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Embryogenesis and acquisition of algal symbionts by planulae of *Xenia umbellata* (Octocorallia: Alcyonacea)

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Abstract

Early embryogenesis of the internally brooding soft coral *Xenia umbellata* and acquisition of algal symbionts in the course of its planular ontogenesis have been examined by scanning and transmission electron microscopy and by light microscopy. The endoderm of adult *X. umbellata* harbours symbionts mainly in the tentacles and in the peripheral solenia system. The colonies are gonochoric brooders. Algal symbionts were never found in the sperm sacs, and were only rarely found in the follicular tissue enclosing the oocytes. Fertilized eggs pass into endodermal brood pouches where embryogenesis occurs. Cleavage is holoblastic and leads to formation of a solid blastula. Algal symbionts are conspicuously embedded in the parental mesoglea that coats the young embryo, most probably transmitted by surface adherence. At a further stage, this integument disappears and the algae reside extracellularly among the cells of the newly-formed blastula. After subsequent cell proliferation developing planulae possess an inner mass of yolk-laden cells that contain numerous symbiotic algae. Gradually the yolk disintegrates, leaving a cavity enclosed by ectoderm, a thin mesoglea and an inner endoderm with intracellular symbionts. The mature planulae have already been provided with numerous intracellular symbionts by the time they are expelled from the brood pouches. The markedly early symbiont acquisition by the embryos of *X. umbellata* may help support their developmental requirements in the course of planular ontogenesis.

Introduction

Many of the soft corals (Octocorallia: Alcyonacea) harbour symbiotic dinoflagellates (zooxanthellae) in their tissues (Berner et al. 1987). Alcyonaceans of the family Xeniidae, widely distributed inhabitants of coral reefs, contain innumerable symbiotic algae in their endodermal cells (Gohar 1940). These algae play a major role in the nutritive physiology of xeniids (Schlichter 1982a, b, Schlichter et al. 1983, 1984).

Several xeniid species reproduce sexually by internal brooding of planulae (Gohar 1940, Benayahu and Loya 1984a, b). Gohar and Roushdy (1961) presented some data on early developmental stages of several xeniids. However, most of ontogeny, including embryogenesis of internally brooding alcyonaceans, remains enigmatic. Presence of algal symbionts in some xeniid planulae has been indicated by Gohar (1940), though no data exist on the infection of these sexually produced offspring by the symbionts during their development.

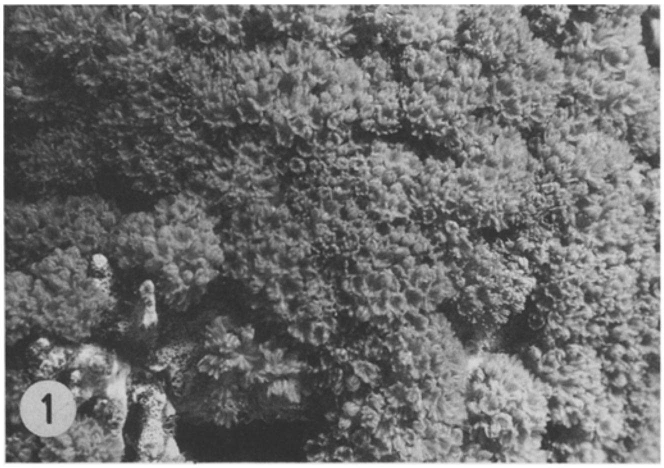
Symbiotic association between a host and symbiotic algae is established in many coelenterates by transmission of symbionts from one generation to the next (Fitt 1984, Trench 1987). Such acquisition of algal symbionts is accomplished either through maternal inheritance by the ovum or the planulae (Kinzie 1974), or alternatively, through uptake from the external environment by mature larvae or juvenile stages (Trench 1987).

Xenia umbellata Savigny, 1816 (Fig. 1) is an abundant soft coral in the Red Sea, with a geographical distribution extending to numerous Indo-Pacific coral reefs (Verseveldt 1965). *X. umbellata* is a brooding species that releases planulae infected with symbionts (Gohar 1940).

The present study deals with histological and ultrastructural relationships of *Xenia umbellata* tissues with their algal symbionts. We examine the developmental stages and morphogenesis of the planulae. This is the first account of embryogenesis in an internally brooded alcyonacean which demonstrates the acquisition of symbionts in the course of planular ontogenesis.

