H); upper branch increasing in length and pointing slightly upward in subsequent setigers, lower branch dividing into maximally 4 digitiform branches that are somewhat shorter and narrower than the upper lobe (Fig. 11.10I, J). Number of branches decreasing gradually after setiger 39 to 46, single gill after setiger 50, rudimentary process on postsetal lobe through about 10 additional setigers. Setae including limbate capillaries and simple hooded hooks throughout entire length of body; hooks slender with very small apex and long hood in anterior setigers, wider with distinct apex bearing crest of several teeth over main fang and short, rounded hood in posterior setigers (Fig. 11.10K-M). Aciculae black, setae clear with dark bases.

Remarks. Moore, in his original description, reported the gills starting from setiger 5 or 6; however, an examination of the holotype revealed that this specimen has gills from setiger 4. Hartman's (1968) notion as to where the gills first appear is incomplete and easily misunderstood, because she only mentioned the first appearance of the second branchial filament (setiger 8), but not of the first filament (setiger 4-6). The distribution of the gills along the body should be used with caution for species discrimination because it may have a wider range of variability than originally thought; however, slow increase of the number of branchial filaments along the length of the branchial region distinguishes *N. gemmea* from the co-occurring *N. palmata* (see below).

Type Locality and Type Specimens. California, Monterey Bay, off Point Piños Lighthouse: holotype (USNM 17348).

Habitat. Soft green or dark mud and sand.

Distribution. Central and southern California, 79 - 1272 m.

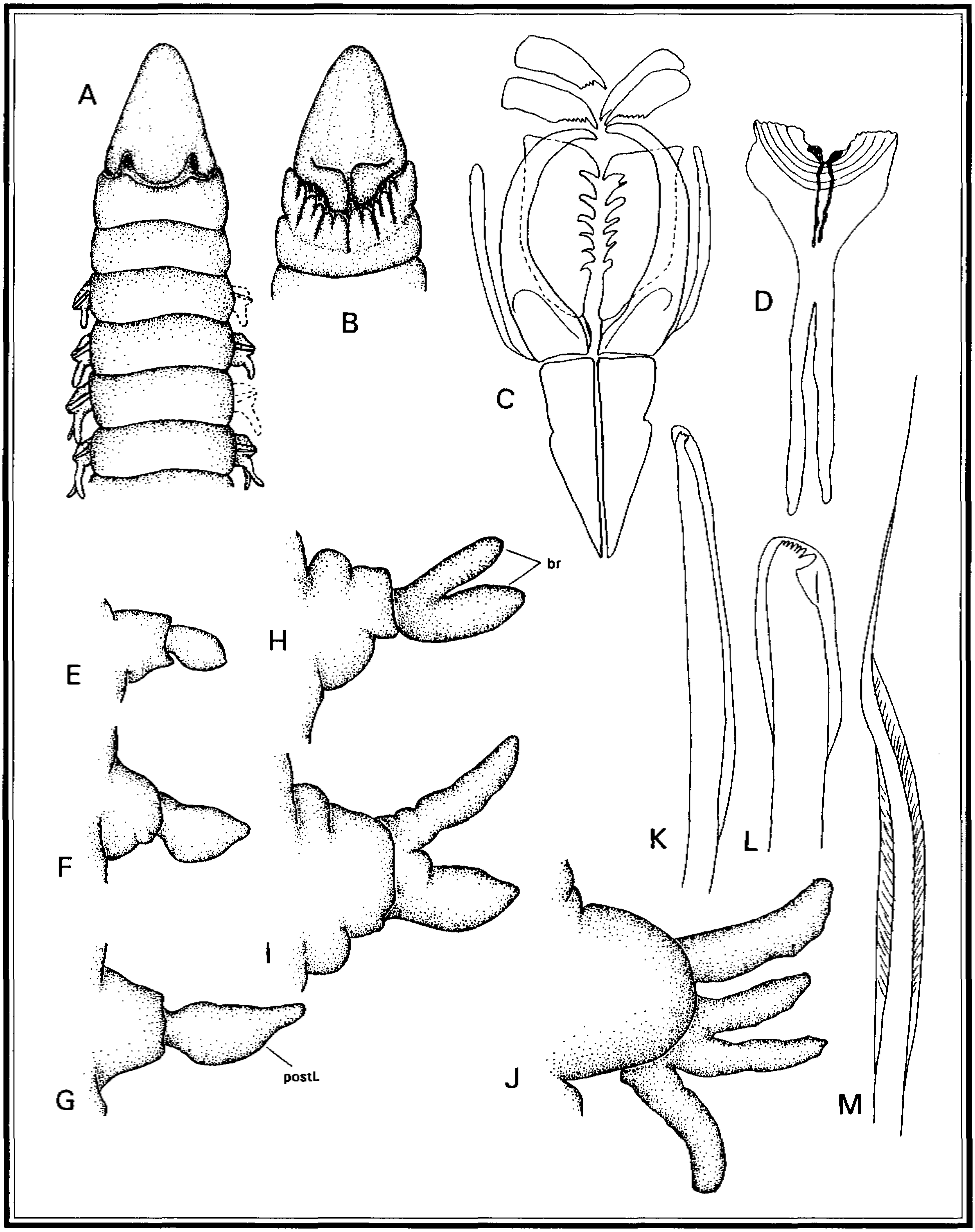

Figure 11.10. *Ninoe gemmea*: A, anterior end, dorsal view; B, same, ventral view; C, maxillae, dorsal view, *in situ*; D, mandibles; E-I, first through fifth parapodium, anterior view; J, 25th parapodium, anterior view; K, hooded hook, setiger 25; L, same, setiger 100; M, limbate capillary seta, setiger 25 (A, B, E-I from holotype; D, K-M after Moore, 1911).

Ninoe palmata Moore, 1903

Figure 11.11

Ninoe palmata Moore, 1903:456-457, pl. XXVI, figs. 69-71.—Izuka, 1912:137-139.—Imajima and Hartman, 1964:264.—Imajima, 1968:141.—Uschakov and Wu, 1965:83-84, fig. 21H-M.—Imajima and Higuchi, 1975:10-12, fig. 3a-m.—Lissner *et al.*, 1986:D-12.
Ninoe nr. *palmata*: Lissner *et al.*, 1986:D-12.
Ninoe nr. *gemmea*: Lissner *et al.*, 1986:D-12.

Material Examined. Japan: Sendai Bay, off Honshu Island, Sta. 3767 (holotype). California: Santa Maria Basin, off Purisima Point, Sta. 42 (1), Sta. 43 (1), Sta. 53 (1); off Point Arguello, Sta. 67 (1).

Description. Length to 51 mm, width to 2 mm excluding parapodia, segments to 158. Body slender, widest in branchial region, gently tapering at both ends. Color in alcohol light tan.

Prostomium conical, slightly longer than wide, with paired nuchal organ at posterior margin (Fig. 11.11A). Maxillae with slender, laterally incised carriers about as long as MI; MII with 6 or 7 teeth, the subterminal one tiny; MIII and MIV unidentate; MIII with whitish center, MIV with serrated cutting edge (Fig. 11.11B, C). Mandibles poorly sclerotized, delicate, fused along proximal half, with 2 large, irregular teeth on cutting edge (Fig. 11.11D).

Parapodia minute in first 2 setigers, with obliquely truncate presetal lobe and conical to foliaceous postsetal lobe, increasing in length in subsequent setigers (Fig. 11.11E). Gills starting on setigers 2 to 4, first developed as 2 subequal halves of postsetal lobe; lower half splitting into additional digitiform branches, number of branches increasing quickly to 6 within about 15 setigers; upper half increasing in size, becoming about twice as long and distinctly thicker than lower branches where best developed, pointing dorsad and curved across dorsum (Fig. 11.11F). Last gill between setigers 30 and 43; postsetal lobes in postbranchial region pointed, conical, distincly longer than presetal lobes (Fig. 11.11G). Setae including limbate capillaries and hooded hooks throughout; anterior hooks slender, with small crest of about 5 teeth and long, narrow hood (Fig. 1011H, I). Posterior hooks stouter, with distinct crest of about 8 teeth over small main fang and shorter, wider hood (Fig. 11.11J). Aciculae dark amber, setae clear, sometimes with amber colored bases.

Pygidium with 2 ventrally inserted anal cirri (Fig. 11.11K).

Remarks. Moore's description of *N. palmata* is unusually short, especially with regard to the branchial development, and examination of the holotype revealed that it is also incorrect. He states that the gills start "as far forward as V," whereas they were found to first appear on setiger 2 on one side of the holotype and on setiger 3 on the other side; the maximum number of filaments is 6 rather than 5 as stated by Moore. Specimens originally identified as *Ninoe* nr. *gemmea* and *N.* nr. *palmata* have been included in *N. palmata* even though the gills start in setigers 4 or 5 rather than 2 or 3. It seems that the first appearance of gills usually varies by about two or three in other species of this genus, so that the assignment to a new species seems unjustified. All other characters agree well with *N. palmata*.

Type Locality and Type Specimens. Japan, Sendai Bay, off Honshu Island, 30-35 m: holotype (USNM 15735).

Habitat. Sandy silt and shells, mixed sand and silt.

Distribution. Japan; Yellow Sea; central California; 30 - 1450 m.

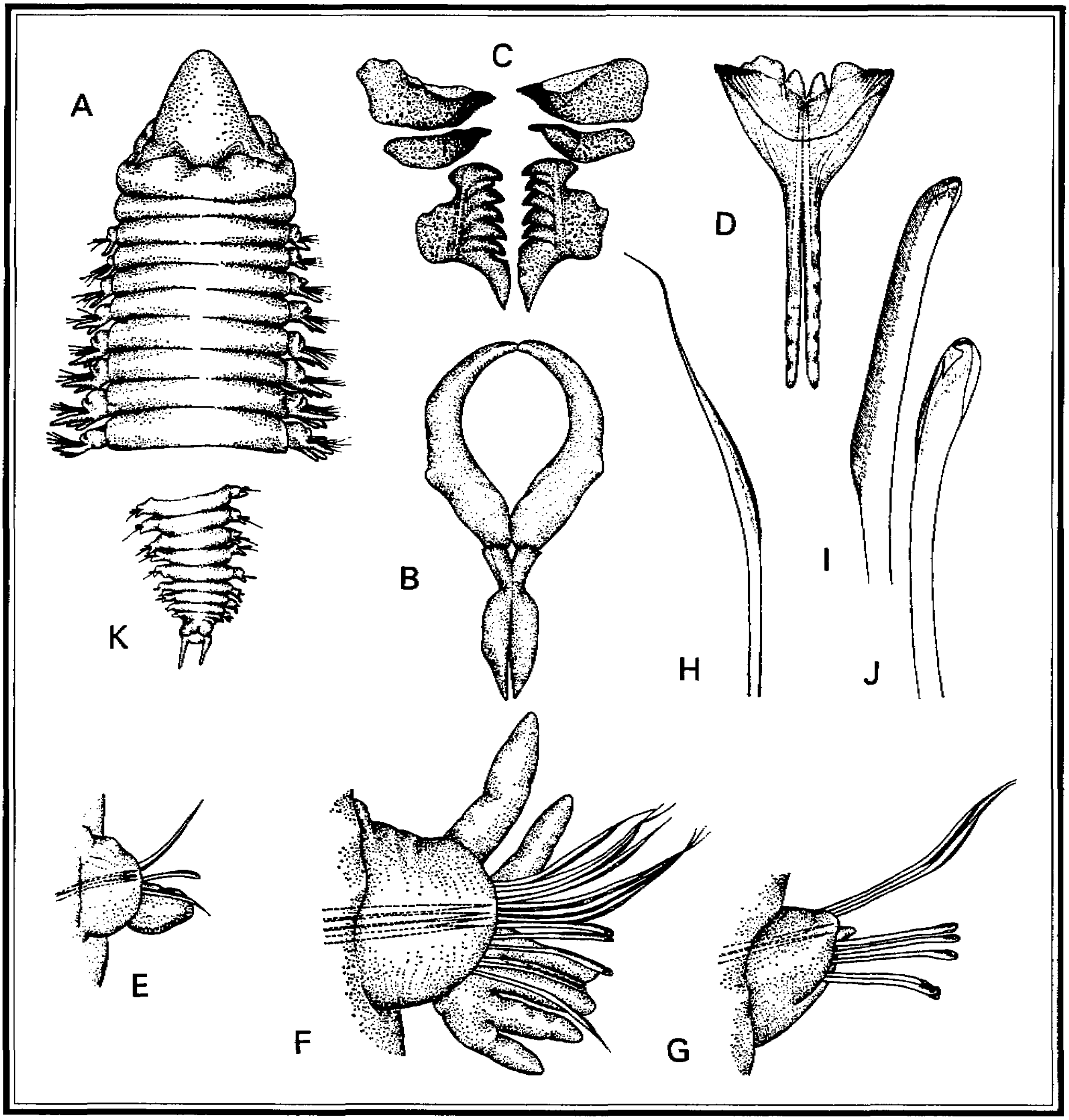

Figure 11.11. *Ninoe palmata*: A, anterior end, dorsal view; B, MI and maxillary carriers, dorsal view; C, MII, MIII, and MIV, dorsal view; D, mandibles; E-G, first, 16th, and 75th parapodium, anterior view; H, limbate capillary seta, setiger 75; I, hooded hook, anterior setiger; J, same, setiger 75 (all from Imajima and Higuchi, 1975).

Ninoe tridentata Hilbig, new species

Figure 11.12

Ninoe sp. A Lissner *et al.*, 1986:D-12.—Hyland *et al.*, 1990:F-1.

Material Examined. California: Santa Maria Basin, off Point Sal, Sta. R-8, 34°55.30'N, 120°45.87'W, 90 m: holotype (USNM 170425) and 3 paratypes (USNM 170426); Sta. 30, 34°54.19'N, 120°47.07'W, 98 m: 1 paratype (SBMNH 142696); off Point San Luis, Sta. 21, 35°06.11'N, 120°44.82'W, 49 m: 1 paratype (LACM-AHF Poly 1658).

Description. Length to 13 mm, width to 1 mm, setigers to 96. Body slender, gently tapering at both ends, widest in pharyngeal region. Color in alcohol light tan.

Prostomium conical, almost twice as long as wide, with faint dorsal longitudinal folds, much narrower than peristomium (Fig. 11.12A). Maxillae with laterally incised carriers, shorter than MI; MII with 7 theeth, MIII with three conical teeth, MIV unidentate with finely serrated cutting edge (Fig. 11.12B). Mandibles delicate, weakly sclerotized.

Parapodia in first two setigers very small, with short, rounded presetal and longer conical, pointed postsetal lobes (Fig. 11.12C, D); subsequent parapodia increasing in size, bearing branchiae from setiger 3 to about 45, with maximally 11 filaments (holotype with up to 7 filaments) and foliaceous upper filament of slightly greater length than lower filaments (Fig. 11.12E-I). Simple capillaries with wide wings and long filiform tip, in postbranchial setigers gradually turning more slender with wing tapering more gradually, absent from far posterior setigers (Fig. 11.12J, K). Hooks first present from setigers 4 to 14, in anterior setigers slender, with medium long hood and small apex bearing crest of about four teeth above main fang; hoods gradually shortening and widening, hooks becoming stouter, bearing larger main fang and crest of five subequal teeth (Fig. 11.12L, M). Aciculae dark amber, setae clear with amber colored bases.

Remarks. *Ninoe tridentata* is easily recognized by the elongate prostomium and the absence of hooded hooks from at least three anterior parapodia. The species resembles *N. palmata* in the distribution and morphology of the gills, but can be distinguished by the tridentate, rather than unidentate, MIII.

Etymology. The epithet refers to the tirdentate thrird maxillae.

Habitat. Sand and sand mixed with silt.

Distribution. Presently known only from the Santa Maria Basin.

Ninoe sp. C

Ninoe sp. C Lissner *et al.*, 1986:D-12.

Material Examined. California: Santa Maria Basin, off Point Arguello, Sta. 69 (8).

Description. All available specimens juvenile; length to 10 mm, width to 0.5 mm, setigers to 45. Body very slender, with prominent parapodia and gills; color in alcohol whitish. Prostomium conical, slightly longer than wide, with indistinct nuchal organs. Maxillae soft, with laterally incised carriers about as long as MI; MII with 4 or 5 teeth, MIII and MIV with serrated cutting edge and one or two teeth (jaws too small for accurate observation). Parapodia conspicuous throughout, with short, bluntly rounded presetal lobes and digitiform, much longer postsetal lobes; branchiae present from setiger 2 to maximally 17 (usually 15), with up to 6 filaments and digitiform to foliaceous upper filament, up to twice as long as lower filaments where best developed. Setae including limbate capillaries and hooded hooks; capillaries with broad wings in anterior

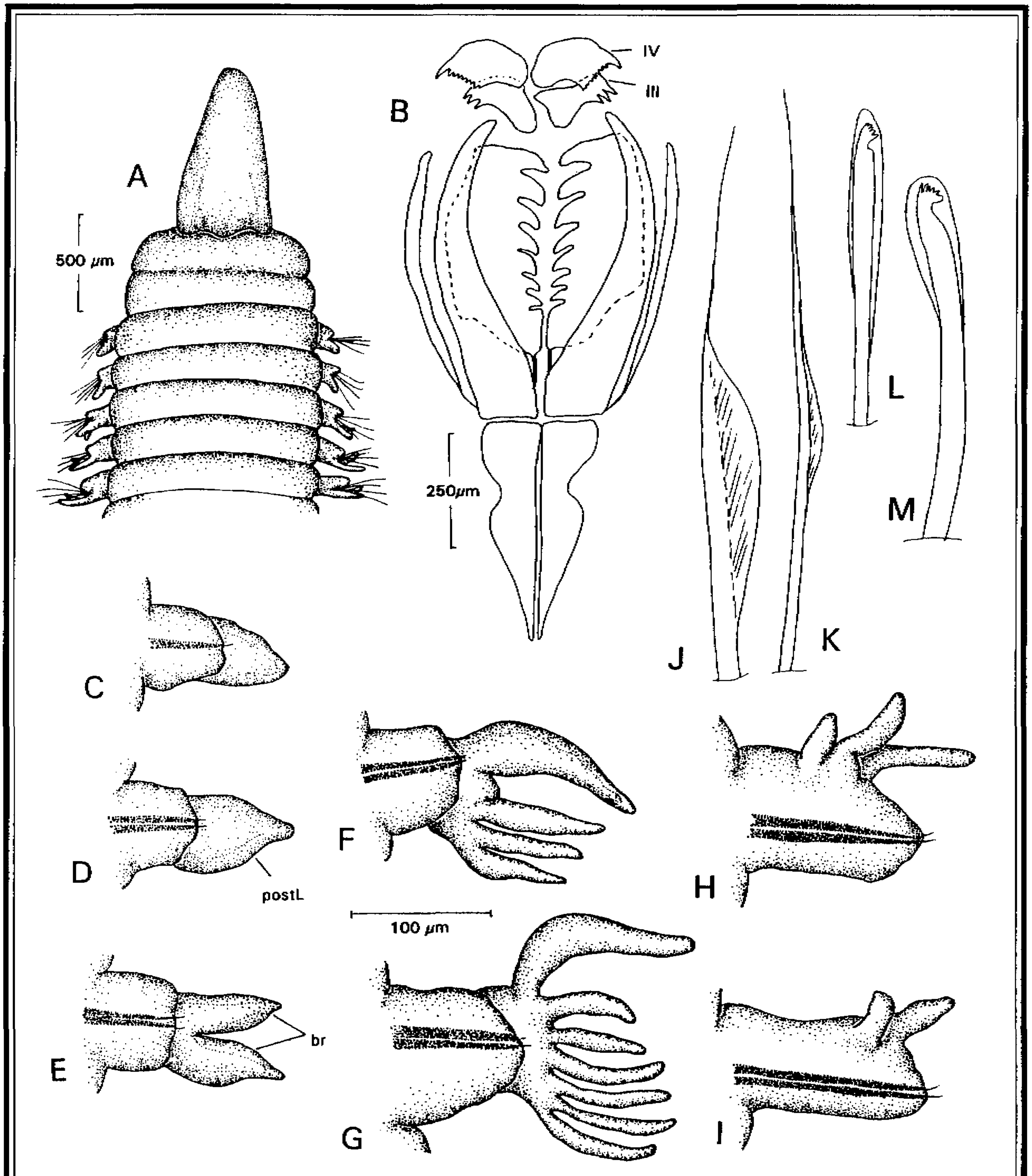

Figure 11.12. ***Ninoe tridentata* Hilbig, new species**: A, anterior end, dorsal view; B, maxillae, dorsal view, *in situ*; C-G, first, second, third, 10th, and 25th parapodium, anterior view; H-I, second-to-last and last gill-bearing parapodium, anterior view; J, limbate capillary seta, anterior setiger; K, same, posterior setiger; L, hooded hook, anterior setiger; M, same, posterior setiger. (A, C-I: paratype USNM 170426; B, J-M: holotype).

setigers, much more slender and with long, narrow wings in postbranchial setigers, absent after setiger 35 to 40; hooks present from setiger 1, very slender with moderately long hoods and small apex in anterior setigers, stouter, with short hoods and large main fangs in posterior setigers. Crest of about 5 teeth forming sharp angle with shaft in hooks from posterior setigers, resembling hooks of *Lumbrineris latreilli*.

Remarks. Specimens assigned to *Ninoe* sp. C are most likely juveniles of *N. longibranchia* Fauchald, 1972, a species found in depths between 1800 and 2600 m off western Mexico. The station where *N.* sp. C was found is about 1000 m deep and may be at the shallow end of the distribution of *N. longibranchia*. The only difference between *N. longibranchia* and *N.* sp. C is the number of teeth on MII (4 or 5 for *N.* sp. C, 6 for *N. longibranchia*) and possibly the shape of the maxillary carriers that are reported to be straight in *N. longibranchia*, but laterally incised in *N.* sp. C. Examination of the holotype of *N. longibranchia* will be necessary to confirm the assignment of *N.* sp. C.

Ninoe sp. D

Ninoe sp. D Lissner *et al.*, 1986:D-12.

Material Examined. California: Santa Maria Basin, off Point Arguello, Sta. 58 (1).

Description. Only one incomplete specimen found during entire program in the Santa Maria Basin and Santa Barbara Channel. Length 19 mm, width 1 mm, 86 setigers; color in alcohol whitish. Prostomium conical, pointed, longer than wide, distinctly narrower than peristomium. Maxillae with very slender, laterally incised carriers, longer than MI; MII with 5 teeth, MIII with 1 tooth and rounded boss, MIV unidentate with serrated cutting edge. Branchiae present from setiger 3, maximally 6 filaments plus superior lobe, the latter foliacous and somewhat longer than lower filaments. Last branchia on setiger 41. Limbate capillaries present throughout length of fragment, with broad wings in anterior setigers and narrow wings in postbranchial setigers; hooded hooks from setiger 15, narrow, with moderately long hoods and very small apex bearing about 6 fine, subequal teeth, gradually becoming stouter with hoods shortening in posterior setigers of fragment. Aciculae dark brown, setae clear with dusky bases.

Remarks. Based on the softness of the maxillary plates, it can be assumed that this specimen is a juvenile; no final assignment of *Ninoe* sp. D, either to a known or a new species, could be made.

Genus *Scoletoma* Blainville, 1828, emended Frame, 1992

Type Species. *Lumbricus fragilis* O.F. Müller, 1776

Diagnosis. Prostomium conical to globular. Setae including simple limbate capillaries and simple, multidentate hooded hooks. Aciculae yellow or black. MII about as long as MI, linked to MI with threadlike ligament. MV, if present, free from MIV.

Remarks. Blainville erected *Scoletoma* for *Lumbricus fragilis* O.F. Müller without stating which characters he considered diagnostic for his new genus. Frame (1992) resurrected *Scoletoma* and provided a generic definition based on the above characters. Although the jaw apparatus is very much like that of *Lumbrineris*, the separation of the two genera based on setal morphology is acceptable because the presence or absence of compound hooks is consistent within all other lumbrinerid genera.

Scoletoma tetraura (Schmarda, 1861)

Figure 11.13

Notocirrus tetraurus Schmarda, 1861:117, 6 figs.
Lumbriconereis tetraura: Ehlers, 1901:137-139, pl. 17, figs. 1-10 (in part).
Lumbrinereis tetraura: Day, 1953:435-436.
Lumbrineris tetraura: Moore, 1911:291.—Augener, 1933:61-62.—Hartman, 1944:147-149, pl. 8, figs. 175, 190, 191, pl. 9, figs. 192-195.
Lumbrineris brevicirra Monro, 1933:83 (in part).

