

OCURRENCE OF TELEPLANIC PELAGOSPHERA LARVAE OF SIPUNCULANS IN TROPICAL REGIONS OF THE PACIFIC AND INDIAN OCEANS

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ABSTRACT

Teleplanic pelagosphaera larvae of sipunculans have been found throughout the tropical epipelagic waters of the Pacific and Indian Oceans. Evidence for their widespread occurrence is based on plankton samples from 849 locations. Among 22 tropical forms distinguished and described, 9 were encountered in the eastern Pacific (east of 140°W), 13 in the central Pacific, 8 in the west Pacific, and 11 in the tropical Indian Ocean. Four of the 13 central Pacific larval forms also occur in the eastern portion of the east tropical Pacific. Sixty-nine percent of the 13 central Pacific larval forms were also to be found in the west Pacific and Indian Oceans. The number of central Pacific forms of pelagosphaera are equal to 65% of the 20 adult shoal water species known to exist there. Among the 22 larval forms described, four were found to range throughout the tropical Pacific and Indian Oceans including the east Pacific; three additional pelagosphaeras were widely distributed throughout the Indo-Pacific as far east as the Polynesian Islands. The evidence suggests that by their dispersal, larval sipunculans play an important biogeographic and evolutionary role, but until a correspondence is established between larval forms and adult species, only tentative conclusions are possible.

The patterns of geographic distribution found among sublittoral benthic invertebrates are, on the one hand, the results of ecological constraints, both physical and biological, which limit where survival and reproduction may occur and, on the other, by the capacity of species to migrate or to be passively dispersed thereby expanding their geographic range or their spatial distribution within that range. Underlying these two contrasting contemporary determinants of spatial distribution are past events on varying time scales; for example, climatic change, changes in sea level, the opening and closing of seaways or corridors, and seafloor spreading or plate tectonics (with attendant increase or decrease in the size of ocean basins or shifts in the positions of islands with respect to major ocean currents). Events in the Holocene or the distant geologic past may well have made important contributions to the present day spatial distribution of genera and species. However, for soft-bodied benthic invertebrates only few if any fossil records survive to make it possible to directly relate such past events with the present-day geographic distribution of species. This is especially so when details of phylogenetic relationships and geographic range are very imperfectly known. Accordingly, to understand the *processes* that can determine geographic distribution of soft-bodied benthic forms today, one is restricted largely to the study of contemporary species. The capacity for dispersal may determine the possibility for a species (a) to cross biogeographic barriers, such as deep ocean basins; (b) to become established in favorable regions within their geographic range and (c) to maintain genetic continuity between disjunct populations over large geographic areas, within their range, e.g., between oceanic islands.

A large anecdotal literature exists on the various commonplace as well as unusual ways in which benthic species have been dispersed (vide: Scheltema, 1986; pp. 310-312) which include migration by adults and rafting of individuals attached to drifting objects. However, among most tropical sublittoral species the most

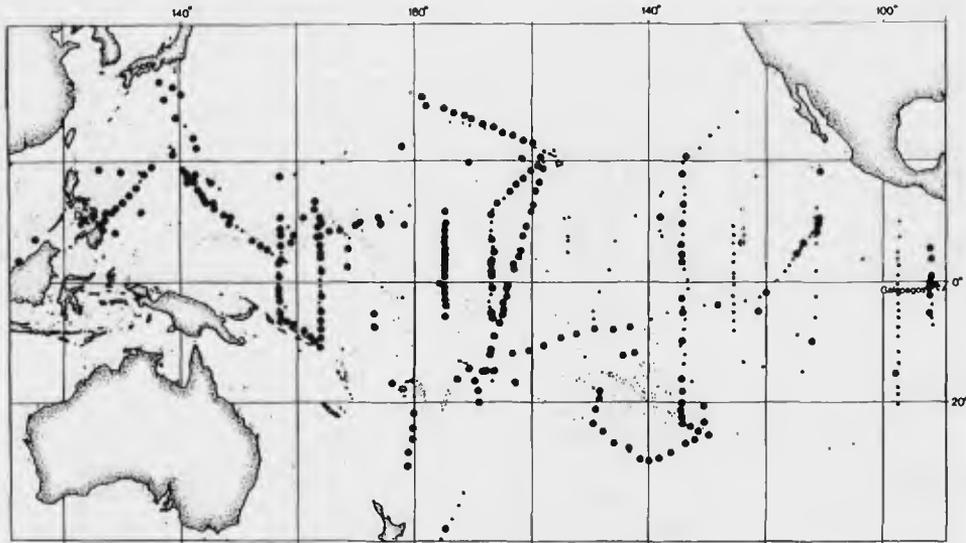


Figure 1. Distribution of teleplanic sipunculan pelagosphaera larvae in the tropical Pacific Ocean. Darkened circles indicate larvae were present; minute open circles show localities sampled where larvae were absent.

obvious means of dispersal is by the advection of planktonic larvae by surface currents. Indeed, there is now considerable evidence to show that larvae of tropical sublittoral invertebrates are carried over very long distances along the major paths of oceanic circulation. Among infaunal sipuncular species, the likelihood of adult migration or rafting is considered very remote indeed, and many such taxa from the tropics include species with planktotrophic larvae with the potential for a long planktonic life. Among such taxa are included those sipunculans that have a planktotrophic pelagosphaera larva with a planktonic development varying from 3 to 8 months (Scheltema and Hall, 1975). The research described here (1) gives evidence for the widespread distribution and dispersal of pelagosphaera larvae in the epipelagic zone of the tropical Pacific and Indian Oceans; (2) attempts to describe the larval species encountered by their external morphological characters (without resort to internal anatomy unless visible externally) (3) maps the geographic distribution of these individual larval forms presumed to belong to individual adult species and (4) considers the biogeographic implications of the dispersal of these pelagosphaera larvae.

MATERIALS AND METHODS

Data on the distribution of pelagosphaera larvae in the tropical Pacific Ocean are based upon the examination of 418 oblique plankton tows. Most of the samples were taken with 1-m diameter nets and collected over a period of 26 years between 1953 and 1979 on 15 different expeditions of the Scripps Institution of Oceanography. Material was examined from the following expeditions in the plankton collection of the Scripps Institution: (1) *Transpac* November 1953 (Snyder and Fleminger, 1965; p. 49, Chart 8) 13 stations; (2) *Capricorn* November 1952–1953 (Snyder and Fleminger, 1965; p. 39, Chart 12) 24 stations; (3) *Troll* March 1955 (Snyder and Fleminger, 1965; p. 63, Chart 25) 47 stations; (4) *Equapac* (R. V. HORIZON) August 1956 (Snyder and Fleminger, 1965; p. 78, Chart 8) 40 stations; (5) *Equapac* (R. V. STRANGER) August–September 1956 (Snyder and Fleminger, 1965; p. 79, Chart 8) 46 stations; (6) *Monsoon* September 1960, March–April 1961 (Snyder and Fleminger, 1965; p. 105, Chart 36–37) 10 stations; (7) *Circe* April 1968 (Snyder and Fleminger, 1972; p. 28, Chart 11) 14 stations; (8) *Scan* June–July 1969 (Snyder and Fleminger, 1972; p. 122, Chart 39) 23 stations; (9) *Antipode* August 1970 (Snyder and Fleminger, 1972; p. 9, Chart 5) 8 stations; (10) *Naga* March 1961

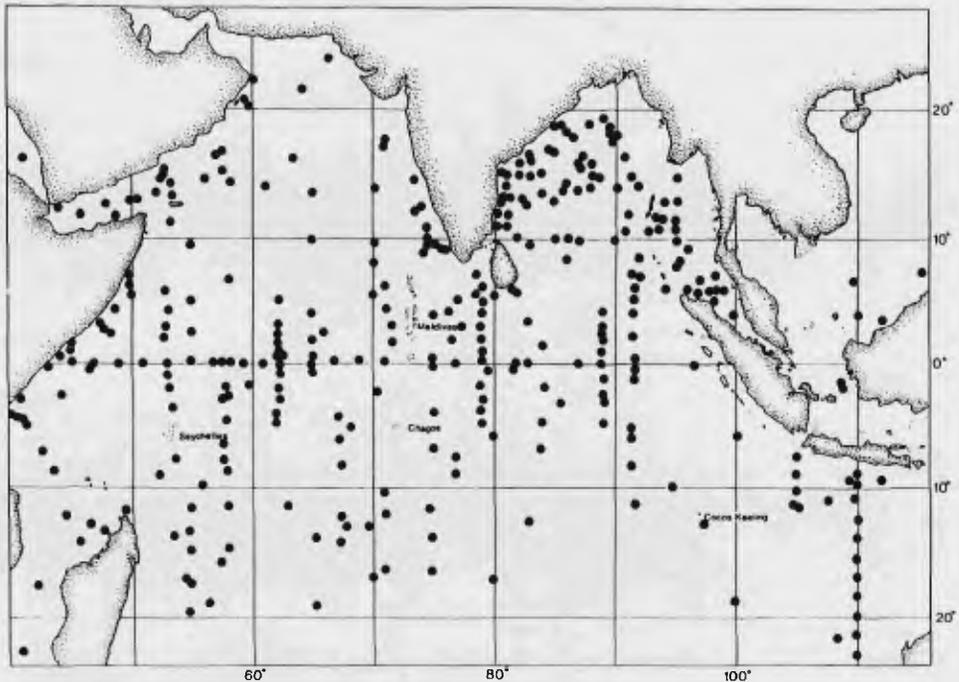


Figure 2. Distribution of teleplanic sipunculan pelagosphaera larvae in the tropical Indian Ocean. Each point shows a location where sipunculan larvae were present.

