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ENTRY OF ALGAL SYMBIONTS INTO OOCYTES OF THE CORAL *LITOPHYTON ARBOREUM*

Keywords: Octocorallia, *Litophyton arboreum*, symbiosis, zooxanthellae, infection, oocyte

ABSTRACT. On the Red Sea coral reefs *Litophyton arboreum* is a common octocoral whose endodermal cells are associated with endosymbiotic dinoflagellates (zooxanthellae). Colonies of this species are gonochoric and brood planulae which, upon release, are already associated with the algal symbionts. Algal cells within membrane-bound vacuoles are observed within the gastrovascular cavity of the polyps, adjacent to the oocytes and are gradually phagocytized by the follicular cells which surround the oocytes. During oogenesis, temporary gaps open in the mesoglea underlying the follicular cells. Symbionts within vacuoles, along with cytoplasm and various organelles derived from the follicular cells, are translocated through these gaps. Subsequently, groups of zooxanthellae accumulate at the perioocytic zone, flanked between the mesoglea and oocytic microvilli. At a later stage, prior to the commencement of the breeding season, symbionts pass through the oolemma and rest inside the periphery of the oocytes. It is proposed that early uptake of zooxanthellae by sexual progeny at the oocyte stage, indicates a highly specialized mode of interaction between this algal symbiont and its host.

Introduction

Tissues of a wide range of marine invertebrates possess endosymbiotic dinoflagellates, also referred to as zooxanthellae (McLaughlin and Zahl, 1966; Trench, 1979). In the course of sexual reproduction of a symbiont-bearing host, algal symbionts are acquired anew by each generation (Benayahu *et al.*, 1988). The mechanisms of an acquisition of dinoflagellate symbionts by sexual progeny of hosts may be divided into two basic categories: (1) acquisition by maternal inheritance, and (2) acquisition from the environment by either larval or adult stages (Trench, 1987). Acquisition during developmental stages, whereby algal cells locate a sexual offspring, require close proximity of both host tissues and algal cells (Trench, 1979). Motile algal symbionts may randomly contact host tissues (Fitt, 1984) or, alternatively, be chemically attracted to them (Kinzie, 1974). An intermediate zooplankter may also transport the algae, which subsequently reside within the final host (Trench, 1979).

Among cnidarians, zooxanthellae are generally restricted within the host endoderm (Muscatine, 1974). Notably, germ cells in anthozoans are considered to be endodermal in origin (Harrison and Wallace, 1990). The earliest recognizable stages of oocytes in alcyonaceans develop from cells in the mesoglea of the mesenteries (Farrant, 1986). Subsequently, each oocyte is attached to the mesenteries by a short pedicle composed of a mesogleal core and surrounded by endoderm (Benayahu, 1991). Histological and ultrastructural studies indicate that alcyonacean oocytes are enveloped throughout their development by mesoglea layer and an outer follicular endoderm, both of which are continuous with the corresponding layers of the pedicle and gastrovascular cavity of the parent polyp (Benayahu, 1991). Shinkarenko (1981) indicated the presence of zooxanthellae in the endodermal follicular layer of the alcyonaceans *Lobophytum crassum*,

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L. pauciflorum and *Sarcophyton trocheliophorum*. Nevertheless, there is no information as to whether these endodermal cells are involved in transmission of algae into the oocytes. Broadcasted eggs of alcyonaceans of the genera *Alcyonium, Cladiella, Lobophytum, Sarcophyton* and *Sinularia* lack algal symbionts upon release (Babcock *et al.*, 1986; Alino and Coll. 1989; Klainman, 1990). Similarly, spawned eggs of the vast majority of scleractinian corals lack symbiotic algae (Harrison and Wallace, 1990). Oocytes of only a few cnidarians have been reported to possess zooxanthellae within their ooplasm: *Anemonia sulcata* (Schäfer, 1984), *Efflatounaria* sp. (Dinesen, 1985), *Montipora* and *Porites* spp. (Harrison and Wallace, 1990), and *Pocillopora damicornis* (Glynn *et al.*, 1991). Most of the evidence on eggs bearing symbiotic algae concerns *Hydra*. In a recent study, Campbell (1990) described the ultrastructural pathway by which symbionts are transferred into mature oocytes of *Hydra viridissima*. In this process, isolated *Chlorella* cells move from the endoderm through the mesolamella into the ectoderm, where they are taken up by oocytes. Additional evidence indicates that eggs of the hydroid *Myrionema amboinense* acquire symbionts from endodermal cytoplasmic processes which bear the algae and pass them into the ooplasm through the mesoglea separating the egg from the endoderm (Trench, 1987).

