

Development of planulae within a mesogleal coat in the soft coral *Heteroxenia fuscescens*

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Abstract

Embryology of the hermaphroditic and dimorphic alcyonacean *Heteroxenia fuscescens* has been examined by scanning electron microscopy and light microscopy. Initial embryonic development in this octocoral occurs while the embryos migrate freely inside the anthocodiae and the tentacles. Immature planulae are extruded externally into intersiphonozooid spaces, where they mature. All stages of planular morphogenesis, from egg to planula, occur while the embryo is coated by the original egg mesogleal coat derived from the parent colony. Hatching from this mesogleal coat occurs as late as immediately prior to planulation. *H. fuscescens* demonstrates highly specialized brood care involving the retention of embryos in internal polyp cavities as well as in external spaces. This highly specialized brood care, coupled with the embryo coating, may provide better protection for the embryo and greater fecundity for the colony.

1985). Its colonies are easily recognized among other xeniids by their large size and long pulsating polyps. Although Gohar (1940) and Gohar and Roushdy (1961) reported some reproductive features of *H. fuscescens*, various aspects of embryogenesis and the structural relationships between the developing planulae and the parent colony remain poorly known.

The objectives of this study are (1) to examine the mode of development of planulae and the brooding procedure in *Heteroxenia fuscescens* and (2) to determine the structural relationships between a gravid colony and its developing embryos.

Using histological sections and scanning electron microscopy (SEM), we examine the morphological features of the eggs and embryos. We describe, for the first time, a peculiar mode of planula development within a coat of parental mesoglea and the consequent hatching of mature larva from this coat at planulation.

Introduction

Several soft corals (Octocorallia: Alcyonacea) have reproduction that involves planulae shedding (Benayahu and Loya 1984b). Alcyonaceans of the family Xeniidae have been observed to brood their embryos to a planula stage (Gohar 1940, Gohar and Roushdy 1961). In *Xenia* species, embryogenesis of the fertilized egg is carried out within internal brooding pouches where the planulae mature (Benayahu and Loya 1984b, Benayahu et al. 1987). All *Heteroxenia* species are characterized by polyp dimorphism, i.e., two kinds of polyps are present in a colony: autozooids and siphonozooids. Some *Heteroxenia* species are hermaphroditic and have a rather complex brooding mechanism that involves the retention of the expelled planulae among the siphonozooids (Gohar 1940).

Heteroxenia fuscescens (Ehrenberg, 1834) is a common shallow-reef xeniid in the northern Red Sea (Benayahu

Material and methods

Colonies of *Heteroxenia fuscescens* were collected during 1986 and 1987 from the coral reef in front of the Marine Biological Laboratory at Eilat. Field collection, underwater observations and photography were conducted while SCUBA diving at depths of 4 to 12 m. Immediately after collection, living colonies were dissected longitudinally and examined under a binocular stereoscope. Gonads and embryos from the colonies were collected and fixed (see below). Additional colonies of *H. fuscescens* were carefully detached from the natural substratum and transferred into aerated aquaria. Released embryos or planulae were pipetted out of these aquaria. Material for light microscopy was fixed in Bouin's solution and then decalcified in a mixture of equal amounts of formic acid (50%) and sodium citrate (15%). Paraffin sections 8 μ m thick were cut and stained in Mallory Trichrome or hematoxylin-eosin. Material for scanning electron microscopy (SEM) was fixed in sea-water 2% glutaral-