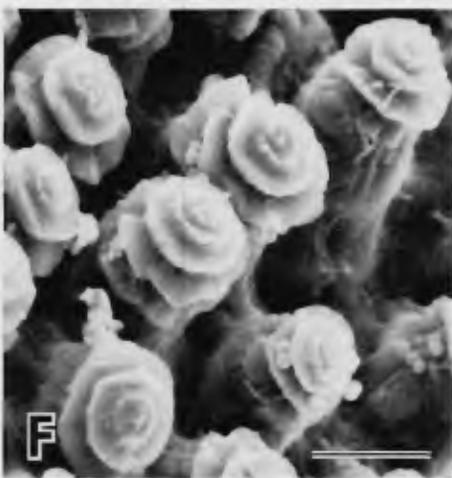
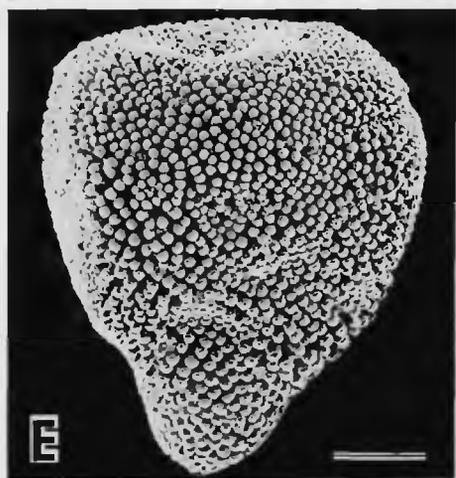
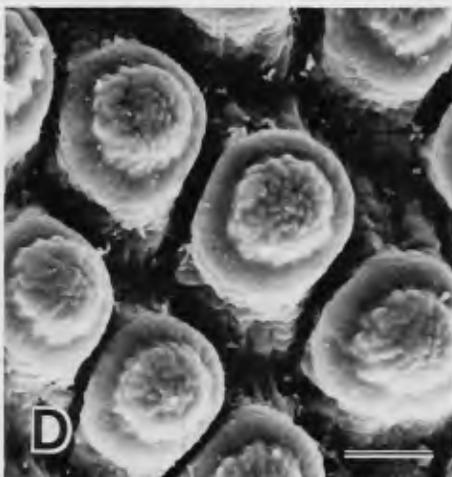
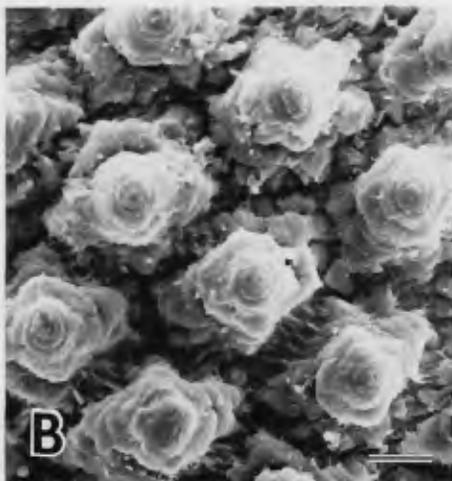
(Snyder and Fleminger, 1972; p. 70, Chart 28) 2 stations; (11) *Navocean* June 1969 (Snyder and Fleminger, 1972; p. 76, Chart 9) 3 stations; (12) *Domes* 1975–1976, 14 stations; (13) *Eastropac* 1967, R. V. ARGO voyage 11; R. V. JORDON voyage 12 and R. V. ROCKAWAY voyage 13, 55 stations. In addition to the above were three recent expeditions in which 0.75-m nets were used. These were the *73rd Scientific Cruise of the R. V. KNORR* January–February 1979 (Woods Hole Oceanographic Institution; collections made for us by Dr. E. M. Hulbert) 38 samples; *Papua* Expedition November–December 1985 (collections made for us by Dr. R. H. Richmond) 33 stations; and the *Helios* expedition September–October 1987, 50 stations.

Data on the distribution of sipunculan pelagosphaeras in the tropical Indian Ocean are based upon 429 plankton samples as follows: (1) *Lusiad Expedition* 1962, (Scripps Institution of Oceanography) 46 stations; (2) *Indian Ocean Expedition* (see Anon. 1969 for station data) including R. V. ANTON BRUUN 1963–1964, 87 stations; R. V. ARGO (*Lusiad*) 1962, 30 stations; R. V. ARGO (*Dodo*) 1964, 4 stations; R. V. METEOR 1964, 32 stations; R. V. KISTNA 1962–1964, 103 stations; R. V. DISCOVERY 1964–1965, 36 stations; R. V. VITIAZ 1960–1965, 42 stations and R. V. DIAMATINA 1962–1965, 49 stations.

More than 2,000 individual larvae from the tropical Pacific and Indian Oceans were examined. Specimens were preserved in formalin and with few exceptions, were contracted with head and metatrochal collar withdrawn into the posterior trunk. Those selected for scanning electron microscopy were rinsed in water, dehydrated through a series of ethanol and acetone and dried in a critical point drier with liquid carbon dioxide. After coating with gold palladium in a sputtering unit, they were viewed and photographed with a NovaScan microscope. Other specimens were photographed with a Zeiss Tessovar photomacrographic apparatus. Voucher specimens have been deposited in the U.S. National Museum (USNM Nos. 121743–121776).

RESULTS

The occurrence of sipunculan pelagosphaera larvae is widespread throughout the tropical Pacific (Fig. 1). In Polynesian waters of the central Pacific, 80% of all samples may include pelagosphaeras; even in the region of the east Pacific “barrier”



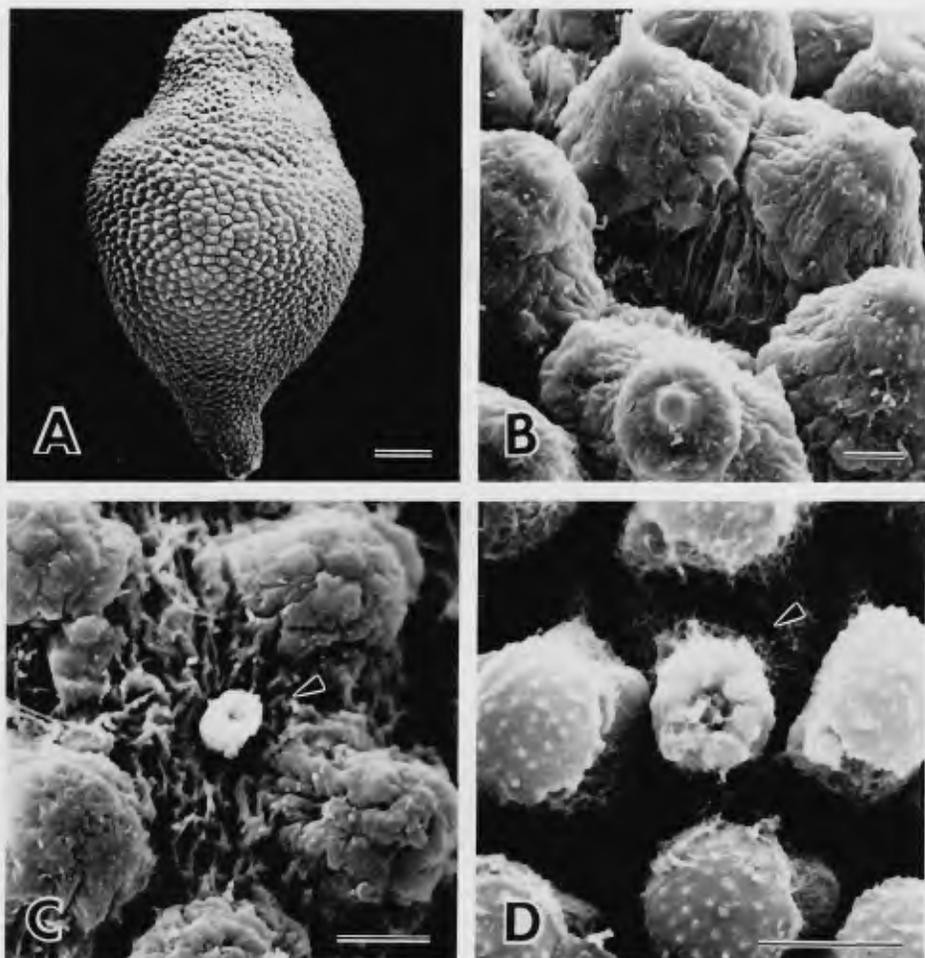


Figure 4. Scanning electron micrographs of teleplanic tropical pelagosphaera larvae of sipunculans: A. *flavida* "e"—Indian Ocean, 0°57'S, 62°19'E, 17 August 1962 (76×). B. *flavida* "e"—same specimen as A showing details of papillae (1,600×). C. *flavida* "e"—west Pacific, 7°58.6'S, 160°58.5'E, 18 August 1956 (2,500×) showing sensory organ (arrow). D. *alba* "e"—east Pacific, 6°00'N, 135°00.4'W, 25 September 1987 (3,800×) showing sensory organ (arrow).

30% contained sipunculans (Scheltema, 1988). Similarly, teleplanic larvae of sipunculans are commonplace in the tropical Indian Ocean (Fig. 2).

Larvae can be sorted into four major groups, based upon the characteristics of the external body surface. These groups are characterized by: (1) the presence of numerous, closely set cuticular papillae, (2) a smooth cuticle, lacking papillae, (3)

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Figure 3. Scanning electron micrographs of sipunculans teleplanic pelagosphaera larvae from the tropical Pacific Ocean belonging to the form *papula flavida*: A. *flavida* "a"—west Pacific, 7°57.5'S, 164°00'E, 16 August 1956 (63×). B. *flavida* "a"—same specimen as A showing details of papillae (840×). C. *flavida* "b"—south of Hawaii, 19°39'N, 159°28'W, 21 August 1956 (80×). D. *flavida* "b"—same specimen as C showing details of papillae (1,200×). E. *flavida* "c"—south of Hawaii, 17°22.6'N, 159°05'W, 7 February 1979 (125×). F. *flavida* "c"—same specimen as E showing details of papillae (1,600×).