Material Examined. California: Santa Maria Basin, off Point San Luis, Sta. 21 (1), Sta. 23 (1), Sta. R-2 (19); Western Santa Barbara Channel, Sta. 79 (2); Tomales Bay, coll. 1958 (1).

Description. Length to 250 mm, width to 5 mm, segments to 280. Body slender, with relatively long parapodia in posterior half; color in alcohol pale, cuticle iridescent.

Prostomium conical, about as long as wide, rounded anteriorly (Fig. 11.13A). Maxillae with short, wide, laterally incised maxillary carriers; MII with 4-5 teeth and large aliform expansion, MIII bidentate, MIV large, roughly triangular, unidentate plates, MV large, squarish plates, free from MIV (Fig. 11.13B). Mandibles relatively short, fused for most of their length (Fig. 11.13C).

Parapodia conspicuous from setiger 1, with short, truncate presetal lobes and conical postsetal lobes; posterior parapodia much longer than anterior ones, with elongate, erect postsetal lobes pointing dorsad, at least three times as long as presetal lobes, often irregularly wrinkled (Fig. 11.13D, E). Simple hooded hooks present from setiger 1; anterior hooks slender, with long hoods and small crest of several fine teeth, posterior hooks stouter, with short rounded hoods and crest of numerous small, subequal teeth above a slightly larger main fang (Fig. 11.13F, G). Limbate setae present through about 40 to 60 setigers. Aciculae yellow to amber, usually present in fascicles of 2 or 3 per parapodium.

Pygidium small, with 2 pairs of short anal cirri.

Remarks. *Scoletoma tetraura* is one of the few species that possess very characteristic hooded hooks that allow for identification without examining the jaws. This character may be helpful for the identification of small specimens where dissection of the jaws is difficult. It also seems that the second tooth on MIII is not present in small individuals (2 to 3 cm length).

Type Locality. Chile.

Biology. Orensanz (1973) reported that gut contents consisted of a variety of algae, detritus, sediment, small crustaceans and pelecypods, and diatoms, suggesting an omnivorous life style. *Scoletoma tetraura* appears to be equally flexible with regard to substatum; it has been reported from mud to sand, mixed sediments, and rocks.

Distribution. Central California to Chile, intertidal - 220 m.

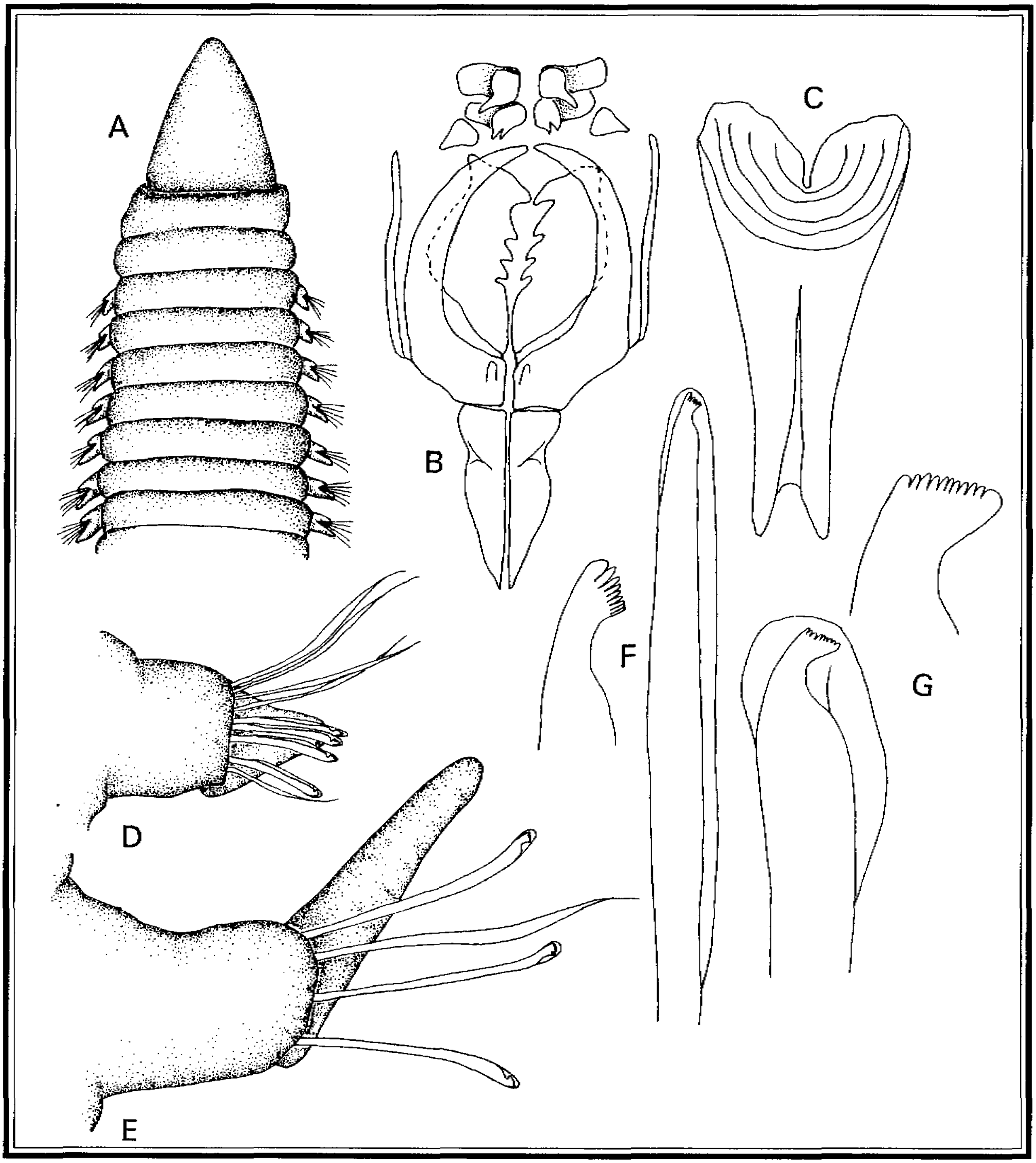

Figure 11.13. *Scoletoma tetraura*: A, anterior end, dorsal view; B, maxillae, dorsal view; *in situ*; C, mandibles; D, 10th parapodium, anterior view; E, posterior parapodium, anterior view; F, hooded hook, anterior setiger, with detail of crest; G, same, posterior setiger (C-G after Orensanz, 1973).

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12. Family Oenonidae Kinberg, 1865, emended Orensanz, 1990

(including Arabellidae Hartman, 1944)

by

Brigitte Hilbig[1]

Introduction

The oenonids superficially resemble the lumberinerids, but differ considerably in several characters, some of which are easily observed. The most obvious difference is the absence of hooded hooks in oenonids, so that only one type of seta is present (limbate capillaries). In many species, these limbate setae are strongly geniculate and serrated or covered with surficial spines. Many oenonids have a characteristically thin and wiry habitus; the cuticle is very rigid and often strikingly iridescent. The prostomium of oenonids is generally dorsoventrally depressed, whereas the typical lumbrinerid prostomium is conical or even globular, although it may flatten, especially in large individuals, when the proboscis is everted. The most important difference between lumbrinerids and oenonids, from an evolutionary and systematic point of view, is the arrangement of the jaw apparatus (see below). Oenonids are distributed worldwide, but never abundant; some species are parasitic, at least through part of their life history, in other polychaetes, bivalves, and echiurans.

Morphology

The prostomium is conical, usually dorsoventrally flattened, and without any appendages except for *Oenone* which has three minute antennae at the posterior margin of the prostomium. Eyes may be present at the posterior prostomial margin as well. The eversible pharynx is armed with five pairs of maxillary plates and paired mandibles that are often very small in relation to the maxillae. Maxillary carriers are much longer than the maxillary plates and consist of a pair of slender dorsal pieces and a usually shorter and broader single ventral piece. The maxillary plates (MI through MV) may be symmetrical, i.e., the corresponding plates are of equal size and have similar numbers of teeth, or they may be asymmetrical, i.e., corresponding plates may be of very different sizes and have clearly different numbers of teeth. An excellent explanation of the origin and evolution of the different maxillary arrangements can be found in Orensanz (1990). The first maxillae are variable in shape; they may be falcate and proximally smooth, much like MI in lumbrinerids, or proximally dentate; some genera have MI that are entirely dentate and have a similar shape to the MII. Intermediate types of MI can be found that have a dentate border over most of their length, but a distinctly larger and hook-shaped distal tooth. The second maxillae are similar in size to the MI and usually bear about 3 to 10 teeth; they are located ventral of the MI and free from the latter (not attached with ligaments as in lumbrinerids). In asymmetrical jaw apparatuses, a smaller MI on one side is accompanied by a larger MII. The third, fourth,

[1] ENSR Consulting and Engineering, 89 Water Street, Woods Hole, Massachusetts 02543

and fifth maxillae are smaller than the first and second ones and located in front of the MI. They are developed as multi- or unidentate plates and usually well sclerotized; MV may be absent in some species. Parasitic species have often greatly reduced maxillae; *Biborin* has no maxillae at all. The mandibles are comparatively small, rod- to diamond-shaped, simple plates that are free from one another. Mandibles are absent in one species of *Drilonereis*.

Because of the paucity of external features, the arrangement of the jaw pieces is one of the most important taxonomic characters in this family. For examination, the pharynx should always be dissected from the dorsum. It may often be useful to dissect out the whole pharyngeal bulb and place it on a slide to view the more delicate parts, such as the unpaired carrier or the mandibles. However, the morphological details especially of MI and MII are size-dependent, and juveniles should be assigned to a species with caution (Colbath, 1987).

The peristomium consists of one or two apodous rings, with the anterior one forming the lower lip on the ventral side. All setigers have essentially the same width as the peristomium; the body tapers only within the last few segments. Parapodia are subbiramous, with the notopodium reduced to a bundle of slender notoaciculae and a minute papilla, except for *Oenone* where the notopodium is developed into a foliaceous lobe extending well beyond the neuropodium. The neuropodium has a short presetal and a typically conical, longer postsetal lobe; it is supported by one to several neuroaciculae and bears a fascicle of limbate, geniculate setae and in some genera single large spines, with or without hood, or bidentate hooks. Dorsal and ventral cirri are absent. Most species of *Drilonereis* have minute parapodia, at least in the anterior part of their body. Generally, the parapodia are about as large as the segmental length. Changes in proportion of the parapodia constitute one of the few external characters useful for species discrimination.

The pygidium bears two or four short anal cirri or two swollen pads; the anus is terminal. Colbath (1989) considered the presence and number of anal cirri an important species specific character, although he acknowledged that obtaining whole specimens is fairly difficult.

Taxonomic History

The family Oenonidae was established by Kinberg (1865) and was defined by a jaw apparatus with long, slender maxillary carriers and mandibles that were shorter than the maxillae. The family included four genera, two of which were subsequently synonymized with *Oenone* Kinberg. The oenonids were distinguished from the closely related Laidea by the presence of foliaceous gills. Hartman (1944) noted that Kinberg's family Laidea did not include the genus *Arabella* Grube, 1851, nor did any of Kinberg's other eunicemorph families. She therefore established the Arabellidae, consisting of *Arabella* and the genera assigned by Kinberg to the Laidea. Because of the presence of superficially similar foliaceous notopodial lobes, the genus *Oenone* was added to the family Lysaretidae, also established by Kinberg (1865), but originally consisting only of the genus *Lysarete*. With the addition of *Oenone*, the Lysaretidae became less well-defined than intended by Kinberg, who had positioned the two genera in two different major groups of genera due to the differences in the jaw apparatus. Colbath (1986, 1989) proposed the restriction of the Lysaretidae to their original definition and recognition of the family Oenonidae to include *Oenone* and two other related genera. He based the definition of those two families not only on morphological details of the jaw apparatuses, but also on the coinciding different chemical composition of the jaw pieces. Lysaretids, like lumbrinerids, have jaws mineralized with calcite crystals, whereas the jaws of oenonids, like those of arabellids, consist only of scleroproteins and lack crystals. Orensanz (1990), in his revision of the eunicemorph polychaete families, subsequently transferred *Lysarete* to the Lumbrineridae because of similarities in the structure of the maxillary apparatus. He also merged the Arabellidae with the Oenonidae, the latter being the older name. The families Lysaretidae and Arabellidae are therefore no longer recognized.

The history of the oenonid genera is as confusing as that of the family, probably because oenonids are never found in abundance. Most of the genera originally assigned to the Oenonidae by Kinberg have subsequently been synonymized, others are indeterminable; within the free-living genera originally assigned to the Arabellidae, the weight of diagnostic characters is not equal. Fauchald (1970) suggested to either split *Arabella* into two genera to separate species with a proximally dentate MI (*Notopsilus*) from those with proximally smooth MI (*Arabella*), or to combine *Drilonereis* and *Notocirrus*, which differ only by the dentate vs. falcate MI. The latter may be more practical because some species of *Notocirrus* have MI with falcate distal teeth. This continuous range in shape of the MI was already noted by Crossland (1924) who, for the first time, attempted to include individual variability of taxonomic characters such as setae and jaw pieces into the species descriptions, especially for lumbrinerids (then including *Arabella* and *Drilonereis*). According to Orensanz (1990), there are five parasitic genera (*Biborin* Chamberlin, *Drilognathus* Day, *Haematocleptes* Wiren, *Labrorostratus* Saint-Joseph, and *Oligognathus* Spengel) and six mostly free-living genera if *Notocirrus* and *Drilonereis* are kept separate (*Oenone* Savigny, *Halla* Costa, *Tainokia* Knox and Green, *Arabella* Grube, *Drilonereis* Claparède, and *Notocirrus* Schmarda). One additional parasitic genus, *Pholadiphila*, has since been described by Dean (1992).

Distribution and Biological Notes

Oenonids are widely distributed in all oceans from intertidal to abyssal depths. Free-living forms burrow in sand and mud, and are carnivorous or highly selective deposit feeders (Fauchald and Jumars, 1979). They do not build tubes, but appear to line their burrows with mucus. Parasitic species live in the body cavity of other polychaetes, such as eunicids, onuphids, spionids, cirratulids, and tricho-branchids, the echiuran *Bonellia*, (Pettibone, 1957) and pholadid bivalves (Dean, 1992). Not much is known about the biology of these parasites; apparently not all of them are parasitic for their entire life, but leave their host's body to become sexually mature as free-living forms. How they enter their host is not known; if they live singly in a host, they often reach a considerable size, occupying the entire body cavity of the host organism. Other species are of small size and may occur in great numbers in a host (Pettibone, 1957). Parasites are not included in the key below; Fauchald (1977) should be used to identify these forms to genus, and Pettibone (1957) is the most reliable reference for identification to species, but more taxa have been added since that time (see Emerson, 1974 and Dean, 1992 for more detail). Uebelacker (1978) can be consulted for the parasitic genus *Labrorostratus*.

Key to the Oenonidae

1A. Parapodia with conspicuous, foliaceous notopodia; prostomium with three antennae along posterior margin .... genus *Oenone*[2]

1B. Notopodia absent or reduced to small papilla, sometimes with fascicle of delicate internal aciculae; prostomium without appendages 2

2A. Setae including limbate capillaries and thick acicular spines, at least in middle and posterior parapodia 3

2B. All setae limbate, thick acicular spines absent 8

[2] Genus not represented in this Atlas

3A. First maxillae falcate; small denticles if present restricted to basal part..... genus *Drilonereis* 4

3B. First maxillae dentate along entire cutting edge .... genus *Notocirrus*[2]

4A. Acicular spines present from setiger 1; anterior parapodia minute, with short pre- and postsetal lobes; postsetal lobes gradually turning digitiform in middle setigers, presetal lobes turning digitiform in posterior setigers and becoming subequal to postsetal lobes, parapodia thus distinctly bilabiate in posterior third of body; MI with 1-5 basal teeth, MII with 3-5 teeth, MIII and MIV with 1 tooth and sometimes additional minute dentitions .... *Drilonereis longa*

4B. Acicular spines first present in setiger 10 or later; parapodia not distinctly bilabiate in posterior setigers 5

5A. Postsetal lobes twice as long as parapodial stem after setiger 70, cirriform, pointing dorsad; all setae with narrow, finely serrated wings; MI with 6-7 basal teeth, MII 8+6, MIII 5-7, MIV 1, MV 1; mandibles large, together forming a horseshoe shape .... *Drilonereis spectabilis*

5B. Postsetal lobes papilliform or conical, as long as parapodial stem at most 6

6A. Mandibles present; parapodia smaller in anterior setigers than in posterior, but proportions of parapodial lobes not changing; acicular spines first present in setiger 10 to 13; MI with 3-4 basal teeth (large specimens up to 7), MII 6-9, MIII 1-5, MIV 1-2, MV 1 (occasionally absent); mandibles large .... *Drilonereis falcata*

6B. Mandibles absent 7

7A. Parapodia minute in anterior setigers, with papilliform postsetal lobes in posterior setigers; acicular spines very large, projecting far beyond postsetal lobes; MI with 4-5 basal teeth .... *Drilonereis mexicana*

7B. Parapodia conspicuous throughout, with digitiform postsetal lobes in posterior setigers; acicular spines first present in setiger 25-30, projecting about as far as postsetal lobes; MI basally smooth . ... *Drilonereis nuda*

8A. Postsetal lobes in posterior setigers digitiform, very long and pointing dorsad; upper supra-acicular and subacicular setae smooth, lower supra-acicular setae with serrated wings .... *Arabella semimaculata*

8B. Postsetal lobes prominent, but not digitiform; surficial structures of setae different 9

9A. All setae with serrated wings; MI with unidentate tips on both sides, MIII and MIV with about 4-5 conical teeth, alternating large and small .... *Arabella iricolor*

9B. Some setae with smooth wings; left MI with bidentate tip 10

10A. Subacicular setae smooth in middle and posterior setigers, supraacicular setae serrated; MIII and MIV with about 4-5 conical teeth, alternating large and small .... *Arabella protomutans*

10B. All setae smooth in anterior setigers, serrated in middle and posterior setigers; MIII and MIV with about 10 needlelike equal teeth, giving comblike shape to maxillae .... *Arabella pectinata*

Description of Species

The Oenonidae are a relatively small family with about 80 species belonging to 12 genera. Only three of these genera, *Arabella, Drilonereis,* and *Notocirrus* consist of ten or more species, while most of the parasitic genera are represented by only one species. In the Santa Maria Basin and Santa Barbara Channel, the only oenonids found belong to *Drilonereis*, including one species new to science, but it is likely that at least some of the species of *Arabella* described below occur in this area, especially in shallower depths. The following species are treated:

Arabella (Arabella) iricolor (Montagu, 1804)
Arabella (Arabella) pectinata Fauchald, 1970
Arabella (Arabella) protomutans Orensanz, 1990
Arabella (Arabella) semimaculata (Moore, 1911)
Drilonereis falcata Moore, 1911
Drilonereis longa Webster, 1879
Drilonereis mexicana Fauchald, 1970
Drilonereis nuda Moore, 1909
***Drilonereis spectabilis* Hilbig, new species**

Genus *Arabella* Grube, 1850

Type Species. *Nereis iricolor* Montagu, 1804

Diagnosis. Prostomium spatulate to conical, without antennae, usually with four eyes along posterior margin; no ventral palps. Peristomium with two rings, separate from one another dorsally and ventrally, anterior one forming a simple lower lip. Mandibles simple, large plates; maxillae usually asymmetrical, MI falcate, with or without basal dentition, or dentate along entire cutting edge; MII, MIII, and MIV multidentate, MV usually unidentate. Parapodia subbiramous with papilliform notopodial rudiment; postsetal lobes longer than presetal lobes. Setae all simple, limbate, with smooth or serrated wings; ventralmost seta modified in some species to blunt-tipped spine with terminal winglike hood; thick acicular spines absent.

Remarks. The genus *Arabella* is somewhat ill-defined within the family Oenonidae because characters that are considered diagnostic for other genera, such as the presence or absence of dentitions on the first maxillae, are variable in *Arabella*. Additionally, the presence of modified setae in some species is unique for the genus *Arabella*; all other genera have very uniform setae. It therefore seems useful to keep some of the genera previously synonymized with *Arabella* as subgenera, as has been done by Orensanz (1976, 1990) and Perkins (1979), even though a cladistic analysis of the oenonids may prove these subgenera, and likely the genus *Arabella*, invalid (Fauchald, personal communication). The subgenera are defined as follows: *Arabella (Arabella)* has falcate MI and unmodified setae; *A. (Cenothrix)* has falcate MI and modified setae, and *A. (Notopsilus)* has dentate MI and unmodified setae.

Arabella (Arabella) iricolor (Montagu, 1804)

Figure 12.1

Nereis iricolor Montagu, 1804:82.

Lumbriconereis opalina Verrill and Smith, 1874:26,38, etc., pl. 13, figs. 69-70.

Arabella opalina: Webster, 1879:242; 1884:321; 1886:145.—Verrill, 1881:291, 301, etc., pl. 4, fig. 4.—Webster and Benedict, 1884:721.

Arabella iricolor: McIntosh, 1910:395, pl. 54, fig. 4, pl. 62, figs. 8-8c, pl. 74, figs. 5-5c, pl. 83, figs. 2-2a.—Hartman, 1944:173 (in part); 1968:789.—Pettibone, 1963:269-271, figs. 71a-e.—Fauchald, 1970:125-128, pl. 20, figs. a-d.—Orensanz, 1974:384-386, pl. 1.—Blake, 1975:205, fig. 194.—Uebelacker, 1984:42-5, figs. 42-1, 42-2a-f.

Material Examined. California: Tomales Bay, det. Olga Hartman (2); Dillon Beach, intertidal, coll. K. Woodwick, 19 June, 1962 (4).

Description. Length to 600 mm, width to 5 mm, segments to 500. Body cylindrical, wiry, of equal width except for short prepygidial region. Color in alcohol pale to reddish brown with iridescent cuticle, head usually the least pigmented.

Prostomium bluntly conical, longer than wide when fully extended, with four subequal eyes in straight line along posterior margin, sometimes obscured by peristomium when prostomium retracted (Fig. 12.1A). Proboscis with large, oval to triangular mandibles (Fig. 12.1B) and five pairs of maxillae; all jaw pieces black, very hard, heavily sclerotized. Paired maxillary carriers very long and slender, free from one another; unpaired piece about two-thirds as long, elongate-oval. First and second maxillae asymmetrical; right MI smallest, with 5 basal teeth, left MI with 10 teeth, both sides strongly falcate; MII curved over distal ends of MI; right MII largest, with 10-16 teeth, left MII with 6-9 teeth. MIII through MV symmetrical; MIII and MIV large, rounded, horny plates with very hard cutting edge bearing 4-7 teeth, large and small ones alternating; MV single, long, sharply pointed tooth arising from very small base (Fig. 12.1B). Peristomium with two rings, the anterior one forming lower lip, both equal to following setigers.

Parapodia similar throughout, with short presetal and conical to digitiform postsetal lobes, the latter longest in posterior setigers (Fig. 12.1D, E). Setae all of one type, geniculate, limbate, with finely to coarsely serrated wings (Fig. 12.1F, G); aciculae in fascicles of about 3 per parapodium, dark amber, with long filiform tips breaking through integument.

Pygidium with 2 to 4 short anal cirri.

Remarks. *Arabella iricolor* is one of the most familiar and widely reported species of this genus, but may have been confused with other species such as *A. pectinata* and *A. protomutans* that have an identical habitus, but differ in details of the setal surface structures and dentition of the maxillae (see below). To positively identify *A. iricolor*, at least the setae should be examined on a slide, preferably those from a posterior parapodium. The first and second maxillae are reported to be asymmetrical by most authors, although there appears to be some variability in this character; for example, McIntosh (1910) described the maxillae as being symmetrical.

Type Locality. Devonshire, England.

Habitat. *A. iricolor* burrows deeply into mud, sand and gravel; it is also found under rocks, in oyster and mussel beds, among *Zostera* holdfasts, among bryozoans and other colonial animals.

