Chapter 19

Phylum Sipuncula

William B. Jaeckle and Mary E. Rice

Introduction

The Sipuncula is a phylum of unsegmented coelomate marine worms that are found in all the world's oceans at depths ranging from the intertidal zone to the abyssal plain. They occupy a variety of habitats including crevices among rocks, oysters, and mussels, among the roots of seagrasses, and in burrows in soft sediments such as sand and mud. In tropical and subtropical waters, they also inhabit burrows, presumably of their own formation, in coral and calcareous rubble. Adult sipunculans range in size from a length of ~ 1 mm to more than 300 mm. Distinguishing features are a complete lack of segmentation, a retractable anterior introvert, a recurved gut leading to a dorsal anus in the middle to upper trunk region, a pair of nephridia, and a single, unpaired ventromedial nerve cord.

The swimming larval form, unique to the Sipuncula, is the pelagosphera (Figure 19.1). The term was first used for a larval sipunculan that was mistakenly described as an adult and named *Pelagosphaera aloysii* (Mingazinni, 1905). The mistake was soon recognized, but the name pelagosphera has remained in the literature to designate the larval form of sipunculans that succeeds the trochophore stage of development (cf. Rice, 1973).

Reproduction

Sipunculans are usually dioecious, with the known exceptions of a hermaphroditic (Åkesson, 1958) and a parthenogenetic species (Pilger, 1978). The gonads are borne on the ventral body wall at the site of attachment of the introvert retractor muscles. Immature gametes are released from the gonads and gametogenesis is completed within the spacious body coelom. Fully developed gametes are collected by each of the paired nephridia and forcibly expelled into the environment via the nephridiopores. Spawning is epidemic with no apparent trend in the timing of male and female gamete release. Sipunculan eggs are typically surrounded by a thick and multilayered envelope that is perforated by small pores that are ≤ 0.8 μm in diameter. Fertilization, subsequent embryogenesis, and larval development occur outside of the female body.

Although both direct and indirect development are known among sipunculans, the majority of species have indirect development and produce two free-living larval forms (Rice, 1967, 1973, 1981). The first larval form, the trochophore, is common to all indirectly developing sipunculans. Similar to those of other spiralian taxa (e.g., Annelida and Mollusca), the trochophore of sipunculans possesses a single circumferential band of ciliated prototroch cells and an apical tuft of cilia. Differing from many other trochophores, the sipunculan trochophore develops within a thick egg envelope, lacks a functional digestive tract, and is lecithotrophic (non-feeding) (Figures 19.2A–D). The duration of this larval stage is relatively short, ranging from 2 to 21 days (Rice, 1976; Rice, unpublished observations). The simplest larval life history of sipunculans with indirect development consists only of a trochophore larva (e.g., *Phascolopsis gouldii*, Gerould, 1906). In this case, metamorphosis of the planktonic larva to a benthic juvenile involves the gradual loss of larval features and acquisition of adult characteristics. Most species studied develop from a fertilized egg to a trochophore larva,

ATLAS OF MARINE INVERTEBRATE LARVAE
ISBN 0-12-773141-5

which then metamorphoses into a new larval form, the pelagosphera (Figures 19.2D–F, 19.3). Unique to the Sipuncula, the pelagosphera larva is characterized by the reduction or loss of the pre-oral prototrochal ciliary band and the development and expansion of a post-oral band of cilia, the metatroch, which serves as the larval locomotory organ (Figures 19.2, 19.2).

There are two general patterns (Rice, 1975, 1976, 1981) among those species whose life history includes these sequential larval forms. In some species (e.g., *Golfingia elongata*, Åkesson, 1961; and *Thysanocardia nigra* (= *Golfingia pugettensis*), Rice, 1975), the lecithotrophic trochophore larva is followed by a relatively short-lived (2–13 days) lecithotrophic pelagosphera larva (Figure 19.4A), which metamorphoses into a benthic juvenile. However, in the majority of species with this biphasic larval life style, the trochophore larva is followed by a potentially long-lived (6–7 months), planktotrophic (feeding) pelagosphera larva (Figures 19.1, 19.3, 19.4B, 19.5A–E). At the end of their planktonic life, planktotrophic pelagosphera larvae undergo settlement and enter the benthos. After 1 to 2 days the settled larva has lost the metatrochal cilia, the trunk has elongated, and anterior tentacles have begun to form (Figures 19.5F, 19.6B,C). The remaining metamorphosis to the juvenile form is gradual and occurs over the ensuing 2 or more weeks (Figures 19.5F–G) (Rice, 1976).

Anatomy of larvae

Trochophore larvae

Trochophore larvae develop in and remain encased within the thick egg envelope. The body of the larva is divided into anterior and posterior hemispheres by the development of the complete prototrochal (pre-oral) ciliary band (Figures 19.2A–C, 19.5A). Cilia extend through the pores in the egg envelope and their beating propels the larva through the water column. The prototroch is commonly the sole or the most prominent ciliary band in the trochophore; however, in a few species, a post-oral metatrochal and pre-prototrochal bands are also apparent. In one species, *Sipunculus nudus*, the entire trochophore is covered with cilia and this ciliature is presumed to be homologous to the prototroch (Gerould, 1903) (Figures 19.7A,B). Each trochophore possesses a pair of eye spots that is associated with the apical plate of the anterior hemisphere. A tuft of long cilia (apical tuft) arises from the epidermis at the apex of the apical plate and extends through the pores of the residual egg envelope (Figures 19.2A–D, 19.5A, 19.7A). No mouth or functional digestive system is present. At the end of the trochophore stage, an invagination of the epidermis forms on the ventral surface, posterior to the prototroch, and denotes the future location of the mouth (Figures 19.2A–D).

Trochophore metamorphosis

Metamorphosis of trochophore larvae follows one of two paths. In some species, the trochophore becomes transformed into a lecithotrophic pelagosphera (Figure 19.4A); in most species, however, the trochophore develops into a planktotrophic pelagosphera larva (Figures 19.2, 19.4B, 19.5A–E, 19.7C–D). Regardless of the outcome of this metamorphosis, several common morphological changes occur that involve the loss of characters of the trochophore larvae and the development of structures characteristic of pelagosphera larvae. The surrounding egg envelope is shed in a few species (Figures 19.7B,C), but more commonly is retained as part of the cuticle of the pelagosphera larva (Figures 19.2, 19.4A). The body elongates and the internal coelomic compartment is expanded, and the once prominent band of prototrochal cilia is lost or significantly reduced (Figures 19.2F, 19.3, 19.5B). A new band of cilia, the metatroch, is formed posterior to the position of the future mouth and the prototroch (Figures 19.1B, 19.2D–F, 19.3B, 19.4, 19.5B–E, 19.7D). At the posterior extremis of the larval body in most species, a retractable attachment organ called the terminal organ develops (Figures 19.2F, 19.3, 19.4B, 19.5C). Internally, at least two pairs of retractor muscles are formed (Figures 19.1B,D, 19.3).

At metamorphosis from the trochophore to planktotrophic pelagosphera larvae, the mouth and anus are opened to the exterior through a rupture of the overlying egg envelope, thus completing the formation of a functional gut. At the same time, an eversion of the ventral stomodeum results in a backward rotation of the head, thus moving the apical head to a more dorsal position, while ventrally interrupting the band of prototrochal cilia and everting the heavily ciliated stomodeal opening to the exterior where it becomes the ventral surface of the head.

Pelagosphera larvae

The body of pelagosphera larvae is divisible into three regions: (1) the anteriormost head, (2) the mid-region, inclusive of the metatrochal ciliary band, and (3) the trunk (Figures 19.1B, 19.4A). The ventral surface of the head of pelagosphera larvae is densely ciliated and medially bisected by a groove or indentation that extends from the ventrally positioned mouth to the anteriormost extent of the head (Figures 19.6A,D,E). Amongst the cilia of the ventral head are openings of numerous gland cells. Below (posterior to) the mouth protrudes an extensible lower lip (Figures 19.6D,E). The medial and proximal surfaces of the lip possess an extensive ciliature,

but the lateral and distal regions of the lower lip may lack cilia, and, in some species, the margin of the lip possesses a series of long cilia (Figure 19.6E). A single pore normally found at the proximal to middle region of the lower lip represents the common opening of paired lip glands. At the base of the lower lip exists a transverse slit that houses the muscular buccal organ (Figures 19.6D,E). The buccal organ can be protruded from or retracted into this slit and, in conjunction with the lower lip, lip glands, and the gland cells of the oral ciliature, is believed to be involved in feeding (Rice, 1975). The mechanism(s) employed by planktotrophic pelagosphera larvae to concentrate and clear suspended particulate foods remains unresolved, but Rice (1976) has reported that pelagospheras of *Apionsoma misakianum* can feed in the laboratory by removing material directly from the surfaces of bowls using structures associated with the larval head. On the dorsal surface of the head, a pair of prominent eye spots is found overlying the apical organ (Figures 19.1A,B). A U-shaped band of cilia extends from the dorsal surface of the larval head to the ventral ciliature (Figures 19.2F, 19.3A, 19.5B). This small ciliary band is believed to be a remnant of the prototrochal ciliary band so prominent in the preceding trochophore larva stage.