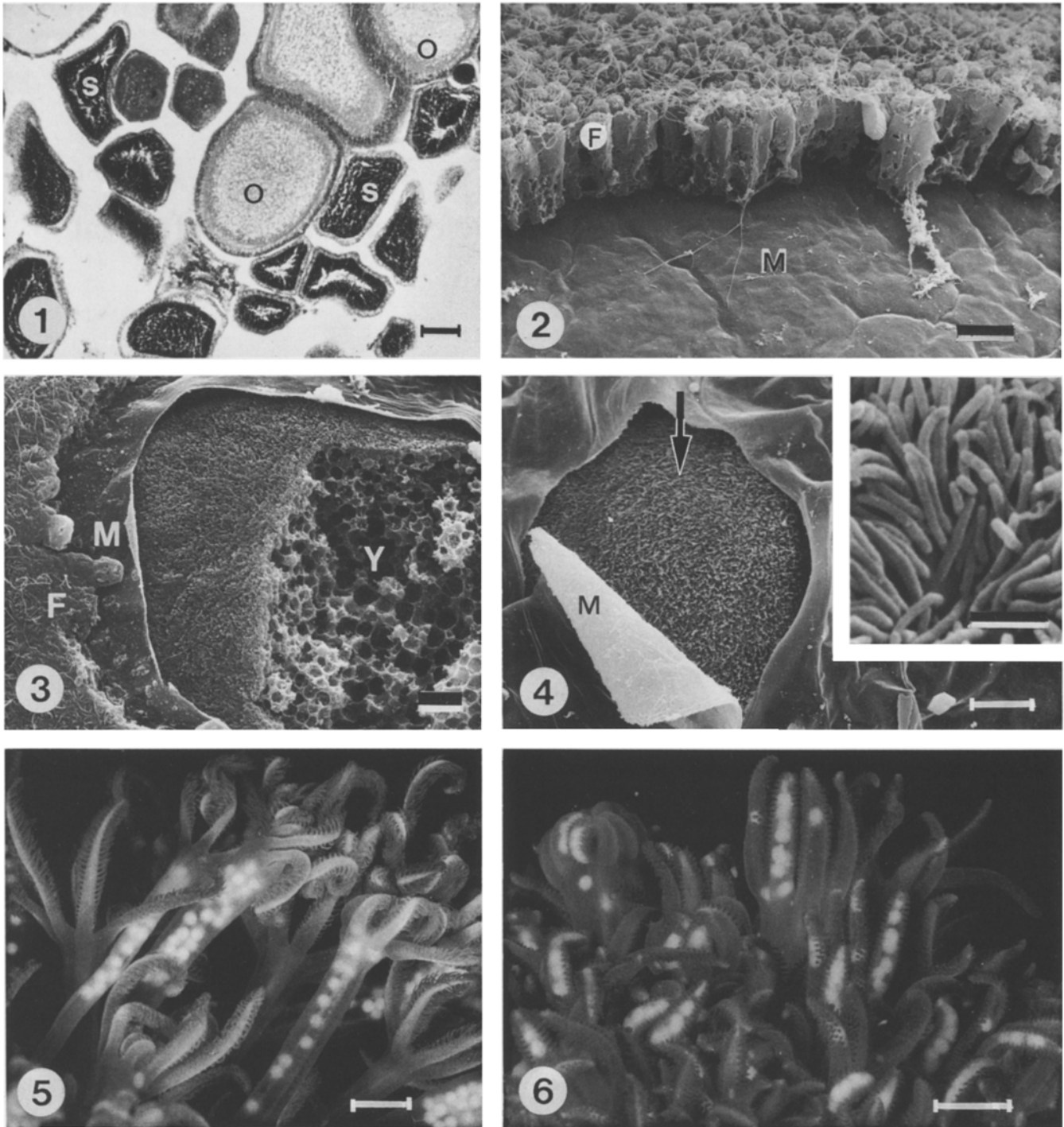


Fig. 1. *Heteroxenia fuscescens*. Photomicrograph of oocytes (O) and sperm sacs (S) inside an autozooid cavity. Scale bar = 100 μ m

Fig. 2. *Heteroxenia fuscescens*. Scanning electron micrograph (SEM) of a portion of an oocyte surrounded by ciliated endodermal follicular layer (F) and mesoglea (M). Scale bar = 10 μ m

Fig. 3. *Heteroxenia fuscescens*. SEM of a fractured oocyte with follicular layer (F), mesoglea (M) and yolk material (Y). Scale bar = 10 μ m

Fig. 4. *Heteroxenia fuscescens*. SEM of an oocyte with partly broken mesoglea (M) and exposed oocyte surface (arrow). Scale bar = 10 μ m. Inset: SEM showing microvilli of the oocyte surface. Scale bar = 1 μ m

Fig. 5. *Heteroxenia fuscescens*. Embryos inside anthocodiae of living colony. Scale bar = 5 mm

Fig. 6. *Heteroxenia fuscescens*. Embryos inside the tentacles of living colony. Scale bar = 5 mm

dehyde, followed by GTGO procedure (Gamliel et al. 1983). Samples were examined using a Joel JSM 840. The terminology of gross morphology and anatomy follows Bayer et al. 1983.