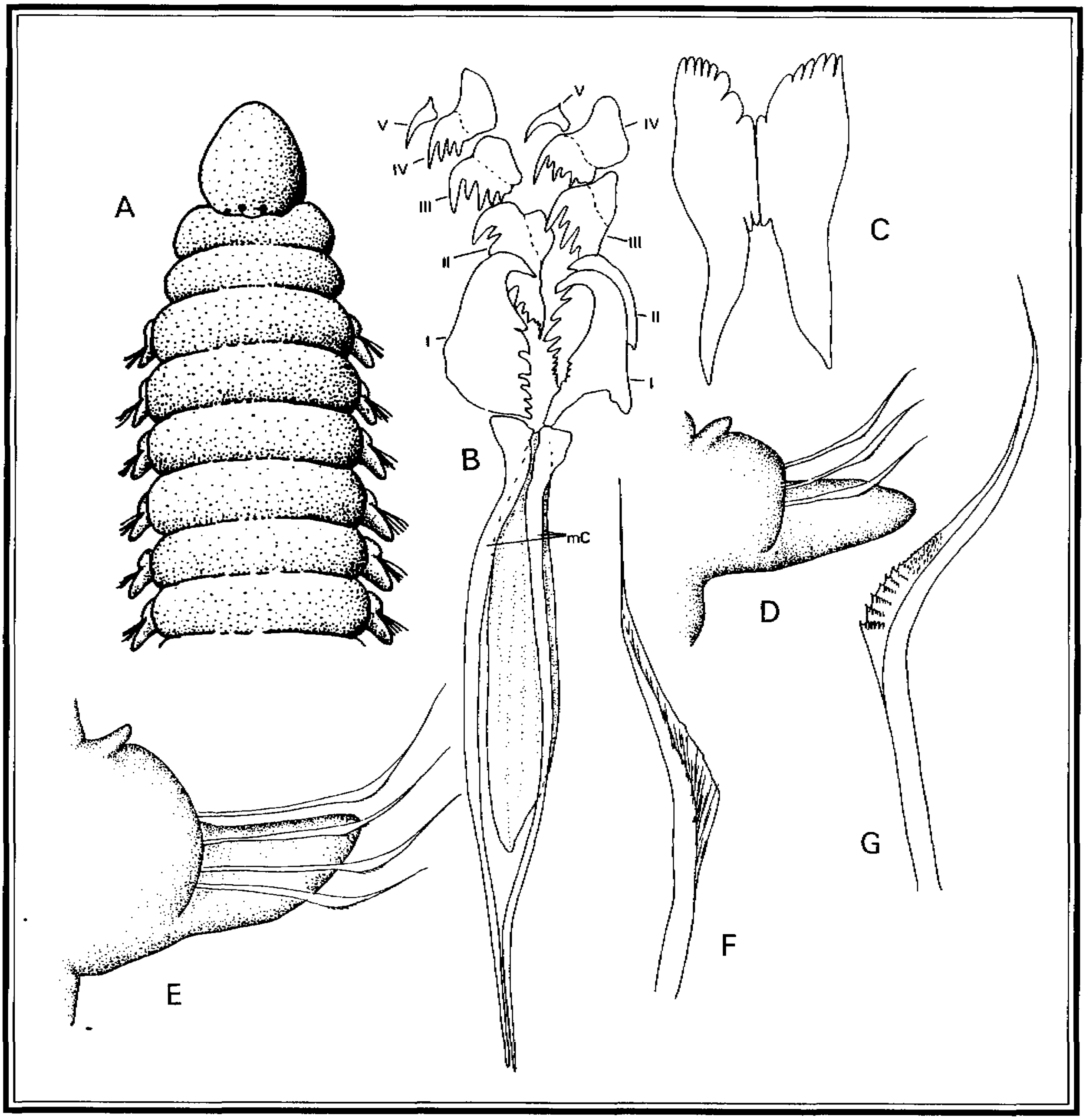

Figure 12.1. *Arabella (A.) iricolor*. A, anterior end, dorsal view (from Blake, 1975); B, maxillae (after Orensanz, 1974); C, mandibles (after Pettibone, 1963); D-E, anterior and posterior parapodium, anterior view (after Fauchald, 1970); F, smooth limbate seta (after Pettibone, 1963); G, serrated limbate seta.

Distribution. Cosmopolitan in temperate and subtropical waters; England, France; Mediterranean Sea; Massachusetts to Florida, Gulf of Mexico, Colombia and Venezuela; Vancouver Island to California, Mexico, Argentina; Japan, China, Persian Gulf, Red Sea, Indian Ocean; Straits of Magellan; West and South Africa; intertidal to 90 m.

Arabella (Arabella) pectinata Fauchald, 1970

Figure 12.2

Arabella pectinata Fauchald, 1970:130-132, pl. 22, figs. a-f.

Material Examined. California: Tomales Bay (1).

Description. Length at least 182 mm, width to 3.5 mm, segments at least 355. Body cylindrical, relatively flexible, increasing in width through pharyngeal region, rest of body of equal width (Fig. 12.2A, B). Color in alcohol copper to purplish brown, highly iridescent.

Prostomium bluntly conical, about as wide as long, less pigmented than rest of body. Peristomium with two equal rings, slightly wider than prostomial base (Fig. 12.2A). Proboscis with mandibles and well-developed maxillae. Mandibles paddle-shaped, fused anteriorly, diverging posteriorly (Fig. 12.2C); maxillae with slender paired carriers, free through most of length, fused anteriorly above insertion of slender unpaired piece. First and second maxillae asymmetrical; both MI of subequal size, falcate, with 7-11 basal teeth, left side with bifid tip; MII curving over distal ends of MI; left MII smallest, with 8-12 teeth, right MII with 14-20 teeth; MIII through MV symmetrical; MIII and MIV large, rounded, horny plates with heavily sclerotized cutting edge bearing 6-11 needlelike teeth, all of equal size, cutting edges looking like combs; MV single long, acutely pointed tooth arising from small base (Fig. 12.2D).

Parapodia similar throughout, with short, rounded presetal lobes and digitiform postsetal lobes about twice as long as presetal ones, thickest in anterior setigers; notopodial rudiments present (Fig. 12.2E, F). Setae of two kinds; anterior parapodia with smooth to very finely serrated, nearly straight limbate setae (Fig. 12.2G), middle and posterior parapodia with very finely serrated setae in uppermost and lowermost position and strongly geniculate, coarsely serrated setae in middle of fascicle (Fig. 12.2H-J).

Remarks. *Arabella pectinata* has most likely been confused with *A. iricolor*, but differs markedly from the latter in the following characters: the setae are all serrated in *A. iricolor*, but smooth at least in uppermost and lowermost position in each fascicle in *A. pectinata*; the third and fourth maxillae have about 5 conical teeth of alternating size in *A. iricolor*, but about 10 needle-like teeth of equal size in *A. pectinata*. The fine structures of the serrated setae that Fauchald (1970) thought to be unique for *A. pectinata* are common to all *Arabella* setae with coarse serrations; the posterior connection of the maxillary carriers were not observed in the examined specimen, but a U-shaped transparent ligament, rather than a rounded plate, was seen that is most likely the same structure. This record is the first one for California.

Type Locality and Type Specimens. Mexico, El Descanso: holotype and 3 paratypes (LACM-AHF).

Distribution. Central California to Mexico (Baja California), intertidal to shallow subtidal depths.

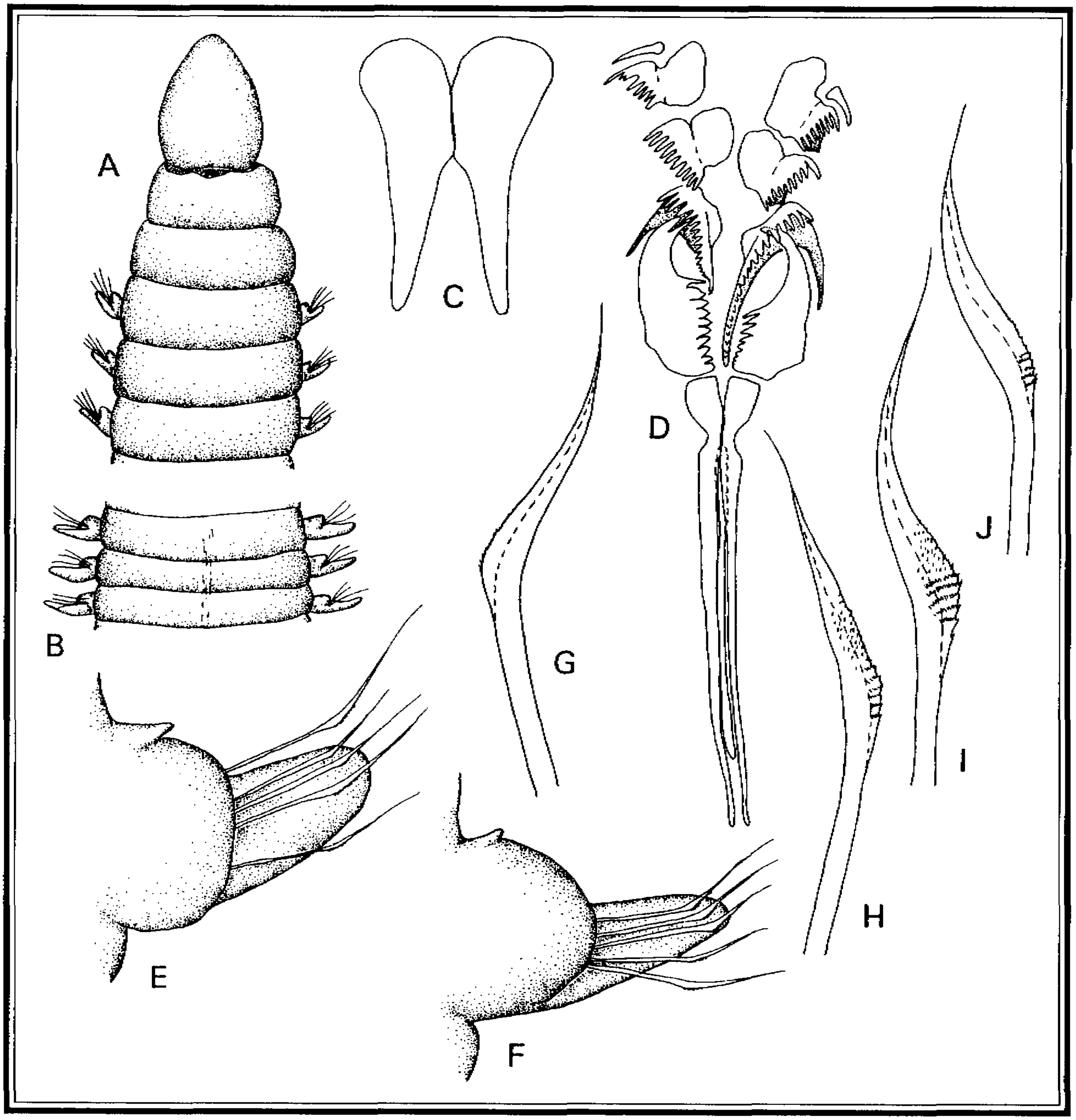

Figure 12.2. *Arabella (Arabella) pectinata*: A, anterior end, dorsal view; B, middle setigers, dorsal view; C, mandibles; D, maxillae; E-F, anterior and posterior parapodium, anterior view; G, finely serrated seta, anterior parapodium; H-J, upper, middle and lower seta from posterior parapodium. (B, E, F after Fauchald, 1970).

Arabella (Arabella) protomutans Orensanz, 1990

Figure 12.3

Arabella protomutans Orensanz, 1990:102-104, pl. 28.
Arabella novecrinita var. *asymmetrica* Crossland, 1924:80-82, figs.103-104 (in part).—Not *Arabella (Cenothrix) asymmetrica* Orensanz, 1974.

Material Examined. California: Tomales Bay, (1), Tomales Point (1); Avila, intertidal, coll. K. Woodwick, 3 March, 1963 (1); Dillon Beach, intertidal, coll. K. Woodwick, 19 June, 1962 (2).

Description. Length to 350 mm, width to 2 mm excluding parapodia, segments to 600. Body cylindrical, wiry, with relatively long segments and small but conspicuous parapodia. Color in alcohol pale to pinkish brown, most segments of Californian specimens with broad band of reddish pigment, head least pigmented.

Prostomium conical, as long as wide, with four eyes in a row along posterior margin (Fig. 12.3A). Proboscis with mandibles and five pairs of maxillae. Mandibles large, paddle-shaped, fused along distal half (Fig. 12.3C). Maxillary carriers with long, slender paired pieces free from one another and ventral unpaired piece of similar shape and almost as long. First and second maxillae asymmetrical; left MI with bifid tip, slightly larger than right MI, both with about 8 basal teeth; left MII much smaller than right MII, with 6-7 unequal teeth; right MII with about 14 unequal teeth. MIII, MIV, and MV symmetrical; MIII and MIV large plates with very hard cutting edges each bearing 4 to 5 unequal teeth, large and small ones alternating; MV single, sharply pointed tooth arising from very small base (Fig. 12.3B).

Parapodia similar throughout, with papilliform notopodial rudiments, low presetal lobes, and conical, elongated postsetal lobes (Fig. 12.3D, E); setae geniculate, with finely to coarsely serrated wings (Fig. 12.3F); subacicular fascicles of posterior parapodia with smooth setae (Fig. 12.3G).

Pygidium with two lateral pads, no anal cirri, anus slitlike.

Remarks. *Arabella protomutans* is closely related and intermediate to both *A. iricolor* and *A. pectinata* (see above), with MI resembling that of *A. pectinata* and the irregular dentition of MIII and MIV being similar to *A. iricolor*. It is most easily recognized by the smooth subacicular setae in posterior parapodia; if only anterior fragments are available, the pharynx should be dissected to examine the first and third maxillae. This record is the first from outside the Magellanic biogeographic province. The Californian specimens are considerably larger than the type material.

Type Locality and Type Specimens. Southwestern Chile, *Eltanin* Sta. 958, 92-101 m: holotype (USNM 98099) and 1 paratype (USNM 98100).

Habitat. This species was found in sandy sediments.

Distribution. Strait of Magellan; central California; intertidal to 118 m.

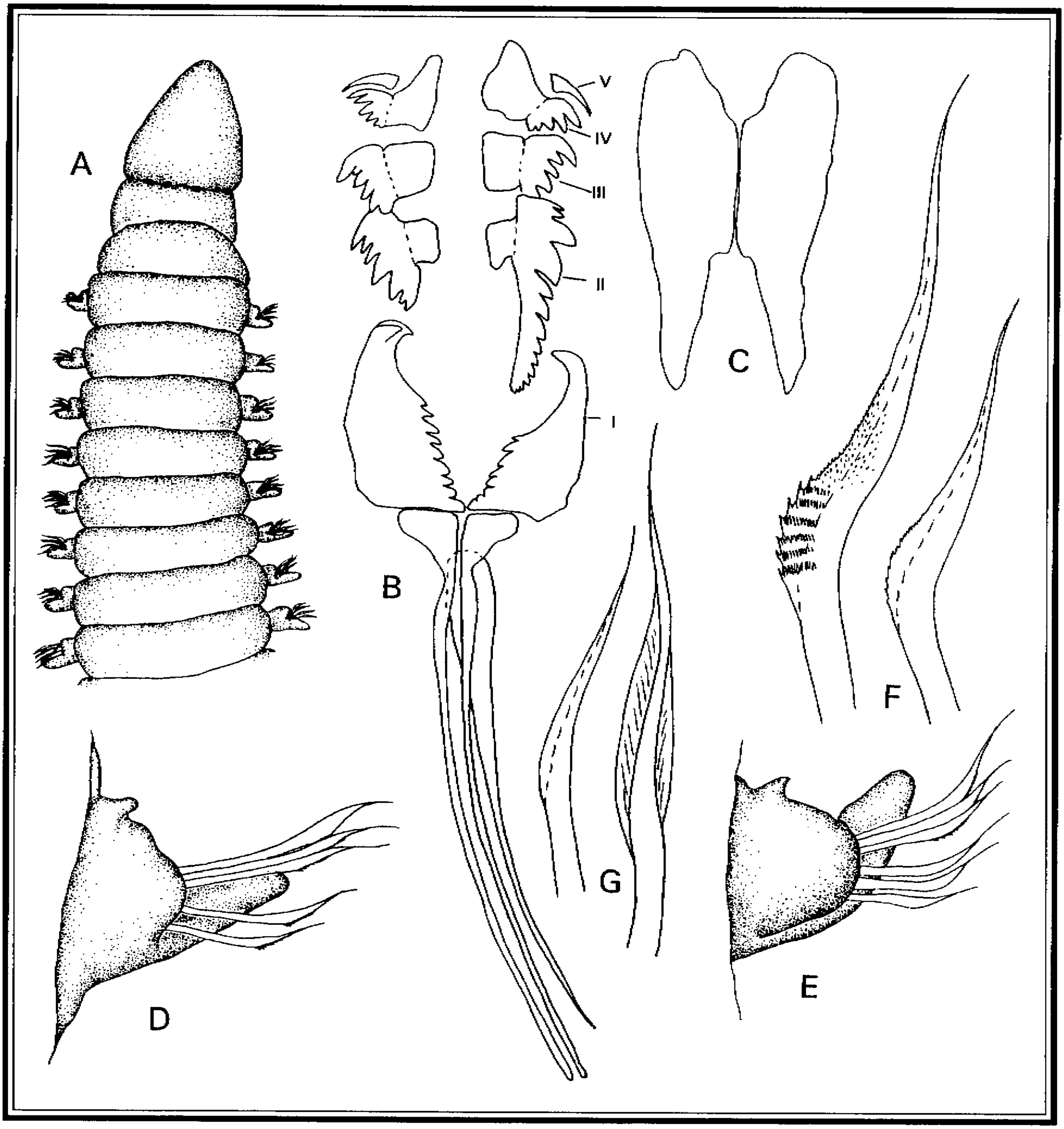

Figure 12.3. *Arabella (A.) protomutans*: A, anterior end, dorsal view; B, maxillae; C, mandibles; D-E, middle and posterior parapodium, anterior view; F, serrated supra-acicular setae, posterior parapodium; G, ventralmost setae, posterior parapodium. (all after Orensanz, 1990 except for left seta in F and right seta in G).

Arabella (Arabella) semimaculata (Moore, 1911)

Figure 12.4

Aracoda semimaculata Moore, 1911:295-297, pl. 20, figs. 143-149.
Arabella semimaculata: Hartman, 1944:173; 1968:793.—Fauchald, 1970:132-133, pl. 20, figs. e-g.—Blake, 1975:205, fig. 197.

Material Examined. California: Dillon Beach, intertidal, coll. K. Woodwick, 19 June, 1962 (1).

Description. Length to 165 mm, width to 2.8 mm, segments to 278. Body slender, cylindrical, appearing widened in middle and posterior setigers because of very prominent parapodia (Fig. 12.4A). Color in alcohol pale greyish, some specimens with three dorsal series of bluish dusky spots and deeply pigmented peristomium.

Prostomium as long as wide or slightly longer, conical, slightly depressed dorsoventrally, with four eyes, may be obscured in very large specimens. Jaw apparatus with large, anteriorly flared mandibles, fused subdistally, divergent proximally and distally. Maxillary carriers with three subequal, long, slender pieces. First and second maxillae asymmetrical; left MI somewhat larger than right one, with 8 to 11 basal teeth, right MI with about 7 to 11 smaller teeth. Left MII much smaller than right one, with 6 to 9 teeth; right MII with about 13 to 17 teeth. MIII, MIV, and MV symmetrical; MIII and MIV rounded plates with cutting edges bearing 4 to 7 unequal teeth; MV with single tooth (Fig. 12.4B, C). Accessory elongate, soft plates present alongside MII.

Parapodia small and inconspicuous anteriorly, with papilliform notopodial rudiments, rounded presetal lobes, and conical postsetal lobes pointing upward and outward (Fig. 12.4D). Parapodia increasing in size after first few setigers; postsetal lobes increasing in length, turning digitiform, pointing dorsad (Fig. 12.4E). Setae few, geniculate, smooth to finely serrated in superior and inferior position of fascicle, distinctly serrated in median position of fascicle (Fig. 12.4 F-H). Notoaciculae delicate, clear, in fascicles of 2 or 3; neuroaciculae stouter, pale, also in fascicles of 2 or 3, with filiform tips breaking through integument.

Pygidium with 2 or 4 very small anal cirri.

Remarks. This species was reported to be the most common of the genus in Mexico by Fauchald (1970).

Type Locality and Type Specimens. California, Monterey Bay, off Santa Cruz Lighthouse: holotype (USNM 16918), 3 paratypes (USNM 17272), 3 paratypes (ANSP 2985).

Habitat. Sand and rocks, mixed sediments.

Distribution. Mexico to central California, intertidal to 80 m.

Genus *Drilonereis* Claparède, 1870

Type Species. *Lumbriconereis filum* Claparède, 1868

Diagnosis. Prostomium spatulate, without eyes or antennae. Peristomium with two rings, separate from one another, the anterior one forming simple lower lip. Setae including limbate capillaries and thick, acicular spines in most setigers; maxillae with falcate, basally smooth or dentate MI.

Remarks. Some species of *Drilonereis* are parasitic; in these forms, jaws, parapodia, and setae may be reduced.

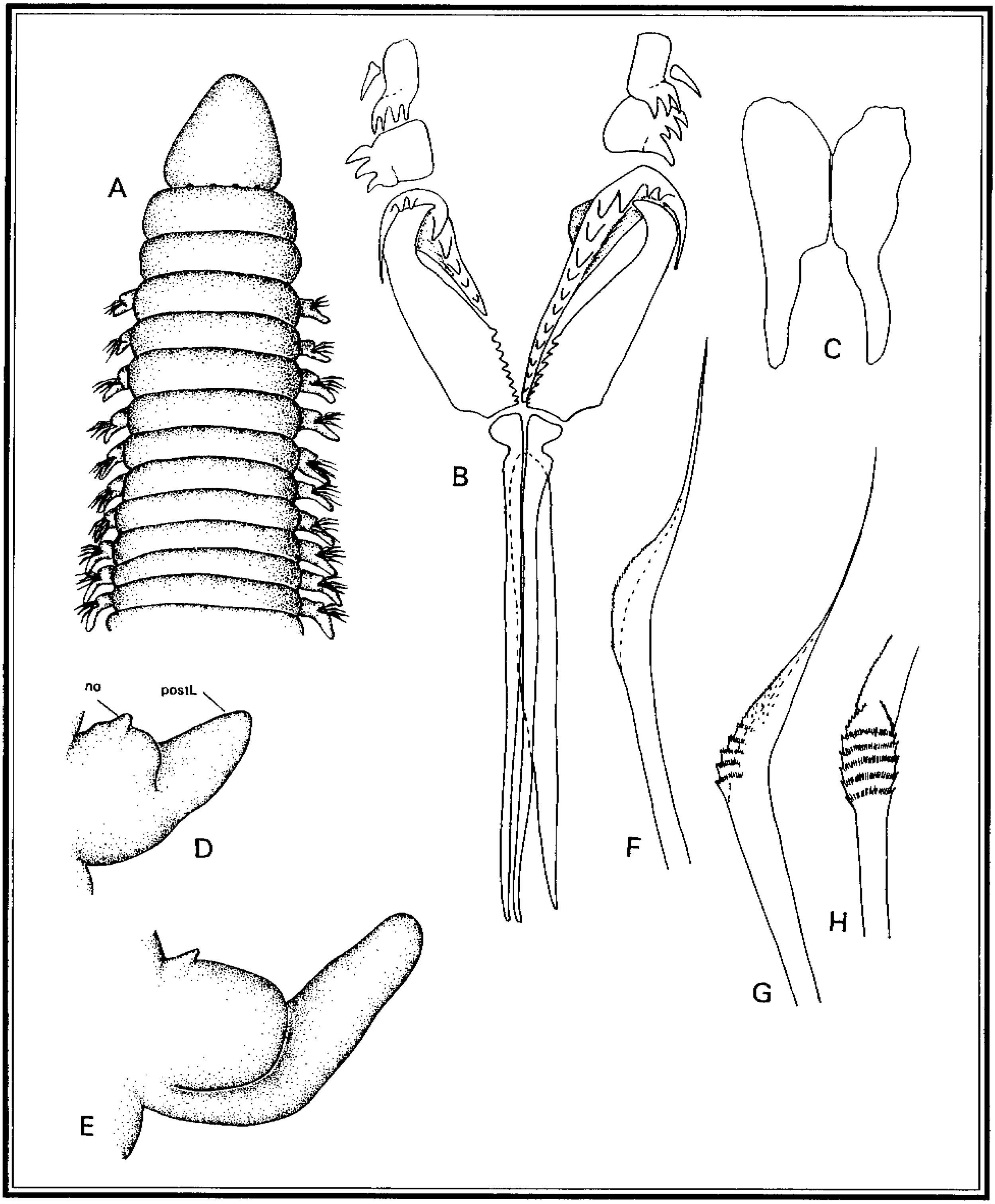

Figure 12.4. *Arabella (A.) semimaculata*: A, anterior end, dorsal view; B, maxillae; C, mandibles (after Moore, 1911); D-E, anterior and posterior parapodium, anterior view (after Fauchald, 1970); F, finely serrated seta; G-H, coarsely serrated seta, lateral and frontal view (detail).