Materials and methods

Colonies of *Xenia umbellata* were collected during summer 1986 from the reef in front of the Marine Biological Laboratory of Eilat. Colonies were sampled randomly by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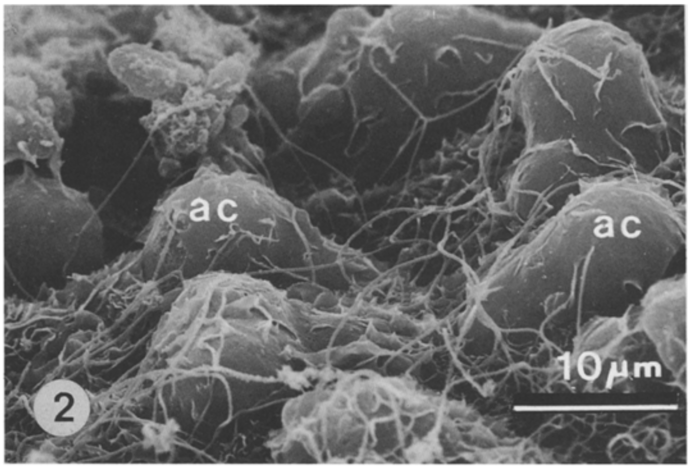
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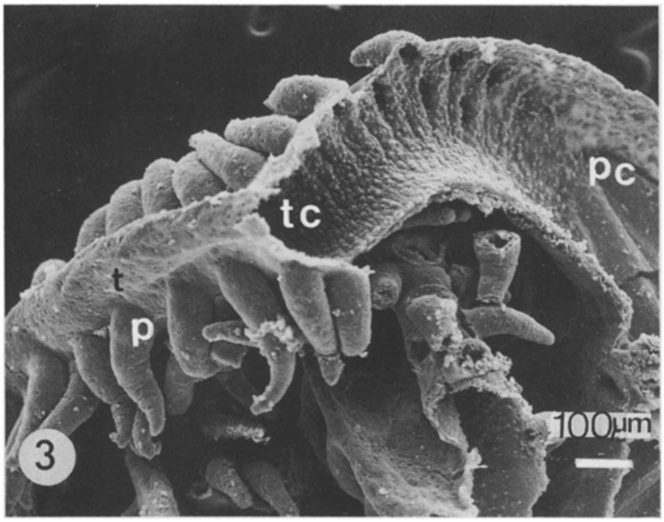
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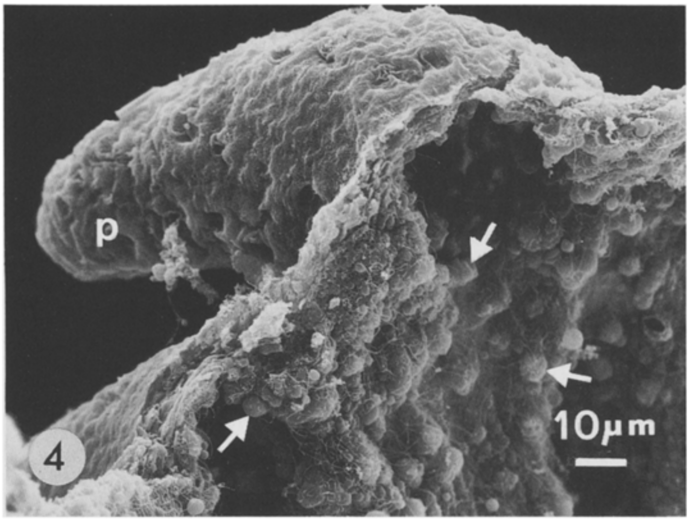
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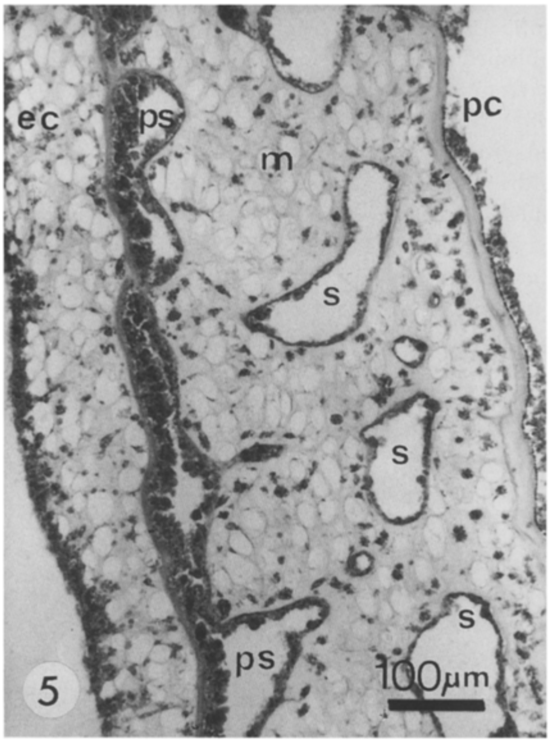
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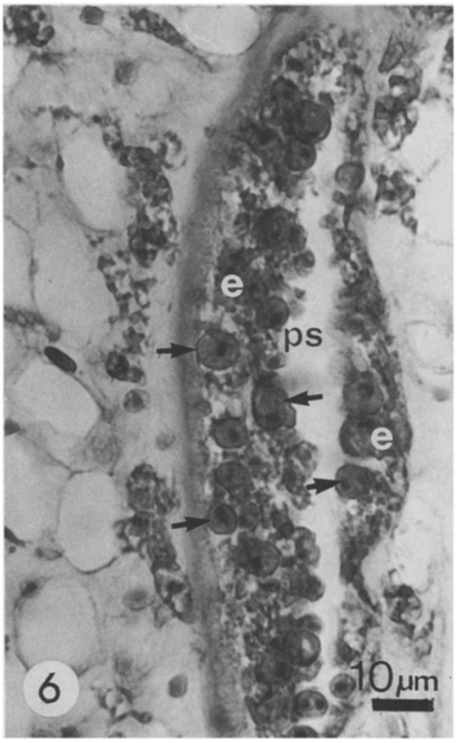
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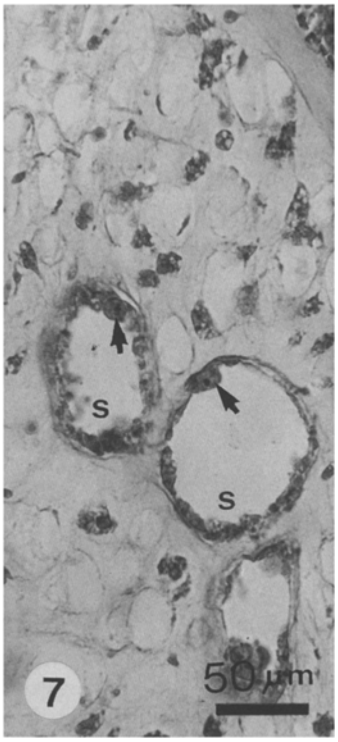
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SCUBA diving at depths of 3 to 6 m. In the laboratory, living colonies were dissected longitudinally and examined under a binocular stereoscope for the presence of gonads or developing planulae in the brooding chambers. Additional colonies were carefully detached from the natural substratum, placed in plastic bags with sea-water, and transferred immediately into aerated aquaria. Colonies shed planulae at dusk, which were then pipetted out. Material for light microscopy was fixed in Bouin's solution and then decalcified in a mixture of equal volumes of formic acid (50%) and sodium citrate (15%). Sections of 8 to 10 μm were stained in Mallory Trichrome or hematoxylin-eosin. Samples for scanning electron microscopy (SEM) were fixed in 2% glutaraldehyde, followed by the GTGO procedure of Gamliel et al. (1983). Samples were examined using an JEOL JSM 840. The procedure for transmission electron microscopy (TEM) followed the methodology described by Berner et al. (1987).