Results

Colonies of *Heteroxenia fuscescens* are hermaphroditic. Each autozooid bears male and female gonads (Fig. 1). The gonads appear on the four lateral and two ventral mesenteries of the polyps, excluding their anthocodial extensions. Within any given polyp the oocytes and the spermaries are densely aggregated at the upper end of the coelenteron below the level of the capitulum, occupying 30–60% of the length of each mesentery. Clusters of gonadal primordia appear at the uppermost part of the autozooid. When alive both male and female gonads are opaque, and creamy-white. Gonadal sex can be determined only by histological sectioning. This reveals that male and female gonads are both present on the same mesentery.

The maximal diameter of mature oocytes is 750 to 900 μm . Each oocyte is surrounded by a follicular layer of ciliated columnar cells and an underlying mesogleal layer (Figs. 2, 3). Both layers are continuous with the parental tissues which form the gonadal pedicel that attaches them to the mesentery. The periphery of the oocytes is covered by microvilli which extend 1 to 2 μm from the surface, toward the mesogleal coat (Fig. 4).

Mature eggs of *Heteroxenia fuscescens* become detached from the mesenteries and are fertilized internally, within the gastrovascular cavity of the autozooids. Subsequent embryonic development is divided into two distinct phases: (1) internally inside the autozooids and (2) externally among the siphonozooids. The embryos migrate freely inside the autozooid cavities. They resemble white-colored strings and are easily observed underwater through the transparent polyp wall (Figs. 5, 6). The embryos are very often driven up into the anthocodiae (Figs. 5, 7) and they are conspicuous in the tentacle cavities (Figs. 6, 8).

All stages of embryogenesis are carried out while the embryo is enveloped within a mesogleal coat, which is apparently the parental mesoglea that surrounds the oocyte (Figs. 2–4). The young embryo is ca. 1.0 mm long (Fig. 9) and covered with the mesogleal coat. Embryos at stereoblastula stage (Fig. 10) were isolated from the autozooids. After further cell divisions the blastomeres are loosely arranged inside the mesogleal coat (Fig. 11) without any recognizable filipodia between them (Figs. 12, 13). At this stage of development the blastomeres are nearly smooth and have no surface specializations (Fig. 13). Further embryonic development leads to the gradual appearance of surface microvilli. Initially they are short and sparsely scattered on the cell (Fig. 14). Then later they become substantially longer and more numerous (Fig. 15). Cilia also develop among the microvilli beneath the mesogleal coat (Fig. 16).

Immature planulae of *Heteroxenia fuscescens* (Fig. 17) are extruded from the autozooids through temporary gono-