The mid-region of the pelagosphera larva is bounded anteriorly by the head and posteriorly by the post-metatrochal sphincter muscles. The most prominent feature of this region is the large band of locomotory cilia, the metatroch (Figures 19.1, 19.2D–F, 19.3, 19.4, 19.5B, 19.7C,D). The mid-region can become significantly expanded while the larva is swimming, exceeding the diameter of the head and the trunk (Figure 19.1C). When a larva is disturbed, the head and the mid-region can be rapidly withdrawn into the larval trunk. This presumably defensive behavior is accomplished by the contraction of the retractor muscles (Figures 19.1, 19.3). Commonly there are two pairs of retractor muscles: one pair extending from the dorsal body wall of the trunk to the larval head; the other pair arising from the ventral body wall of the trunk and attaching to the body wall lateral to the mouth region.

The largest of the three regions of pelagosphera larvae is the trunk (Figures 19.1B, 19.4A, 19.7D). The trunk of pelagosphera larvae is extensible, expanding and retracting through contractions of the outer circular and inner longitudinal muscle bands of the body wall. A cuticle covers the epidermis of the entire larval trunk (Figures 19.2F, 19.3, 19.4A). Housed within the trunk are the stomach, intestine, rectum, and paired nephridia, and a spacious body cavity, the coelom (Figures 19.1, 19.3). The esophagus leads from the mouth (head region) through the mid-region to the trunk where it joins a slightly enlarged, bulbous stomach. The intestine is U-shaped with a portion descending toward the posterior end of the trunk and an ascending region that fuses with the rectum and terminates at the anus on the dorsal surface of the midtrunk (Figures 19.1, 19.3). The paired nephridia open separately in ventrolateral positions commonly near the level of the anus (Figures 19.1, 19.3). In many species, 'sacciform organs' of unknown function open to the exterior in dorsolateral positions at the middle to posterior level of the trunk. An unpaired ventral nerve cord extends the length of the trunk (Figure 19.1D, 19.3). At its anterior terminus, the nerve cord bifurcates to form circumesophageal connectives that pass around the esophagus at the level of the lower lip and fuse with the larval brain within the head. At the posterior terminus of the larval body, a retractable terminal organ (Figures 19.2F, 19.3, 19.4, 19.5C, 19.9) is generally present. This structure is a composite of both secretory and sensory elements (Ruppert and Rice, 1983). It functions as an attachment organ and also may be associated with both feeding behavior and site selection at settlement.

Planktotrophic pelagosphera larvae reared in the laboratory from spawnings of known adults rarely reach the size or degree of development of the oceanic pelagospheras (Figures 19.1, 19.10) and in only one case have they been observed to undergo metamorphosis to the juvenile stage (Rice, 1981; 1988). The oceanic larvae, mostly of unknown adult affinities, possess the same basic morphological features, but may have relatively different body proportions (e.g., a more elongate trunk) and greater elaboration of such features as cuticular structures, thickness of body wall, and prominence of the metatrochal ciliary band.

Morphological diversity

Significant diversity is manifested in the essential morphological features among the fully mature pelagosphera larvae found in the oceanic plankton. Ranging in size from approximately 200 μm to more than 5000 μm in length, these oceanic pelagospheras are believed to be teleplanic (i.e. larvae that can be advected across oceanic basins, Hall and Scheltema, 1975). Variation among species is evident in pigmentation, body wall transparency, and cuticular development over the exterior of the larval body (Figures 19.1, 19.8, 19.10, 19.11). Larval color ranges from yellow, pink, and orange, to green or brown (Figure 19.10). In certain species, the body wall is sufficiently transparent that internal organs are readily identifiable (Figure 19.1); in others, the body wall is relatively thick and opaque (Figure 19.10). There is also considerable variation in the development and elaboration of the trunk body wall and cuticular covering. The cuticle of some larvae is smooth, lacking cuticular elaboration (Figures 19.1, 19.8C,D, 19.10B,C,D,F). Other

species, however, are replete with papillae of a variety of forms (Figures 19.8A,B, 19.10A,E, 19.11). Although the structure of the papillae may vary among species (Figure 19.11), within a species the morphology of the papillae is generally consistent. Still others lack cuticular papillae, but possess a body wall that is defined by a series of transverse and longitudinal grooves (Figures 19.1, 19.8C,D). In papillate forms, scattered amongst the papillae of the body wall are smaller structures, of sensory and glandular function, that open to the exterior (Figure 19.11). The terminal organ may be absent or may vary in size from a relatively small, tarely extended, stick-like structure to a highly developed, extensible organ that functions in attachment of the larva to the substratum (Figures 19.8A, 19.9).

Metamorphosis from a pelagosphera larva to the juvenile

Metamorphosis of the pelagosphera larva has been observed mostly in planktotrophic oceanic larvae in the laboratory. If provided with an appropriate substratum, the larvae, when competent, will burrow into the sediment and subsequently begin the morphological transformation from a planktonic larva to a benthic juvenile. The cues for larval settlement are not entirely understood, but (Rice, 1986) reported that metamorphosis of the oceanic pelagosphera larvae of *Apionsoma misakianum* was considerably increased over that of controls when larvae were exposed to a combination of sediment and seawater that had previously been in contact with conspecific adults. Metamorphosis of the pelagosphera involves significant morphogenesis of the head and mid-region of the larva (Figures 19.5, 19.6). The ciliation of the head is lost and the mouth migrates from an anterior and ventral position to an anterior and terminal position; a series of tentacles develops and typically (but not always) surrounds the mouth (Figure 19.6). The metatrochal cilia are lost and the mid-region elongates to form the extensible introvert of the adult (Figure 19.5G). During these alterations of the anterior portion of the body, the larval trunk elongates and the terminal organ is resorbed (Figure 19.5G).

Pelagosphera larvae are common components of the surface plankton of the warm water currents of the world's oceans (Hall and Scheltema, 1975; Scheltema and Rice, 1990). In Scheltema's studies of the North Atlantic, pelagosphera larvae were found in 75% of the stations at which collections were made. Known to exist in the larval stage for 6–7 months, pelagosphera larvae have the potential for serving to disperse the species over great geogtaphical distances and maintaining gene flow between widely separated populations (e.g., Hall and Scheltema, 1975; Scheltema and Rice 1990; Staton and Rice, 1999).

Acknowledgements

We would like to thank Dr Elizabeth Balser for het tireless efforts in assisting with the construction of figures for this chapter, Julie Pitaino for het assistance thtoughout this ptoject, and Hugh Reichardt and William Lee for collecting the sipunculan larvae examined fot this chaptet. This work represents Smithsonian Marine Station Contribution number 498.

Literature cited

Åkesson, B. (1958). A study of the nervous system of the Sipunculoideae, with some remarks on the development of two species *Phascolion strombi* Montagu and *Golfingia minuta* Keferstein. *Undersökningar över Öresund* **38**, 1–249.

Åkesson, B. (1961). The development of *Golfingia elongata* Keferstein (Sipunculidae) with some remarks on the development of neurosecretory cells in sipunculids. *Ar. Zool.* **2**, 511–534.

Gerould, J.H. (1903). *Studies on the Embryology of the Sipunculidae, I. The Embryonal Envelope and its Homologue.* Mark Anniversary Volume, pp. 439–452. Henry Holt and Co., New York.

Gerould, J.H. (1906). Studies on the embryology of the Sipunculidae, II. The development of *Phascolosoma. Zool. Jahrb. Abt. Anat. Ontog. Thiere* **23**, 77–162.

Hall, J.R. and Scheltema, R.S. (1975). Comparative morphology of open-ocean pelagosphaera. In *A Proceeding of the International Symposium on the Biology of the Sipuncula and Echiura* (eds M.E. Rice and M. Todorovic), pp. 183–197. Naucno Delo Press, Belgrade.

Mingazinni, P. (1905). Un Gifireo pelagico: *Pelagosphaera aloysii* n. gen., n. sp. *Rend. Acad. Naz. Lincei* **14**, 713–720.