Results

Distribution of algal symbionts in endodermal tissues

The endoderm of *Xenia umbellata* harbours symbiotic algae (Fig. 2). The anthocodial part of the polyp contains high densities of symbionts in the endodermal lining of the tentacles and pinnules (Figs. 3 and 4). Numerous algae are found in the endodermal cells of peripheral solenia in the coenenchyme (Figs. 5 and 6). A marked decrease in algal abundance is observed in inner endoderm located deeper inside the coenenchyme. The superficial solenia contain low numbers of symbionts (Figs. 5 and 7), while in interior solenia and the basal part of the polyp cavity algae are hardly ever seen.

Gonads

The gonads of *Xenia umbellata* develop along the ventral and the lateral mesenteries of the polyp cavities. The colonies are gonochoric brooders. The development of both female and male gonads follows an annual cycle (Benayahu in preparation). Early gonadal tissue appears as a cluster of primordial-endodermal cells, each cluster being attached by a stalk to the edge of the mesentery. The mesoglea of the stalk and its surrounding endoderm are continuous with the polyp cavity tissues. As the gonads grow in size they come to fill most of the polyp cavity (Fig. 8). In females each oocyte is enveloped by a mesogleal layer and by an outer layer of endodermal follicular cells (Fig. 9). A nucleus with a nucleolus lies at the periphery of the oocyte (Fig. 8). No algal symbionts are found inside the oocytes. However, their follicular tissue occasionally contains disintegrated algae (Fig. 10).

Each sperm sac contains a dense mass of sperm, enveloped by an endodermal sheath devoid of algal cells (Fig. 11). Dissected living colonies and histological sections indicated that mature sperm sacs are of various sizes and their variable shapes are probably determined by space availability within the polyp cavity (Fig. 12).

Embryogenesis

Ripe eggs of *Xenia umbellata* detach from the mesenteries and enter the gastrovascular cavities of the polyps. In *Xenia* after fertilization the zygotes pass into endodermal brooding chambers (see Benayahu and Loya 1984a, b), where embryogenesis takes place. These brooding chambers are located at the distal part of the polyp cavities (Fig. 13). Cleavage is initiated after detachment of the follicular layer from the mesoglea surrounding the eggs. The first stages of embryogenesis occur while the embryo is still coated by a thin layer of parental mesoglea (Fig. 14). Holoblastic cleavage of the embryo leads to formation of a solid blastula (Fig. 15). Dense, short microvilli appear on the surface of the blastomeres (Figs. 16 and 17). Symbiotic algae are embedded conspicuously within the mesogleal coating of the embryo (Figs. 18 and 19). At a later developmental stage this mesogleal integument disappears and a naked round stereoblastula is recognized (Fig. 15). At this stage algal cells appear to be on the surface of the cells of the newly formed blastula (Fig. 20). Thus, symbionts are incorporated by the embryo very early in development.

Subsequent cell divisions lead to development of young planulae within the brood chambers (Fig. 21). The peripheral cell layer of the planula gives rise to ectoderm, which is attached to a thin mesoglea (Fig. 22). Immature planulae contain an inner mass of undifferentiated yolk-laden cells with intracellular algal symbionts embedded in the yolk (Figs. 23 and 24). The yolk is gradually utilized leaving a cavity enclosed by a wall of two tissue layer, separated by a thin mesoglea (Fig. 25).