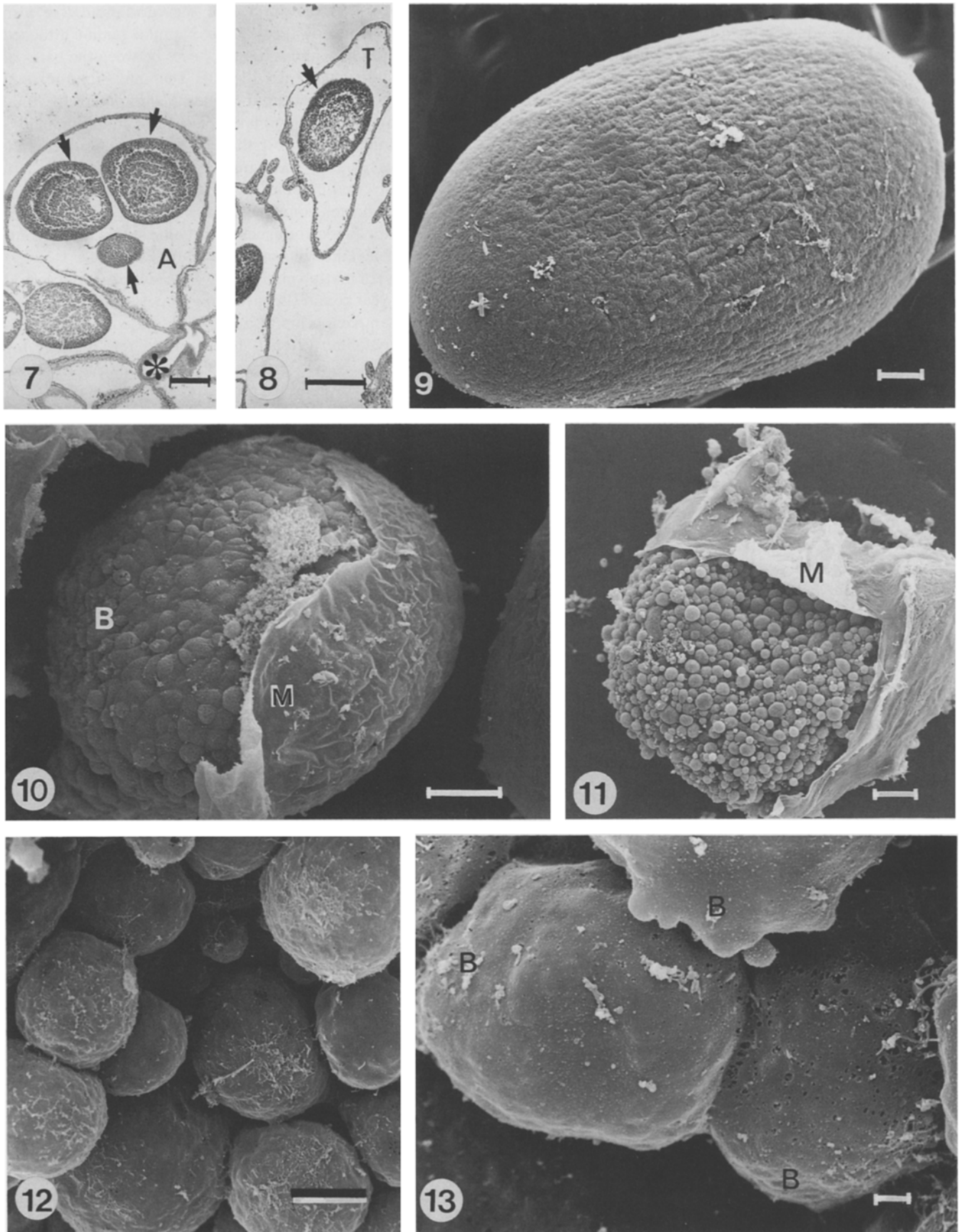
pores opened in the surface of the capitulum (see also Gohar and Roushdy 1961). These planulae remain attached externally on the capitulum, in spaces between the bases of the siphonozooids (Figs. 18–20). The inter-siphonozooid spaces are used as external brooding sites where the final stage of larval maturation takes place. The immature planulae are elongated or pear-shaped (Fig. 19), about 1.5 mm and surrounded by the parental mesoglea coat (Fig. 20). Severely stressed colonies of *H. fuscescens* tend to release numerous aborted young white embryos and immature planulae. In the laboratory such embryonic stages fail to complete their metamorphosis into mature larvae.

Release of mature planulae by *Heteroxenia* was observed nearly all year round (Benayahu in preparation). Release of mature planulae occurs at dusk. Within a colony this process is rapid, and often it takes only a few minutes for hundreds of larvae to emerge from the inter-siphonozooid spaces. Planulation occurs when the planulae hatches from the mesogleal coat and escapes from these spaces. Mature planulae of *H. fuscescens* are elongated, 3.5–4 mm long (Fig. 21), ciliated (Fig. 22), and opaque white, because their tissues lack symbiotic algae. The planulae are capable of contraction and, hence, tend to change their shape. Larval movement is slow, performed both by body contractions and ciliary movement on the substratum.

Discussion

Heteroxenia fuscescens is a hermaphroditic soft coral which broods its planulae. Among alcyonaceans hermaphroditism has been recorded for only a few other species, e.g. *H. elizabethae*, *H. gardagensis* and *Xenia viridis* Ashworth 1899, (Gohar 1940). To date, available information indicates that most soft corals are gonochoric (Gohar 1940, Hartnoll 1975, Benayahu and Loya 1983, 1984a, 1986, Farrant 1986, Benayahu 1987, Uehara et al. 1987). Observations derived from several earlier publications supply additional evidence that gonochorism is the dominant pattern among alcyonaceans (Pratt 1903, Nutting 1912, Thorpe 1928, Hickson 1931). However, caution is necessary in interpreting these observations as they are based on small samples. Furthermore, while Gohar (1940) indicated that *H. elizabethae* in the Red Sea is hermaphroditic, Shinkarenko (1981) pointed out that the same species is gonochoric at the Great Barrier Reef, Australia. Such a mixed breeding system within the same species in different zoo-geographical areas would be remarkable if true, and requires further study.