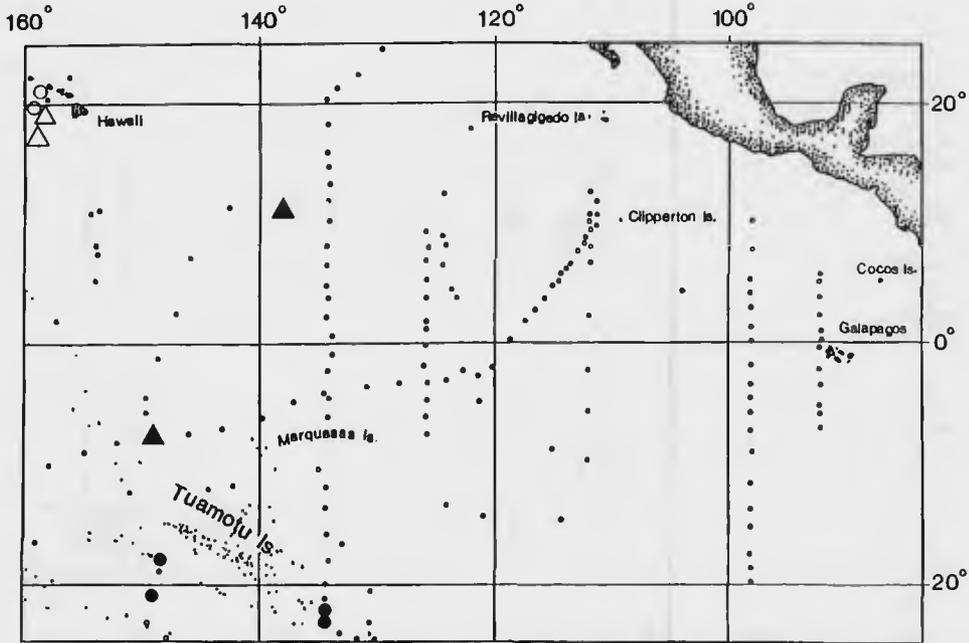


Figure 5. Eastern and east central tropical Pacific Ocean showing locations where teleplanic pelagosphaera larvae of form *papula flavida* occurred. Filled circles = "a"; open circles = "b"; open triangles = "c"; filled triangles = "d"; minute circles = locations sampled where no *papula flavida* occurred.

elevations of the body wall (cuticle plus epidermis) to form knobs or projections over the surface, and (4) annular constrictions of the body wall to form a series of transverse grooves around the body. Within these major groups a total of 22 larval forms were distinguished by such additional characters as pigmentation, structure of papillae, body shape, position of anus and nephridiopores on the trunk, and, in the case of transparent specimens, such internal structures as the number of longitudinal muscle bundles. These 22 larval forms are assumed to represent different species but until reared to identifiable adults, the specific identity of the larvae remains uncertain.

Description of Larvae

Larvae with Cuticular Papillae.—Pelagosphaeras with papillae can be separated into two categories, each having five species. The first includes those that are yellow or amber, termed by us the form *papula flavida*; the second group, those white or nearly so we call form *papula alba*. The two designated names are not to be construed as having a formal taxonomic significance. These two forms can be further distinguished by the structure of their cuticular papillae, which consist of a base and cap often separated by one or more intervening collars. The collar and cap differ from the base in composition as indicated by differences in staining properties (Rice, 1976). There are many elaborations of this basic structure. The base is a continuation of the cuticle and may be elongate or truncate. The collar, when present, may appear as one or more tiers separating cap from base. The cap itself may be variously ornamented by ridges or projections and is sometimes distinguished by a central knob or point. Variations in size and shape of papillae may occur in different regions of the trunk. Scattered among the papillae are

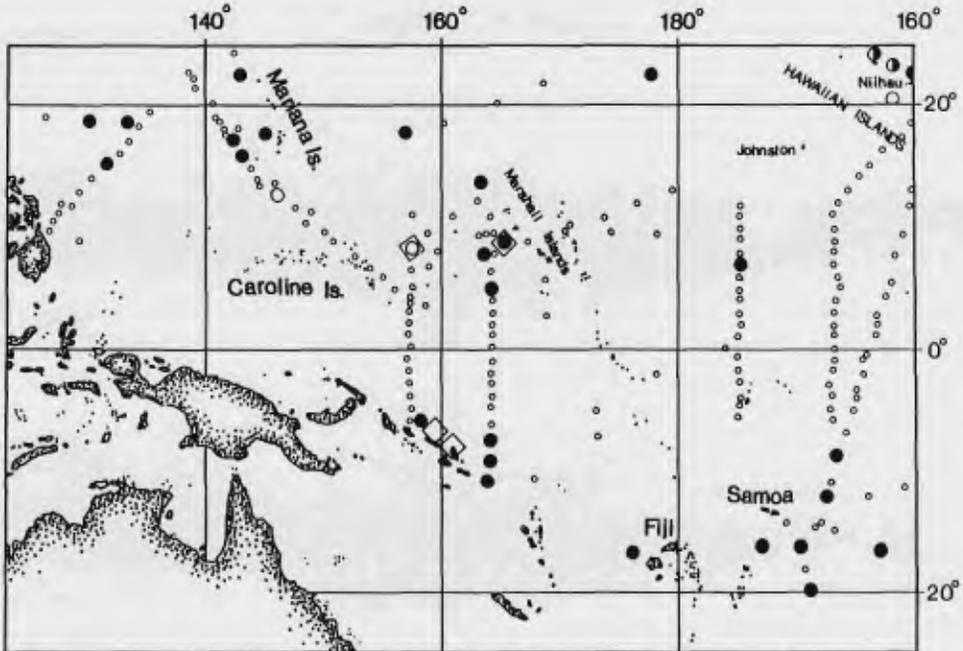


Figure 6. West central and western tropical Pacific Ocean showing locations where teleplanic pelagosphera larvae of form *papula flavida* occurred. Filled circles = "a"; open circles = "b"; divided half-filled circle = "a" and "b"; open diamond = "e"; filled circle enclosed by diamond = "a" and "e"; open circle enclosed by diamond = "a" and "e"; minute circles = locations sampled where no *papula flavida* occurred.

smaller epidermal organs which can be useful as additional characters to distinguish larval types and considered both sensory and secretory in function (Rice, 1976). Epidermal organs vary in shape and are often surrounded by a modified cuticular papilla.

FORM *papula flavida*.—*flavida* "a": When contracted, typically rounded with a posterior knob (Fig. 3A). Papillae regularly arranged in oblique rows and consisting of low broad basal protuberances surmounted by apical caps often of irregular shape and characteristic central knobs (Fig. 3B). Sensory organs cylindrical sporadically disposed among papillae. This larva is similar to *Baccaria citrinella* (Häcker, 1898) which has been assigned to the genus *Aspidosiphon* by Hall and Scheltema (1975) and by Rice (1976) who reared the larvae to a juvenile stage. Occurs among French Polynesian islands, and throughout tropical central and western Pacific (Figs. 5, 6).

flavida "b": Round or somewhat elongate with pointed posterior when contracted (Fig. 3C). Paler yellow than in *flavida* "a." Papillae in diagonal rows, larger posteriorly, rounded with a flattened, often obscure collar; apical cap lacking a central knob and characteristically crenulated (Fig. 3D). Sensory organs similar to those of *flavida* "a." Found in central Pacific (off Hawaii) west tropical Pacific and in the Indian Ocean southwest of Sri Lanka (Figs. 5, 6, 7).

flavida "c": Body form not as rigid as in *flavida* "a" and "b," anterior trunk wide, tapering posteriorly; anterior sphincter of retracted introvert not tightly contracted (Fig. 3E); pale yellowish-orange. Papillae elongate, filiform with 3 to 4 tiers of collars decreasing in diameter distally, capped by an apical floret (Fig.

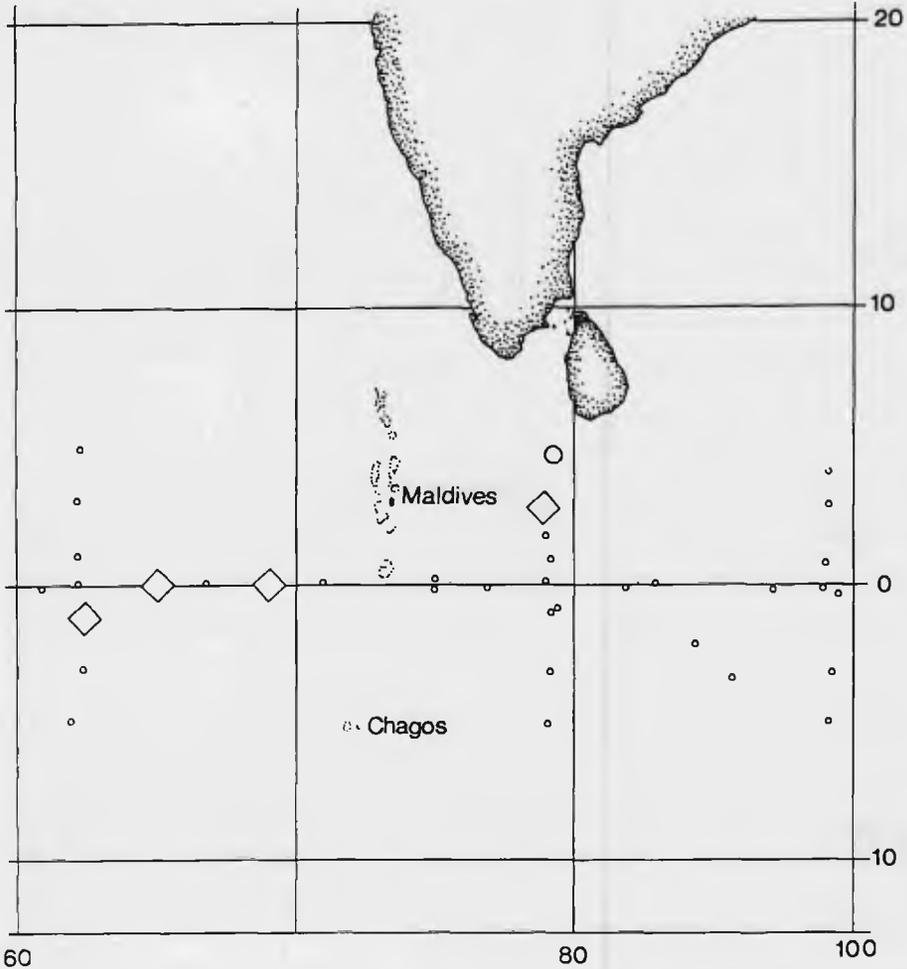


Figure 7. Central tropical Indian Ocean showing locations where teleplanic sipunculan pelagosphera larvae that belonged to the form *papula flavida* were encountered. Open circle = "b"; open diamond = "e"; minute circles = other locations sampled but where no *papula flavida* occurred.

3F). Sensory organs encircled by small rounded papillae (9 to 12) which lack tiered apical structure. Off Hawaiian Islands only (Fig. 5).

flavida "d": Distinguished from *flavida* "b" by several broad, brown bands encircling trunk. Papillae similar to "b" but apical crenulation less developed. Represented by 2 specimens north of the Society Islands and at ca. 11°N–139°W (Fig. 5); variant of *flavida* "b."

flavida "e": Translucent, internal organs discernible through the body wall. Body round when contracted but tapering anteriorly and posteriorly (Fig. 4A). White with a yellowish tinge overall. Orange pigment around anus and on body at level of anterior retraction. Papillae not regularly arranged in oblique rows; apical caps surmounted by central knobs, smaller than found in *flavida* "a" and elongated to sharp point (Fig. 4B). Sensory organs between papillae (Fig. 4C). West Pacific Ocean (near the Solomon, Marshall, and Caroline Islands) and central tropical Indian Ocean (Figs. 6, 7).