The mature planulae are slender, reaching 2.0 mm or more in length (Fig. 26). They are broad at the oral end and taper gradually towards the aboral end. In life their colour is brownish due to presence of symbionts. The columnar ectoderm of the planula is covered with cilia (Figs. 27 and 28), and many cilia are surrounded by collars (Fig. 28). Endodermal cells containing algae adhere to the thin mesoglea (Fig. 27) and in the mature planulae they also bear cilia and numerous microvilli on the surface lining of the polyp cavity (Fig. 29).

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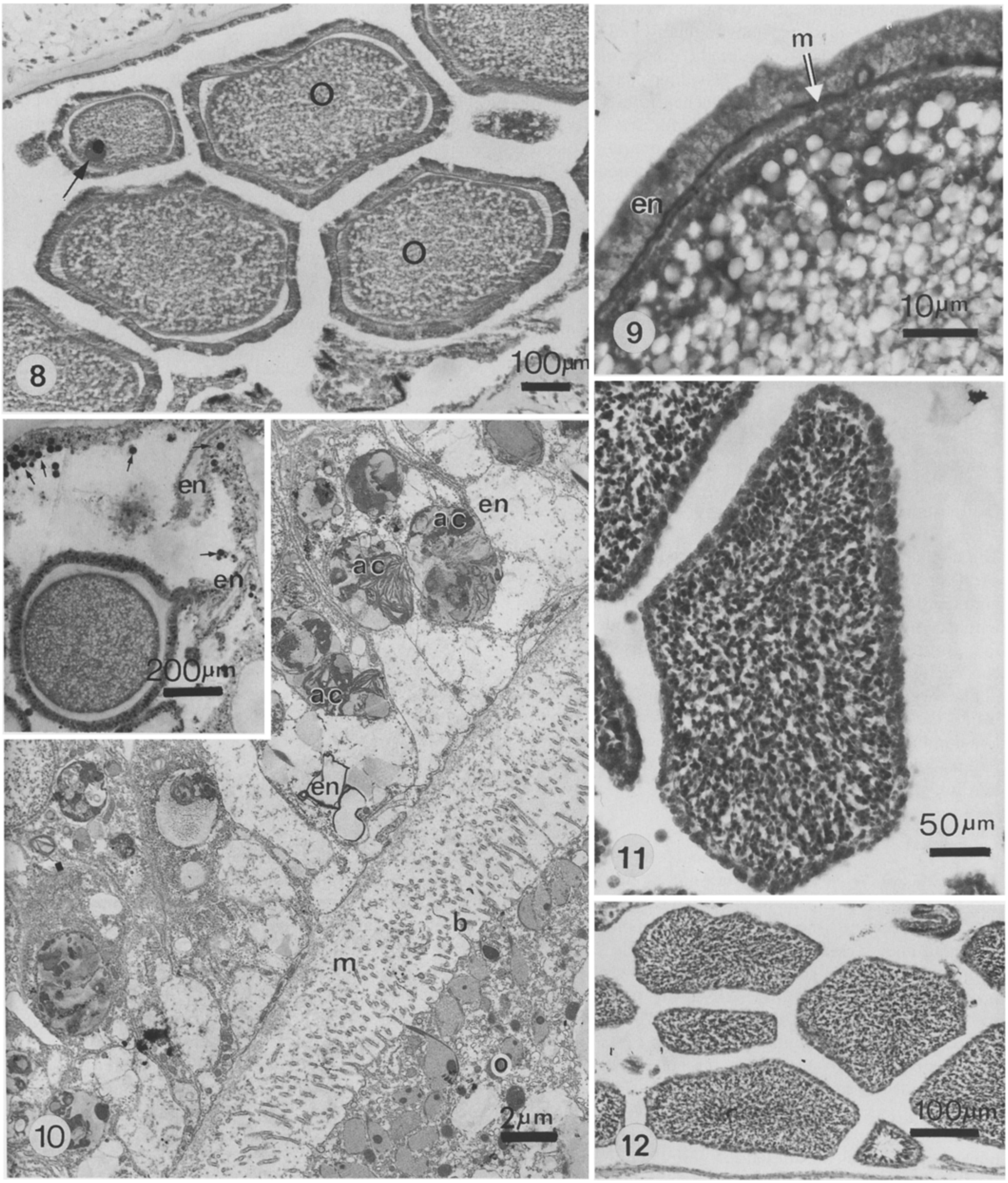
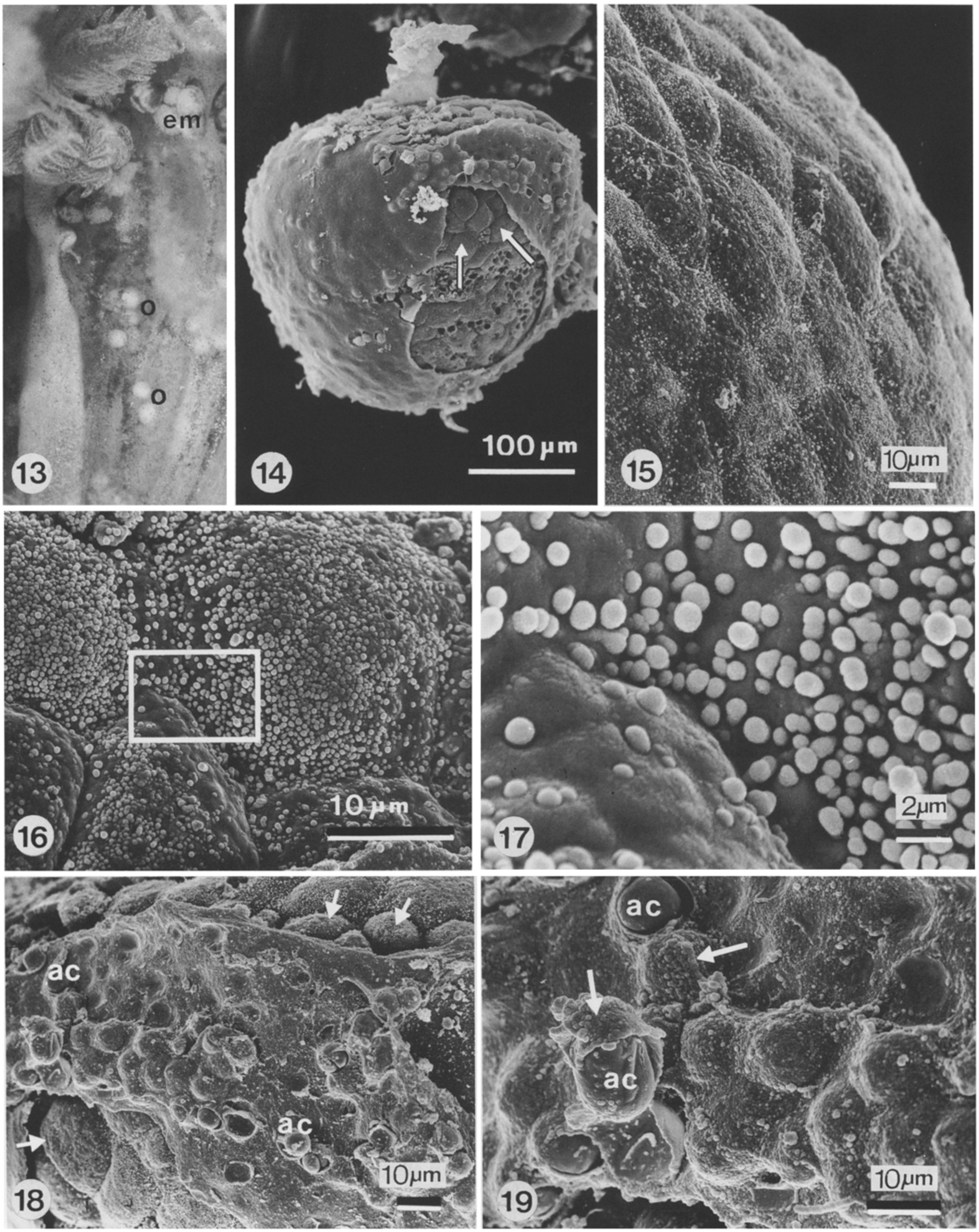
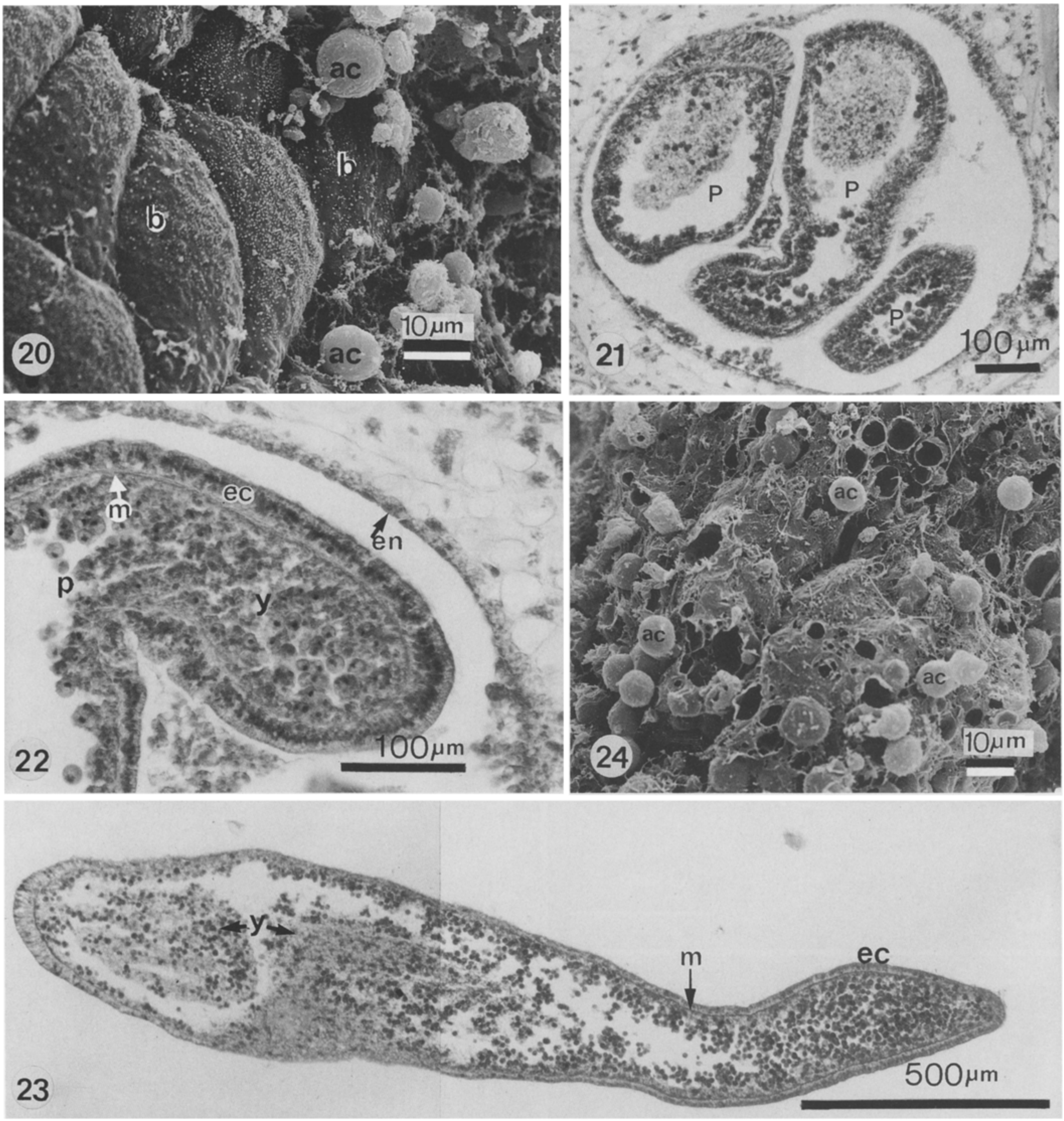
Figs. 1–7. 1: Living colonies of *Xenia umbellata;* **2:** Scanning electron micrograph (SEM) of ciliated endoderm showing algal cells (ac); **3:** SEM of a fractured tentacle (t) with lateral pinnules (p). Tentacle cavity (tc) protrudes into polyp cavity (pc); **4:** SEM of fractured pinnule (p) with algal symbionts in its endoderm (arrows); **5:** Photomicrograph of the outer surface of colony stalk. Ectoderm (ec) is outermost cell layer. Endodermal cavities run through mesoglea (m) comprising longitudinal peripheral solenia (ps), cross-sectioned inner solenia (s) and a polyp cavity (pc); **6:** Photomicrograph of longitudinally sectioned peripheral solenium (ps). Numerous algal symbionts (arrows) are found in its endodermal lining (e); **7:** Photomicrograph of cross-sectioned inner solenia (s) with very few algal cells (arrows)