Heteroxenia fuscescens has a number of features that would be useful in promoting outcrossing. The spermaries are shed intact into outside water through temporary gonopores (Gohar 1940). This mechanism, in which spermaries do not break open inside the polyp cavities, reduces the probability of self-fertilization in hermaphroditic species (see also Szmant 1986). In histological sections of polyps (Fig. 1) spermaries often outnumber the oocytes (Benayahu in preparation). *H. fuscescens* colonies grow in clusters on the reefs of Eilat (Benayahu 1975), a pattern which would also favor cross-fertilization.



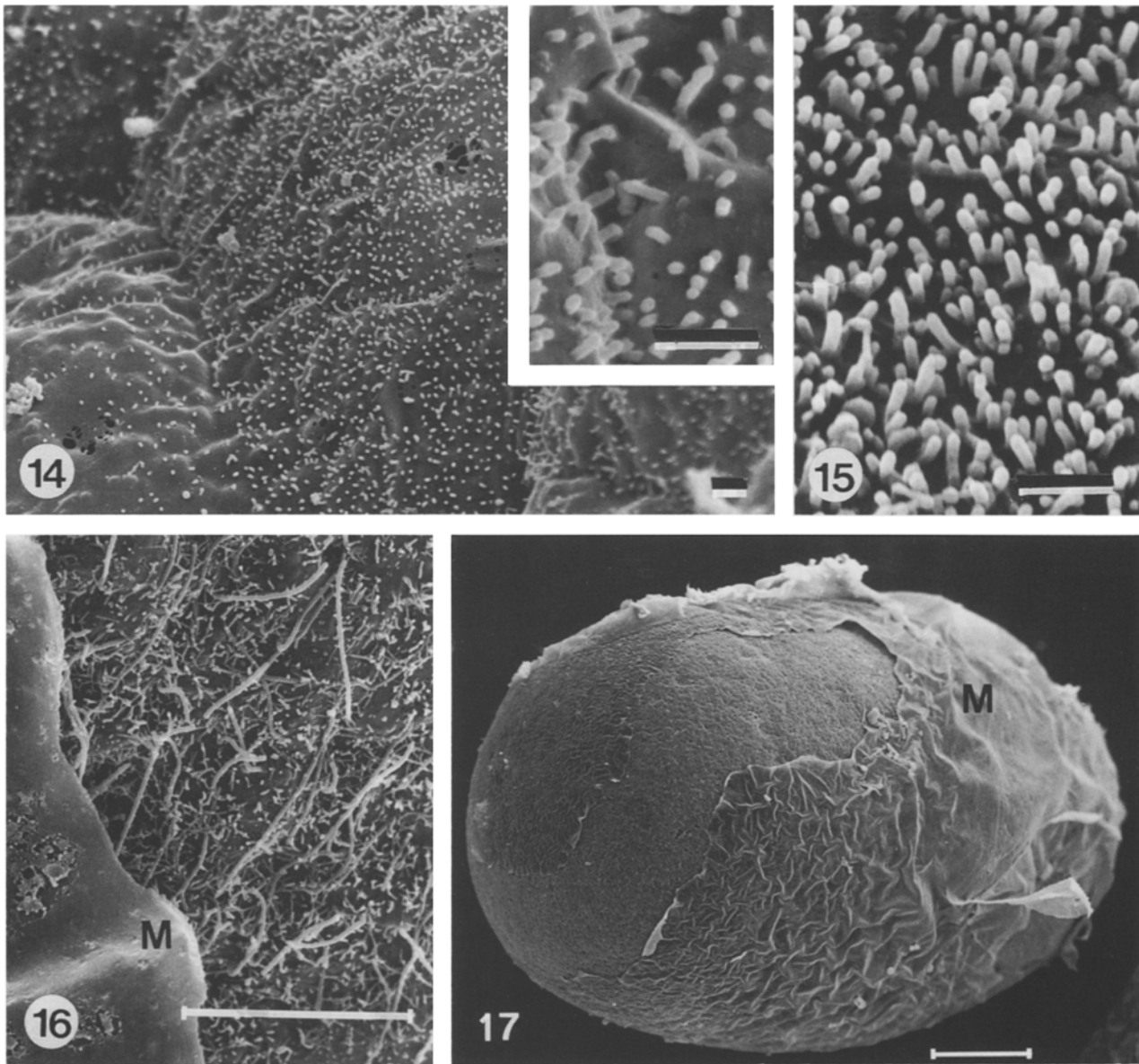


Fig. 14. *Heteroxenia fuscescens*. SEM of exposed blastomeres with microvilli. Scale bar = 1 μm . Inset: high magnification of a region on these blastomeres. Scale bar = 1 μm