Drilonereis falcata Moore, 1911

Figure 12.5

Drilonereis falcata Moore, 1911: 289-299, pl. 20, figs. 150-154.—Hartman, 1944:179; 1968:797.—Fauchald, 1970:135-136, pl. 21, fig. g.—Orensanz, 1974:397-399, pl. VII.—Lissner *et al.*, 1986:D-12.—Steinhauer and Imamura, 1990:F-1.

Material Examined. California: Santa Maria Basin, off Point Buchon, Sta. 12 (1); off Point San Luis, Sta. 21 (1); off Point Sal, Sta. R-8 (1).

Description. Length at least 120 mm, width to 1.2 mm, segments to 230. Body thin, wiry, cylindrical, with anteriorly small but conspicuous parapodia throughout; anterior segments about twice as long as parapodial width, middle and posterior segments much more crowded, only as long as parapodial width (Fig. 12.5A, B). Color in alcohol light tan to purplish brown.

Prostomium spatulate, about as long as wide, with median dorsal furrow; nuchal organs inconspicuous (Fig. 12.5A, C). Mandibles well sclerotized, roughly triangular, about half as long as MI, fused along short distal area (Fig. 12.5D); maxillae with long, slender carriers and lanceolate unpaired ventral piece; MI large, strongly falcate, with 3 or 4 large basal teeth; MII with 6 to 9 teeth, subdistal one smallest; MIII with 3 teeth, 1 large and 2 small; MIV and MV each with one pointed tooth, MIV occasionally with additional serrations along cutting edge; MV may be absent (Fig. 12.5 E). Peristomium consisting of two rings, each as long as following setigers and sligthly wider than prostomial base. All setigers uniform except for gradually decreasing length within anterior part of body; parapodia with minute notopodial papilla supported by bundle of slender notoaciculae, neuropodia with short presetal and longer, conical postsetal lobes throughout; length of parapodial stems doubling or tripling between anteriormost and posterior setigers, proportions of pre- and postsetal lobes practically unchanged (Fig. 12.5F). Limbate setae with narrow wings, covered with minute surficial spines, finely serrated in side view (Fig. 12.5 G, H). Single thick, acicular spines present from about setiger 10, protruding furthest in posterior setigers, almost reaching length of postsetal lobes (Fig. 12.5 I).

Pygidium with 4 anal cirri.

Remarks. The unchanging proportions of the parapodial lobes along the body and the basal teeth on MI are diagnostic for this species.

Type Locality and Type Specimens. California: Monterey Bay, off Point Piños lighthouse: holotype (USNM 17283), 1 paratype (USNM 17282), 2 paratypes (ANSP 2984).

Habitat. *Drilonereis falcata* is free-living and occurs in mud, sand, and gravel and in mixed sediments.

Distribution. Central California to Argentina; South Africa; intertidal to 350 m, possibly cosmopolitan.

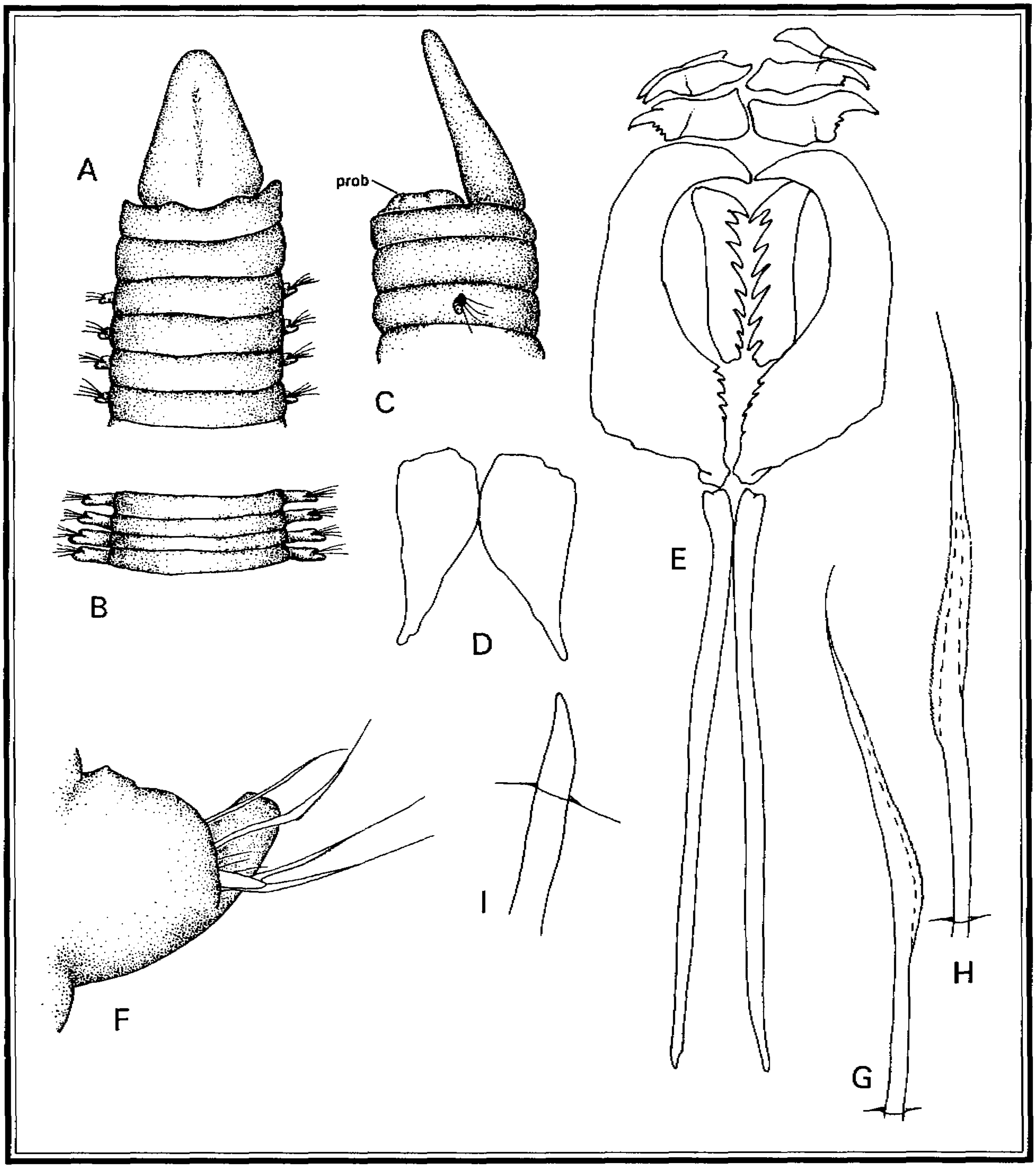

Figure 12.5. *Drilonereis falcata*: A, anterior end, dorsal view; B, middle setigers, dorsal view; C, anterior end, lateral view; D, mandibles; E, maxillae; F, middle parapodium, anterior view; G-H, seta in lateral and frontal view; I, spine. (D-F after Orensanz, 1974).

Drilonereis longa Webster, 1879

Figure 12.6

Drilonereis longa Webster, 1879:240-241, pl. 7, figs. 84-88.—Pettibone, 1963:272-273, fig. 72.—Hartman, 1968:801.—Uebelacker, 1984:42-12 - 42-15, figs. 42-9, 10a-d.
Drilonereis nr. *longa*: Lissner *et al.*, 1986:D-12.—Steinhauer & Imamura, 1990:F-1.
Drilonereis sp. B Lissner *et al.*, 1986:D-12.

Material Examined. California: Santa Maria Basin, off Purisima Point, Sta. R-5 (1); Western Santa Barbara Channel, Sta. 79 (2).

Description. Length to 710 mm, width to 1.5 mm, segments several hundreds. Body very thin, flexible, cylindrical, with tiny parapodia in anterior setigers (Fig. 12.6A). Color pale, iridescent, maxillae jet black and usually visible through body wall.

Prostomium spatulate, somewhat longer than wide, with median furrow dorsally. Pharynx armed with mandibles and 4 pairs of maxillae. Mandibles small, triangular, free from one another, anterior to maxillae; maxillae with long carriers, at least twice as long as MI, and oval, elongate unpaired piece about as long as MI. First maxillae strongly falcate, heavily sclerotized, with 2 to 3 large basal teeth; MII about half as long, with 3 or 4 teeth; MIII and MIV each with 1 very sharply pointed tooth, MIII occasionally with few additional minute denticles; MV absent (Fig. 12.6B).

Setigers shortest in anterior part of body, equal to peristomial rings, bearing inconspicuous parapodia with few limbate capillaries and single acicular spine (Fig. 12.6C); middle and posterior setigers becoming longer than wide, parapodia gradually increasing in length; postsetal lobes turning from short papilla into conical lobes after setiger 30 to 40; presetal lobes gradually becoming conical after about 50 more setigers (Fig. 12.6D); in posterior region, both lobes conspicuous and divergent. Setae including limbate capillaries with very narrow, smooth wings anteriorly and somewhat wider, smooth to very finely serrated wings in middle and posterior parapodia (Fig. 12.6E); and single, thick acicular spines about as thick as postsetal lobes and longer than the latter in middle setigers, about half as wide in posterior setigers and about as long as postsetal lobes.

Pygidium with 4 short anal cirri.

Remarks. Most of the specimens from the Santa Maria Basin and Santa Barbara Channel were originally identified as *D.* nr. *longa*, but no differences could be found between those specimens and any of the available descriptions, and they are here considered as *D. longa*. One specimen, identified as *Drilonereis* sp. B, had been dissected for examination of the jaws. Mandibles are absent, but all other characters match the description of *D. longa* so closely that it was concluded by the author that the small mandibles may have been overlooked during the dissection of the pharyngeal bulb. It is also possible that *Drilonereis* sheds its jaws in the same manner as is known for lumbrinerids (Colbath, 1987) with the mandibles not yet regenerated in the present specimen. Establishment of a new species seems unjustified; the specimen was therefore assigned to *D. longa*.

Type Locality. Virginia.

Habitat. The species appears to be most common in silt and clay, but has been reported from sand, fine gravel, and shell rubble as well. The specimens from the Santa Barbara Channel were found in sediments with more than 70% sand.

Distribution. Massachusetts to Georgia; Gulf of Mexico, West Indies; Washington to southern California, intertidal to 2450 m.

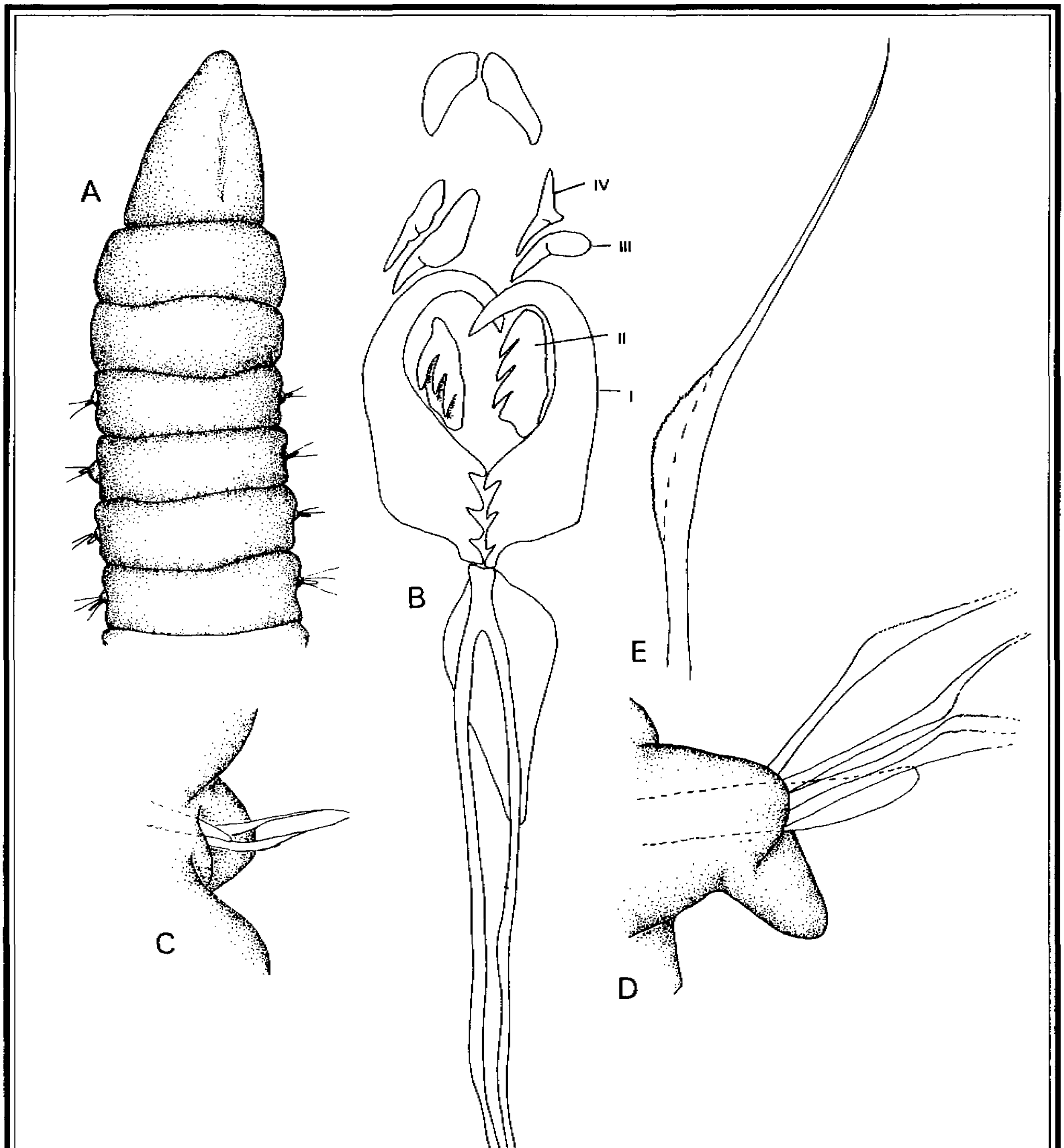

Figure 12.6. *Drilonereis longa*: A, anterior end, dorsal view; B, maxillae and mandibles; C-D, anterior and posterior parapodium, anterior view; E, limbate seta. (A-D after Uebelacker, 1984; E after Pettibone, 1963).

Drilonereis mexicana Fauchald, 1970

Figure 12.7

Drilonereis mexicana Fauchald, 1970:138-140, pl. 23, figs.a-c.

Description. Length to 240 mm, width to 1.5 mm including setae, segments to 800. Color evenly reddish brown.

Prostomium short, conical, as long as both peristomial rings together. Jaw apparatus consisting of 4 pairs of maxillae; mandibles absent. Paired maxillary carriers very long and slender, almost three times as long as first maxillae, fused anteriorly; unpaired carrier roughly rectangular, about as long as first maxillae. MI falcate, with 4 or 5 basal teeth; MII with 4 teeth, MIII with 2 teeth, and MIV with 1 pointed tooth (Fig. 12.7B).

Anterior setigers about two to three times as wide as long, gradually lengthening, twice as long as wide in far posterior setigers. Parapodia minute and inconspicuous in anterior setigers, slightly increasing after about 30 setigers, with short, papilliform postsetal lobes throughout (Fig. 12.7A). Setae geniculate, finely serrated, with moderately wide wings and long, slender tips (Fig. 12.7C). Acicular spines very large, projecting much further than postsetal lobes. Aciculae with long filamentous tips.

Remarks. Although no specimens of *D. mexicana* were reported during the Phase I and Phase II programs, this species may co-occur with *D. nuda* and may have been misidentified as the latter because of the easily observed absence of mandibles shared by both species. Hartman (1944) described a mixture of these two species as *D. nuda*, and she used the same erroneous species concept in the Atlas (1968). The differences in the proportions of the parapodia—minute anteriorly and increasing toward the middle of the body, postsetal lobes papilliform for *D. mexicana*, of almost equal size throughout and with digitiform postsetal lobes for *D. nuda*—and the presence or absence of serrations on the setae may be sufficient characters to discriminate between those two species without having to dissect the maxillae.

Type Locality and Type Specimens. Mexico, San Cristobal Bay (LACM-AHF).

Habitat. *D. mexicana* was found in medium to coarse sand, mixed with mud or shells.

Distribution. Southern California to Baja California, 30 - 130 m.

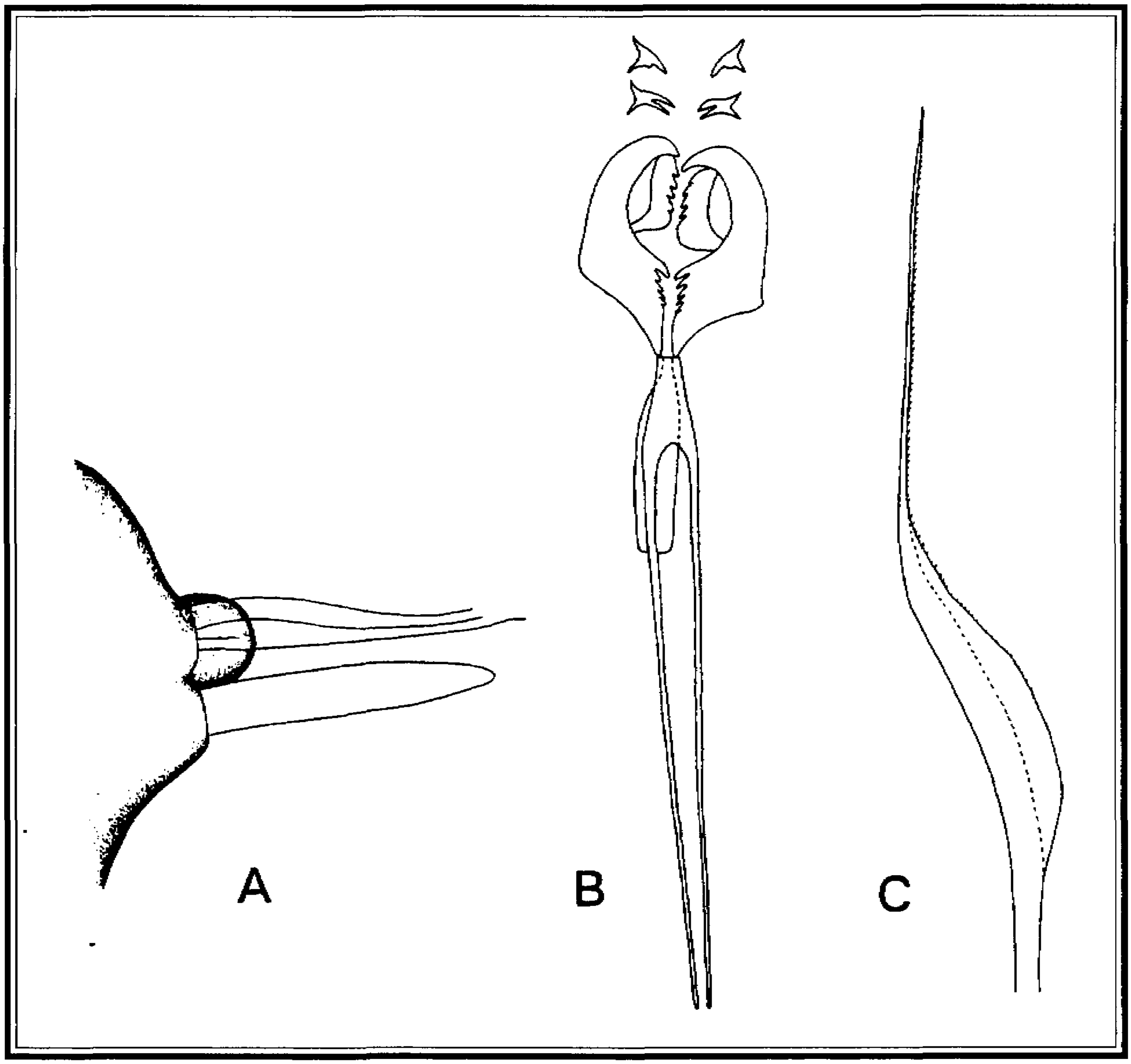

Figure 12.7. *Drilonereis mexicana*: A, parapodium, anterior view; B, maxillae; C, seta (all from Fauchald, 1970).

Drilonereis nuda Moore, 1909

Figure 12.8

Drilonereis nuda Moore, 1909:254-256, pl. 8, figs. 21-23.—Hartman, 1944:178-179, pl. 13, figs. 297-302 (in part); 1968:803 (in part).—Fauchald, 1970:140-141, pl. 22, fig. g.—Lissner *et al.*, 1986:D-12.

Material Examined. California: Santa Maria Basin, off Point Estero, Sta. 6 (rock) (1).

Description. Length to 630 mm, width to 1.3 mm, segments to 935. Body long, cylindrical, of nearly uniform diameter, with conspicuous parapodia throughout. Color in alcohol brown to light golden, with dark spots at parapodial bases, sometimes with 2 dark rings across each setiger, with iridescent cuticle.

Prostomium about as long as wide, spatulate, rounded anteriorly, with median dorsal furrow. Nuchal organs not discernible; examined specimen with 4 pigment spots on brain, possibly subdermal eyes (Fig. 12.8A). Peristomium with 2 rings, the anterior one indistinctly separated from prostomium, about as wide as prostomial base and of equal length to second ring and subsequent setigers. Pharynx armed with 4 to 5 pairs of maxillae, mandibles absent. Maxillae with slender carriers, about twice as long as MI, anteriorly fused over short distance; ventral unpaired piece short, oval. MI strongly falcate, very hard, basally smooth; MII more delicate, but cutting edge with 5 to 7 massive teeth. MIII and MIV each with 1 sharply pointed tooth, MIII sometimes with additional tooth or boss at base of main tooth. MV usually absent, when present much smaller than MIII and MIV, with 2 minute teeth (Fig. 12.8B).

Parapodia conspicuous and of equal shape throughout length of body, smallest in few anterior setigers; presetal lobes truncate, postsetal lobes conical, pointing dorsad; notopodial papilla minute (Fig. 12.8C). Setae narrowly limbate with smooth wings, strongly geniculate in anterior and middle setigers, more straight and slender in far posterior setigers. Acicular spine first present around setiger 25 to 30, golden, projecting about as far as postsetal lobes, usually single, sometimes two per parapodium (Fig. 12.8D-F). Neuroaciculae fine, with very long filiform tips breaking through integument.

Pygidium without anal cirri, with 2 padlike lobes surrounding slitlike anus.

Remarks. The species is defined here as originally described by Moore (1909), with basally smooth first maxillae; Fauchald's (1970) notion that Hartman (1944) included two species in her definition, one with smooth MI and the other with dentate MI, is accepted. The latter was referred to *Drilonereis mexicana* by Fauchald (1970). The two species may co-occur, but can be distinguished from one another without dissection of the jaws by the following differences: the setae are smooth in *D. nuda*, but finely serrated in *D. mexicana*; and the acicular spines project about as far as the postsetal lobes in *D. nuda*, but far beyond in *D. mexicana*.

Type Locality and Type Specimens. California, Monterey Bay: holotype (CASIZ 56, ANSP slide 2.24), 2 paratypes (CASIZ 77), 2 paratypes (ANSP 2578).

Habitat. *Drilonereis nuda* typically occurs on rocky bottom; the type locality was a large tide pool.

Distribution. Central California to Mexico (Baja California), intertidal to about 100 m.