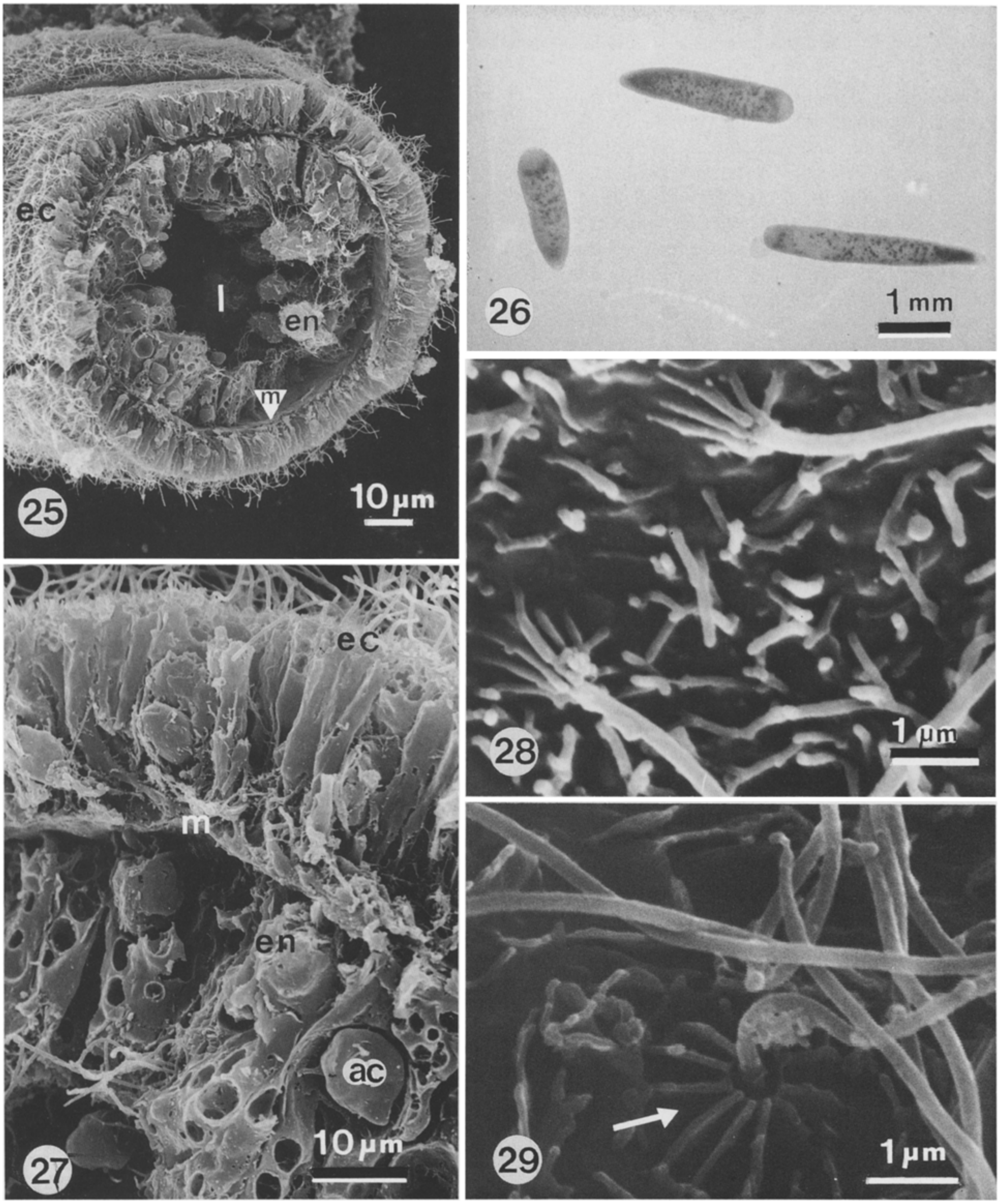
Figs. 8–12. 8: Photomicrograph of mature oocytes (o) inside polyp cavity. Arrow indicates nucleus with deeply stained nucleolus; **9:** Photomicrograph of a portion of large oocyte with cortex composed of thin mesoglea (m) and outer follicular endodermal layer (en); **10:** TEM micrograph of sectioned oocyte showing outer part of oocyte (o) covered with brush-like surface (b) and mesoglea (m). Follicular endodermal tissue (en) contains disintegrated algal walls (ac). Inset: Photograph of oocyte without algal walls attached to mesentery by stalk of parental mesoglea and endoderm (en) with symbionts (arrows); **11:** Photomicrograph of sperm sac with darkly stained spermatids; **12:** Photomicrograph of mature spermaries within a polyp cavity