Fig. 15. *Heteroxenia fuscescens*. SEM of exposed blastomeres of an advanced embryo with dense microvilli. Scale bar = 1 μm

Fig. 16. *Heteroxenia fuscescens*. SEM of a partly removed mesogleal coat (M) showing microvilli and cilia on the embryo surface. Scale bar = 10 μm

Fig. 17. *Heteroxenia fuscescens*. SEM of immature planula with partly removed mesogleal coat (M). Scale bar = 100 μm

Fig. 7. *Heteroxenia fuscescens*. Photomicrograph of fertilized eggs (arrows) inside anthocodium (A), at the level of the pharynx (asterisk). Scale bar = 200 μm

Fig. 8. *Heteroxenia fuscescens*. Photomicrograph of fertilized egg (arrow) inside a tentacle (T). Scale bar = 200 μm

Fig. 9. *Heteroxenia fuscescens*. SEM of an embryo coated with parental mesoglea. Scale bar = 100 μm

Fig. 10. *Heteroxenia fuscescens*. SEM of a stereoblastula with partly removed parental mesogleal coat (M) exposing the blastomeres (B). Scale bar = 100 μm

Fig. 11. *Heteroxenia fuscescens*. SEM of an advanced cleaved stereoblastula with partly removed mesogleal coat (M). Scale bar = 100 μm

Fig. 12. *Heteroxenia fuscescens*. SEM of exposed blastomeres indicating no junctional filipodia between cells. Scale bar = 10 μm

Fig. 13. *Heteroxenia fuscescens*. SEM of exposed cleaved blastomeres (B) indicating no surface specializations. Scale bar = 1 μm