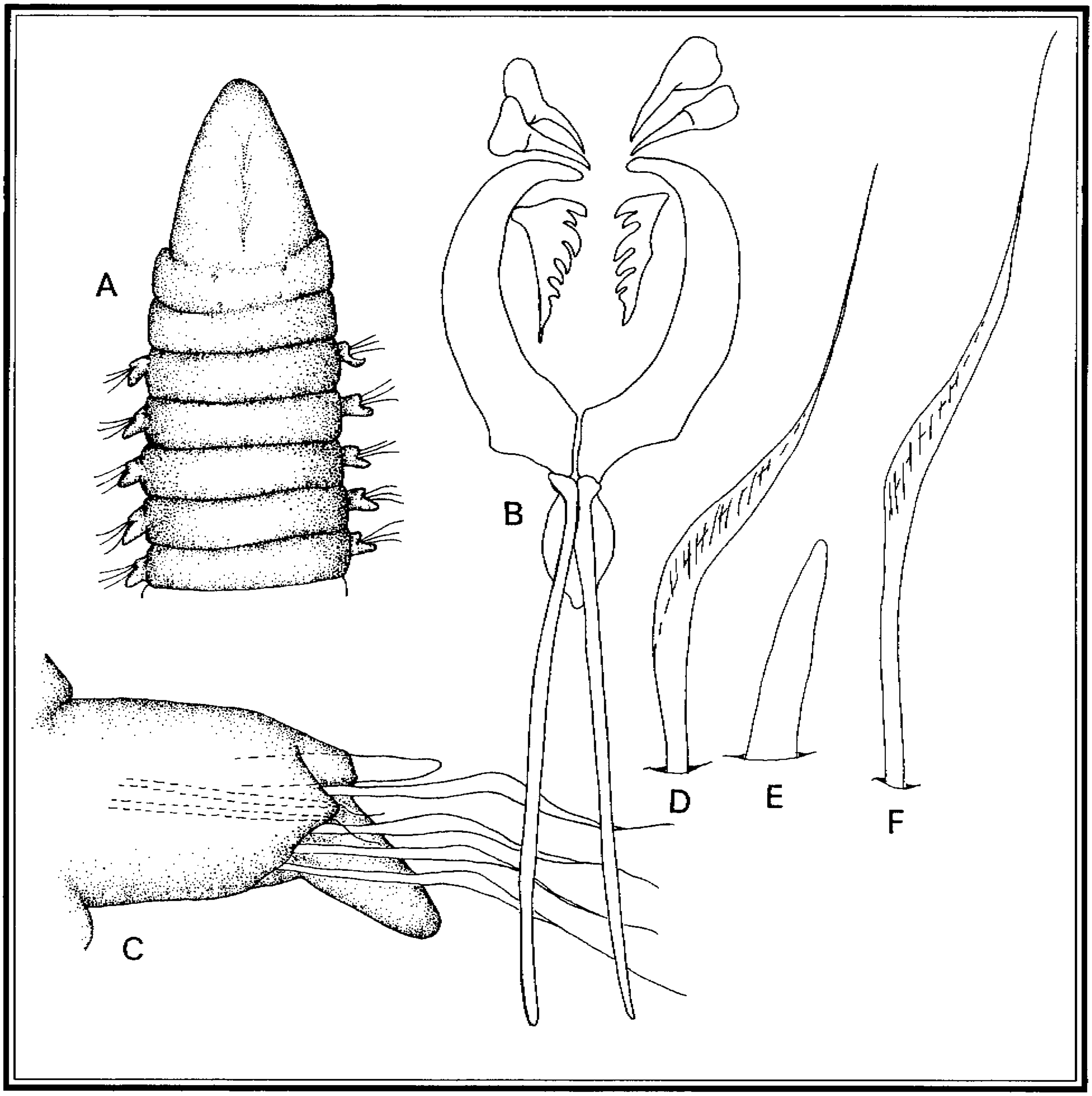

Figure 12.8. *Drilonereis nuda*: A, anterior end, dorsal view; B, maxillae; C, posterior parapodium, anterior view; D, supraacicular seta; E, spine; F, subacicular seta.

Drilonereis spectabilis Hilbig, new species

Figure 12.9

Drilonereis sp. A Lissner *et al.*, 1986:D-12.

Material Examined. California: Santa Barbara Channel, off Point Conception, Sta. 74, 34°26.84'N, 120°38.61'W, 201 m: holotype (USNM 170424).

Description. Length of anterior fragment 100 mm, width 5 mm excluding parapodia; length of posterior fragment 40 mm, width 3 mm. Body very robust, large for the genus, tapering slightly toward prostomium and more distinctly toward pygidium, almost cylindrical, with several hundreds of setigers. Anterior segments crowded, 8-10 times as wide as long, only as long as parapodial bases; posterior segments only 3-4 times as wide as long, longer than parapodial bases (Fig. 12.9A, B). Color in alcohol uniformly tan.

Prostomium spatulate, as long as wide, distinctly narrower than peristomium. Pharynx with well-developed maxillary plates and relatively large, rodlike, slightly curved mandibles resembling a black horseshoe (Fig. 12.9C). Both mandibles and maxillary carriers broken during previous dissection performed from the ventral side, details not readily observed. Maxillary carriers with slender paired pieces, about twice as long as MI, and slender, conical unpaired piece about as long as MI. MI very strongly falcate, with 4 large and about 2-3 small basal teeth; MII sligthly asymmetrical, left one with 8 large and 3 small basal teeth, right one with 6 large and about 3 small teeth; MIII with main fang and group of 4 small teeth; MIV and MV with single tooth, the latter with very small base (Fig. 12.9D). Peristomium with 2 rings resembling subsequent setigers.

Parapodia small in first few setigers, rapidly increasing in size after 10 to 15 setigers; presetal lobes in anteriormost parapodia obliquely truncate, in middle and posterior parapodia developed into short conical lobes; postsetal lobes conical, very conspicuous throughout, about as long as parapodial stem to about setiger 70; after setiger 70, postsetal lobes turning digitiform to almost foliaceous, at least twice as long as parapodial stem, inserting ventrally and pointing dorsad (Fig. 12.9E). Limbate setae weakly geniculate, with finely serrated wings; acicular spines present on all setigers, longest in posterior fragment; all setae amber colored (Fig. 12.9F-H). Notoaciculae delicate, clear, in fascicles of about 3; neuroaciculae amber, about half as thick as acicular spines, in fascicles of about 5 (Fig. 12.9E).

Remarks. The presence of long, digitiform to foliaceous postsetal lobes is unique in the genus, so that the establishment of a new species based on only a single incomplete specimen is justifiable. The habitus of *D. spectabilis* is similar to *Arabella (A.) semimaculata.*

Etymology. The species name was chosen to indicate the very unusual outer appearance of this species.

Habitat. The type specimen was found in silt mixed with sand (27%) and clay (16%).

Distribution. Known only from type locality, central California, 220 m.

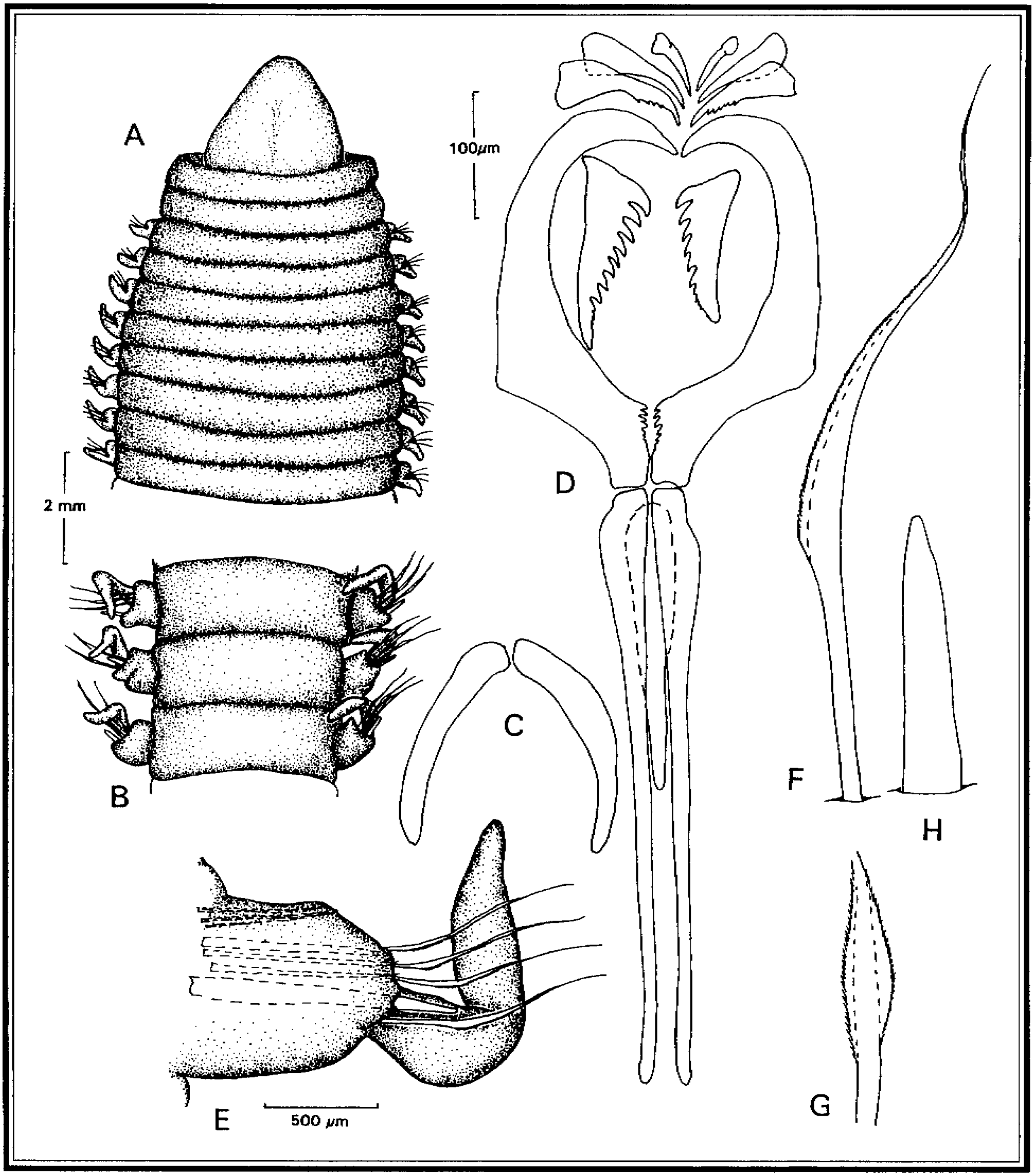

Figure 12.9. ***Drilonereis spectabilis* Hilbig, new species**: A, anterior end, dorsal view; B, posterior segments, dorsal view; C, mandibles; D, maxillae; E, posterior parapodium, anterior view; F-G, seta, lateral and frontal view; H, spine. (all from holotype).

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13. Family Dorvilleidae Chamberlin, 1919

by

Brigitte Hilbig[1]

Introduction

The dorvilleids are mostly small, only a few millimeters in length, and most species have been discovered and described only in the last 30 years when samples were more routinely sieved through fine mesh screens. Some species of *Ophryotrocha* have been investigated extensively because of their role as pollution indicators, and quantitative sampling of the deep-sea floor has resulted in a wealth of new genera and species of unexpected morphological diversity. Among the Eunicida, the dorvilleids are considered phylogenetically the oldest group because they are the only extant family with a ctenognath jaw apparatus, i.e. the maxillae consist of several rows of small denticles rather than 4 to 6 pairs of larger pieces. They also differ from all other Eunicida in having an even number of prostomial appendages.

Morphology

The prostomium may be pear-shaped, conical, or rounded, with or without one or two pairs of eyes, a pair of antennae, and a pair of palps. The antennae may be simple, papilliform to digitiform, or they may be biarticulate or moniliform; the palps are simple or biarticulate. The presence or absence, relative lengths, and shapes of the prostomial appendages are of great taxonomic importance. Usually the prostomium bears one or two ciliary bands and sometimes an apical ciliary tuft. The pharynx is eversible and forms a muscular proboscis armed with numerous maxillary plates and a pair of mandibles. The jaws differ a great deal in composition among the dorvilleids and are therefore the most important taxonomic character. The maxillae may be present in two, four, or up to 14 rows, consisting of several plates that may be heavily sclerotized and bear large fangs and smaller teeth along the cutting edges, or be more delicate, soft, and bear fine serrations along the cutting edge. Maxillary carriers, located dorsal to the denticle rows, are present in *Dorvillea*, *Meiodorvillea*, and *Protodorvillea* (Fig. 13.2A, C). Posterior denticles may be fused to form basal plates (Fig. 13.2A); in *Ophryotrocha*, *Exallopus*, and *Parophryotrocha*, the posterior maxillae may be icetong-shaped and much larger than the anterior free denticles (Fig. 13.2B). The maxillae are reduced in a number of interstitial forms such *Coralliotrocha*, *Microdorvillea*, *Eliberidens*, and *Pseudophryotrocha* (Fig. 13.2D), and generally in deep-sea species. The genus *Pettiboneia* is characterized by the presence of numerous very thin denticles covered with surficial spines that give the anterior end of the pharynx a rasp-like surface. The mandibles are either triangular with several coarse teeth along the cutting edge (*Dorvillea* and related genera, Fig. 13.2F), elongate bifid with finely serrated cutting edges (*Ophryotrocha*, Fig. 13.2G; also *Anchidorvillea*, Fig. 13.2H), or L-shaped with variable shapes and degrees of dentition (Fig. 13.2I).

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[1] ENSR Consulting and Engineering, 89 Water Street, Woods Hole, Massachusetts 02543

The peristomium consists of two achaetous rings, not true segments, that are usually encircled by a ciliary band. The setigerous segments are usually ciliated as well, either bearing segmental bands or ciliary tufts at the parapodial bases. Parapodia are uniramous or subbiramous, with the notopodia consisting of the base of the dorsal cirri and a fine acicula extending into the dorsal cirrus (Fig. 13.1L). *Pettiboneia* possesses subbiramous parapodia on a species-specific number of anterior parapodia. The neuropodium may bear a conical, retractable ventral lobe in addition to the acicular lobe (Fig. 13.3C). Dorsal and ventral cirri are generally simple and often very small, and one or both may be absent in small forms. Branchiae are present in a few species of *Ophryotrocha*, *Pettiboneia*, and *Diapharosoma* as simple digitiform or cushion-like structures on the dorsal or ventral side of the parapodium. Notopodia often contain large vessel loops and thus are functional gills.

All setae are neuropodial; they are generally simple above the neuroacicula and compound below, with the exception of *Parophryotrocha* that has simple setae only and *Ikosipodus* that has compound setae only. Supraacicular setae include smooth or serrated capillaries and spines and, in some genera, furcate and geniculate setae (Fig. 13.1A-D). Subacicular setae are homogomph or heterogomph, smooth or serrated, and the blades may be falcigerous or spinigerous (Fig. 13.1E-G). Sometimes the inferiormost seta in a fascicle is a simple capillary or cultriform seta (Fig. 13.1K). In the genus *Exallopus*, all or some setae in anterior setigers may be greatly modified into recurved hooks (Fig. 13.1H-J).

The pygidium bears a central or slightly dorsal anus and often one or two pairs of anal cirri that may be simple or articulated; sometimes a conical dorsal stylus is also present.

Taxonomic History

Due to the small size of the dorvilleids, the history of their classification is relatively short, and its beginning is marked by confusions and errors. In 1865, Kinberg established the Staurocephalidea, and a number of genera had been established during the first half of the 19th century for *Dorvillea*-like forms, most of which are now synonymized. *Staurocephalus*, erected by Grube in 1855, was found to be preoccupied by Verrill (1900), and he proposed *Stauronereis* (and the family name Stauronereidae) as a replacement. However, since he also changed the type species from *S. rubrovittatus* to *S. rudolphi* (which had actually been described as *Nereis rudolphi* by delle Chiaje in 1828), he violated an ICZN rule, and the genus *Stauronereis* became invalid. McIntosh (1910) moved *S. rubrovittatus* to *Dorvillea*, a genus established by Parfitt in 1866 with the type-species *Dorvillea lobata*, which McIntosh synonymized with *Stauronereis rubrovittatus*. *Dorvillea* and *Ophryotrocha* Claparède and Mecznikov, 1869, were the only valid genera used for the dorvilleids for nearly 100 years, with the former containing a mixture of many different forms.

Pettibone's (1961) revision of the family was the beginning of a substantial change in dorvilleid systematics, even though two of her four genera have since become invalid. In her generic definitions, she relied on setal types and the presence of notopodia, and she removed forms with furcate setae, but without notopodia from *Dorvillea* and placed them in a new genus *Protodorvillea*. In the 1970's, the importance of structural details of the jaw apparatus was recognized, mainly by two authors. Orensanz (1973) described a new genus with a very unique maxillary structure fully described by Blake (1979), *Pettiboneia*. Jumars (1974) was the first to describe deep-sea dorvilleids, a group that since has proven to include a host of genera and many unusual species. Two of his new genera, *Meiodorvillea* and *Exallopus*, are still valid, and *Schistomeringos* now exists as a subgenus of *Dorvillea*. Hartmann-Schröder (1971) established the genus *Parophryotrocha* based on the absence of compound setae. At the same time, Åkesson had worked extensively with shallow-water species of *Ophryotrocha*, and he found many new species that were quite uniform morphologically, but differed in their reproductive behavior and the number of chromosomes (Åkesson, 1967, 1973a-b, 1975a, 1976).

During the following decade, important contributions were made by Wolf (1986a-b) and Westheide and his coauthors (Westheide, 1982; Westheide and Riser, 1983; Westheide and von Nordheim, 1986; von Nordheim, 1987). Wolf divided the *Dorvillea*-like forms into *Ougia* and *Parougia*, based on the anatomy of the maxillae, and described some very unusual genera from the Gulf of Mexico, including *Westheideia, Eliberidens,* and *Diapharosoma*. Westheide and his colleagues discovered a number of minute interstitial dorvilleids, including *Petrocha, Arenotrocha, Pusillotrocha,* and *Apodotrocha*. In 1990 and 1991, the description of deep-sea dorvilleids initiated by Jumars was continued by Hilbig and coauthors (Hilbig and Ruff, 1990; Hilbig, 1991; Hilbig and Blake, 1991), including the description of two new genera, *Anchidorvillea* and *Pseudophryotrocha*.

The publication of Orensanz' (1990) revision of the eunicemorph polychaetes, including fossil species, proposed further change in the systematics of the dorvilleids. He thought the split within the family into *Ophryotrocha*-like and *Dorvillea*-like species to be significant enough to divide the family. The two main types of ctenognath maxillae—many free denticles in several rows in the *Drovillea* group and large, fused proximal pieces and free distal denticles in the *Ophryotrocha* group—have been separate from each other since the Jurassic. Orensanz therefore proposed to join *Ophryotrocha* and related genera, including his new genera *Palpiphitime*, *Pinniphitime*, and *Mammiphitime*, together with the dinophilids, with the Iphitimidae. This proposition is rejected here, mainly because of findings in Hilbig and Blake (1991) of which Orensanz was not aware while preparing his revision. In particular, the genus *Anchidorvillea* would fall between the two families, because it is linked to *Dorvillea*-like forms by its long antennae and palps, but to the *Ophryotrocha*-like genera by the uniramous parapodia and the arrangement of its maxillae that is reminiscent of P-type forceps and a (reduced) number of free denticles. Furthermore, Orensanz (1990) overstated Westheide's (1982) position on the relationship between dinophilids and dorvilleids. Although Westheide's and Westheide and Riser's (1983) cladograms suggest that the dinophilid genera should be moved to the dorvilleids, these authors never actually merged these two families; in fact, in Westheide and Riser (1983), they specifically state the possibility of different evolutionary pathways leading to neotenic species like the dinophilids. It may be difficult to resolve this issue because neotenic interstitial forms have so few characters that could be used to identify them as sister groups to any morphologically complex taxa.

Distribution and Biological Notes

Dorvilleids are mostly shallow-water forms, although a great number of deep-sea species have been found during the last 20 years. Many species are opportunists and flourish in organically enriched environments, such as sewer and pulp mill outfalls and, in the deep sea, locations of temporal enrichment such as whale carcasses (Hilbig, personal observations). These opportunistic species are likely to be exposed to pollutants, and Åkesson (1975b) developed a bioassay method using *Ophryotrocha labronica* as test organism.

The heavily sclerotized, elaborate maxillae of many forms belonging or related to *Dorvillea* suggests that they are predatory, and the fact that they are usually captured with empty guts supports that assumption. However, occasionally specimens are seen with sediment-filled intestines, and *Ophryotrocha* can be cultured and raised both with plant matter such as algae or spinach and with small prey such as crustacean larvae (Åkesson, 1975a). The rasp-like surface of most denticles of *Pettiboneia* may be used to graze, much as gastropods use the radula.

One of the most interesting features in dorvilleid biology, and probably one of the reasons for their success, is the plasticity of their reproductive behavior. It has been extensively investigated in the genus *Ophryotrocha*. Åkesson (1975, 1976) described a number of species that were morphologically similar, but differed in their reproductive cycles; he also divided the genus into several species groups characterized by their reproductive mode (gonochoric, hermaphroditic, and viviparous), chromosome numbers, and morphology of egg cases. Sex determination by environmental factors, a phenomenon known as Paarkultureffekt (pair culture effect), was first observed for *O.puerilis* by Hartmann and Huth (1936), and further investigated mainly in Italy by Bacci and coworkers (see, for example, Bacci & Bortesi (1967)) and in Germany by Pfannenstiel and coworkers (see Kegel & Pfannenstiel (1983a, b) for synopsis). Richards (1967) investigated the reproduction and development of a species of *Dorvillea*, probably *D. longicornis*, in the laboratory. He was able to raise two generations to maturity within approximately two years. Eggs and sperm are released directly into the water, and larvae settle and start to feed after 8 days. Recently, Akesson & Rice (1992) described two new species of *Dorvillea* with obligate asexual reproduction. Both species autotomize into small pieces of about 5-10 setigers which develop new heads and tails within a matter of days.

Key to the Dorvilleidae

The following key can be used not only to identify the species described in this chapter, but to identify all known genera. The presentation of such an extensive key seems to be appropriate because of the large number of recently described new genera and species and the likelihood that many previously unreported genera will eventually be found in California. If jaw structures have to be examined and the specimens are too small for dissection, the whole animal should be cleared in 10% KOH for about 30 to 60 minutes or until the muscular tissue is macerated away and the body is transparent. The clearing process should be checked every 10 to 20 minutes to avoid loss of the specimen. Details of the setae must be examined under oil immersion.

1A. Notopodia (= "dorsal cirri" with embedded acicula) present in at least some setigers (Fig. 13.1L) 2

1B. Notopodia absent; dorsal cirri if present short, never with acicula (Fig. 13.1M) 10

2A. Notopodia present throughout body (may be absent on setiger 1); antennae and palps well developed, antennae moniliform, palps biarticulate; maxillae in 4 rows, with or without maxillary carriers, with at least 1 pair of basal plates (Fig. 13.2A) 3

2B. Notopodia with aciculae present on limited number of anterior setigers; antennae and palps well developed or reduced; maxillae in 2, 4, or numerous rows, consisting of free denticles only 8

3A. Maxillae with maxillary carriers and both superior and inferior basal plates; furcate setae if present with short tines (Fig. 13.1D) .... genus *Dorvillea* 6

3B. Maxillae without inferior basal plates; furcate setae if present with long, slender tines (Fig. 13.1C) 4

4A. Maxillary carriers present .... genus *Ougia*[2]

4B. Maxillary carriers absent .... genus *Parougia* 5

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[2] Genus not treated in this Atlas. For recent diagnoses or revisions, see Hilbig and Blake (1991) for *Anchidorvillea*, *Exallopus*, *Ophryotrocha*, and *Pseudophryotrocha*, Jumars (1974) for *Meiodorvillea*, von Nordheim (1987) for *Petrocha*, Orensanz (1990) for *Pinniphitime*, Pettibone (1961) for *Protodorvillea*, Wainwright and Perkins (1982) for *Gymnodorvillea*, Westheide (1982) for *Ikosipodus*, Westheide and von Nordheim (1985) for *Arenotrocha*, *Coralliotrocha*, *Microdorvillea*, and *Pusillotrocha*, and Wolf (1986a) for *Diapharosoma*, *Eliberidens*, and *Ougia*.