FORM *papula alba*.—*alba* "a": Contracted specimens typically barrel-shaped (Fig. 8A, B). Cuticle varies from translucent to almost transparent; white internal gut sometimes obvious. Nephridia from colorless to pale orange to brown. Papillae large, arranged in regular diagonal rows; rounded, with flattened collars and highly lobulated apical caps (Fig. 8B). Specimens from east Pacific (Fig. 8C, D) with smaller lobulated cap than those of west Pacific and the Indian Ocean (Fig. 8A, B). East Pacific S.W. of Clipperton Island, French Polynesia, westward throughout the tropical Pacific and Indian Oceans to East Africa (Figs. 10, 11, 12).

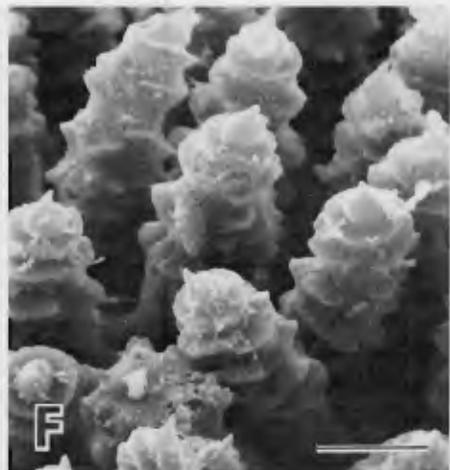
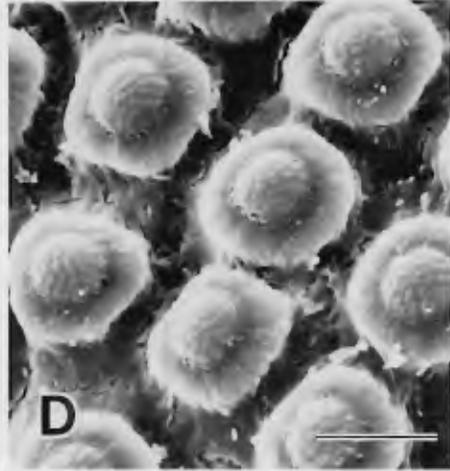
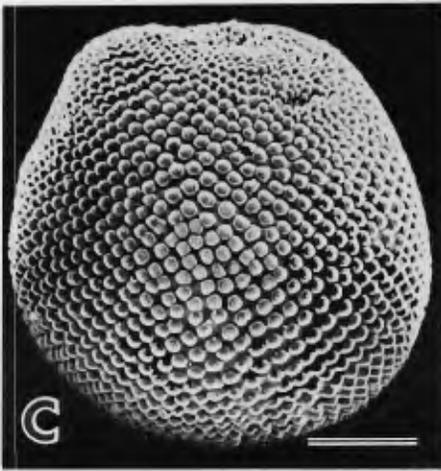
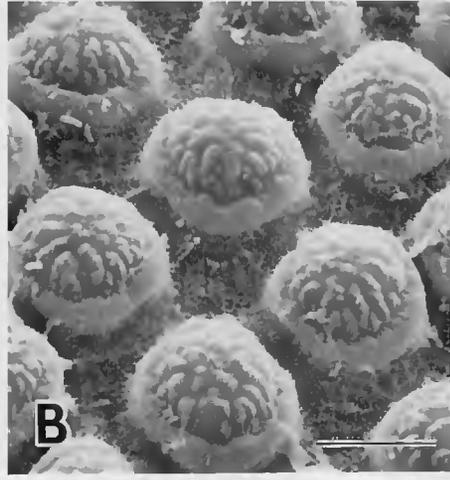
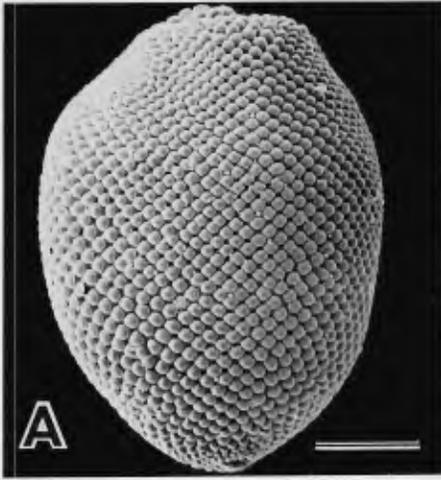
alba "b": Shape variable when contracted: round or top-shaped posteriorly with wide opening at anterior retraction, posterior tapering; tight closure at the anterior retraction (Fig. 8E). Body wall almost opaque, but often with internal orangish-yellow nephridia visible. Papillae very fine and pointed without obvious arrangement over body (Fig. 8F) and uniform in size over entire trunk. Papillae elongate, collar consisting of 3 to 4 tiers, apical cap well defined, smaller in diameter than the rest of the papilla and either rounded, flattened or pointed. Sensory body on modified, flattened papilla, diameter greater than of other papillae and lacking tiers. East Pacific (S.W. Clipperton Island), central and west Pacific (south of Hawaii and Fiji) and Indian Ocean (south of Sri Lanka between 60°E and 80°E at the equator and northward) (Figs. 10, 11, 12). Indian Ocean specimens larger, more opaque, pinkish and lacking the orange-colored nephridia.

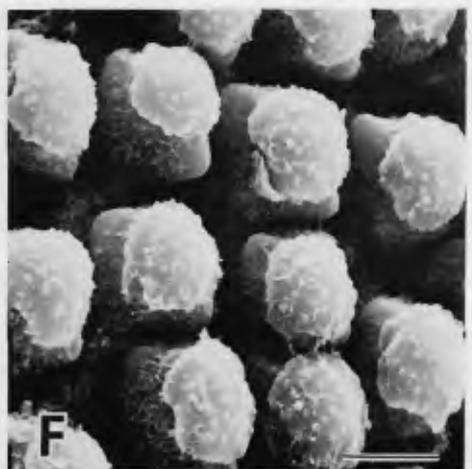
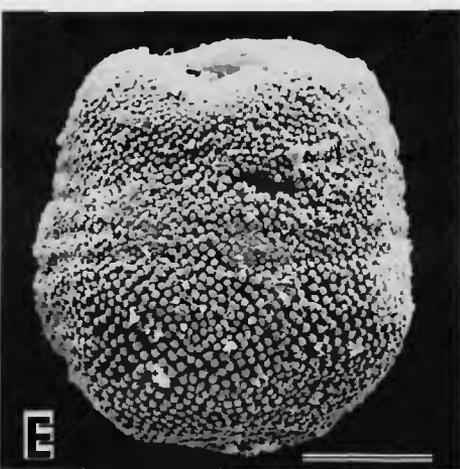
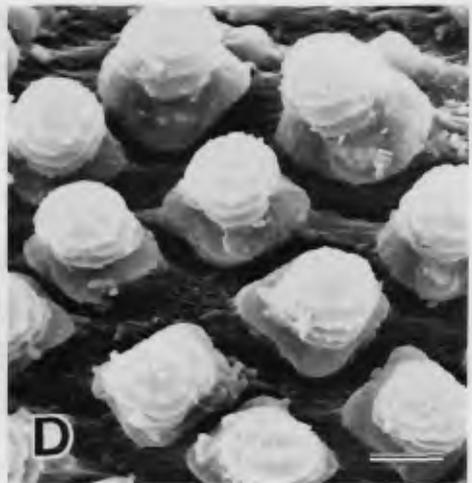
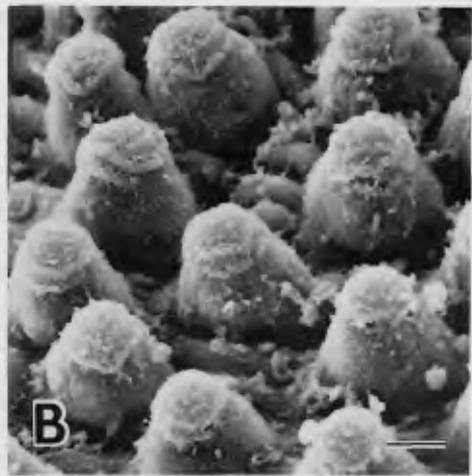
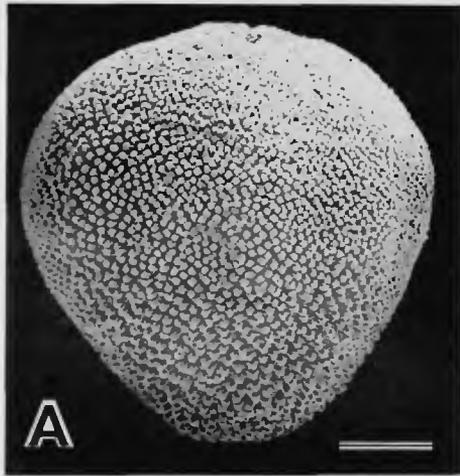
alba "c": Shape, when contracted, broader anteriorly, tapering posteriorly and resembling a top (Fig. 9A). Rigid shape distinguishes it from flexible body shape of *alba* "b." Color white, to pale yellowish or pinkish. Body wall opaque but with white intestinal mass usually visible posteriorly. Papillae vary in size and distribution over trunk, anteriorly small and crowded, posteriorly larger and more rounded. Papilla morphology varies in different regions of body and also between specimens; base usually broad and pyramidal; cap rounded with collar region ill-defined, having one or two incomplete ridges, but varying from smooth and rounded to flattened with ridges (Fig. 9B). Variation of papillae needs further study. Western tropical Pacific (at 20°N, north of the Marshall Islands) and Indian Ocean (E. of the Maldives and N.E. of the Seychelles, Fig. 11, 12).

alba "d": Body translucent, when contracted spherical or ovoid (Fig. 9C); nephridia, gut and retracted head region green. Anus in upper third of trunk; nephridia opening slightly anterior to anus. Trunk covered with regularly spaced papillae, smaller anteriorly. Papilla broad at base mounted by a distinctive rounded apical cap with two or three circular ridges or tiers (Fig. 9D). Epidermal or sensory organs scattered among the papillae, appear to open in the centers of

Figure 8. Scanning electron micrographs of teleplanic pelagosphaera larvae belonging to form *papula alba*. A. *alba* "a"—Indian Ocean, 0°02'S, 74°59'E, 11 July 1962 (140×). B. *alba* "a"—same specimen as A showing details of papillae (1,600×). C. *alba* "a"—east central Pacific 15°41'N, 159°33'W, 6 February 1979 (143×). D. *alba* "a"—same specimen as C showing details of papillae (1,600×). E. *alba* "b"—central Pacific south of Fiji, 21°47.8'S, 179°57.6'E, 24 January 1979 (120×). F. *alba* "b"—same specimen as E showing details of papillae (1,500×).