Pilger, J. (1978). Reproduction of a parthenogenetic sipunculan. *Am. Zool.* **18**, 663 (Abstract).

Rice, M.E. (1967). A comparative study of the development of *Phascolosoma agassizii, Golfingia pugettensis,* and *Themiste pyroides* with a discussion of developmental patterns in the Sipuncula. *Ophelia* **4**, 143–171.

Rice, M.E. (1973). Morphology, behavior, and histogenesis of the pelagosphera larva of *Phascolosoma agassizii* (Sipuncula) *Smith. Contrib. Zool.* **132**, 1–51.

Rice, M.E. (1975). Sipuncula. In *Reproduction of Marine Invertebrates* (eds A. Giese and J. Pearse), vol. 2, pp. 67–127. Academic Press, New York.

Rice, M.E. (1976). Larval development and metamorphosis in Sipuncula. *Am. Zool.* **16**, 563–571.

Rice, M.E. (1978). Morphological and behavioral changes at metamorphosis in the Sipuncula. In *Settlement and Metamorphosis of Marine Invertebrate Larvae* (eds F.S. Chia and M.E. Rice), pp. 83–102. Elsevier North-Holland Biomedical Press, New York.

Rice, M.E. (1981). Larvae adrift: Patterns and problems in life histories of sipunculans. *Am. Zool.* **21**, 605–619.

Rice, M.E. (1986). Factors influencing larval metamorphosis in *Golfingia misakiana* (Sipuncula). *Bull. Mar. Sci.* **39(2)**, 362–375.

Rice, M.E. (1988). Observations on development and metamorphosis of *Siphonosoma cumanense* with comparative remarks on *Sipunculus nudus* (Sipuncula, Sipunculidae). *Bull. Mar. Sci.* **42(1)**, 1–15.

Ruppert, E.E. and Rice, M.E. (1983). Structure, ultrastructure, and function of the terminal organ of a pelagosphera larva (Sipuncula). *Zoomorphology* **102**, 143–163.

Scheltema, R.S. and Rice, M.E. (1990). Occurrence of teleplanic pelagosphera larvae of sipunculans in tropical regions of the Pacific and Indian Oceans. *Bull. Mar. Sci.*, **47**, 159–181.

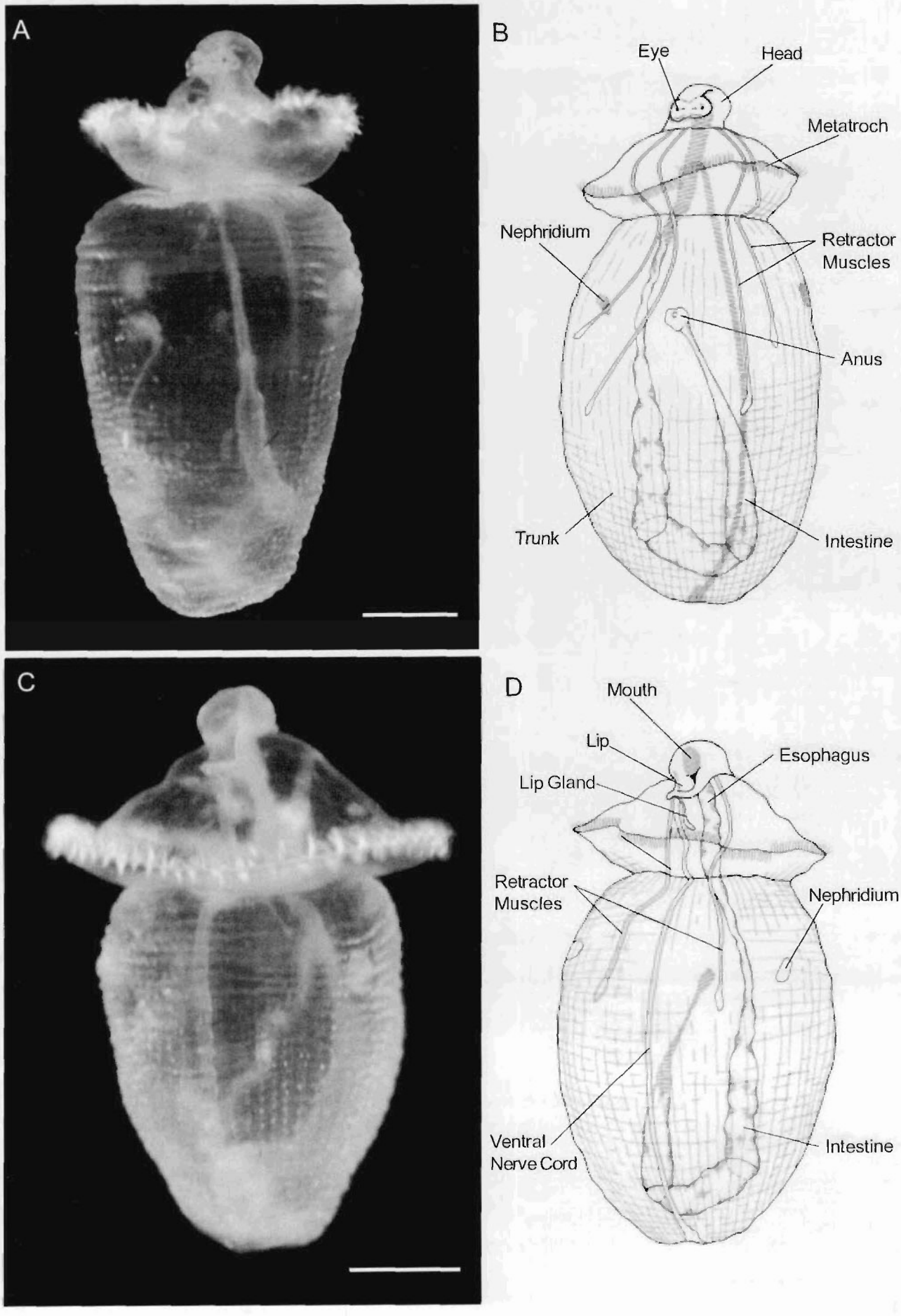
Staton, J.L. and Rice, M.E. (1999). Genetic differentiation despite teleplanic larval dispersal: allozyme variation in sipunculans of the *Apionsoma misakianum* species-complex. *Bull. Mar. Sci.* **65**, 467–480.

FIGURE 19.1

Oceanic giant pelagosphera larvae of *Sipunculus* sp. (family Sipunculidae)

This figure is reproduced in color between pages 606 and 607

A. Dorsolateral view of living larva. Scale bar: 100 µm. (Photograph by M.E. Rice).
B. Line drawing (dorsolateral view) depicting major structures in A. (Drawing by Bonnie Dennis.)
C. Ventrolateral view of living larva. Scale bar: 100 µm. (Photograph by M.E. Rice.)
D. Line drawing (ventrolateral view) depicting major structures in C. (Drawing by Bonnie Dennis.)


A
B
Eye
Head
Metatroch
Nephridium
Retractor
Muscles
Anus
Trunk
Intestine
C
D
Mouth
Lip
Esophagus
Lip Gland
Retractor
Muscles
Nephridium
Ventral
Nerve Cord
Intestine