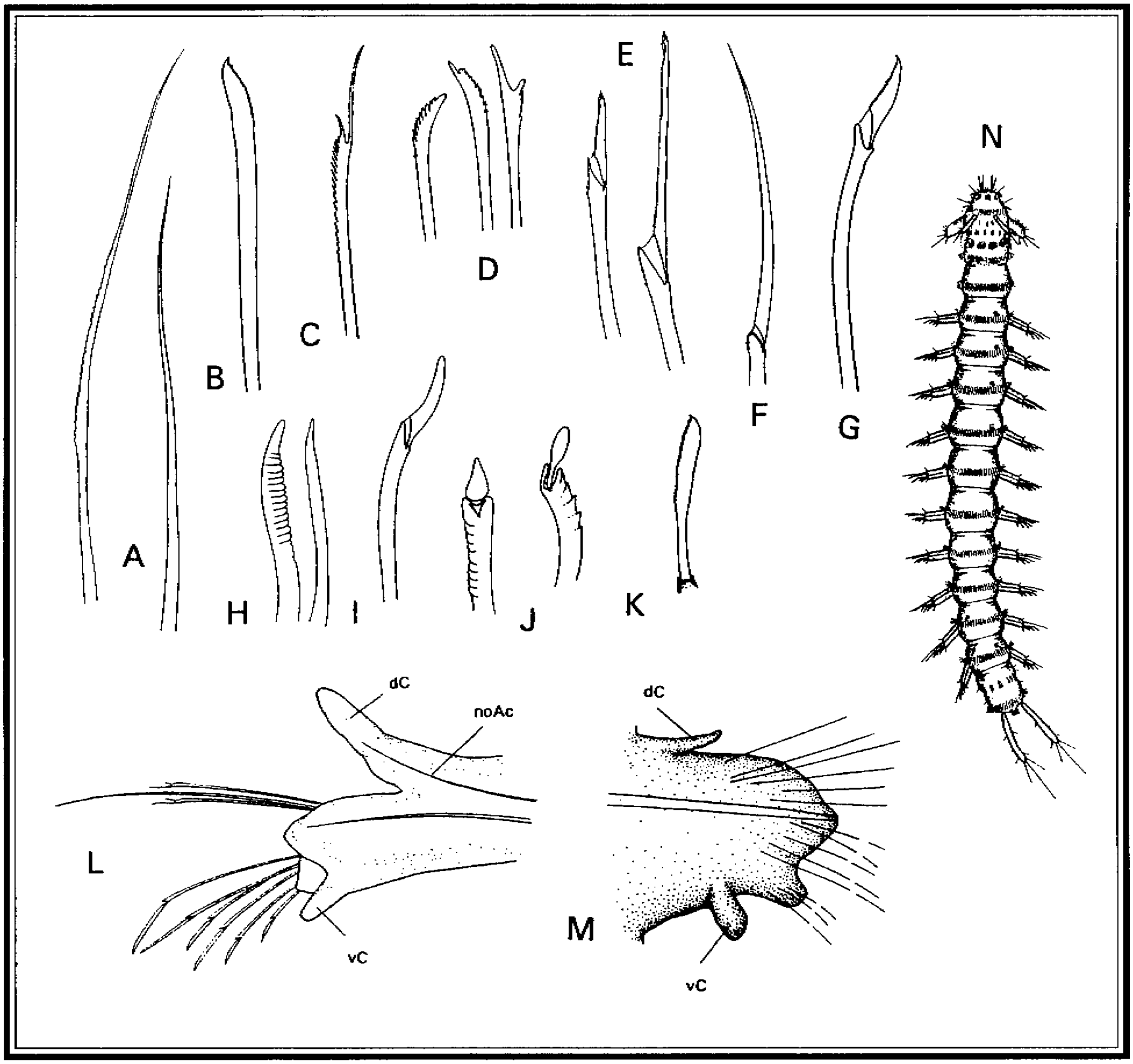

Figure 13.1. Dorvilleidae: A, capillary supraacicular setae; B, cultriform supraacicular seta (*Ophryotrocha*); C, long-tined furcate seta; D, geniculate and short-tined furcate setae; E, bidentate subacicular setae; F, spinigerous subacicular seta (*Exallopus*); G, falcigerous subacicular seta (*Ophryotrocha*); H, modified supraacicular setae (*Exallopus*); I-J, modified subacicular setae, heterogomph and homogomph (*Exallopus*); K, cultriform ventralmost seta (*Ophryotrocha*); L, subbiramous parapodium; L, uniramous parapodium; N, habitus of interstitial species (*Arenotrocha*). (from various sources).

5A. Body large (more than 10 mm long), rigid; furcate setae usually present; all setae with serrations at least distally; maxillae heavily sclerotized, visible through body wall as V-shaped structure; mandibles triangular, dark .... *Parougia caeca*[3]

5B. Body small (about 5 mm long), fragile; furcate setae absent; all setae smooth and very slender; maxillae reduced, transparent, not visible through body wall; mandibles L-shaped with transparent center (Fig. 13.6C) .... *Parougia batia*

[3] Although no specimens were present in either Phase 1 or Phase 2 material, the species is likely to occur in the area

6A. Furcate setae absent (check several parapodia) .... subgenus *Dorvillea*[2]

6B. Furcate setae present .... subgenus *Schistomeringos* 7

7A. Dorsal cirri tapering, with cirrophores as long as cirrostyles; ventral cirri inserting subdistally; furcate setae with short tines half as long as long tines; anterior denticles with straight, finely serrated cutting edge .... *Dorvillea (Schistomeringos) annulata*

7B. Dorsal cirri cylindrical, distally inflated, with cirrophores much longer than cirrostyles; ventral cirri inserting distally (may look like subdistal insertion when ventral setal lobe is extended); furcate setae with short tines one-third as long as long tines (setiger 10); most anterior denticles with crescentic, wing-like serrated cutting edge and some larger distal teeth ....
.... *Dorvillea (Schistomeringos) longicornis*

8A. Maxillae in 8 rows, most denticles covered with surficial spines; antennae simple, palps biarticulate, shorter than antennae, palpophores very short; notopodia slightly longer than neuropodia, present in setigers 2 to 12 .... *Pettiboneia brevipalpa*

8B. Maxillae in 2 or 4 rows, none covered with surficial spines 9

9A. Maxillae in 4 rows, maxillary carriers absent; antennae moniliform, palps biarticulate, palpophores much longer than palpostyles; anterior notopodia with aciculae, posterior ones without aciculae ....
.... genus *Diapharosoma*[2]

9B. Maxillae in 2 rows, maxillary carriers present; antennae indistinctly articulate, palps biarticulate; palpophores about as long as palpostyles; notopodia present in limited number of anterior setigers
.... genus *Westheideia*[2]

10A. Antennae and palps well developed, antennae moniliform; maxillae in 2 rows (Fig. 13.2E); ventral cirri much longer than dorsal cirri .... genus *Anchidorvillea*[2]

10B. Antennae and palps well developed or reduced, antennae never moniliform; ventral cirri always shorter than dorsal cirri 11

11A. Maxillae with superior and inferior free denticles and forceps or icetongs formed by fused carriers and basal plates (Fig. 13.2B); prostomial appendages and parapodial cirri present or absent, well developed or reduced 13

11B. Maxillae in 2 or 4 rows, without forceps or icetongs 12

12A. Maxillae in 2 rows 20

12B. Maxillae in 4 rows, with superior and inferior free denticles, superior and inferior basal plates, and maxillary carriers (some elements may be reduced); antennae and palps well developed or reduced
.... 15

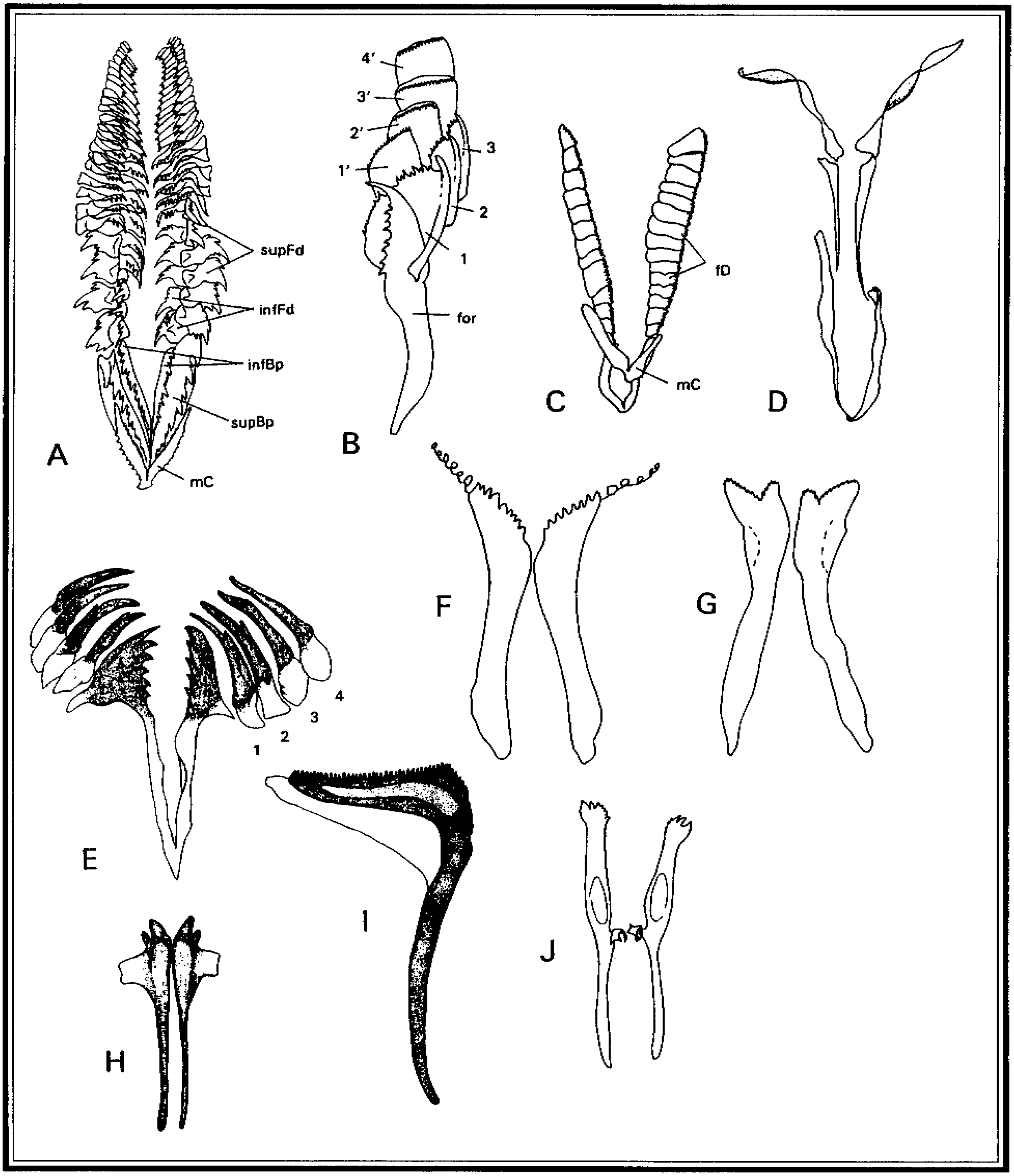

Figure 13.2. Dorvilleidae: A-E, maxillae; A, with maxillary carriers, two pairs of basal plates, and and four rows of free denticles; B, with forceps and seven pairs of free denticles in four rows (*Ophryotrocha*); C, with two rows of denticles; D, reduced to smooth, soft plates (*Pseudophryotrocha*); E, modified, woth two rows of denticles (*Anchidorvillea*); F-J, mandibles; F, *Dorvillea*; G, *Ophryotrocha*; H, *Anchidorvillea*; I, modified, L-shaped (*Ophryotrocha*); J, rodlike (*Pseudophryotrocha*). (from various sources).

13A. All setae simple; prostomium wider than long, with well-developed clavate antennae and palps; median and posterior setigers with dorsolateral and ventrolateral segmental lobes; setae including smooth spines and fine capillaries .... *Parophryotrocha brevicapitis*

13B. Supraacicular setae simple, subacicular setae compound (ventralmost seta may be simple) 14

14A. Some or all setae in anterior setiger(s) greatly modified into recurved hooks (Fig. 13.1H-J) .... genus *Exallopus*[2]

14B. Anterior setae if modified only slightly different from regular setae, never recurved; prostomial appendages and parapodial cirri usually short and simple .... genus *Ophryotrocha*[2]

15A. Maxillae consisting of basal plates only; antennae and palps short, digitiform .... genus *Eliberidens*[2]

15B. Maxillae including free denticles 16

16A. Minute interstitial forms, about 1 mm long, with maximally 15 setigers (Fig. 13.1N) 17

16B. Animals not interstitial, adults several millimeters long; antennae papilliform, palps multiarticulate, much longer than antennae; maxillary apparatus well-developed .... genus *Protodorvillea*[2]

17A. Maxillae with superior and inferior basal plates and superior and inferior free denticles 18

17B. Maxillae with superior basal plates and superior and inferior free denticles; antennae simple, palps biarticulate, palpophores as long as palpostyles; all supraacicular setae simple spines .... genus *Microdorvillea*[2]

18A. Antennae moniliform, palps biarticulate, with long palpophore; supraacicular setae including furcate setae with long, slender tines (Fig. 13.1C) .... genus *Coralliotrocha*[2]

18B. Antennae simple or absent; furcate setae absent 19

19A. Setae including serrated capillaries and compound falcigers with serrated shaft and blade; prostomium with simple palps, antennae absent; parapodia without cirri; mandibles ornate; maxillae with at least 2 pairs of free denticles .... genus *Petrocha*[2]

19B. Both simple setae and blades of compound falcigers unidentate; capillaries serrated, compounds smooth; prostomium with simple palps, antennae absent; maximally 18 setigers, parapodia without cirri .... genus *Pusillotrocha*[2]

20A. Maxillae consisting of 3 pairs of plates, the posteriormost pair basally fused or linked 21

20B. Maxillae consisting of serrated, rounded free denticles 22

21A. Maxillary plates smooth, elongate, weakly sclerotized (Fig. 13.2D); mandibles rodlike or L-shaped (Fig. 13.2J); furcate or geniculate setae absent .... genus *Pseudophryotrocha*[2]

21B. Maxillary plates dentate, oval, heavily sclerotized; mandibles subterminally fused along symphysis (Fig. 13.2K) .... genus *Pinniphitime*[2, 4]

22A. Small, interstitial forms with reduced prostomial and parapodial appendages 24

22B. Adults several millimeters long, not interstitial 23

23A. Maxillary carriers absent; supraacicular setae including serrated capillaries, furcate setae with short tines (anterior setigers), and geniculate setae (median and posterior setigers); inferiormost subacicular seta cultriform; antennae and palps absent .... genus *Gymnodorvillea*[2]

23B. Maxillary carriers present (Fig. 13.2C); supraacicular setae including capillaries and furcate setae with short tines, occasionally replaced by geniculate seta in one or few anterior parapodia (Fig. 13.1D); antennae and palps present (palps may be absent) .... genus *Meiodorvillea*[2]

24A. All setae compound; maximally 10 setigers, parapodia lacking cirri; prostomium with palps, antennae and eyes absent .... genus *Ikosipodus*[2]

24B. Supraacicular setae simple, serrated, bidentate; compound falcigers with smooth, distally bidentate blades; up to 10 setigers, parapodia without cirri; prostomium with digitiform antennae and thicker palps of equal length, eyes absent; nuchal organs with 4 ciliated pads .... genus *Arenotrocha*[2]

Description of Species

As a result of the many recent publications, the Dorvilleidae have become a large family with well over 100 species in 22 genera. The dorvilleid fauna in the Santa Maria Basin and Santa Barbara Channel is depauperate with only five species, none of which belong to *Ophryotrocha*. The following species are treated:

Dorvillea (Schistomeringos) annulata (Moore, 1906)
Dorvillea (Schistomeringos) longicornis (Ehlers, 1901)
***Parophryotrocha brevicapitis* Hilbig, new species**
Parougia batia (Jumars, 1974), **new combination**
Pettiboneia brevipalpa Hilbig and Ruff, 1990

[4] The other two genera described by Orensanz (1990), *Palpiphitime* and *Mammiphitime*, are considered doubtful and are therefore not included in this key.

Genus *Dorvillea* Parfitt, 1866

Type Species. *Staurocephalus rubrovittatus* Grube, 1855

Diagnosis. Parapodia subbiramous throughout (except for setiger 1), with notopodium consisting of base of dorsal cirrus and acicula projecting into the cirrostyle; setae including simple capillaries and heterogomph falcigers (subgenus *Dorvillea*) or capillaries, furcate setae with short tines, and heterogopmph falcigers (subgenus *Schistomeringos*). Antennae and palps well-developed, antennae usually moniliform, palps biarticulate. Maxillae heavily sclerotized, visible through body wall, consisting of maxillary carriers and 4 rows of denticles, the posterior ones fused to form superior and inferior basal plates; mandibles dark, triangular, with few large teeth along cutting edge and often several lateral free conical teeth.

Remarks. Thanks to the revisions by Pettibone (1961) and Wolf (1986a-b), the formerly ill-defined genus now has a clear and concise definition. It appears that true *Dorvillea* are limited to shelf depths, whereas species from deep water are assigned to *Ougia* and *Parougia*.

Dorvillea (Schistomeringos) annulata **(Moore, 1906)**

Figure 13.3

Stauronereis annulatus Moore, 1906:225-227, pl. 10, figs. 12-13, pl. 11, figs. 18-22.
Stauronereis rudolphi: Pettibone, 1963:231-233, fig. 60a-f (in part).
Dorvillea annulata: Fauchald, 1970: 152-154.
Schistomeringos nr. *annulata*: Lissner *et al.*, 1986:D-12.
Schistomeringos longicornis: Lissner *et al.*, 1986:D-12 (in part).

Material Examined. California: Santa Maria Basin, off Point Buchon, Sta. 6 (1), Sta. 13 (2).

Description. Length to 13 mm, width to 1 mm, segments to 72. Body slender, dorsoventrally compressed, with conspicuous parapodia, widest in pharyngeal region, gently tapering toward pygidium within last 10 setigers or so. Color in alcohol light tan.

Prostomium rounded, somewhat longer than wide, with antennae and palps of equal length and about twice as long as prostomium. Antennae with 7 to 8 moniliform articles, palps with long palpophore and short, conical palpostyle. Two pairs of eyes near antennal base, side by side or arranged in a square; anterior (inner) pair large, posterior (outer) pair minute spots (Fig. 13.3A). Proboscis with well-developed mandibles and maxillae. Maxillae with smooth to finely serrated carriers, posteriorly fused or free from one another; superior basal plates large, with 6 to 7 large teeth alternating with smaller ones; superior free denticles about 30; proximal denticles with narrow base and wide cutting edge bearing large main fang and several smaller lateral teeth; remaining free denticles gradually becoming elongate, more delicate plates, main fang diminishing in size and eventually completely absent, cutting edge with several fine, long teeth. Inferior basal plates smaller and more delicate than superior ones, with about 5 large fangs alternating with several smaller teeth. Inferior free denticles also numbering about 30, resembling corresponding superior ones, but generally less sclerotized (Fig. 13.3B). Mandibles large, anteriorly flared, with about 10 teeth on cutting edge and 4 to 8 free conical teeth (Fig. 13.3C).

Parapodia uniramous in setiger 1, subbiramous from setiger 2, with notopodium reduced to base of dorsal cirrus and fine acicula projecting into cirrostyle; with rounded acicular lobe, conical postsetal lobe, and retractable ventral lobe. Ventral cirri inserting subdistally, projecting about as far as postsetal lobe; dorsal cirri slender, with conical cirrostyle about as long as cirrophore (Fig. 13.3D). Supraacicular setae including

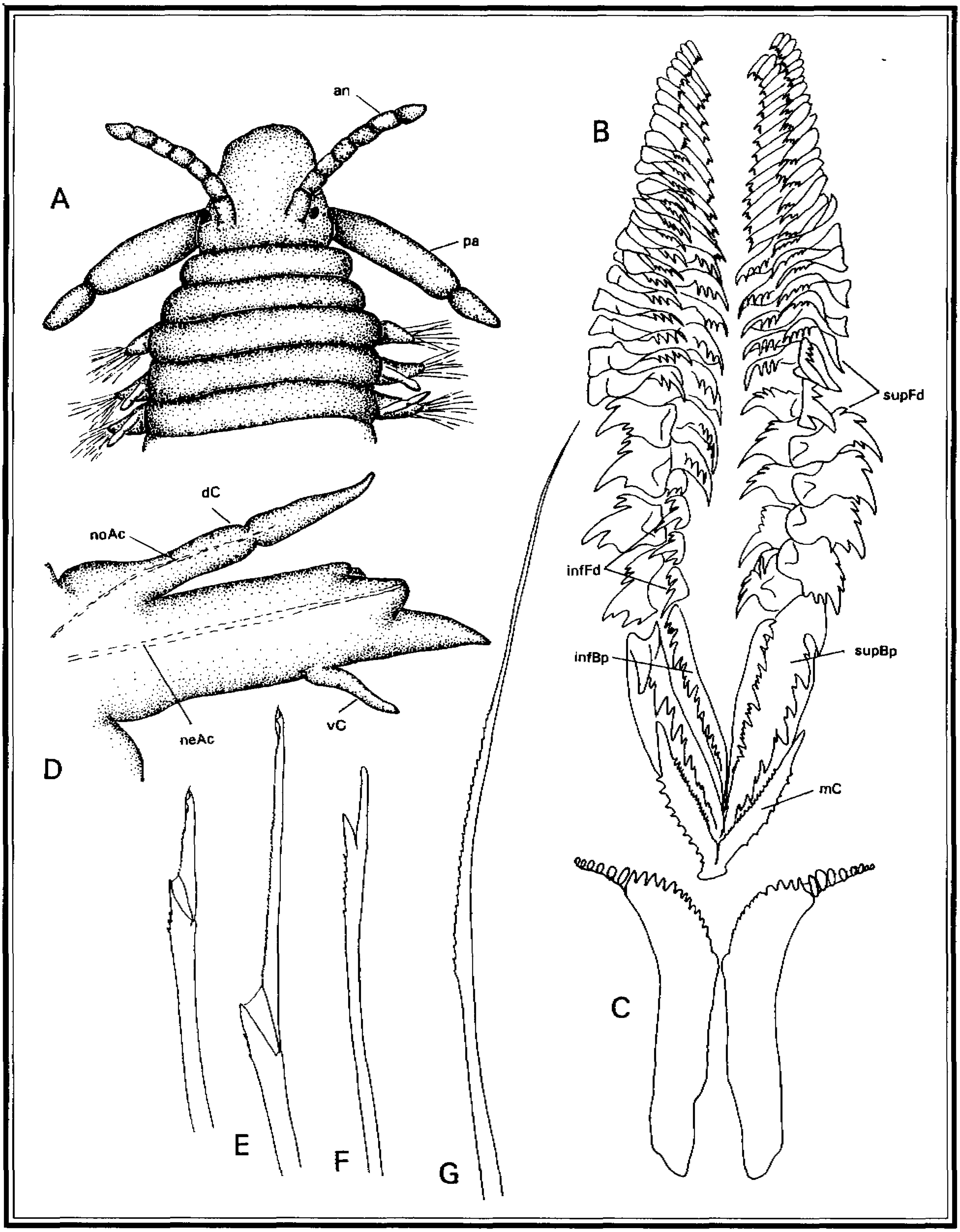

Figure 13.3. *Dorvillea (Schistomeringos) annulata*: A, anterior end, dorsal view; B, maxillae; C, mandibles; D, middle parapodium, ventral setal lobe extended; E, subacicular setae, shortest and longest blade of fascicle; F, furcate supraacicular seta; G, capillary supraacicular seta (after Fauchald, 1970).

2 to 3 finely serrated capillaries and usually one or two furcate setae with long tines about twice as long as short tines; shaft serrated subdistally below shorter tine (Fig. 13.3F, G). Subacicular setae numerous compound setae with bidentate blades of varying length; longest blades on dorsalmost setae, about 3 times as long as shortest blades (Fig. 13.3E).

Remarks. The largest Phase I specimen examined was originally identified as *Schistomeringos* nr. *annulata*, probably because of the differences in the jaw apparatus to Fauchald's (1970) redescription. However, since characters such as the number of free denticles and the number of teeth on a denticle or basal plate appear to be growth-dependent (Hilbig, personal observations), the only remaining discrepancy is the shape of the maxillary carriers, which were found to be fused and serrated in the specimen at hand, but were described as being smooth and posteriorly free from one another by Fauchald (1970). All other characters, such as the proportions of the parapodia and setae, agree very well with Moore's (1906) original description, and it seems unlikely that two species would differ only in details of the maxillary carriers. The specimen is therefore considered to be *D. annulata*.

Type Locality and Type Specimens. Quarantine Rock, Port Townsend, Washington: holotype (USNM 5541) and paratype (ANSP 1980).

Habitat. Silt, silty and shelly sand.

Distribution. Washington to western Mexico, 80 - 220 m.