Figs. 13–19. 13: Dissected living female colony with oocyte (o) and brooding chamber with developing embryos (em); **14:** SEM of an early cleavage embryo coated by mesogleal cover isolated from brood chamber. Double arrows mark exposed blastomeres, where mesoglea was removed; **15:** SEM of portion of blastula after detachment of mesogleal sheath; **16:** SEM of microvilli associated with blastomeres of exposed embryo. Box outlines region similar to that shown at higher magnification in Fig. 17; **17:** SEM of microvilli arising from blastomeres; **18:** SEM of mesogleal sheath around embryo, with embedded algal cells (ac). Arrow points to exposed blastomeres; **19:** SEM of a mesogleal coating of embryo with algal cells (ac). Partial exposure of algal cells is due to removal of mesoglea (arrows)



Figs. 20–24: 20: SEM of fractured embryo. Algal cells (ac) reside on surface of blastomeres (b); **21:** Photomicrograph of sectioned brood chamber with developing young planulae (p); **22:** Photomicrograph of portion of young planula (p) inside brood chamber. This chamber is lined with endodermal tissue (en). Developing planula is differentiated into ectoderm (ec), thin mesoglea (m) and yolk content (y); **23:** Photomicrograph of immature planula showing ectoderm (ec), mesoglea (m) and inner yolk laden mass (y) with numerous darkly stained algal cells (ac); **24:** SEM of a fractured immature planula with nutritive content and numerous algal cells (ac)



Figs. 25–29. 25: SEM of transversely fractured mature planula prior to liberation, differentiated into ectoderm (ec), thin mesoglea (m), and endoderm (en) with interior lumen (l); **26:** Living planulae with zooxanthellae visible as dark patches; **27:** SEM of fractured mature planula showing ciliated columnar ectoderm (ec), mesoglea (m) and endoderm (en) inhabited by algal cells (ac); **28:** SEM of ectoderm of mature planula showing cilia which cover surface. Each cilium is surrounded by collar of microvilli cover surface; **29:** SEM of endoderm cells lining cavity of a mature planula showing collar of microvilli (arrow) and cilia