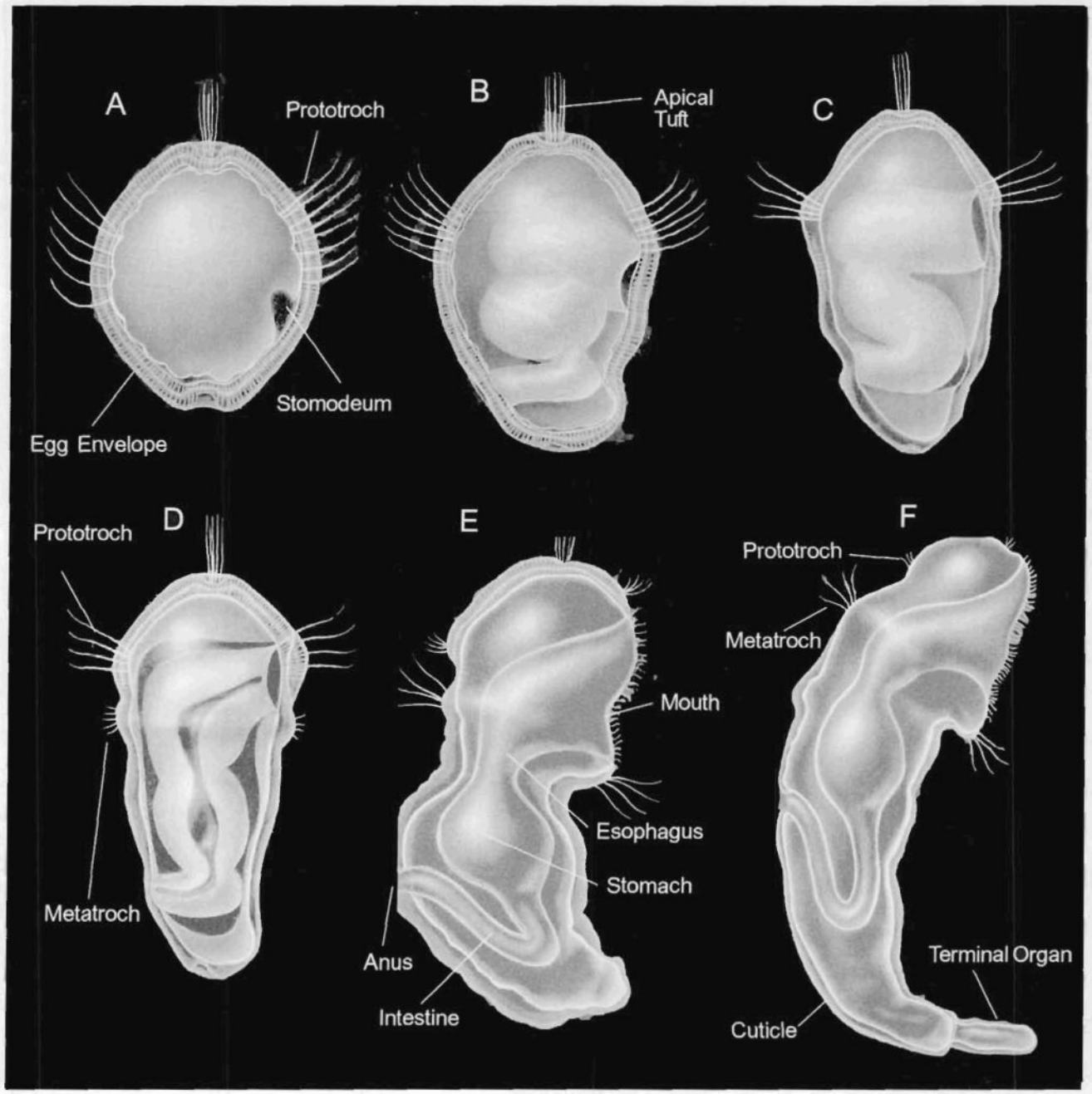


FIGURE 19.2

Diagrammatic representation of developmental stages of *Phascolosoma perlucens* (family Phascolosomatidae)

A. Early trochophore larva. (All drawings reproduced with permission from Rice, 1975.)

B. Late trochophore larva.

C and D. Premetamorphosis stages.

E. Planktotrophic pelagosphera larva, immediately after metamorphosis from trochophore stage, 2½ to 3 days of age.

F. Planktotrophic pelagosphera larva, about 1 week old.

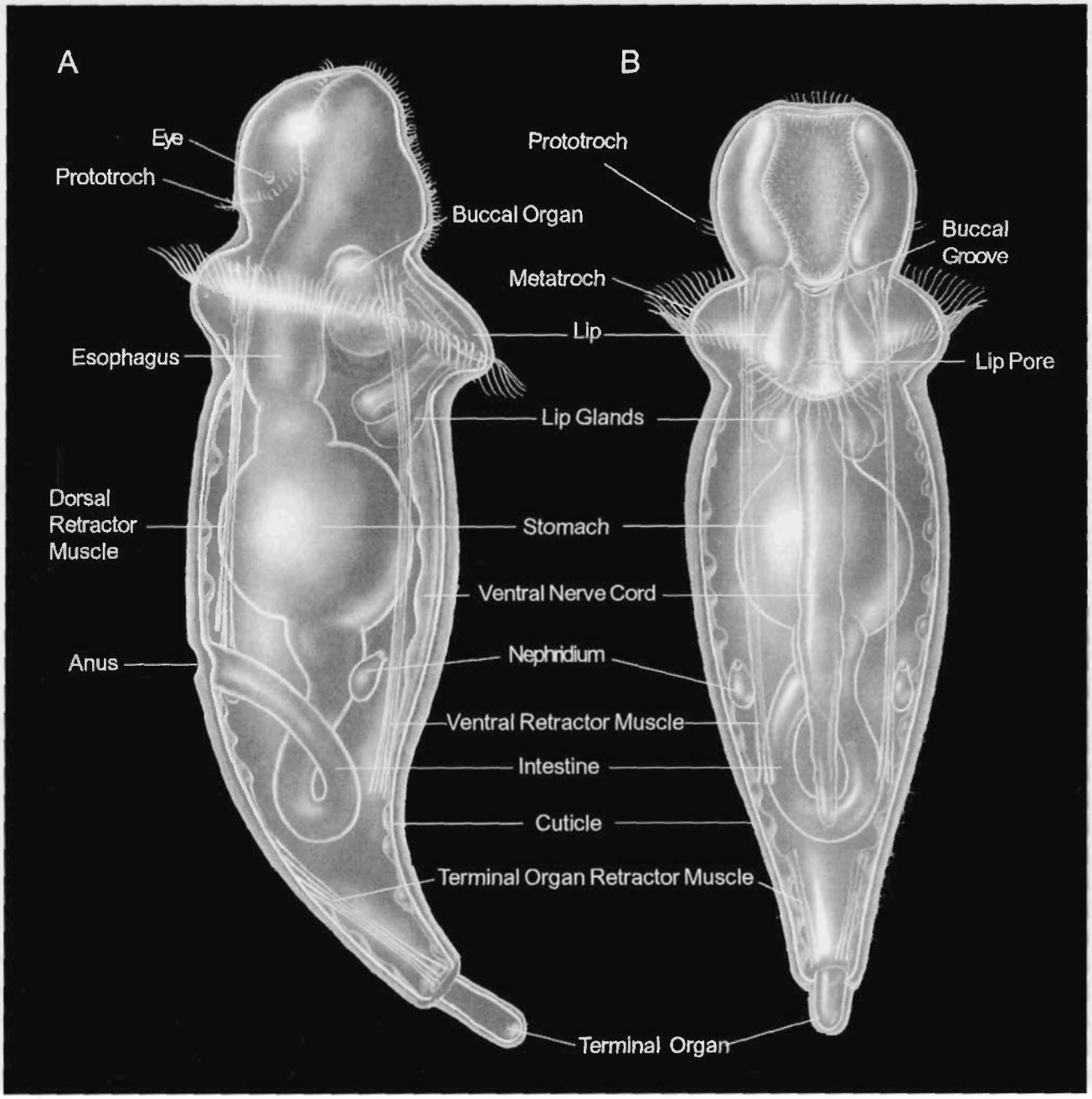


FIGURE 19.3

Internal structures of a 1-week-old planktotrophic pelagosphera larva of *Phascolosoma perlucens* (family Phascolosomatidae)

A. Bilateral view.

B. Ventral view. (Drawings reproduced with permission from Rice, 1975.)

FIGURE 19.4

Living pelagosphera larvae

A. Dorsal view of a lecithotrophic larva of *Thysanocardia nigra* (= *Golfingia pugettensis*) (family Golfingiidae), 3 days old. Scale bar: 50 µm. (Photograph by M.E. Rice.)

B. Right lateral view of a planktotrophic larva of *Nephasoma pellucidum pellucidum* (= *Golfingia pellucida*) (family Golfingiidae), about 7 days old. Scale bar: 50 µm (Photograph by M.E. Rice.)