Figure 9. Scanning electron micrographs of teleplanic pelagosphaera larvae belonging to the form *papula alba*. A. *alba* "c"—central Indian Ocean, 1°54'N, 79°01'E, 30 August 1962 (124×). B. *alba* "c"—same specimen as A showing details of papillae (1,500×). C. *alba* "d"—east Pacific, 26°50.8'S, 134°24.0'W, 9 October 1987 (107×). D. *alba* "d"—same specimen as C showing details of papillae (1,900×). E. *alba* "e"—east Pacific, 6°00.3'N, 135°00.4'W, 25 September 1987 (170×). F. *alba* "e"—same specimen as E showing details of papillae (2,500×).





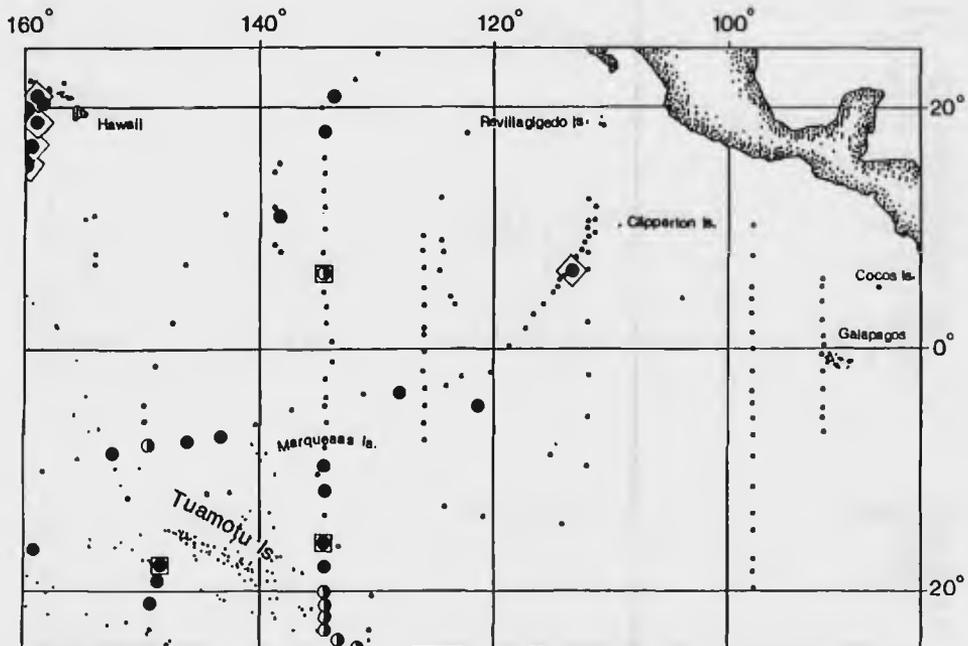


Figure 10. Eastern and east central tropical Pacific Ocean showing where teleplanic pelagosphaera larvae of the form *papula alba* occurred. Filled circle = "a"; filled circle enclosed in diamond = "a" and "b"; divided half-filled circle = "a" and "d"; filled circle enclosed in square = "a" and "e"; divided half-filled circle enclosed in square = "a," "d" and "e"; minute circles = locations sampled where no *papula alba* occurred.

smaller modified papillae. East-central Pacific only (S.E. French Polynesia; Fig. 10).

alba "e": Small, "snow white" variable shape when contracted, papillae fine (Fig. 9E). Cuticle nearly opaque, black to dark green nephridia. Papillae with squat base topped by a simple, thin apical cap with minute projections (Fig. 9F). Epidermal or sensory organ on small, modified papillae with a lobulated cap (Fig. 4D). East central Pacific only (off S.E. French Polynesia, the Society Islands and approximately 8° north of the equator at 135°W; Fig. 10).

Larvae with Smooth Cuticle.—The term "smooth" was first used by Jägersten (1963) to distinguish pelagosphaeras without papillae from those having a papillate surface. Hall and Scheltema (1975) described a larva from the North Atlantic "Type B" that they considered the same as Jägersten's "smooth." Rice (1981) placed a similar pelagosphaera in the family Sipunculidae. Six "smooth"-larval types, include two with variants, from the Pacific and Indian Oceans; we term these forms *leura*. In addition to the commonly encountered opaque forms of Jägersten are smooth transparent pelagosphaeras also considered here within this group. Some forms show considerable variation.

FORM leura.—*leura* "a": Large transparent, or translucent, body wall often "milky" with white flecks (Fig. 13A). Gut broad, flat, white to yellowish, fills posterior $\frac{2}{3}$ or $\frac{3}{4}$ of the ventral trunk cavity in contracted specimens. Anus located in anterior $\frac{1}{3}$ of trunk. Pair of long, white nephridia attach slightly anterior or at same level as the anus. Distinguished by long, coiled nephridia and lack of clearly

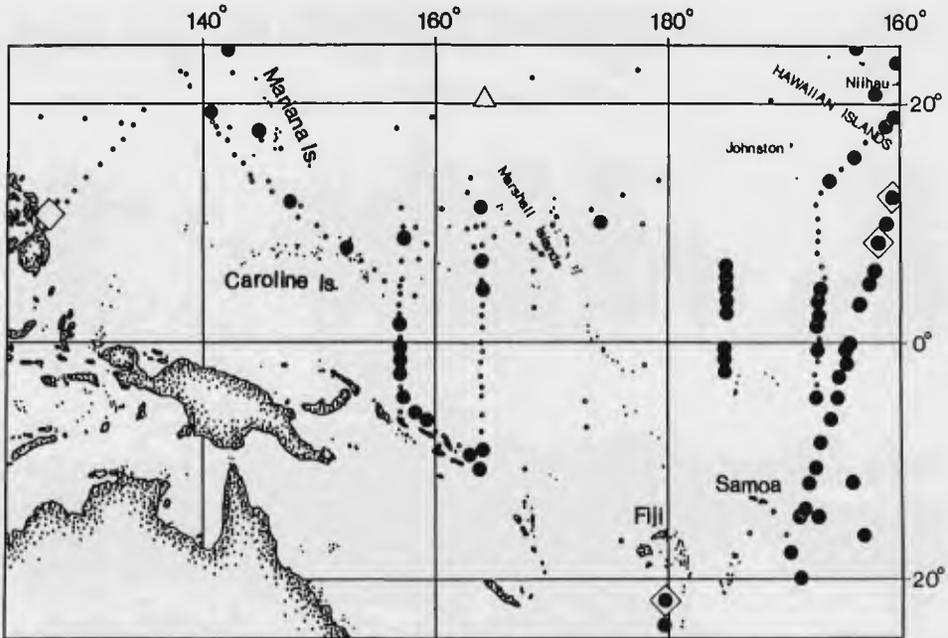


Figure 11. West central and western tropical Pacific Ocean showing where teleplanic pelagosphera larvae of the form *papula alba* occurred. Filled circles = "a"; open diamonds = "b"; open triangles = "c"; diamonds enclosing filled circles = "a" and "b"; minute circles = locations sampled where no *papula alba* occurred.

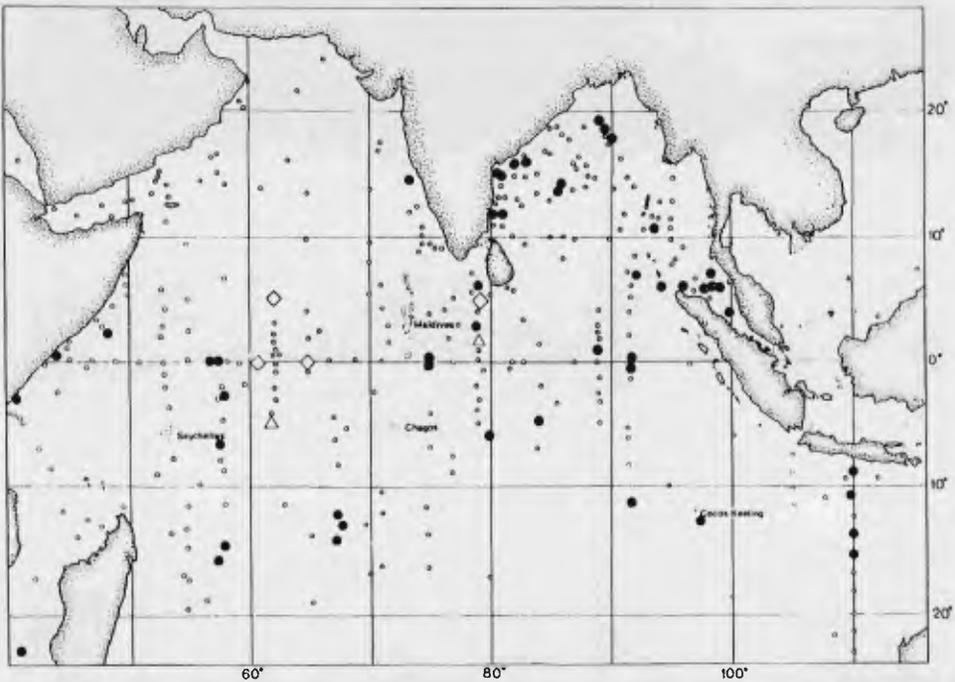
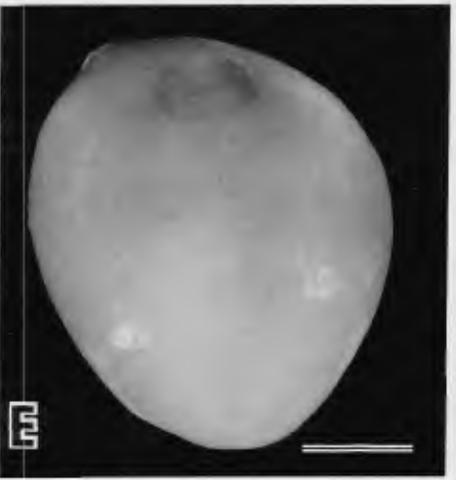
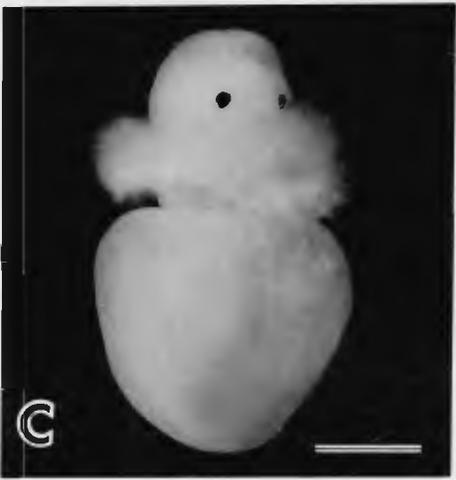
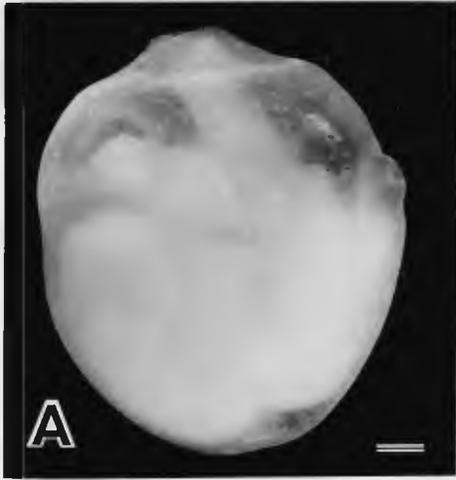


Figure 12. Tropical Indian Ocean showing where teleplanic pelagosphera larvae of the form *papula alba* occurred. Filled circles = "a"; open diamonds = "b"; open triangles = "c"; minute circles = locations with pelagosphera but no *papula alba* occurred.