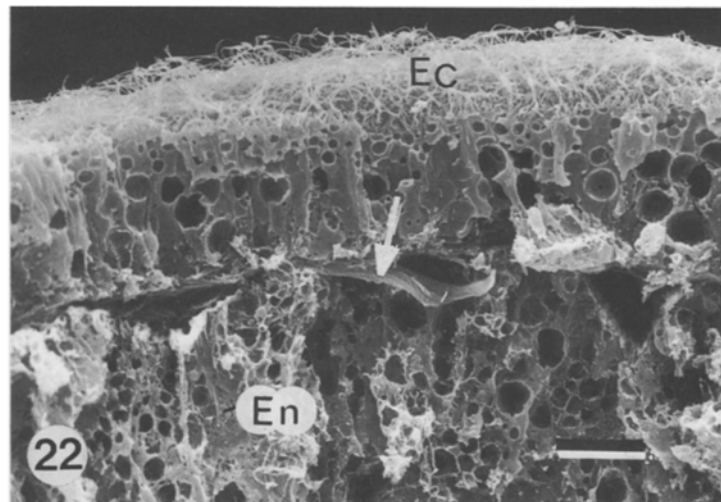
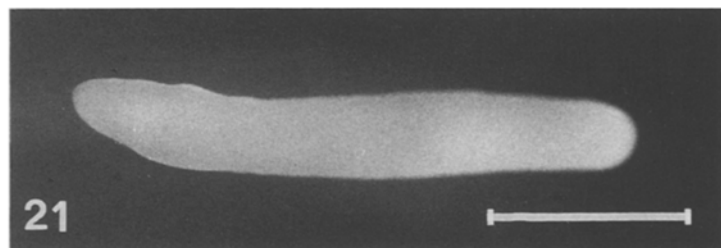
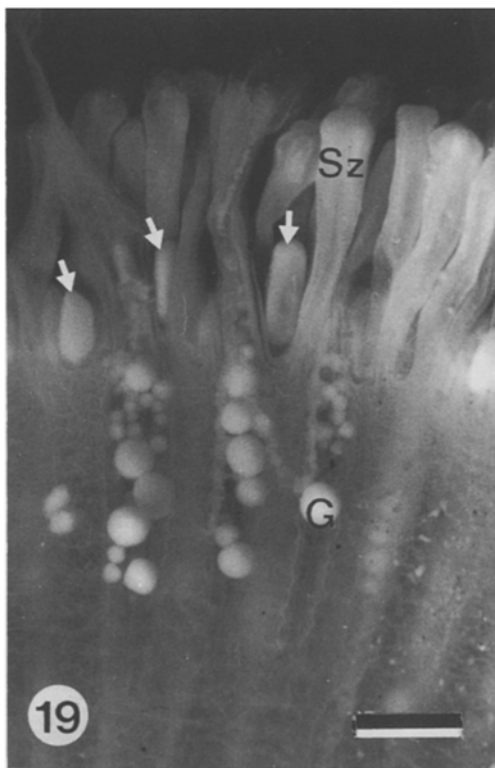
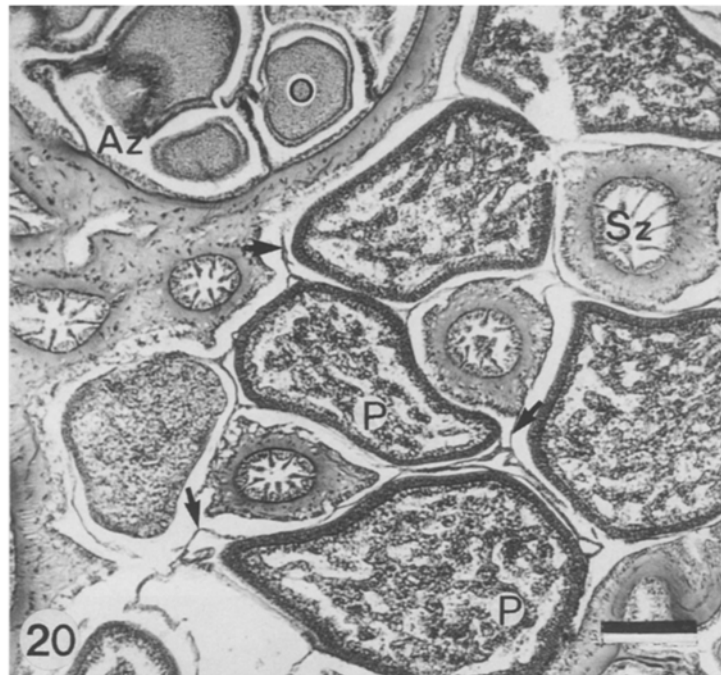
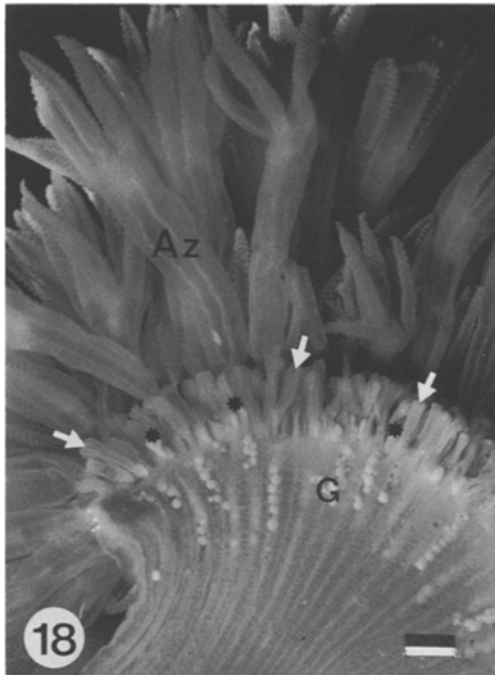


Fig. 18. *Heteroxenia fuscescens*. Longitudinal section through living colony showing autozooids (Az), siphonozooids (arrows), gonads (G) in autozooids, planulae between siphonozooids (asterisks). Scale bar = 5 mm

Fig. 19. *Heteroxenia fuscescens*. Longitudinal section through living colony showing clusters of gonads (G) in autozooids and brood planulae (arrows) between siphonozooids (Sz). Scale bar = 2 mm

Fig. 20. *Heteroxenia fuscescens*. Photomicrograph of cross section through autozooid (Az) with oocytes (O) and through the siphonozooids (Sz). Immature planulae (P) are found in the intersiphonozooid spaces. Each planula is surrounded by the parental mesogleal coat, indicated by arrows. Scale bar = 100 μ m

Fig. 21. *Heteroxenia fuscescens*. Living planula. Scale bar = 1 mm

Fig. 22. *Heteroxenia fuscescens*. SEM of a fractured mature planula showing ciliated ectoderm (Ec), mesoglea (arrow) and endoderm (En). Scale bar = 10 μ m