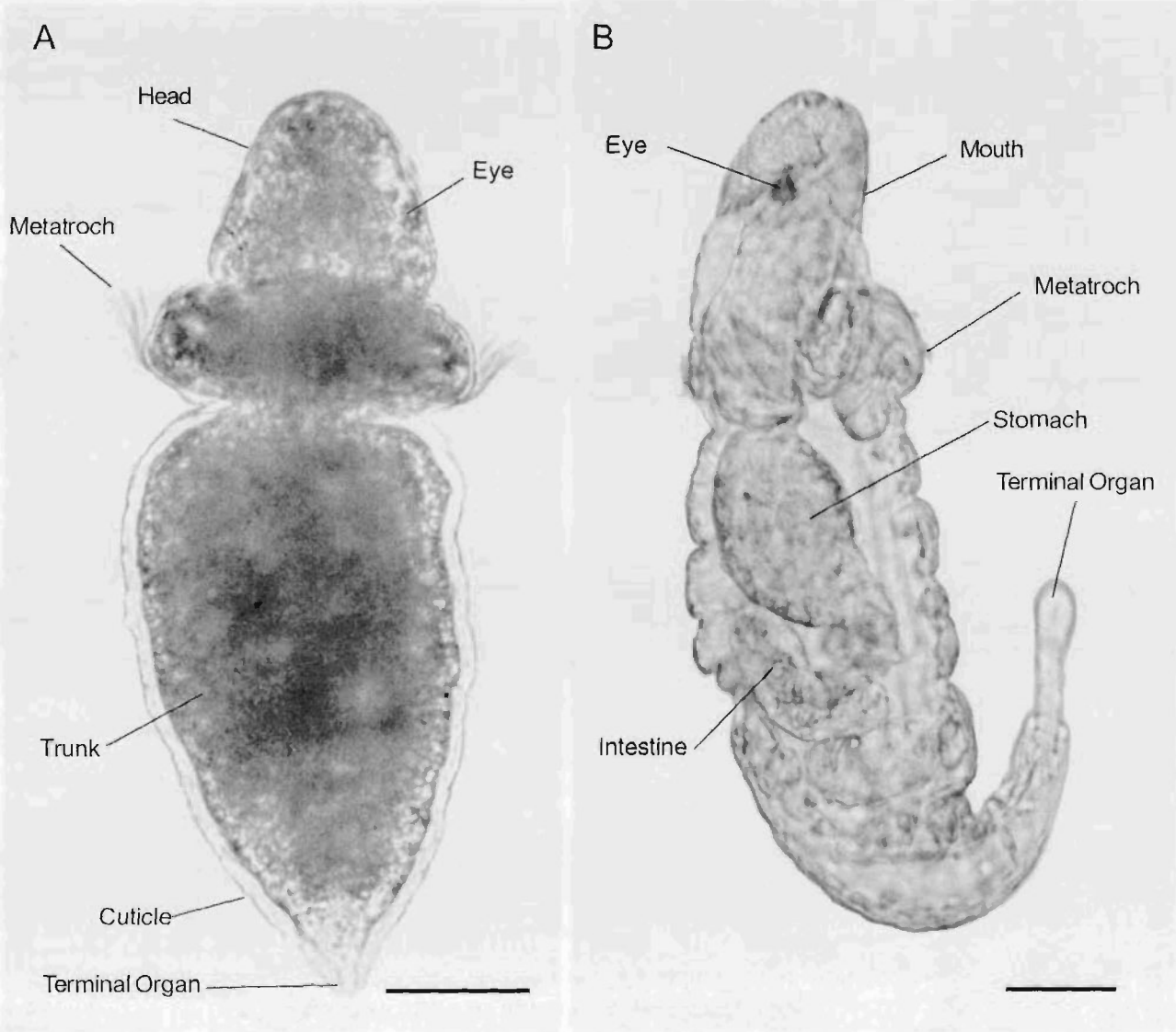

A
Head
Eye
Metatroch
Trunk
Cuticle
Terminal Organ
B
Eye
Mouth
Metatroch
Stomach
Terminal Organ
Intestine

FIGURE 19.5

Development of *Apionsoma misakianum* (family Phascolosomatidae) from trochophore larva to benthic juvenile

A. Trochophore larva. Scale bar: 10 µm. (Scanning electron micrographs A–D reproduced with permission from Rice, 1981.)

B. Early pelagosphera larva. Scale bar: 10 µm.

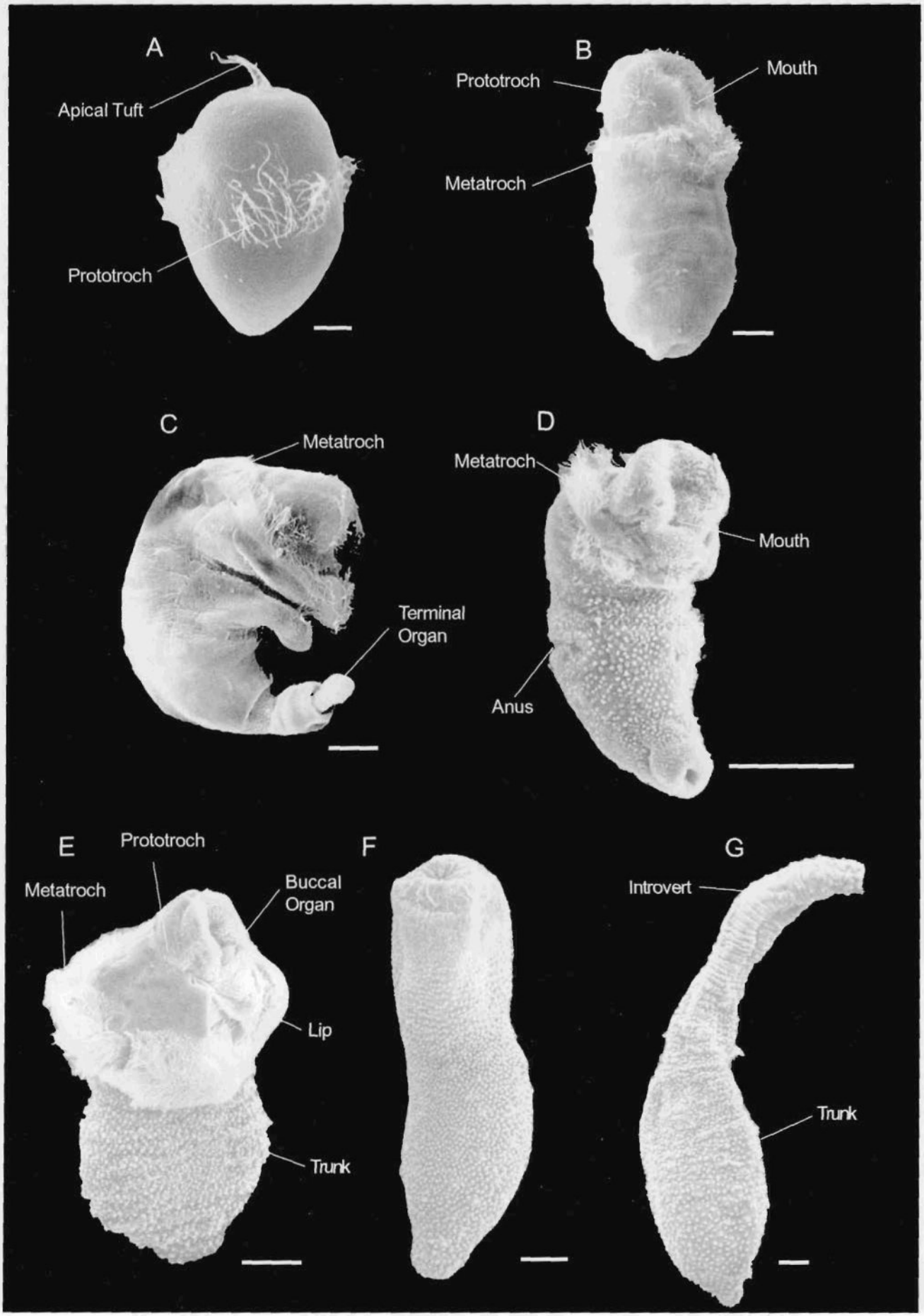
C. Late pelagosphera larva. Scale bar: 10 µm.

D. Field-collected oceanic pelagosphera larva. Note that the terminal organ is retracted into the larval trunk. Scale bar: 100 µm.

E. Oceanic pelagosphera. Scale bar: 100 µm. (Scanning electron micrographs E–G reproduced with permission from Rice, 1978.)