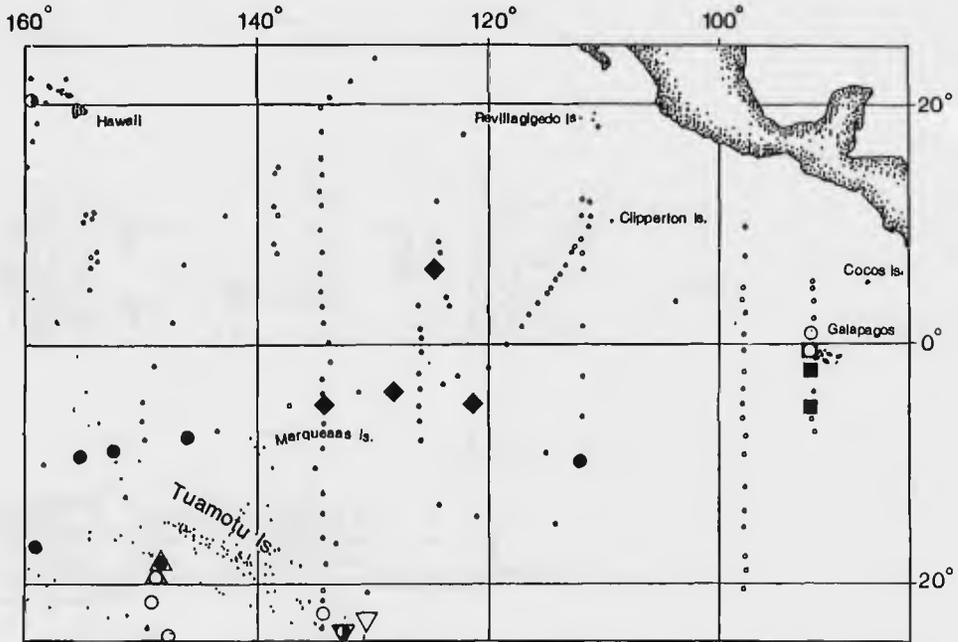


Figure 14. Eastern and east central tropical Pacific Ocean showing where teleplanic sipunculan pelagosphaera larvae of the form *leura* occurred. Filled diamond = "a"; filled circle = "b"; open circle = "c"; filled square = "e"; open inverted triangle = "f"; divided half-filled circle = "b" and "c"; filled circle enclosed by open triangle = "b" and "d"; divided half-filled circle enclosed in inverted triangle = "b," "c" and "f"; open circle enclosed by open triangle = "c" and "d"; open circle enclosed by filled square = "c" and "e"; minute circles = locations sampled where no *leura* occurred.

distinguishable longitudinal muscle bundles. Four specimens from east tropical Pacific (N.E. of the Marquesas; Fig. 14).

leura "b": Body wall opaque, surface smooth, shiny; cuticle shows reticulated pattern beneath. Orange pigment flecks sometimes in cuticle along longitudinal muscle. Anus in anterior 1/5 of the trunk, openings of the yellowish-orange nephridia posterior to anus. Body pear-shaped when retracted (Fig. 13B) with a posterior knob. Terminal organ when retracted slightly ventral to the posterior extremity. East tropical Pacific, abundant in the west tropical Pacific and Indian Oceans (Figs. 14, 15, 16).

leura "c": Anus in the mid-trunk. Small nephridia proximately anterior to the anus, pigmented orange, open on longitudinal muscle five. Contracted body spherical (Fig. 13D); 25–32 prominent longitudinal muscle bundles; four retractors attached at the level of anus with well developed ciliated metatrochal band, postmetatrochal spinchter and two orange eyespots (Fig. 13C). Off the Galapagos, French Polynesia, the Austral Archipelago (Fig. 14); widely distributed in the

Figure 13. Photographs of teleplanic sipunculan pelagosphaera larvae belonging to the form *leura*. A. *leura* "a"—east Pacific, 3°36.7'S, 128°00.3'W, 13 December 1985 (21×). B. *leura* "b"—central Pacific, 16°52.8'S, 159°08.2'W, 15 October 1987 (57×). C. *leura* "c"—east Pacific—introvert extended, 24°35.5'S, 147°54.1'W, 15 October 1987 (47×). D. *leura* "c"—Indian Ocean, introvert withdrawn, 2°56'N, 78°59'E, 30 August 1962 (43×). E. *leura* "e"—east Pacific, 0°18.55'S, 92°03'W, 12 March 1967 (48×). F. *leura* "i"—Indian Ocean, 0°08'S, 46°52'E, 22 August 1962 (13×).

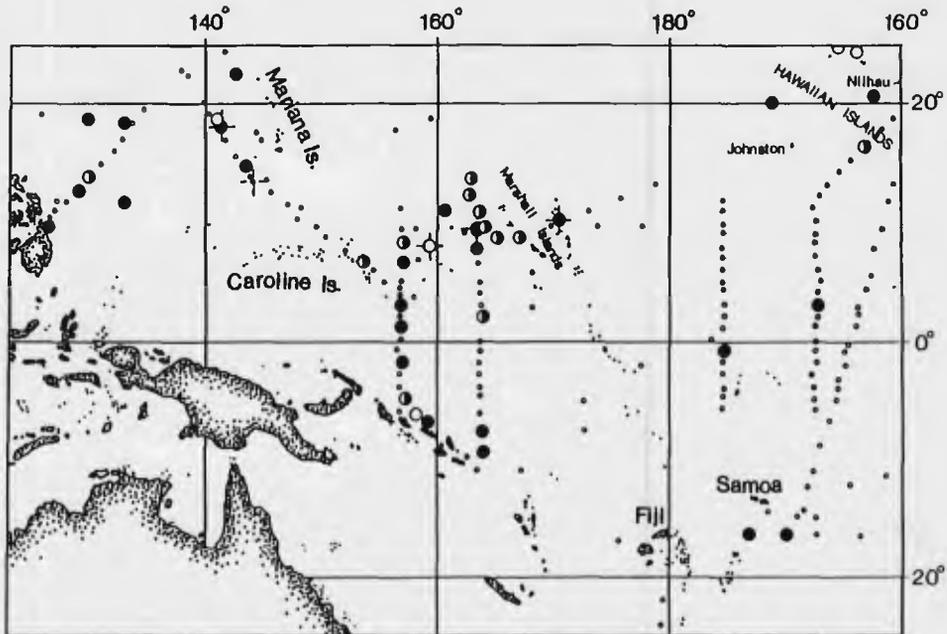


Figure 15. West central and west tropical Pacific Ocean showing where teleplanic pelagosphere larvae of the form *leura* occurred. Filled circle = "b"; open circle = "c"; divided half-filled circle = "b" and "c"; filled circle with rays = "b" and "g"; open circle with rays = "c" and "g"; rays = "g"; minute circles = locations sampled where no *leura* occurred.

western tropical Pacific and Indian Oceans (Figs. 15 and 16). Specimens from the west Pacific and Indian Ocean were sometimes larger.

leura "d": Body shape ovoid, opaque, but with longitudinal muscle bands discernible. Anus in anterior 1/5 of the trunk as in *leura* "b," orange nephridia open posterior to the anus. Stomach deep purple; cuticle with purple tinge. Except for purple pigment closely resembles *leura* "b," and probably is variant form thereof. East Pacific Ocean southwest of the Tuamotu Archipelago (Fig. 14).

leura "e": Body rounded to ovoid when contracted, with posterior knob. Surface shiny, opaque, with reticulated pattern in cuticle not so prominent as *leura* "b," pigmentation pale orange. Retracted introvert slightly ventrolateral rather than apical. Anus anterior, only slightly subapical (Fig. 13E). East Pacific at three locations near Galapagos (Fig. 14).

leura "f": Body wall opaque buff-colored elongate with a prominent terminal knob when contracted. Clear spots on smooth and shiny surface. Anus in the anterior 1/5 of the trunk. Nephridiopores at or slightly posterior to anus. Southeast French Polynesia only (Fig. 14).

leura "g": Shape spherical, body wall translucent. Anus in the mid-trunk, nephridiopores when visible slightly anterior to anus. Longitudinal muscle bands discernible only with difficulty. Differs from *leura* "c" by presence of irregularly shaped white bodies in the coelom, possibly aggregations of coelomocytes. Stomach large, white globular. Probably variant of *leura* "c." Central and west Pacific, off the Marshall, Mariana, and Caroline Islands (Fig. 15).

leura "i": Exceptionally large; 40 longitudinal muscle bands (Fig. 13F). Nephridiopores on longitudinal muscle band 8. Two ventral and 2 dorsal retractors