Studies on reinfection of aposymbiotic host tissues by zooxanthellae are far behind those on zoochlorellae (Muscatine, 1974). This is in contrast to the tremendous amount of information which has been accumulated, meanwhile, on reproduction of corals (Harrison and Wallace, 1990). The presence of zooxanthellae in eggs of planulae of corals is considered to be a major feature of their development (Richmond and Hunter, 1990). Planulae competency (the ability of larvae to successfully settle and metamorphose) is highly dependent on the presence of zooxanthellae and, therefore, greatly affects the species distribution (Richmond, 1987). Nevertheless, no information exists on the histological pathway by which zooxanthellae infect either eggs or planulae of any coral species.

On the Red Sea coral reefs, *Litophyton arboreum* is a common alcyonacean and possesses zooxanthellae in its endodermal cells (Berner *et al.*, 1987). It is a gonochoric planulae brooder (Benayahu *et al.*, 1990) those planulae, upon release, are already associated with algal symbionts (Weil, 1990). This study describes how oocytes of *L. arboreum* become infected by parental zooxanthellae. This is the first study to demonstrate the ultrastructural pathway of symbiont uptake by the follicular layer, and successive translocation into the oocytes of an alcyonacean coral.

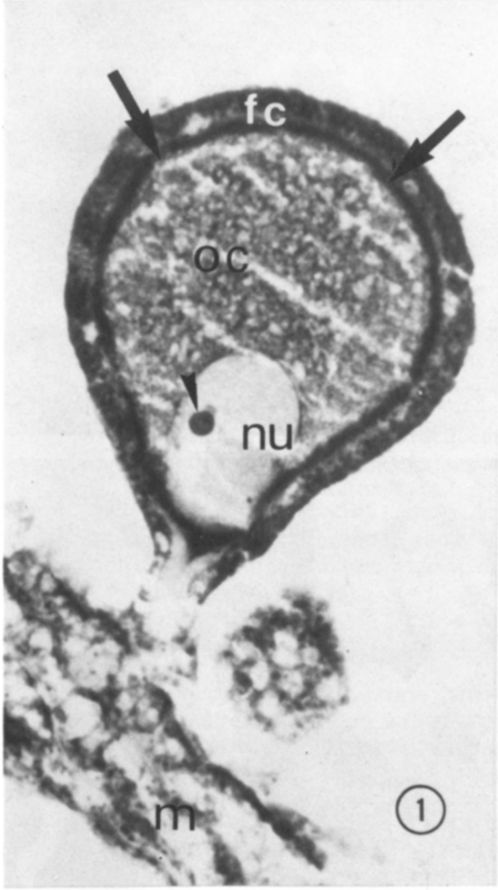
Materials and Methods

The reproductive cycle of *L. arboreum* was studied from February 1988 to January 1991 at Eilat, Gulf of Eilat, Red Sea. Monthly samples of female colonies were fixed in 4% formalin in sea water formalin for 24 hr, rinsed in fresh water and transferred into 70% alcohol. The preserved material was

Fig. 1. Young oocyte (oc) with nucleus (nu) and nucleolus (arrowhead) surrounded by follicular endodermal cells (fc) lying over mesoglea (arrows). The oocyte is attached by a pedicle (pe) to the mesentery (m). ×1500.

Fig. 2. Apical surface of follicular cells (fc) with microvilli (mv) some with a reticulate structure (arrowheads). Zooxanthellae (zx) within a vacuole (vc) ensheathed with thin layer of cytoplasm. Hemijunction-like desmosomes (arrows) are formed between the surface microvilli and this cytoplasm. Sections through flagella (fl) are shown in the vicinity of the zooxanthella. ×7500.