F. Oceanic pelagosphera in E, 5 days after beginning metamorphosis. Scale bar: 100 µm.

G. Oceanic pelagosphera in E, 10 days after beginning metamorphosis. Scale bar: 100 µm.


A
Apical Tuft
Prototroch
B
Prototroch
Mouth
Metatroch
C
Metatroch
Terminal
Organ
D
Metatroch
Mouth
Anus
E
Prototroch
Metatroch
Buccal
Organ
Lip
Trunk
F
G
Introvert
Trunk

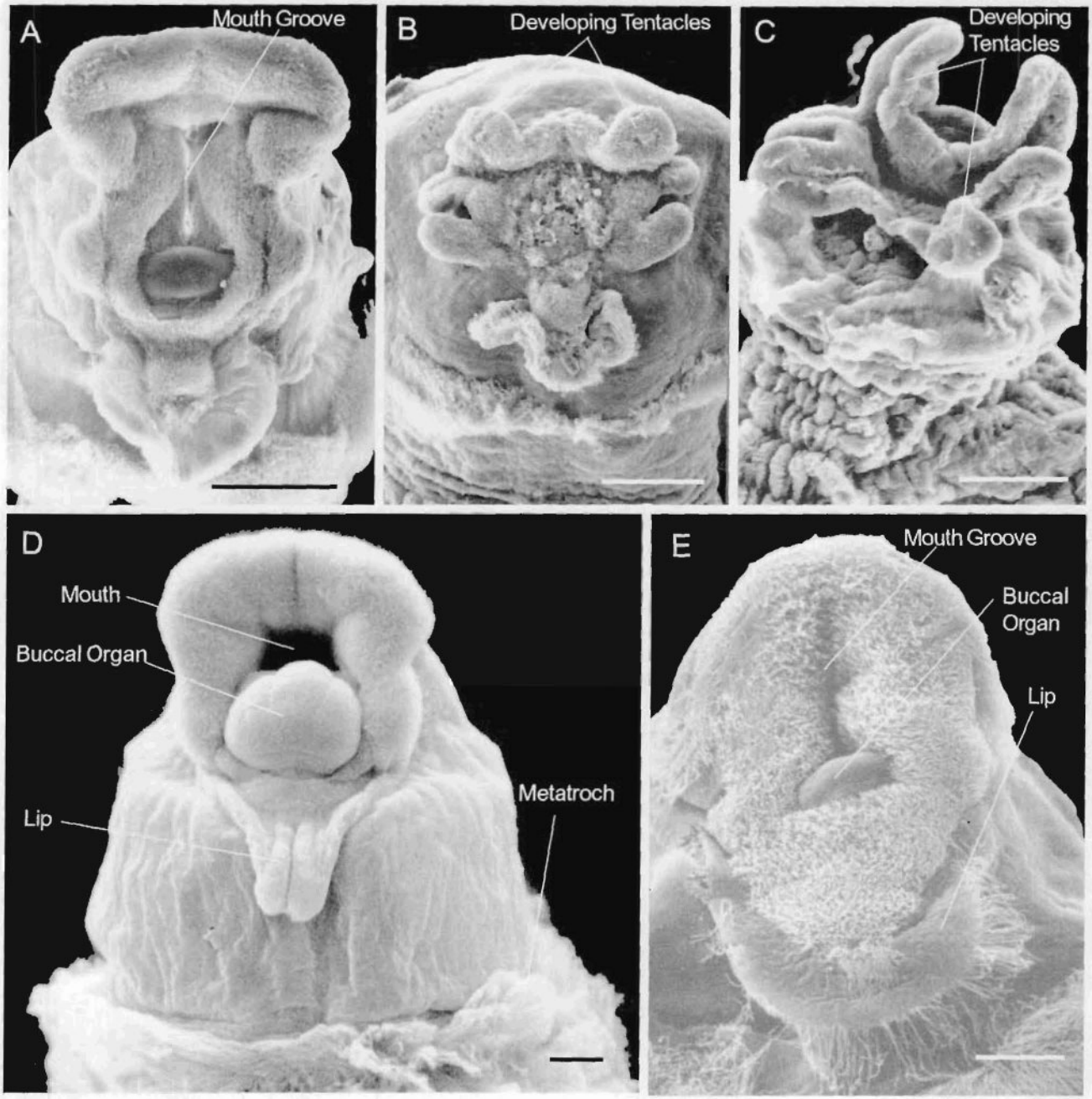


FIGURE 19.6

Head morphology and morphogenesis of the head in pelagosphera larvae

A. Ventral view of the head of an oceanic pelagosphera, *Siphonosoma cumanense* (family Sipunculidae). Scale bar: 50 µm. (Scanning electron micrographs A–E by M.E. Rice).

B. Head of *S. cumanense* showing developing tentacles during the transition to a settled juvenile. Scale bar: 50 µm.

C. Head of a benthic juvenile of *S. cumanense.* Scale bar: 50 µm.

D. Ventral surface of the head of an oceanic planktotrophic pelagosphera in the genus *Sipunculus* (family Sipunculidae). Scale bar: 40 µm.

E. Ventral view of the head of a pelagic pelagosphera, *Apionsoma misakianum* (family Phascolosomatidae) from the Gulf Stream, off Florida. Scale bar: 40 µm.

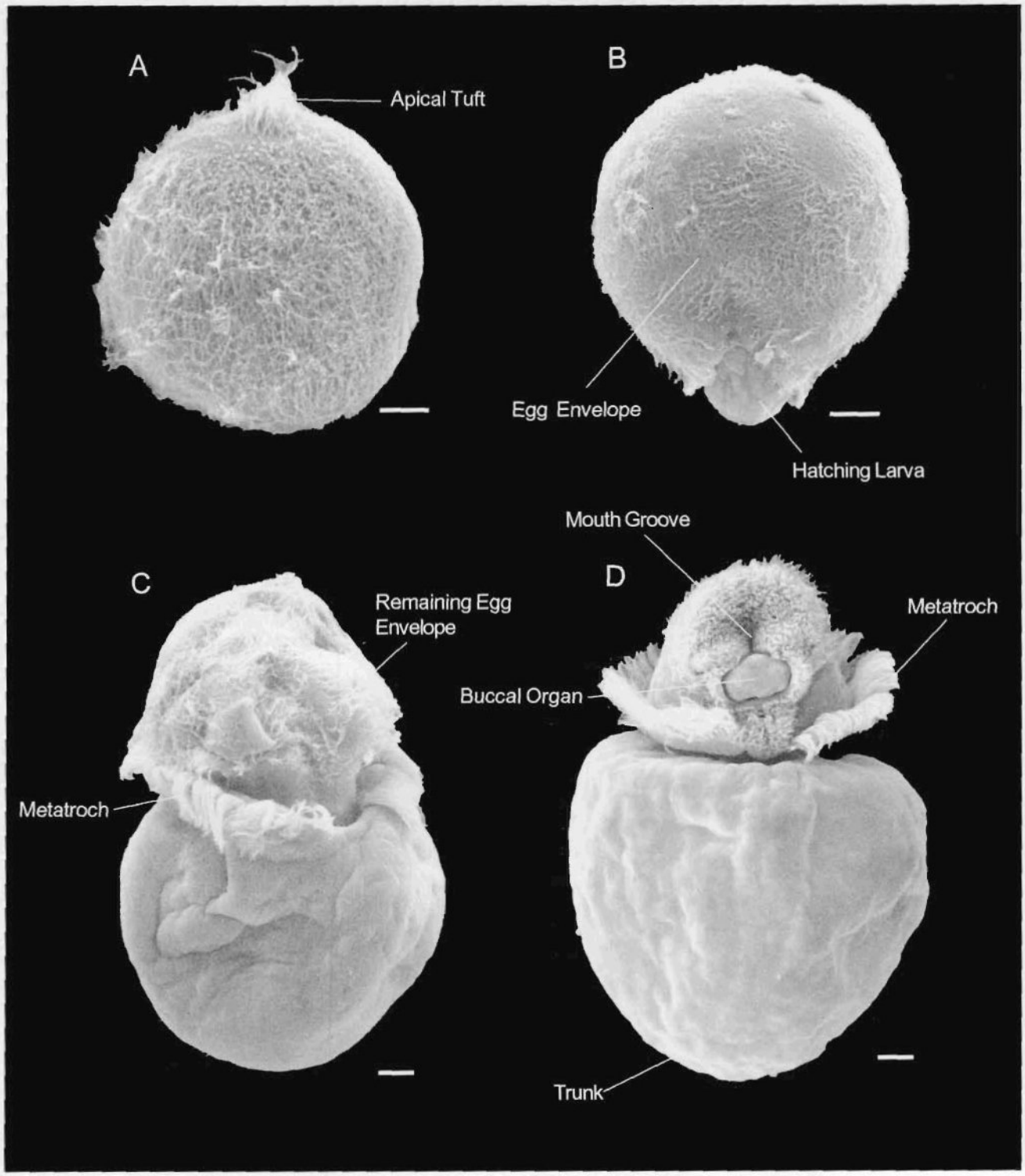


FIGURE 19.7

Scanning electron micrographs of developmental stages of *Sipunculus nudus* (family Sipunculidae)

A. Embryo at about 50 h, completely ciliated with apical tuft. All scale bars: 20 µm. (Scanning electron micrographs A–D reproduced with permission from Rice, 1988.)