Utinomi and Imahara (1976) described gonadal development both in autozooids and siphonozooids of the dimorphic alcyonacean *Minabea robusta*. However, in *Heteroxenia fuscescens*, as in other dimorphic soft corals that have been studied (Gohar 1940, Shinkarenko 1981, Benayahu and Loya 1986, Uehara et al. 1987), the gonads are confined only to the autozooids. Like gonads of other alcyonaceans (Farrant 1986), the gonads of *H. fuscescens* bulge out from the mesenteries into the gastrovascular cavity of each polyp. Each oocyte is enclosed by a follicular endoderm and a thin mesogleal layer (Figs. 2–3). The dense, short microvilli found on the oocyte surface (Fig. 4) are remarkable and have not been described previously for corals. Eggs of some sea anemones are covered by longer microvilli (10 to 20 μm), usually extending as tufts of cytopines (Siebert 1974, Spaulding 1974, Siebert and Spaulding 1976, Larkman and Carter 1984, Schäfer 1984). It has been suggested that these tufts of microvilli may afford the egg a certain mechanical protection (Larkman and Carter 1984). However, oocytes of *H. fuscescens* are enclosed within a mesogleal coat (Figs. 2–4) which would provide an adequate protection. During cleavage the surfaces of the blastomeres are nearly smooth with no indication of microvilli (Figs. 10–11), and therefore, differ markedly from the oocyte surface. This dramatic morphological change is presumably associated with the cortical reaction following fertilization. Eggs of some sea anemones equipped with similar microvilli lose their projections immediately after fertilization and, subsequently, have a smooth oolema (Clark and Dewel 1974, Schäfer 1984). In other species the conspicuously long cytopines are retained as late as gastrulation (Siebert 1974, Siebert and Spaulding 1976). It has been suggested that microvilli on eggs of some hydroids serve for nutritional exchange between the oocyte and its surrounding epithelium (Boelsterli 1975). We also propose that microvilli of *H. fuscescens* eggs play a nutritional role throughout oogenesis, and that their complete disruption is probably associated with sperm-egg interaction. Further ultrastructural evidence is required in order to shed light on cortical reaction and related events in alcyonaceans.

The blastomeres of broadcasting alcyonaceans are connected by numerous filipodia (Benayahu and Loya 1983, Benayahu 1987). However, embryos of *Heteroxenia fuscescens* lack this type of cell-to-cell adhesion complex (Figs. 9–10), and during embryogenesis the mesogleal coat, most probably helps hold the blastomers together. The mechanism of cell-to-cell adhesion in the developing embryos of alcyonaceans is as yet unknown.

Heteroxenia fuscescens has elaborate brood care involving structural and behavioral adaptations. All stages of embryogenesis of this species, from egg to mature planula, occur within the parental mesoglea coat that originally covered the egg. Early cleavage within a mesogleal coat has recently been recorded in *Xenia umbellate* (Benayahu et al. 1987). However, unlike *H. fuscescens*, subsequent morphogenesis of *X. umbellate* occurs while the embryo is within the brood pouch. Among other cnidarians embryonic development of the sea anemone *Actinostola spetsbergensis* occurs in

a peculiar non-cellular envelope of unknown origin (Rieman-Zürneck 1976) and embryos of *Hydra carnea* are surrounded by a protective cellular embryotheca secreted by the blastomeres (Honegger 1981). Our study demonstrates for the first time retention of a coat of parental mesoglea throughout the entire process.

The brooding of planulae by *Heteroxenia fuscescens* inside cavities of the anthocodia or the tentacles, has not been recorded for any other alcyonacean. Such a mechanism utilizes the non-gonad producing polyp cavities for the brooding planulae. Extrusion of immature planulae from the cavities into the inter-siphonozooid spaces (Figs. 16–17) is presumably associated with increasing final embryo size. Planulae of *H. fuscescens* are the largest known among alcyonaceans (Benayahu and Loya 1984b, Benayahu 1987), reaching 3.5 to 4 mm in the inter siphonozooids spaces. This allows the inner polyp cavities to be used by the following smaller embryonic stages, substantially increasing the brooding capability of *H. fuscescens* and probably leading to higher fecundity of individuals in this species.

Hatching of embryonic stages or larvae from their coat has been studied in various echinoderms (Holland 1981). This is the first study to show hatching of a cnidarian larva from a parental mesogleal coat at planulation. The brood care of *Heteroxenia fuscescens* exhibits a previously undescribed mode of planular development with highly specialized brooding habits, which seem to maximize the protection and survival of the embryo.

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