Dorvillea (Schistomeringos) longicornis (Ehlers, 1901)

Figure 13.4

Stauronereis longicornis Ehlers, 1901:150-151, pl. 19, figs. 18-21, pl. 20, figs. 4-6.
Stauroneries articulatus Hartman, 1938:101-102, figs. 39-44.
Dorvillea articulata: Hartman, 1968:817, figs. 1-5.
Stauronereis rudolphi: Pettibone, 1963:231-233, fig. 60a-f (in part).
Dorvillea rudolphi: Fauchald, 1970:156-159, pl. 27, figs. a-j (in part).
Dorvillea atlantica: Hartman, 1968:819, figs. 1-5.
Schistomeringos longicornis: Jumars, 1974:107-109, fig. 2.—Lissner *et al.*, 1986:D-12.
Schistomeringos annulata: Lissner *et al.*, 1986:D-12 (in part).

Material Examined. California: Santa Maria Basin, off Point Sal, Sta. 104 (1), Sta. 103 (1); off Purisima Point, Sta. R4 (1).

Description. Length to 70 mm, width to 1 mm, segments to 80. Body stout, with rounded dorsum and slightly flattened ventrum, widest in middle, tapering toward pygidium and slightly toward prostomium. Color in alcohol uniformly light tan.

Prostomium bluntly rounded, longer than wide, in alcohol sometimes divided into 2 or 3 rings, bearing 2 pairs of eyes, the anterior pair largest; antennae somewhat longer than prostomium, moniliform, with 5 to 12 articles; palps about as long as antennae, with long palpophore and short palpostyle (Fig. 13.4A). Maxillae with fused, serrated carriers; superior basal plates fused posteriorly, with about 14 large fangs alternating with smaller teeth (Fig. 13.4B); superior free denticles about 30 to 40 elongate plates with cutting edges bearing different kinds of dentitions from proximal to distal position within row; denticles close to basal plate with comb-shaped cutting edge bearing several equal teeth (Fig. 13.4C); more distal denticles with main fang and small lateral teeth (Fig. 13.4D, E); main fangs gradually diminishing in size, cutting edges becoming crescentic with progressingly finer dentitions, distalmost denticle soft, with delicate, rounded teeth (Fig. 13.4F, G). Inferior basal plates free, smaller than superior ones, also bearing about 14 large fangs and several smaller teeth; about 40 to 50 inferior free denticles present, similar in shape to corresponding superior denticles,

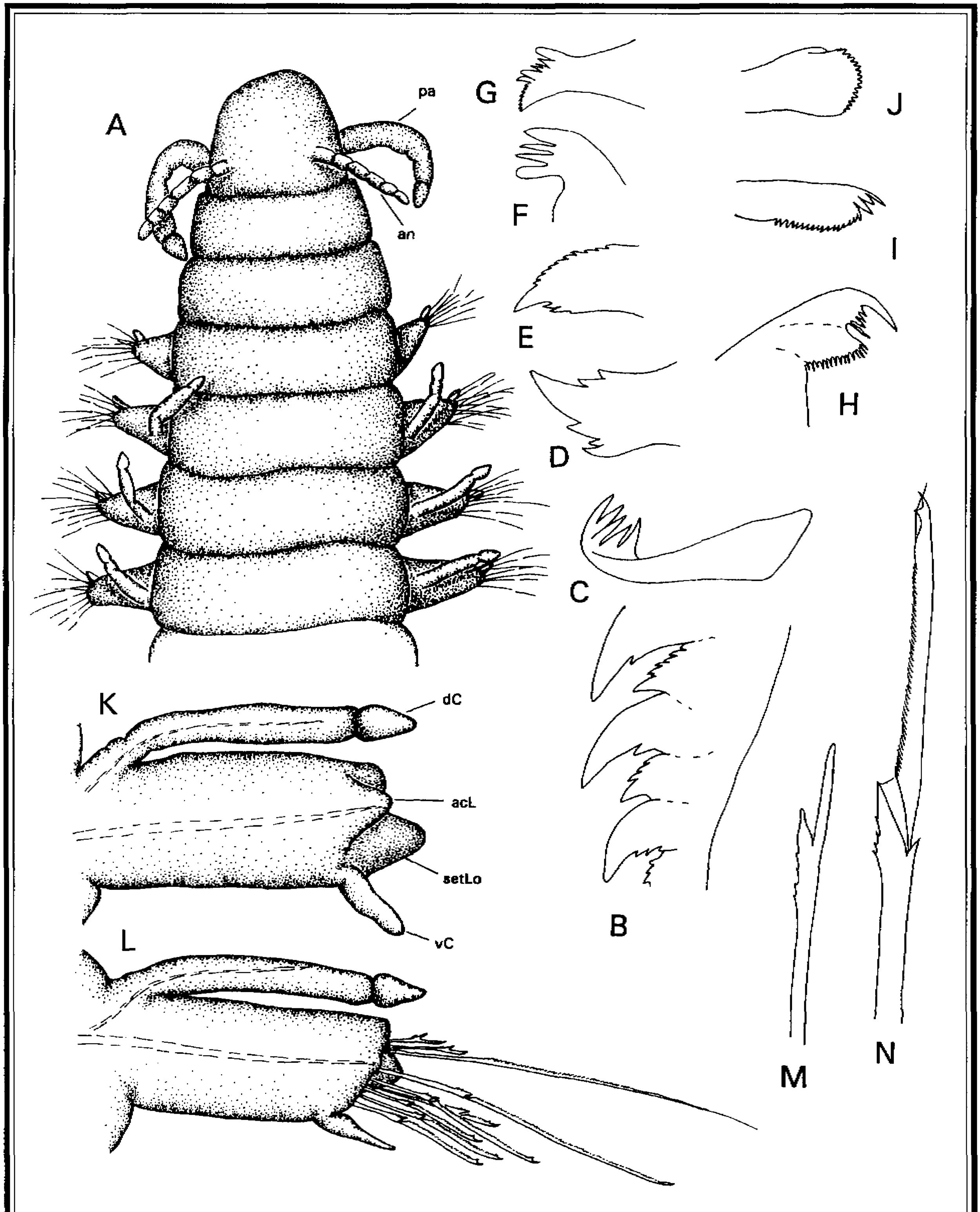

Figure 13.4. *Dorvillea (Schistomeringos) longicornis*: A, anterior end, dorsal view (eyes faded); B, superior base plate, detail of proximal teeth; C-G, superior free denticles from proximal to distal: C, very close to base plate, D-E, middle of superior row, F-G, first and fifth denticle; H-J, distal inferior free denticles; K, parapodium, anterior view, ventral setal lobe extended; L, same, ventral setal lobe retracted; M, furcate supraacicular seta; N, subacicular seta. (D, E, G after Fauchald, 1970).

generally somewhat more delicate; distal inferior denticles soft, oblong plates with numerous very fine teeth (Fig. 13.4H-J). Mandibles heavily sclerotized, flared anteriorly, with about 10 teeth on cutting edge and several free conical teeth.

Parapodia uniramous in setiger 1, subbiramous from setiger 2 (Fig. 13.4K, L); with low presetal lobe, conical postsetal lobe, and retractable ventral lobe. Ventral cirri inserted distally, insertion appearing subdistal when ventral parapodial lobe fully extended (Fig. 13.4K); dorsal cirri with long cylindrical cirrophore and short, conical, slightly inflated cirrostyle, extending about as far as postsetal lobe. Supraacicular setae including serrated capillaries and furcate setae with subdistally serrated shafts and unequal tines; around setiger 10, long tine about 3 times as long as short tine (Fig. 13.4M). In anterior setigers occasionally one of the furcates replaced by bidentate geniculate seta. Subacicular setae compound falcigers with bidentate, serrated blades of varying length, dorsalmost setae with longest blades, up to 4 times as long as shortest blades in same fascicle (Fig. 13.4N).

Pygidium with 2 short ventral and 2 longer ventrolateral anal cirri.

Remarks. Among the Phase I voucher material, some specimens were misidentified as *Schistomeringos annulata*, most likely because the overall shape of the parapodia resembles that species when the ventral lobe is extended; the ventral cirrus then seems to arise from the middle of the ventral parapodial edge rather than distally. However, the shape of the dorsal cirrus is a good character to discriminate between those two species; the cirrostyle is slender and as long as the cirrophore in *D. annulata*, but much shorter than the cirrophore and somewhat inflated in *D. longicornis*. The cresecentic, wing-like cutting edges of the anterior free denticles are also characteristic for *D. longicornis* and can be easily observed through a short dorsal incision just below the prostomium. The length ratio between the shorter and longer tines of a furcate seta from setiger 10, recommended for species discrimination between *D. longicornis* and *D. rudolphi* by Jumars (1974), can also be used to distinguish *D. longicornis* from *D. annulata*; the ratio is about 2 for *D. annulata* and 3 for *D. longicornis*. However, several setae should be examined because this character is somewhat variable.

Type Locality and Type Specimens. According to Jumars (1974), Ehlers' type specimens have to be considered lost. Type locality is Chile.

Habitat. The species is found in mixed sediments, mud with high silt content, and ooze.

Distribution. Alaska to Chile, intertidal to 575 m.

Genus *Parophryotrocha* Hartmann-Schröder, 1971

Type Species. *Ophryotrocha isochaeta* Eliason, 1962

Diagnosis. Parapodia uniramous, with simple setae of one or two kinds in both supra- and subacicular fascicles; compound setae absent. Antennae and palps if present short and simple. Maxillae with icetong-shaped posterior pieces, formed through fusion of maxillary carriers and superior and inferior basal plates, and usually 7 pairs of free denticles in 4 rows.

Remarks. This genus is very similar to *Ophryotrocha* except for the absence of compound falcigers in the subacicular fascicle.

Parophryotrocha brevicapitis Hilbig, new species

Figure 13.5

Dorvilleidae sp. A Hyland *et al.*, 1990:F-1.

Material Examined. California: Santa Maria Basin, off Point San Luis, Sta. R-1, 35°05.83'N, 120°49.16'W, 91 m: holotype (USNM 170427).

Description. Length 2 mm, width 0.2 mm, segments 19. Body long, slender, widest in pharyngeal region, gently tapering toward pygidium. Median and posterior setigers drawn out to rounded dorsolateral and ventrolateral lobes extending over the parapodial bases, ventral lobes largest (Fig. 13.5A, B). Ciliation including ring on prostomium between antennae and palps and tufts at dorsal and ventral parapodial bases and along edge of lateral segmental lobes. Color in alcohol pale.

Prostomium bluntly triangular, wider than long, with two digitiform antennae arising from ridge running across middle of prostomium and large biarticulate palps inserted at postectal corners of prostomium; cirrophores short, cylindrical, bases as wide as lateral edges of prostomium; cirrostyles slender, digitiform (Fig. 13.5A). Jaws observed through body wall only; maxillae with P-type forceps, weakly sclerotized, and probably 7 pairs of free denticles arranged as typical for the genus; mandibles L-shaped, anteriorly flared, with smooth cutting edge, also weakly sclerotized except for median rod-shaped handles. Peristomium with 2 equal rings, similar to subsequent setigers.

Parapodia simple, with long, slender base and conical acicular lobe; dorsal and ventral cirri absent, but ciliated pad present just above insertion of dorsalmost seta; no retractable parapodial lobes observed (Fig. 13.5C). Setae all simple, in fascicles of 4 or 5, of 2 kinds: (1) 3-4 slender, smooth, fine-tipped spines, (2) in ventralmost position single, very thin capillary (Fig. 13.5D, E).

Pygidium unknown.

Etymology. The species is named for its characteristically short head (brevis= Latin for short, caput= Latin for head).

Remarks. Although only one incomplete specimen was available for examination, the establishment of a new species is justifiable because of the very unusual external appearance of this animal. The other two known species of *Parophryotrocha*, *P. isochaeta* and *P. gesae*, resemble typical shallow-water *Ophryotrocha* species, whereas *P. brevicapitis* is most similar to a group of somewhat aberrant species within *Ophryotrocha* including four provisional SCAMIT species from polluted environments in California and the hydrothermal vent species *O. platykephale*. The most characteristic features of *P. brevicapitis* are the large biarticulate palps and the heavily ciliated segmental lobes above and below the median and posterior parapodia.

Distribution. Only known from the type locality.

Genus *Parougia* Wolf, 1986

Type Species. *Schistomeringos nigridentata* Oug, 1978

Diagnosis. Parapodia subbiramous throughout except for setiger 1, with notoaciculae projecting into dorsal cirrostyles; supraacicular setae simple capillaries, in some species also 1 or 2 furcate setae with long tines; subacicular setae compound falcigers or spinigers. Antennae and palps well-developed; antennae simple or moniliform, palps biarticulate. Maxillae with superior basal plates and superior and inferior free denticles; maxillary carriers and inferior basal plates absent. Mandibles dark, triangular, with conical teeth along cutting edge, or more delicate, wing-shaped, and smooth anteriorly.

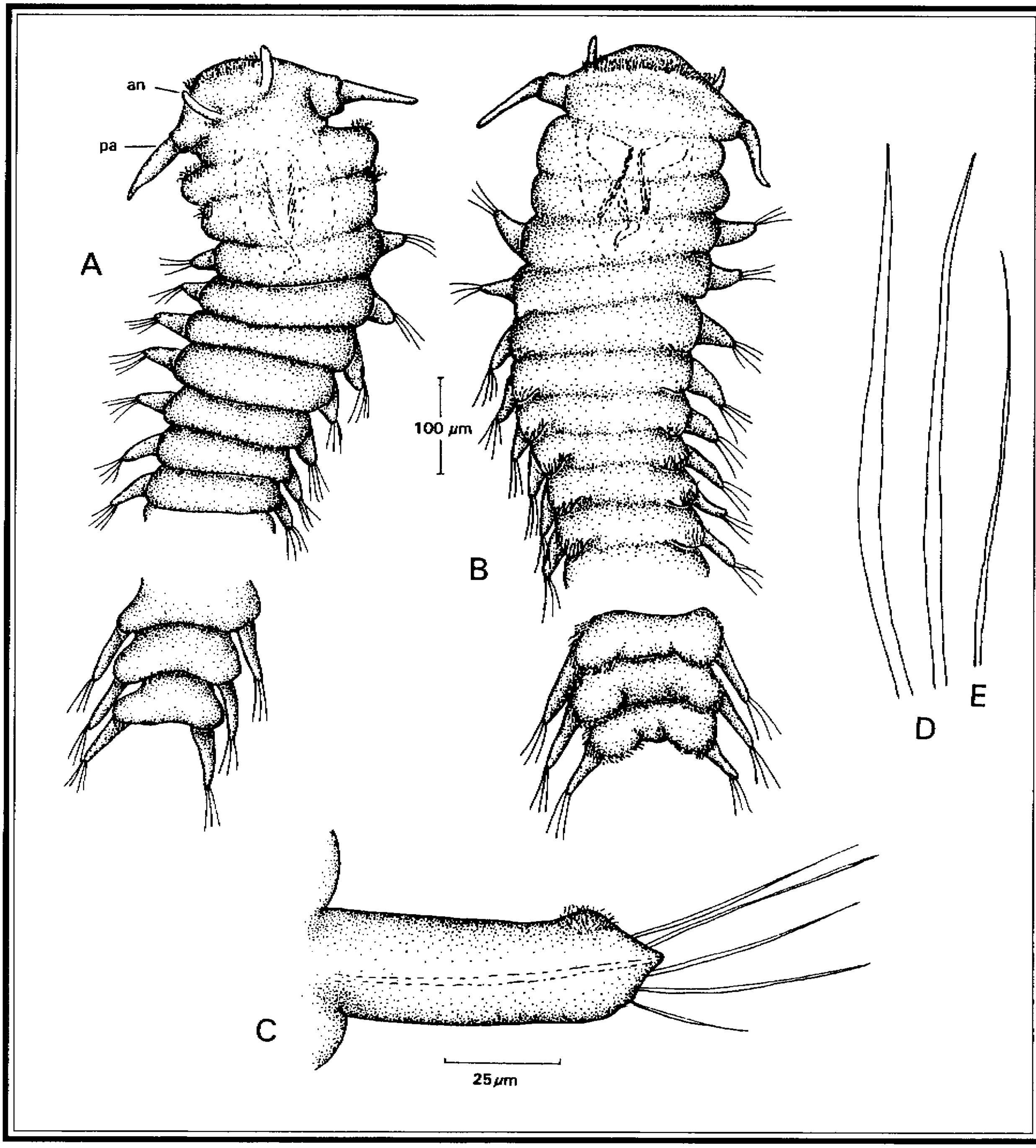

Figure 13.5. ***Parophryotrocha brevicapitis* Hilbig, new species**: A, anterior end and last setigers of fragment, dorsal view; B, same, ventral view; C, parapodium; D, spines; E, ventralmost capillary seta. (all from holotype).

Remarks. *Parougia* contains some species formerly assigned to *Schistomeringos* as defined by Jumars (1974). The presence of furcate setae seems to be a fairly inconsistent character; for example, *Parougia caeca*, one of the most common species in this genus, is found with furcate setae in all parapdia, along a certain portion of the body (sometimes only on one side), or with none at all. The inconsistency of this character was one of the initial reasons to restrict *Schistomeringos* (as a subgenus of *Dorvillea*, see above) to those forms that possess short-tined furcates which occur regularly in all parapodia.

Parougia batia (Jumars, 1974), new combination

Figure 13.6

Dorvillea batia Jumars, 1974:115-117, fig.6.—Hyland *et al*., 1990:F-1.
Dorvillea sp. 2: Blake *et al*., 1987:C-2.

Material Examined. California: Santa Maria Basin, off Point Sal, Sta. R-7 (2). North Carolina: Cape Hatteras, MMS ACSAR Sta. S9, 35°28.3'N, 74°47.6'W, 604 m (6); Cape Lookout, MMS ACSAR Sta. S1, 34°16.2'N, 75°45.8'W, 583 m (1).

Description. Length to 3.3 mm, width to 0.3 mm, segments to 44. Body slender, dorsoventrally flattened; color in alcohol pale.

Prostomium bluntly rounded, wider than long, with antennae arising close to posterior margin at outer edges of central transverse ridge; palps slightly shorter than antennae, with short palpophores located at postectal margin of prostomium and tapering, cirriform palpostyles (Fig. 13.6A); eyes absent. Peristomium with 2 rings, the first one much shorter and narrower than the second one, bearing large, bilobed, heavily ciliated nuchal organs. Maxillae weakly sclerotized, reduced; superior basal plates fused, with 5 large fangs alternating with several small teeth, fusion lines of original denticles visible as typical for the genus; 5 superior free denticles present, all but distal one with main fang and long serrated cutting edges below main fang; distal superior denticle reduced to very thin, finely serrated plate. Inferior row consisting of 5 free denticles, all soft, oblong plates with rounded cutting edge bearing numerous very fine teeth (Fig. 13.6B). Mandibles wing-shaped, with short posterior handle and medially serrated cutting edge; center of mandible soft, transparent, margins and cutting edge relatively heavily sclerotized and visible through body wall even in dorsal view (Fig. 13.6C).

Parapodia uniramous in setiger 1, subbiramous from setiger 2; neuropodia conical, with retractable ventral lobe, bearing large setal fascicles arranged in broad fan; ventral cirri short, inserted subdistally; dorsal cirri about as long as neuropodia, indistinctly divided into cirrophore and short, slightly inflated cirrostyle (Fig. 13.6D). Supraacicular setae numerous smooth capillaries, subacicular setae compound spinigers with blades of varying lengths, shortest blades almost falcigerous; shafts with very few serrations distally (Fig. 13.6E-G).

Pygidium with two articulated anal cirri and middorsal style.

Remarks. Unlike typical members of this genus, *P. batia* does not preserve well, and proportions of the soft body parts, such as prostomial appendages and parapodial cirri, vary somewhat depending on the condition of the specimens. The soft, small body, smooth setae, indistinctly articled dorsal cirri, and characteristic outline of the mandibles readily distinguish this species from its congeners and from co-occurring species of *Dorvillea*. An examination of the maxillae *in situ* after clearing in 10% KOH revealed that maxillary carriers and inferior basal plates are absent, and consequently the species is transferred to *Parougia*. Jumars, in his original description, had interpreted the superior basal plates as being a fusion product of the carriers and both pairs of basal plates. *P. batia* belongs to a group of deep-water species within the genus that are all characterized by reduced, weakly sclerotized maxillae and mandibles of aberrant shapes. At least one Atlantic and one Pacific species are still awaiting description.

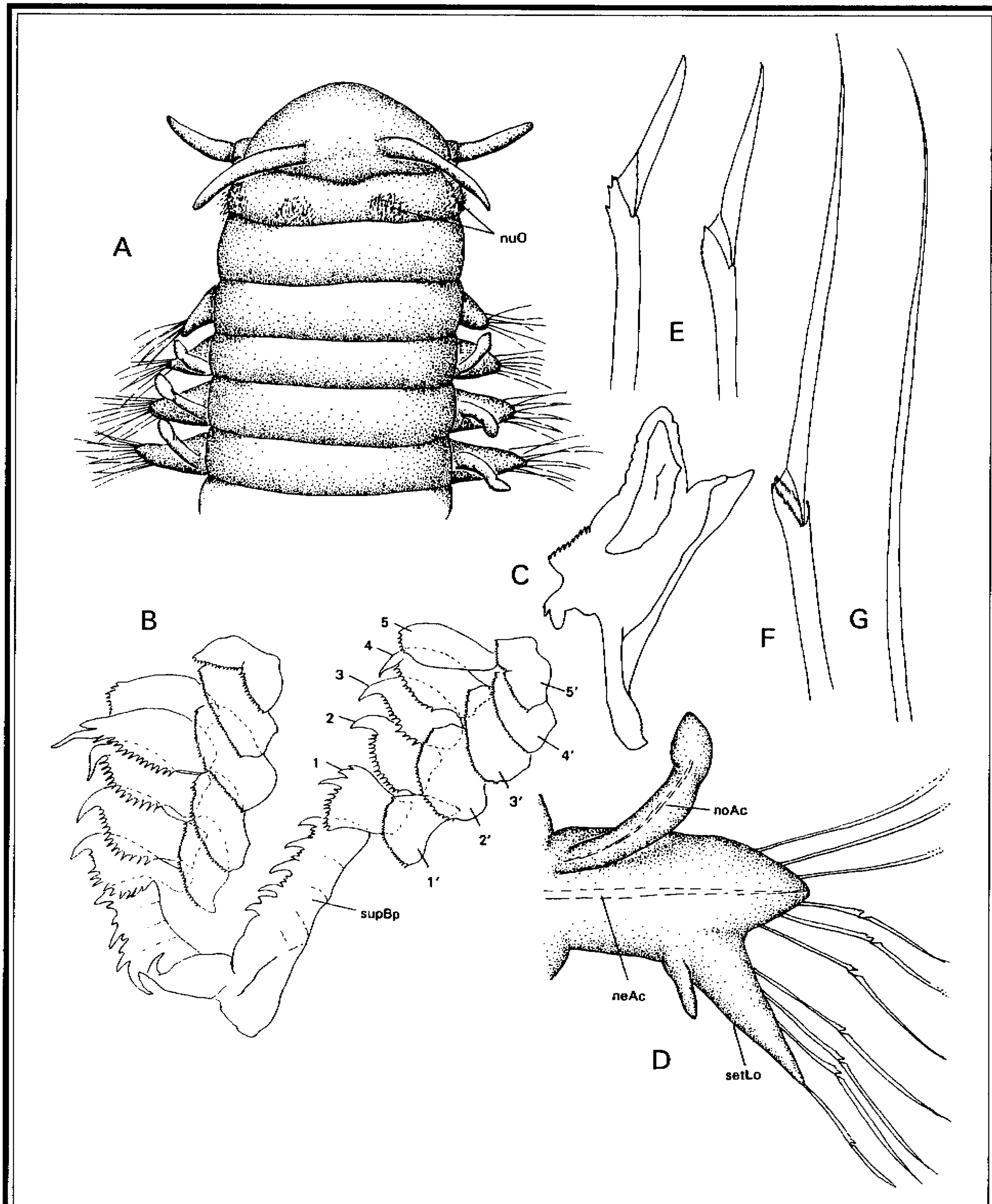

Figure 13.6. *Parougia batia*: A, anterior end, dorsal view; B, maxillae; C, right mandible (after Jumars, 1974); D, parapodium, anterior view; E-F, two upper, short-bladed and one lower, long-bladed subacicular seta; G, supraacicular seta.

Type Locality and Type Specimens. San Diego Trough, California: holotype (LACM-AHF Poly 1074) and 4 paratypes (LACM-AHF Poly 1075, 1076).