B. Hatching from the egg envelope begins at about 50 h.

C. Advanced stage of hatching with the egg envelope covering the head at about 58 h.

D. Planktotrophic pelagosphera larva at 9 days of age.

FIGURE 19.8

Field-collected oceanic pelagospheras, showing variation in body form and cuticular structure

A. Unknown oceanic pelagosphera. All scale bars: 125 μm. (Scanning electron micrographs A–D by M.E. Rice and W.B. Jaeckle.)

B. Unknown oceanic pelagosphera (family Aspidosiphonidae).

C. Unknown oceanic pelagosphera larva (family Sipunculidae).

D. *Siphonosoma cumanense* (family Sipunculidae), note that the terminal organ is retracted into the larval trunk.

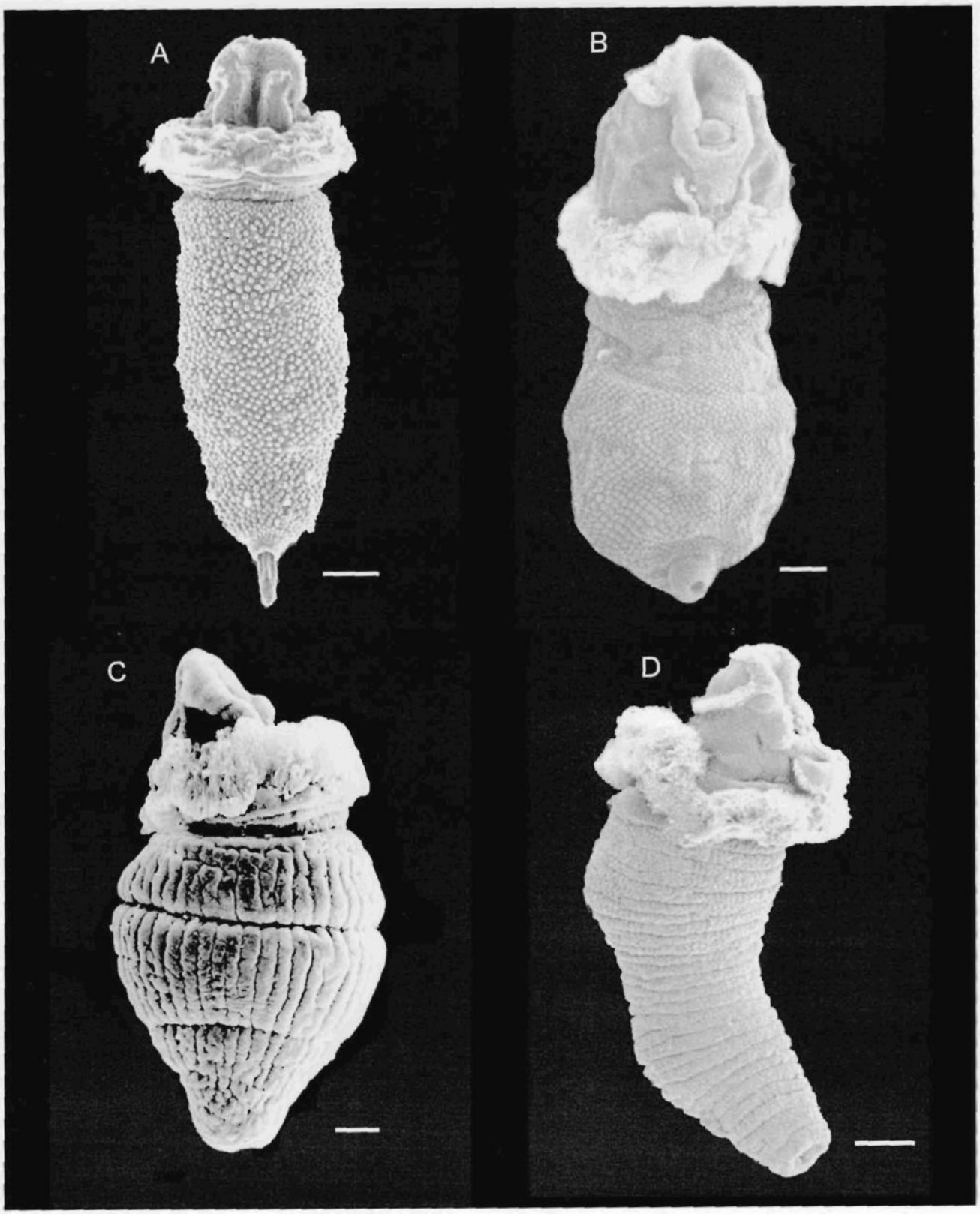

A
B
C
D

FIGURE 19.9

Scanning electron micrographs (A and B) showing differing extension of the terminal organ in an unknown oceanic pelagosphera larva

Scale bars: 50 μm. (Scanning electron micrographs by M.E. Rice.)

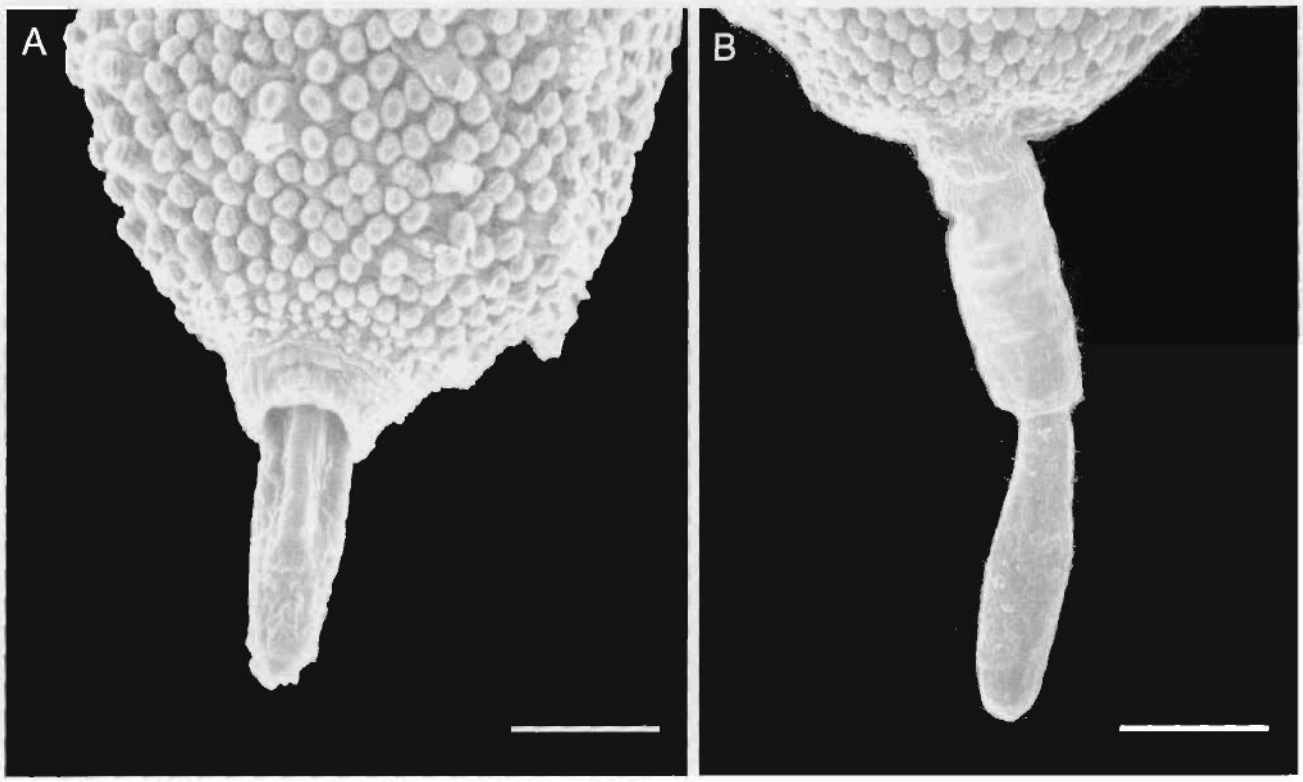

A
B

FIGURE 19.10

Photomacrographs of living oceanic pelagosphera larvae depicting diversity of form and coloration

This figure is reproduced in color between pages 606 and 607

A. Left lateral view of unknown oceanic pelagosphera (family Aspidosiphonidae). All scale bars: 150 μm. (Photograph by M.E. Rice.)