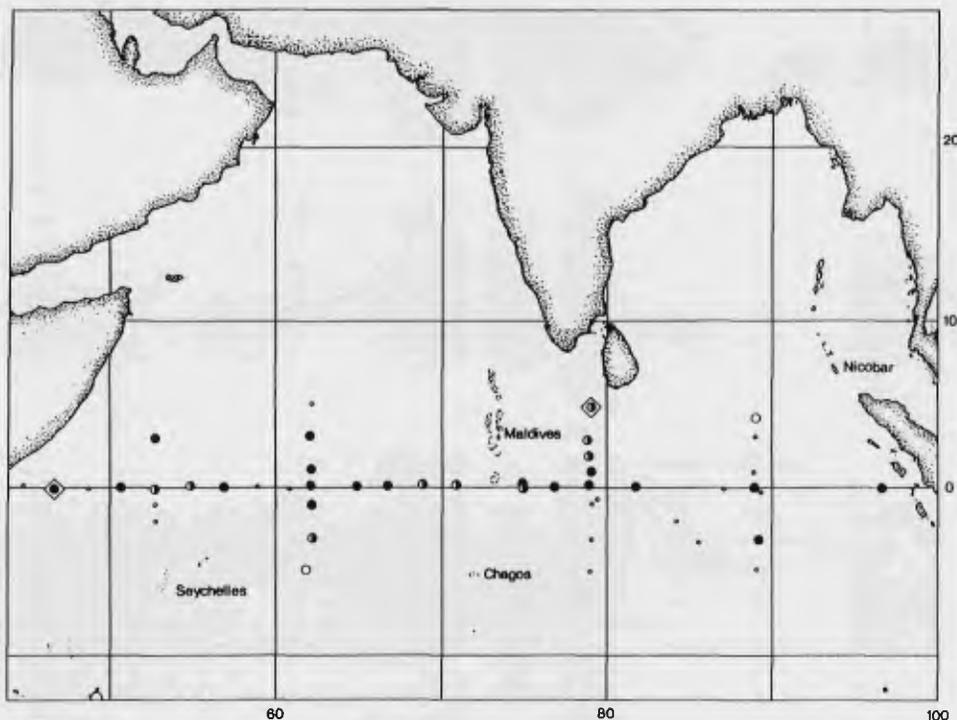


Figure 16. Tropical Indian Ocean showing where teleplanic pelagosphaera larvae of the form *leura* occurred. Filled circles = "b"; open circles = "c"; divided half-filled circles = "b" and "c"; filled circles enclosed in diamonds = "c" and "i"; divided half-filled circle enclosed in diamonds = "b," "c" and "i."

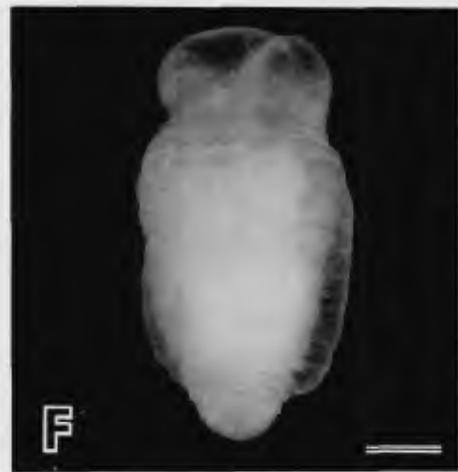
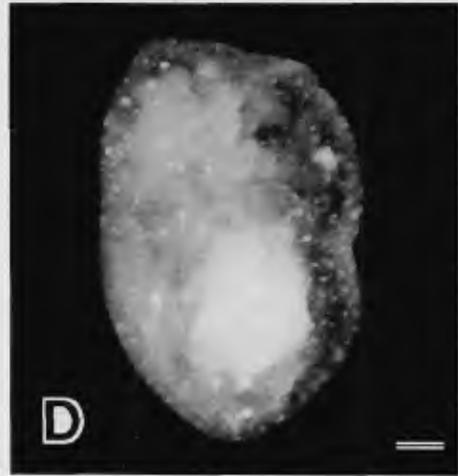
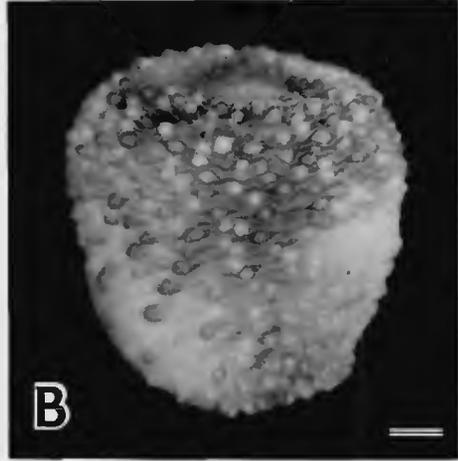
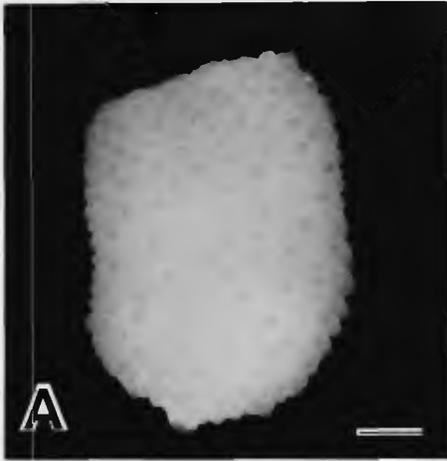
attach at level of anus. Transparent body wall with small, white flecks. One specimen Indian Ocean S.W. of Sri Lanka (Fig. 16). Single small individual off tropical East Africa tentatively placed here though nephridiopores are slightly anterior to anus.

FORM *tuberosa*.—A larva from the North Atlantic, designated by Hall and Scheltema (1975) as "Type F," has external characters similar to *tuberosa* "a," described below. This same larva has also been figured by Rice (1975), but no affiliation to an adult form has been proposed.

tuberosa "a": Body generally opaque, brown to reddish pigmentation around large, characteristic papillae (Fig. 17A). Cuticular papillae differ from those of other types described above, and are projections of body wall (probably) beneath cuticle; larger and more widely spaced than cuticular papillae. Hawaii, N.W. of Tuamotu Archipelago, common west of 160°W longitude in tropical central and west Pacific; Indian Ocean south of Sri Lanka and westward along equator (Figs. 18, 19, 20).

tuberosa "b": Papillae and grooves intense green; remainder of body wall pale green. Pigment densest at the base of papillae extending out from base into grooves (Fig. 17B). External morphology otherwise similar to *tuberosa* "a." Eastern Pacific, ca. 5° north of the equator along 135°W longitude only (Fig. 18).

FORM *annulata*.—A pelagosphaera characterized by presence of transverse or annular grooves or constrictions at regular intervals along length of trunk was



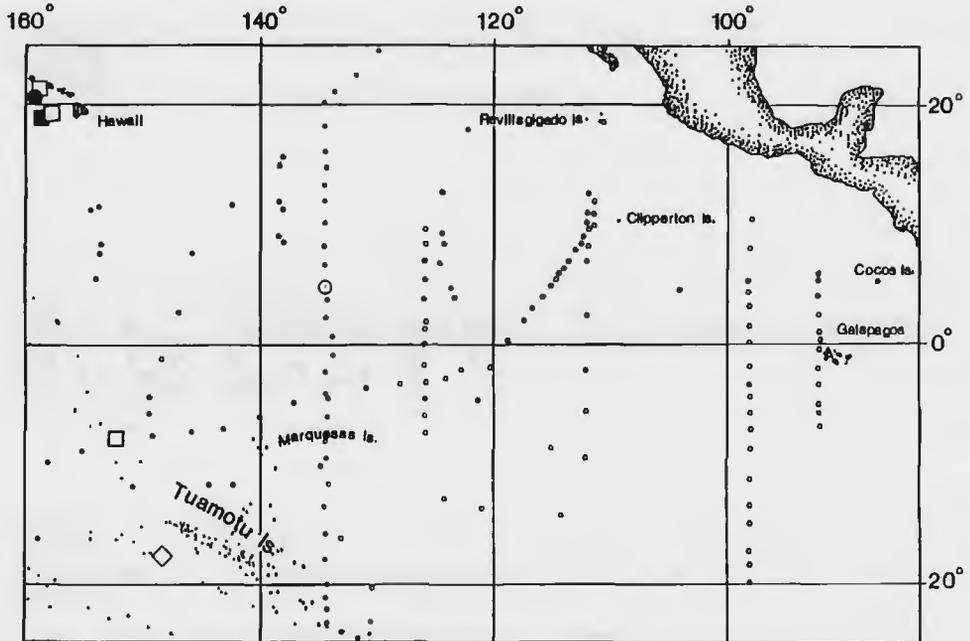


Figure 18. Eastern and east central tropical Pacific Ocean showing where teleplanic pelagosphaera larvae of the forms *tuberosa* and *annulata* occurred. Filled circle = *tuberosa* "a"; open circle = *tuberosa* "b"; open square = *annulata* "a"; filled square = *annulata* "c"; open diamond = *annulata* "d"; minute circles = locations sampled where no *tuberosa* or *annulata* occurred.

first described and designated as type "E" by Hall and Scheltema (1975) from the North Atlantic. Since then this larval form has been referred to by Rice (1976, 1981, 1988) who reared it from the Florida Current into the juvenile of *Siphonosoma cumanenese*. Four types within this category (genus?) were found in the Pacific and Indian Oceans.

annulata "a": Body assumes various shapes, but usually ovoid with elongated posterior end or "tail" (Fig. 17C). Annuli numerous and closest together posteriorly. Body wall transparent to translucent, with reddish glands, visible throughout trunk. Body cavity often packed with small circular bodies (probably coelomocytes). Anus in anterior third of trunk, nephridiopores slightly anterior to anus. Approximately 20 longitudinal muscle bundles, white bodies embedded in epidermis. Society Islands, near Hawaii (Fig. 18), most of central and west tropical Pacific, equatorial Indian Ocean (Figs. 18, 19, 20).

annulata "b": Body wall clear; cavity filled with clumped clear, irregular shaped white inclusions and also particles including coelomocytes (Fig. 17D). Numerous, closely spaced annular grooves along length of trunk, white flecks scattered over the body wall. Clear saccular glands located laterally in anterior third of the trunk

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Figure 17. Photographs of teleplanic pelagosphaera larvae belonging to the forms "*tuberosa*" and "*annulata*". A. *tuberosa* "a"—west central Pacific, 4°00'N, 174°56'W, 17 August 1956 (45×). B. *tuberosa* "b"—east Pacific, 5°09.0'N, 135°00.2'W, 25 October 1987 (36×). C. *annulata* "a"—west Pacific, 12°16'N, 163°07'E, 14 March 1955 (33×). D. *annulata* "b"—central Pacific, 18°00.5'S, 169°26.5'W, 28 January 1979 (31×). E. *annulata* "c"—S.W. of Hawaii, 19°05.6'N, 158°35.0'W, 7 February 1979 (33×). F. *annulata* "d"—east central Pacific, 17°52.8'S, 148°07.4'W, 18 October 1987 (50×).