Fig. 3. Endocytosis of zooxanthella (zx) by cellular extensions of a follicular cell (fc). Note numerous sections through flagella (fl) associated with the symbiont uptake. Hemijunction-like desmosomes between microvilli and cytoplasm of the algal cell are indicated by arrows. ×11,600.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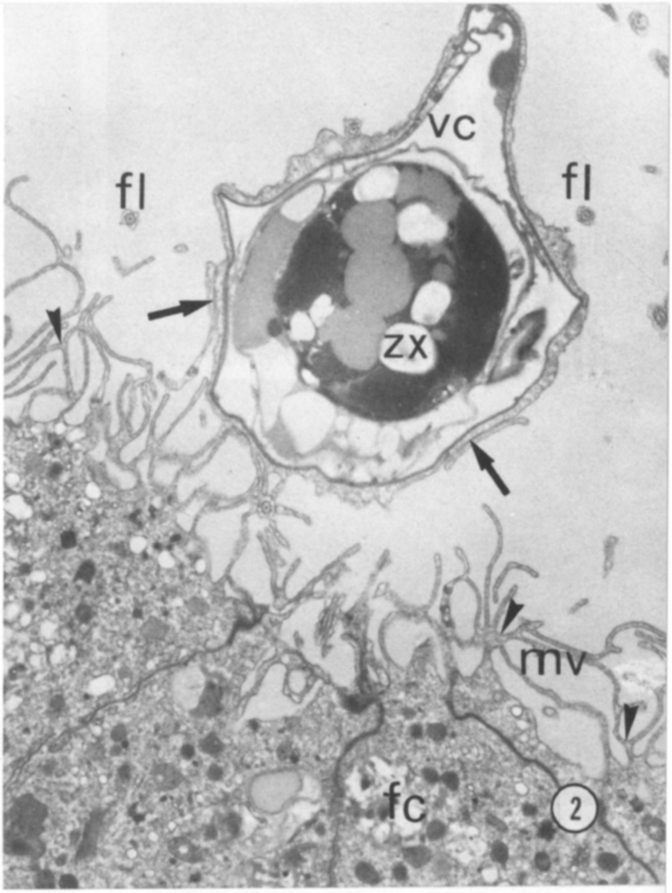