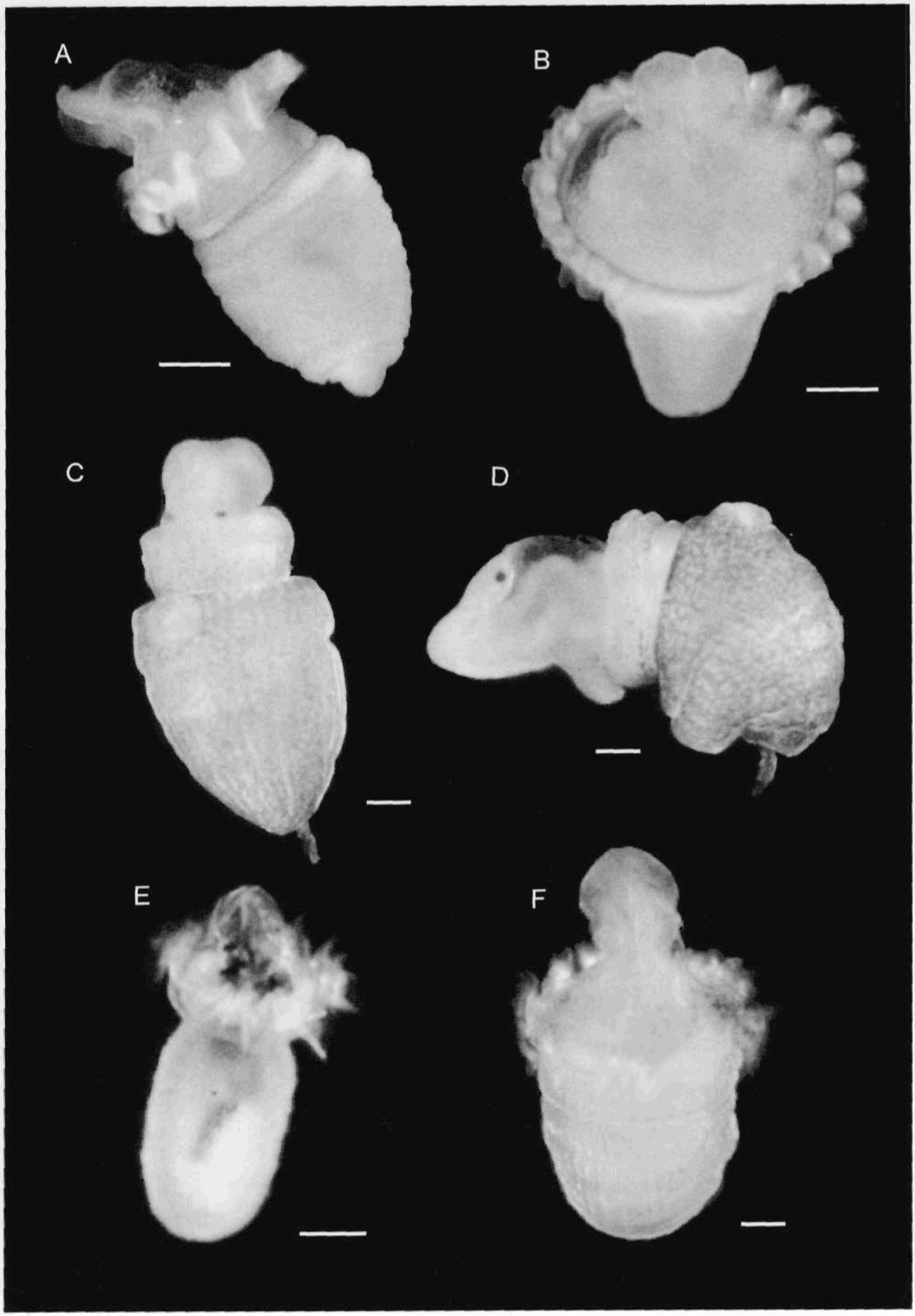
B. Dorsal view of a pelagosphera of *Siphonosoma cumanense* (family Sipunculidae). (Photograph by Elizabeth J. Balser.)

C. Dorsal view of an unknown oceanic pelagosphera (family Sipunculidae). (Photograph by M.E. Rice.)

D. Left lateral view of an unknown oceanic pelagosphera (family Sipunculidae). (Photograph by M.E. Rice.)

E. Ventrolateral view of a larva of *Apionsoma misakianum* (family Phascolosomatidae). (Photograph by Elizabeth J. Balser.)

F. Ventral view of an unknown oceanic pelagosphera. (Photograph by M.E. Rice.)


A
B
C
D
E
F

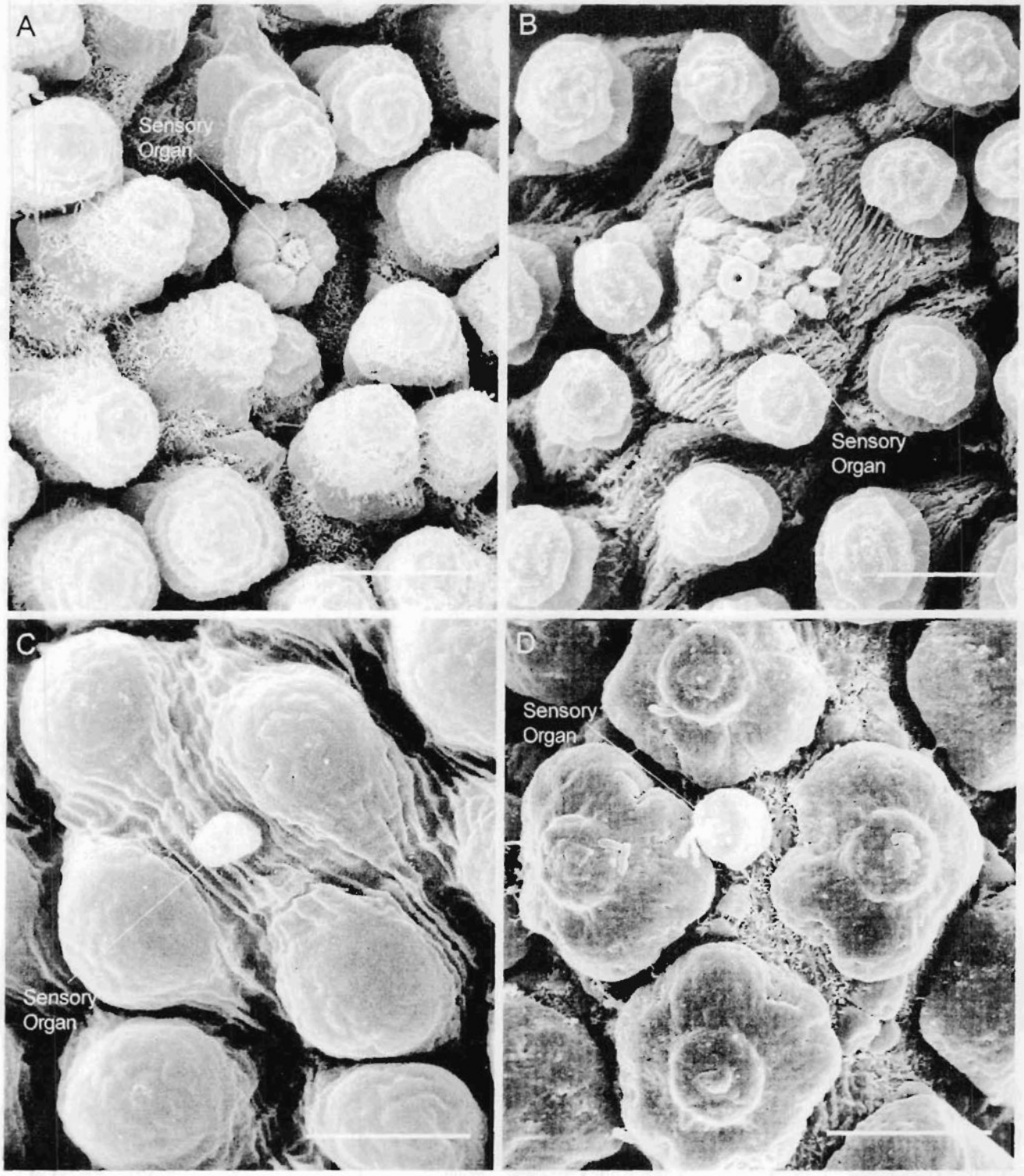


FIGURE 19.11

Diversity of papillae and sensory organs in four field-collected oceanic pelagosphera larvae from Florida

A. *Apionsoma misakianus* (family Phascolosomatidae). All scale bars: 10 μm. (Scanning electron micrographs A–D by M.E. Rice.)

B. Unknown pelagosphera larva.

C. Unknown pelagosphera larva (family Aspidosiphonidae).

D. Unknown pelagosphera larva (family Aspidosiphonidae).