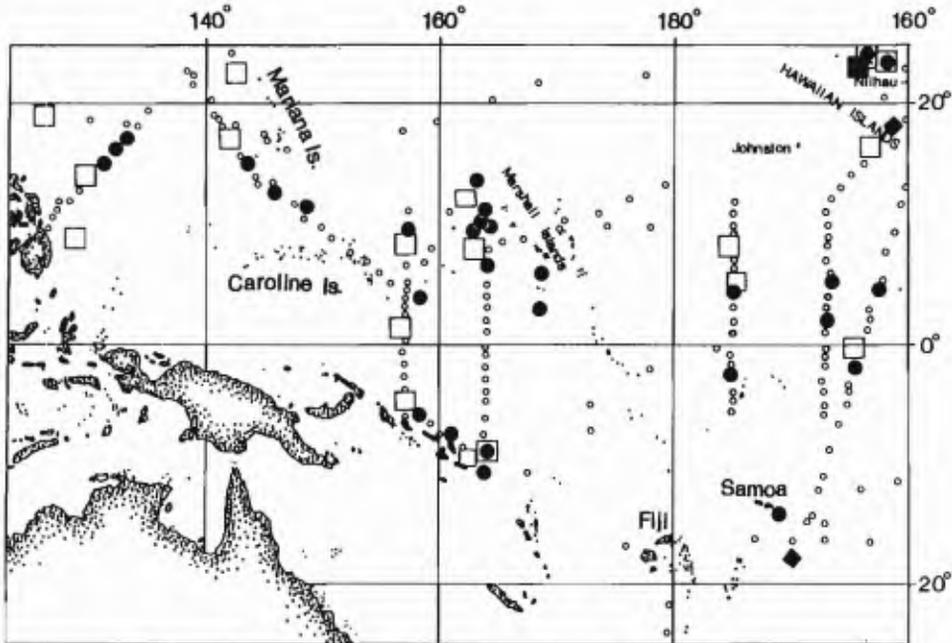


Figure 19. West central and west tropical Pacific Ocean showing where teleplanic pelagosphaera larvae of the forms *tuberosa* and *annulata* occurred. Filled circle = *tuberosa* "a"; open square = *annulata* "a"; filled diamond = *annulata* "b"; filled square = *annulata* "c"; filled circles enclosed in open squares = *tuberosa* "a" and *annulata* "a"; minute circles = locations sampled where no *tuberosa* or *annulata* occurred.

at level of anus. Posteriorly body with a conspicuous white gut. Small, transparent ventrolateral nephridia open anterior to the anus. Southwest of Hawaii, south of Samoa and in Indian Ocean on the equator south of Sri Lanka (Figs. 19, 20).

annulata "c": Thick, opaque body wall, prominent annular grooves; posterior end tightly contracted into tail-like appendage (Fig. 17E). Two specimens both from near Hawaii (Figs. 18, 19).

annulata "d": Small green granules underlying transparent cuticle but otherwise opaque, white, body wall. Green granules in rings correspond with the position of the annulations (Fig. 17F). Society Islands only (Fig. 18).

DISCUSSION

A total of 22 larval forms have been described from the tropical Pacific and Indian Oceans. However, it is not possible to assign any of these pelagosphaeras to an adult species; this can only be done by rearing larvae through metamorphosis to an identifiable stage. Thus the specimens from our plankton collections can only be relegated to larval types based upon their external characteristics. Notwithstanding, some generalizations about their identity can be made from what is known about tropical Atlantic pelagosphaera larvae taken alive from the plankton and reared to recognizable stages in the laboratory (Rice, 1976). Based upon such observations, it is predicted that larvae with cuticular papillae (form *papula flavida* or *alba*) belong to the family Aspidosiphonidae or Phascolosomatidae and that those with annuli or "transverse grooves" (form *annulata*) belong to the Sipunculidae, most likely the genus *Siphonosoma*. Larvae with smooth cuticles (i.e., form *leura*) lacking obvious elaborations, also probably belong to the family

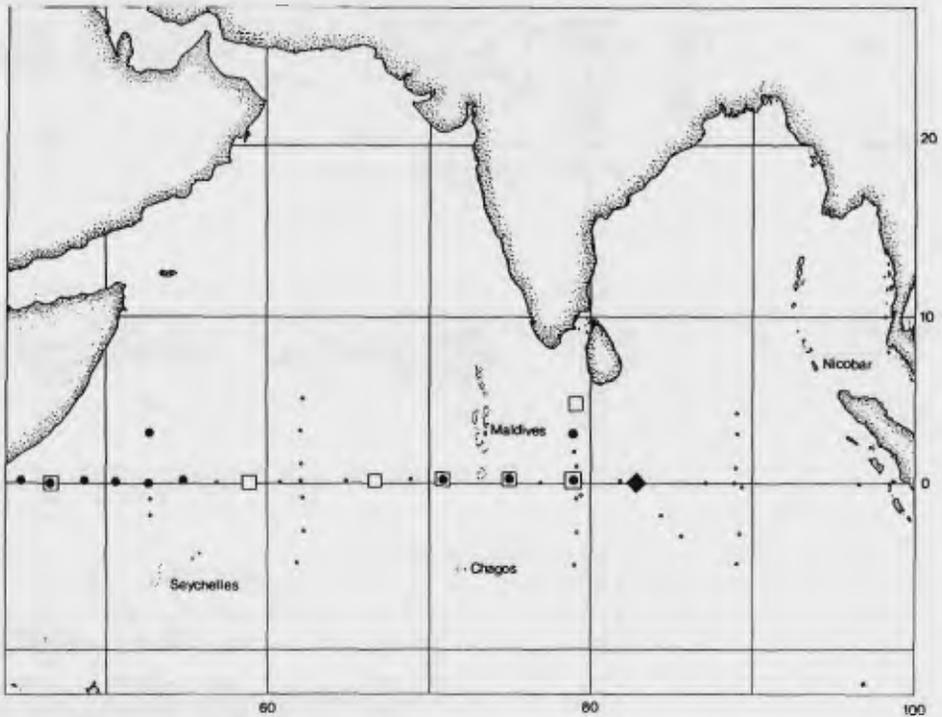


Figure 20. Tropical Indian Ocean showing where teleplanic sipunculan pelagosphere larvae belonging to the forms *tuberosa* and *annulata* were encountered. Filled circle = *tuberosa* "a"; open square = *annulata* "a"; filled diamond = *annulata* "b"; filled circle enclosed in open square = *tuberosa* "a" and *annulata* "a"; minute circles = locations sampled where no *tuberosa* or *annulata* occurred.

Sipunculidae, possibly the genus *Sipunculus* or *Xenosiphon*. The larvae with epidermal papillae or "knobs" (i.e., form *tuberosa*) have not yet been reared to identifiable juveniles.

Even though it is not possible to assign species names to any of the larval forms, some biogeographical observations can be made. It is estimated that there are approximately 84 sublittoral species known from tropical waters of the Pacific and Indian Oceans. This figure was derived by tallying all tropical shoal-water species cited in the monograph of Stephens and Edmonds (1972) and modifying the resultant list, where appropriate, by the subsequent published revisions (Cutler and Cutler, 1982, 1985). Included are all species recorded between the Tropics of Cancer and Capricorn with the exception of those known only from the type localities (viz. 67 species of arguable validity) and all deep-sea forms. This may be a conservative estimate. Among these eighty-four species, seventy (83 percent) occur in the tropical Indian Ocean, and only twenty from the list are known from the central tropical Pacific. None of these twenty species is endemic to the central Pacific. Note, however, that some central Pacific endemic species may have been removed from the list because of the way in which it was compiled, i.e., removing those known from only a single location.

The central tropical Pacific, for the present purpose, is here defined to include the Marquesas, French Polynesia and westward to the Marshall and Caroline Islands. Eighty percent (16 of these 20 species) are Indo-Pacific forms i.e., they also occur in the Indian Ocean; the remainder extend only as far as the western Pacific including Fiji, New Caledonia, the Philippines, New Guinea and eastern

Australia. Sipunculans of the central Pacific can be regarded as an attenuated Indo-Pacific fauna.

The foregoing compilation of adult species can now be compared with the occurrence of pelagosphaera larvae. Thirteen of the twenty-two larval forms described from the present plankton collections were found to exist in the central Pacific. Among these 13 pelagosphaeras, eight or about two-thirds also occurred in the Indian Ocean, while one extended only as far as the western Pacific. The remaining four larval forms were found only in the central tropical Pacific. There appears, therefore, to be a rough general correspondence between larval and adult distribution, namely a strong Indo-Pacific connection. The present information on systematics of larvae is too incomplete for the Indian Ocean to carry the argument further (8 larvae out of 70 known species i.e., 11 percent), but the results are nonetheless suggestive.

A list of the known east Pacific sublittoral tropical sipunculans, arrived at in a fashion already described above (Stephens and Edmonds, 1972) includes 18 species. Among these 9 (50 percent) are known to be Indo-Pacific, 6 appear to be "endemic," restricted within the Pacific to the eastern tropical portion including Central and South America between the Tropics of Cancer and Capricorn and the outlying islands such as the Clipperton and Galapagos Islands. Three species are shared with the central Pacific only.

Turning now to the pelagosphaera larvae, nine species are described from plankton samples in the eastern Pacific. Three of these are found only in the easternmost Pacific, two in the east central Pacific (French Polynesia) and westernmost east Pacific; the remaining four larval types are widely distributed Indo-Pacific forms. Thus of the nine pelagosphaera, at least four (somewhat over a third of the known larvae) are apparently able to cross the east Pacific barrier and all of these are widely distributed Indo-Pacific species. Previously it has been demonstrated that around 33 percent of the one hundred plankton samples taken in the eastern Pacific contained pelagosphaera larvae (Scheltema, 1988; Table I) whereas 78 percent of the 129 samples from the central Pacific included pelagosphaeras (difference significant; χ^2 test of homogeneity $P = 0.001$). Previous and present results both suggest that the east Pacific acts as a filter rather than a complete barrier to the dispersal of invertebrate larvae in general and to sipunculan pelagosphaeras in particular. The evidence appears to support the hypothesis that larvae may play an important role in maintaining geographic distribution and the genetic continuity of widely distributed sipunculan species (Scheltema, 1975). Further systematic, biogeographic and genetic studies using biochemical techniques are needed to support or refute such an hypothesis, but until the correspondence is established between the larval and adults forms, only tentative conclusions will be possible.

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