Discussion

Development of planulae

Soft coral alcyonaceans demonstrate a variety of reproductive patterns (Benayahu and Loya 1983, 1984a, Uehara et al. 1987). Embryogenesis and early larval development of gamete-spawning alcyonaceans has been examined in *Alcyonium digitatum* (Linnaeus, 1758) (Hartnoll 1975) and recently in *Lobophytum crassum* Marenzeller, 1886 (Uehara et al. 1987). In addition, these ontogenetic phases have been described for several other alcyonaceans with external brooding of planulae, e.g. *Clavularia crassa* (Milne Edwards, 1848), *Cornularia komaii* Utinomi, 1950, *C. sagamiensis* Utinomi, 1950, *Parerythropodium fulvum fulvum* (Forskål, 1775) (ref. in: Benayahu and Loya 1983) and *Clavularia hamra* Gohar, 1940 (Benayahu 1987). The only existing data concerning transition of an alcyonacean egg into planula through internal brooding are derived from scanty illustrations of *Heteroxenia fuscescens* Ehrenberg, 1834 (Gohar and Roushdy 1961). The current study is the first to demonstrate ultrastructural features associated with embryogenesis of a planulating alcyonacean.

Embryogenesis and larval development of numerous gamete-spawning hermatypic corals have been well documented (Fadlallah 1983, Babcock and Heyward 1986). However, similar aspects of development in brooding scleractinians remain enigmatic, despite extensive studies (Fadlallah 1983, Szmant-Froelich et al. 1985). Even in the well studied scleractinians, e.g. *Stylophora pistillata* Esper, 1797 (Rinkevich and Loya 1979) and *Pocillopora damicornis* (Linnaeus, 1758) (Stoddart and Black 1985), the developmental stages connecting ova and the mature planulae have never been observed. Absence of embryos in brooding colonies has led to speculations concerning the mode of planula development (Stoddart and Black 1985). Babcock and Heyward (1986) suggest that retention of larvae by parent hermatypic corals produces difficulties while searching for their brood embryos. Embryogenesis of xeniid alcyonaceans takes place in brood pouches (Benayahu and Loya 1984b). Presence of embryos in colonies of *Xenia umbellata* 2 to 3 wk prior to the reproductive season (Benayahu in preparation) leads us to suspect that planular maturation is completed within this period. Therefore, further examining of embryogenesis within the brood pouches will provide a unique opportunity to clarify an enigmatic phase of xeniid ontogenesis.

Aquisition of symbiontic algae

Gametogenesis and embryogenesis of symbiotic coelenterates occur in intimate proximity to tissues containing symbionts. Therefore, two questions may be posed: (1) To what extent does this structural association ensure transmission of symbiotic algae to the next generation? and (2) At what ontogenetic stage is a structural association between alga and offspring initiated? There is no evidence in the literature that sperm carry symbionts. In contrast, oocytes of various coelenterates have been reported to possess algal symbionts, either inside their ooplasm (Krupp 1983, Schäfer 1984, Dinesen 1985, Babcock et al. 1986), or in their follicular layer (Rinkevich and Loya 1979, Shinkarenko 1981). Incorporation of algal symbionts into the oocytes prior to spawning may ensure infected offspring. However, there is currently insufficient information on which to base conclusions about the role of follicular algae in offspring infection. Oocytes of *Xenia umbellata* as other alcyonaceans are differentiated from clusters of endodermal cells found in the mesoglea (Farrant 1986, Benayahu in preparation). During advanced oogenesis the oocytes are coated with the parental mesoglea and endoderm which are continuous with the parent tissues. Shinkarenko (1981) indicated the presence of algal cells in the endodermal follicular layer of the alcyonaceans *Lobophytum crassum* Marenzeller, 1886; *L. pauciflorum* (Hemprich and Ehrenberg, 1832) and *Sarcophyton trocheliophorum* Marenzeller, 1886. Nevertheless there is no information as to whether this tissue is involved in algal transmission into further developmental stages. Endodermal tissues of *X. umbellata* are not uniformly infected by symbionts (Figs. 4–7). Although these symbionts are found in the lining of the polyp cavities, they are only rarely present in the follicular sheath of *X. umbellata.* We suggest that the presence of disintegrating algal cells in the follicular cells may indicate a possible prevention of symbiont acquisition from this tissue.

There is substantial ultrastructural evidence for a role played by the egg surface in transmitting algal symbionts to hosts. Thorington et al. (1979) demonstrate maternal transport of symbionts through the sexual cycle of *Hydra* sp. via adherence to the egg surface. Trench (1987) further describes the passage of symbionts in the hydroid *Myrionema* through the mesoglea separating the egg from the endoderm. Algal symbionts adhere to sticky externally-brooded embryos of the alcyonacean *Capnella gaboensis* Verseveldt, 1977, thus suggesting an algal trap by the dividing embryo (Farrant 1985, 1986). The mechanism of establishing a contact between blastomeres of *X. umbellata* and the symbionts is also associated with surface adherence of the algae (Figs. 18, 19), which are first probably transmitted extracellularly and later attain their intracellular position within the endoderm.

For corals that brood planulae internally the present study is the first to document maturation of eggs lacking symbiotic algae and subsequent infection of an early blastula. We assume that incorporation of symbiotic algae into such an early embryogenic stage may help support its metabolic requirements. Nevertheless further studies are needed to provide a more detailed understanding of the developmental pathways of corals along with their algal associates. Such information is essential for assessment of the structural and functional significance of endosymbiotic algae throughout the life cycle of the coral host.

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