Biology. *Parougia batia* was found in silty mud; Jumars (1974) suggested that the species grazes on epifauna of astrorhizid foraminiferans. It is possible that *P. batia* feeds in a similar way on epifauna of another large foraminiferan characteristic for the slope off Cape Hatteras, *Bathysiphon filiformis*.

Distribution. Central and southern California; North Carolina, Cape Hatteras to Cape Lookout, 560-1229 m.

Genus *Pettiboneia* Orensanz, 1973

Type Species. *Pettiboneia sanmatiensis* Orensanz, 1973

Diagnosis. Parapodia subbiramous in a limited number of anterior setigers (usually about 8 to 12), with notoaciculae projecting into dorsal cirrostyles; median and posterior parapodia uniramous. Setae including simple capillaries and geniculate or furcate setae in supraacicular fascicles and compound falcigers in subacicular fascicles. Antennae simple, palps biarticulate. Maxillae in 8 to 22 rows, with free denticles only; most denticles weakly sclerotized, rounded, rasplike plates densely covered with surficial spines. Mandibles delicate, wing- or L-shaped, with scalloped cutting edge.

Remarks. The often spectacular maxillae, although usually visible only after clearing, and the presence of notopodia in a defined number of anterior setigers makes this genus easy to recognize. To date, three species of *Pettiboneia* have been reported from California: the type species *P. sanmatiensis* that was found in Tomales Bay, *P. dibranchiata* with the type locality in the Santa Catalina Basin, and *P. brevipalpa* which was found during Phase I and is described below. Descriptions of the other two species can be found in Blake (1979) and Blake and Hilbig (1990).

***Pettiboneia brevipalpa* Hilbig and Ruff, 1990**

Figure 13.7

Pettiboneia brevipalpa Hilbig and Ruff, 1990:115-118, fig. 1.
Pettiboneia sanmatiensis Lissner *et al.*, 1986:D-12. *Not* Orensanz, 1973.

Material Examined. California: Santa Maria Basin, off Point San Luis, Sta. 28 (1); Pioneer Canyon, Sta. C-3, 37°20.21'N, 123°08.84'W, 1400 m (1); north of Pioneer Canyon, Sta. 3-4, 37°27.83'N, 123°11.60'W, 1040 m (1), Sta. 3-5, 37°27.39'N, 123°14.42'W, 1195 m (2), Sta. 3-10, 37°26.00'N, 123°10.83'W, 985 m (1), Sta. 3-11, 37°25.50'N, 123°15.02'W, 1225 m (3), Sta. 3-15, 37°24.71'N, 123°12.16'W, 1010 m (3), Sta. 3-16, 37°23.20'N, 123°14.44'W, 1220 m (2),Sta. 3-17, 37°22.18'N, 123°16.76'W, 1457 m (1); south of Pioneer Canyon , Sta. 4-2, 37°15.29'N, 123°07.13'W, 995 m (1).

Description. Length to 4.5 mm, width to 0.1 mm, segments to 66. Body slender, fragile, unpigmented in alcohol.

Prostomium pear-shaped, about as long as wide (Fig. 13.7A); antennae clavate, about as long as greatest prostomial width; biarticulate palps half antennal length, inserted ventrolaterally behind antennae, with short, inconspicuous palpophores; eyes absent; narrow band of cilia encircling prostomium between antennae and palps; large yellowish-brown nuchal organs on posterior margins of prostomium. Maxillae with two main rows of free denticles and about six additional rows on each side; maxillary carriers and basal plates absent (Fig. 13.7F). Basal teeth of main rows smooth, delicate, rounded plates with serrated cutting edge;

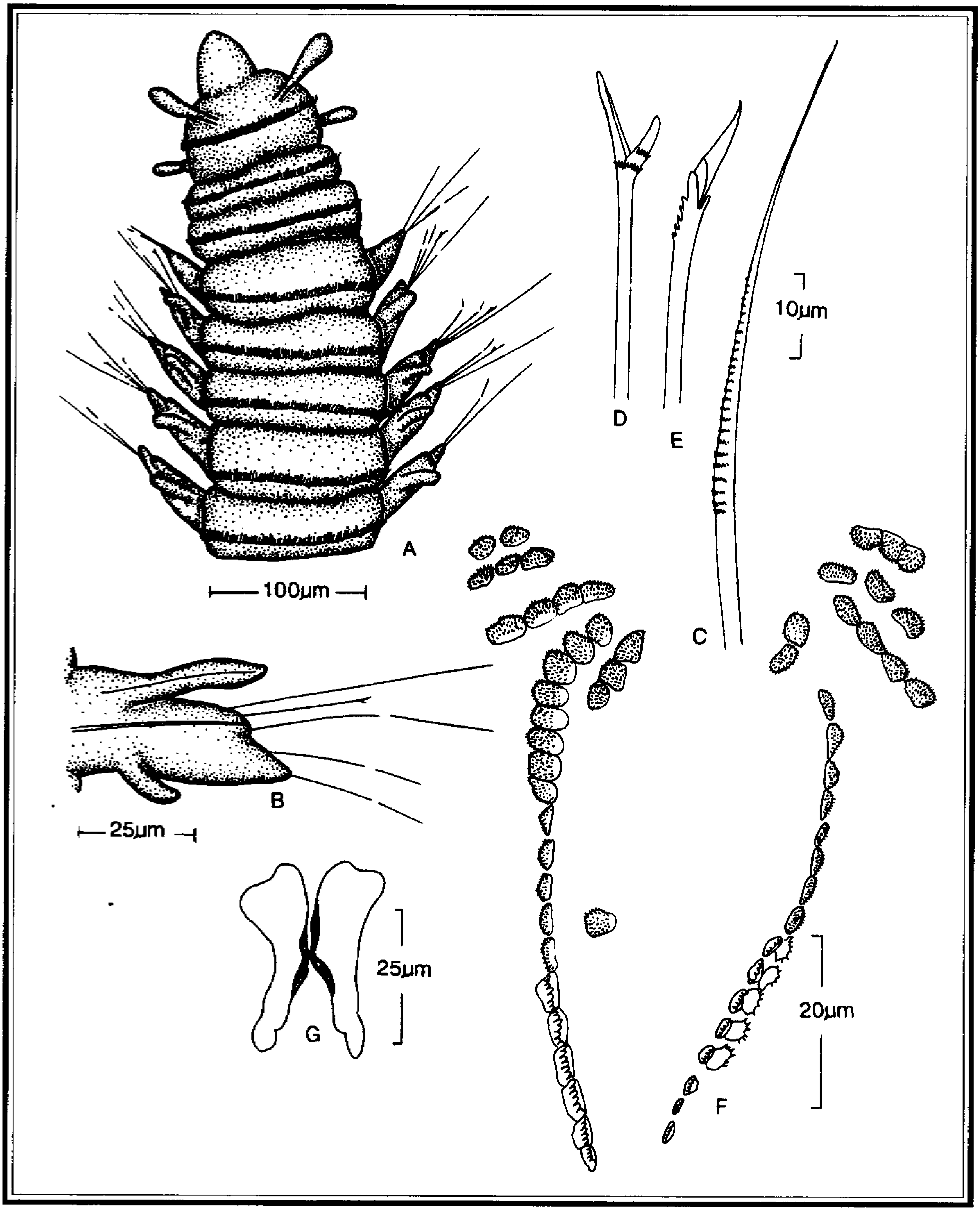

Figure 13.7. *Pettiboneia brevipalpa*: A, anterior end, dorsal view; B, anterior parapodium; C-D, capillary and furcate supraacicular setae; E, subacicular seta; F, maxillae; G, mandibles. (from Hilbig & Ruff, 1990).

middle and upper teeth rounded plates covered with surficial spines. Teeth of additional rows including smooth, anteriorly serrated plates proximally and spinose plates distally. Mandibles elongate, slightly curved, anteriorly flared, smooth and weakly incised (Fig 13.7G). Two subequal asetigerous peristomial rings, shorter than setigerous segments; complete ciliary bands on both rings and on anterior setigers.

Cirriform notopodia with embedded acicula present from setiger 2 through setiger 8-12, as long as or slightly longer than neuropodial acicular lobe. Neuropodia with conical acicular lobe and inferior retractable setal lobe supported by inferiormost seta (Fig. 13.7B); ventral cirri short, cirriform. Supraacicular setae including 1 to 3 serrated capillary setae (Fig. 13.7C) and 1 (occasionally 2) furcate seta with unequal tines and 1-2 rows of fine serrations below shorter tine; longer tine with delicate wing on inner side (Fig. 13.7D). Subacicular fascicle with 2-4 compound setae having unidentate, finely serrated blades of varying lengths; shafts bifid with coarse subdistal serrations (Fig. 13.7E). Far posterior setigers occasionally with simple pointed inferior setae.

Pygidium rounded, longer than preceding setigers, with 2 pairs of clavate subterminal cirri.

Remarks. To date, three species of *Pettiboneia* have been reported from California: the type species *P. sanmatiensis* Orensanz, 1973, *P. dibranchiata* (Armstrong and Jumars, 1978), and *P. brevipalpa* Hilbig and Ruff, 1990. *Pettiboneia brevipalpa* is similar to *P. sanmatiensis* in the number of notopodia, the shape of the prostomium, the number of maxillary rows, and the size and shape of the pygidial cirri. However, it is easily distinguished from the latter species by the palps that are much shorter than the antennae, with palpophores shorter than the palpostyles. In addition, *P. brevipalpa* lacks eyes, and the notopodia are longer in relation to the neuropodia than in *P. sanmatiensis*.

Type Locality and Type Specimens. Boca de Quadra, Alaska: holotype (USNM 130084) and 15 paratypes (USNM 130086 - 130091), 3 paratypes (BMNH ZB 1990.29-31), 1 paratype (ZMH P-20325); Smeaton Bay, Alaska: 1 paratype (BMNH ZB 1990.32).

Biology. Hilbig and Ruff (1990) reported the occurrence of mature males and females in Alaska between April and July. There are up to 8 round or elongated eggs per setiger averaging 40 ìm in length and 27 ìm in width. The eggs are first present between setigers 14 and 21, and the sperm appear between setigers 15 and 19. The gametes are associated with the bases of the parapodia and continue for most of the length of the worm. The species is found in fine silts and silt mixed with sand.

Distribution. Alaska to central California, 140 - 1457 m.

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Appendix A

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, or acLa, acicular lobe
acS, acicular seta
ai, aileron or wing on jaw
an, antenna
ap, accessory papilla
br, branchia
buS, buccal segment
bv, blood vessel
ca, capsule
car, caruncle
cer, ceratophore
cG, chromophile gland
ch, chevron
co, cortex
cP, cephalic peak of prostomium
cph, cirrophore or base of cirrus
cr, crotchet
ct, ctenidium or ciliated cushion
cutPl, cutting plate
D, dorsal
dC, dorsal cirrus or notocirrus
dLa, dorsal lamella
dT, or dTu, dorsal tubercle
DtC, dorsal tentacular cirrus
el, elytron or scale
elph, elytrophore
ey, eye
fAn, frontal antenna
fPa, frontal palp (in onuphids)
fTu, facial tubercle
g, gap
gl, gland
hG, hyaline gland
iLan, inner lateral antennae
InfLatAn, inferior lateral antenna
intC, interramal cirrus or intercirrus
intSo, interramal sensory organ
lAn, lateral antenna
lC, lateral cirri
li, ligule
lig, ligament
lo, lobe
lPa, labial palps (in onuphids)
lSup, lateral support piece (lumbrinerid jaw)
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
lLan, outeral lateral antennae
oR, oral ring
ov, ovary
pAn, palpal antenna
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
st, style
sty, stylodes of parapodia or parapodial fringe
subF, subpodial fringe or ventral pad
SupLatAn, superior lateral antenna
supNeL, superior neuropodial lobe
subPap, subpodial lateral papilla or ventral cirrus
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

Appendix B

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.

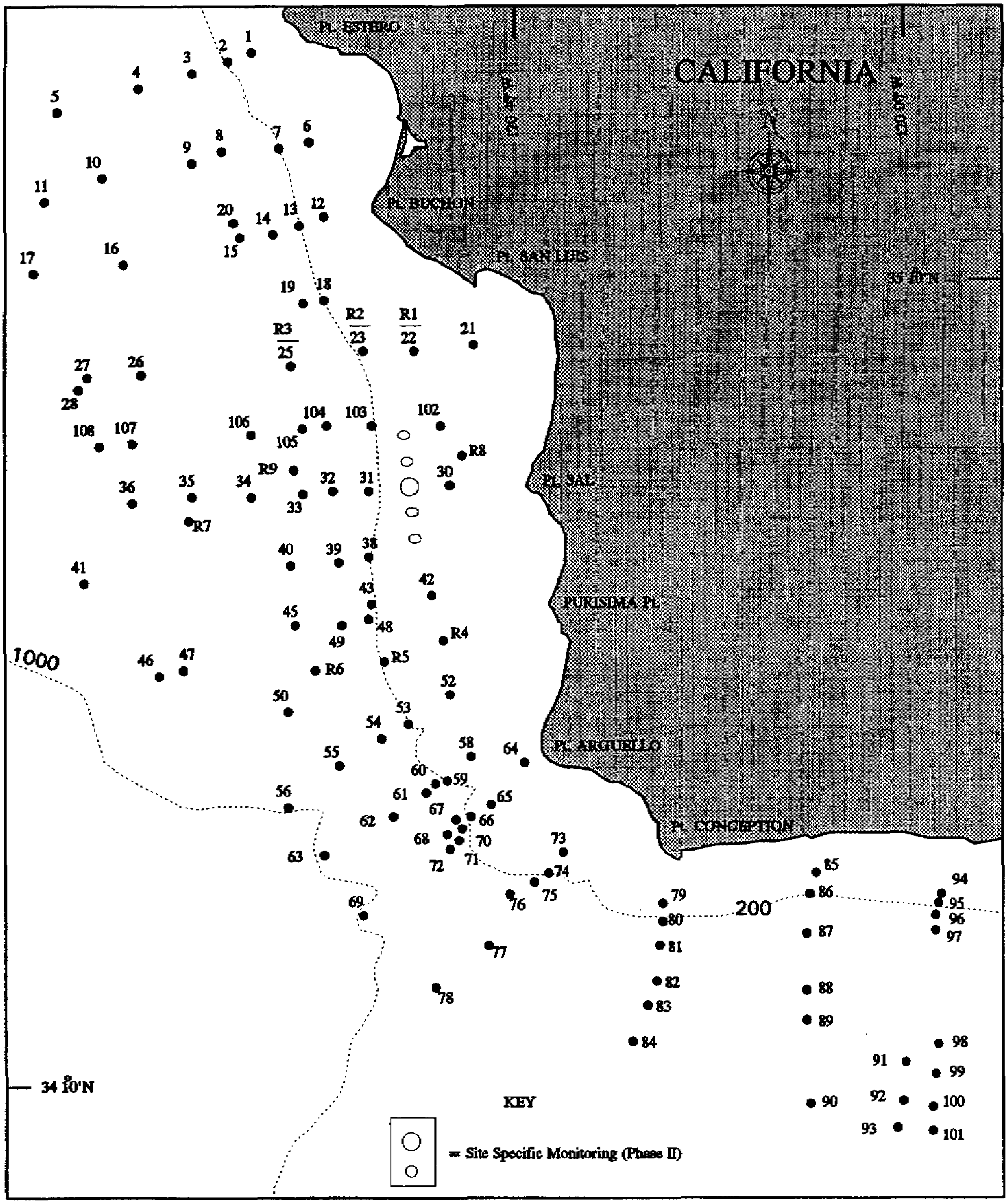

Figure A.1. Map showing location of soft substrate stations from Phase I and Phase II MMS Reconnaissance and Monitoring Programs.

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. Sampling dates of MMS Phase II Monitoring Program.

Cruise	Date
1-1	October 1986
1-2	June 1987
1-3	May 1987
1-4	July 1987
2-1	October 1987
2-2	January 1988
2-3	May 1988
3-1	October 1988
3-2	May 1988

Table A.4. MMS Phase I - Locations of hard-substrate transects.

Station	Beginning Latitude	Longitude	End Latitude	Longitude	Depth (m)
1 A/B	34°24.454′N	120°01.876′W	34°24.464′N	120°00.878′W	69-73.5
1 C/D	34°24.076′N	120°00.443′W	34°24.184′N	120°01.480′W	73.5-78
2 A/B	34°11.377′N	120°29.318′W	34°11.289′N	120°28.774′W	110-126
2 C/D	34°10.984′N	120°28.094′W	34°10.780′N	120°27.554′W	120-123
4 A/B	34°27.539′N	120°40.364′W	34°28.162′N	120°40.189′W	168-237
6 A/B	34°30.246′N	120°35.555′W	— —.—	— —.—	54-63
6 C/D	— —.—	— —.—	34°30.421′N	120°34.315′W	54-63
13 A/B	34°42.570′N	120°47.899′W	34°42.107′N	120°48.253′W	92-100
13 C/D	34°42.556′N	120°48.147′W	34°42.974′N	120°47.424′W	88.5-100.5
14 A/B	34°43.589′N	120°49.093′W	34°42.826′N	120°48.370′W	96-105
14 C/D	34°43.244′N	120°49.406′W	34°42.893′N	120°48.822′W	105-117
16 A/B	34°46.544′N	120°50.197′W	34°45.912′N	120°49.726′W	91.5-123
17 A/B	34°49.382′N	120°50.768′W	34°49.600′N	120°50.688′W	160.5-168
19 A/B	34°47.833′N	120°51.425′W	34°47.097′N	120°50.793′W	148.5-177
20 A/B	34°46.470′N	120°50.289′W	34°46.140′N	120°49.885′W	90-130.5
21 A/B	34°47.335′N	120°45.903′W	34°47.548′N	120°46.123′W	75-90
22 A/B	34°50.365′N	120°48.221′W	34°50.990′N	120°48.365′W	114-115.5
23 A/B	34°49.868′N	120°47.393′W	34°50.003′N	120°47.480′W	93-102
25 A/B	35°05.662′N	120°47.562′W	35°06.036′N	120°47.652′W	64.5-72
26 C/D	35°11.586′N	120°55.556′W	35°11.555′N	120°55.233′W	108-111
27 A/B	35°20.906′N	120°59.657′W	35°21.035′N	120°59.603′W	96-126
28 A/B	35°21.539′N	120°59.641′W	35°21.867′N	120°59.299′W	96-105
29 A/B	35°27.864′N	121°05.331′W	35°27.805′N	121°05.277′W	102-106.5

Table A.5. MMS Phase II - Locations of hard-substrate photosurvey stations.

Station	Latitude	Longitude	Depth (m)
PH-E	34°30.26′N	120°42.76′W	119
PH-F	34°30.81′N	120°42.36′W	105
PH-I	34°29.96′N	120°41.68′W	107
PH-J	34°29.82′N	120°41.82′W	117
PH-K	34°29.37′N	120°42.26′W	160
PH-N	34°29.21′N	120°42.05′W	166
PH-R	34°29.11′N	120°42.67′W	213
PH-U	34°31.48′N	120°43.51′W	113
PH-W	34°31.52′N	120°45.86′W	195

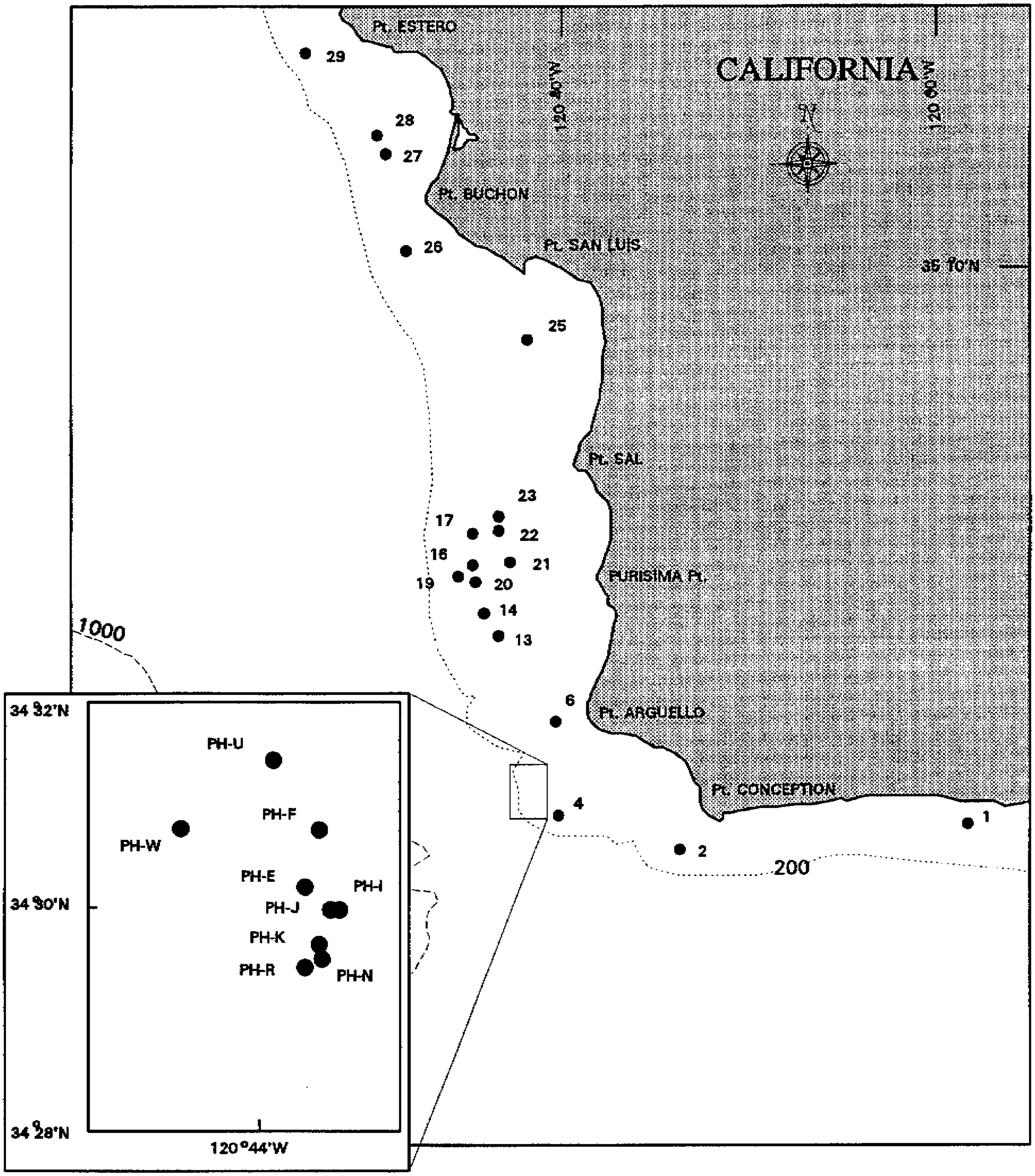

Figure A.2 Map showing locations of hard substrate stations from Phase I and Phase II MMS Reconnaissance and Monitoring Programs.

The Department of the Interior Mission

As the Nation's principal conservation agency, the Department of the Interior has responsibility for most of our nationally owned public lands and natural resources. This includes fostering sound use of our land and water resources; protecting our fish, wildlife, and biological diversity; preserving the environmental and cultural values of our national parks and historical places; and providing for the enjoyment of life through outdoor recreation. The Department assesses our energy and mineral resources and works to ensure that their development is in the best interests of all our people by encouraging stewardship and citizen participation in their care. The Department also has a major responsibility for American Indian reservation communities and for people who live in island territories under U.S. administration.

The Minerals Management Service Mission

As a bureau of the Department of the Interior, the Minerals Management Service's (MMS) primary responsibilities are to manage the mineral resources located on the Nation's Outer Continental Shelf (OCS), collect revenue from the Federal OCS and onshore Federal and Indian lands, and distribute those revenues.

Moreover, in working to meet its responsibilities, the **Offshore Minerals Management Program** administers the OCS competitive leasing program and oversees the safe and environmentally sound exploration and production of our Nation's offshore natural gas, oil and other mineral resources. The MMS **Royalty Management Program** meets its responsibilities by ensuring the efficient, timely and accurate collection and disbursement of revenue from mineral leasing and production due to Indian tribes and allottees, States and the U.S. Treasury.

The MMS strives to fulfill its responsibilities through the general guiding principles of: (1) being responsive to the public's concerns and interests by maintaining a dialogue with all potentially affected parties and (2) carrying out its programs with an emphasis on working to enhance the quality of life for all Americans by lending MMS assistance and expertise to economic development and environmental protection.