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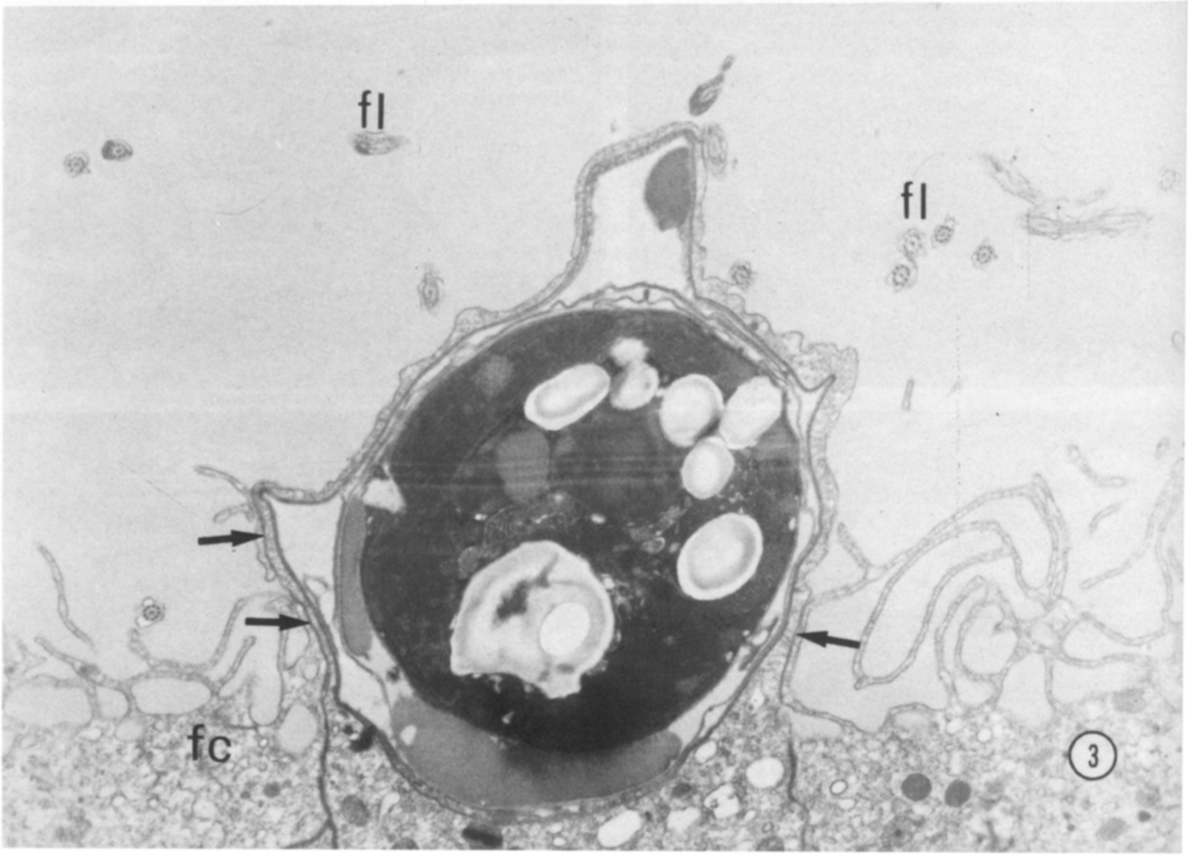
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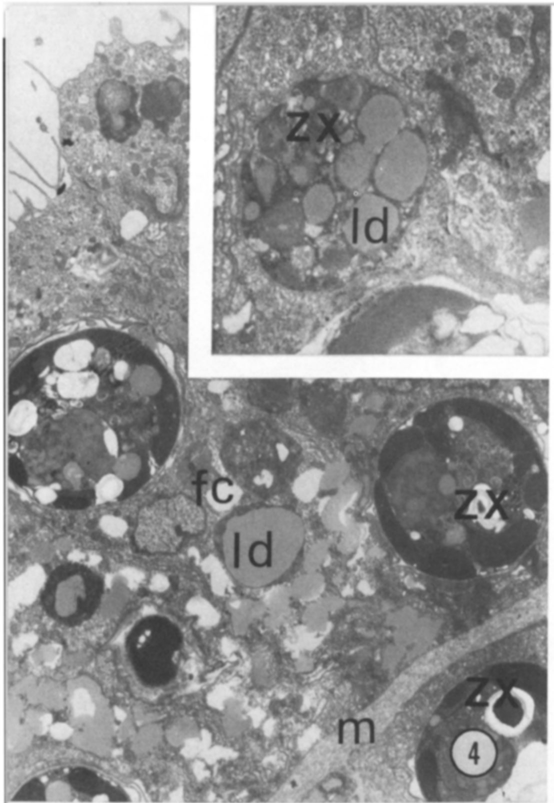
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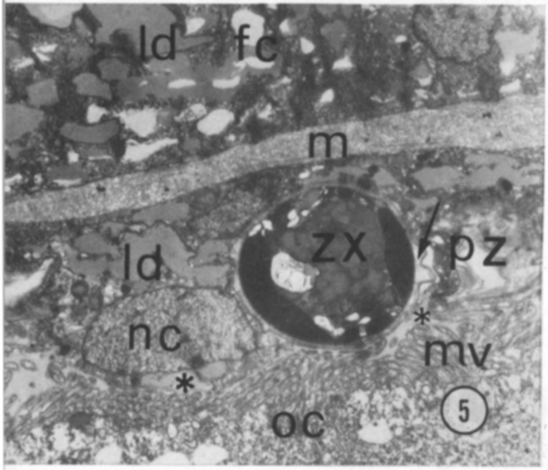
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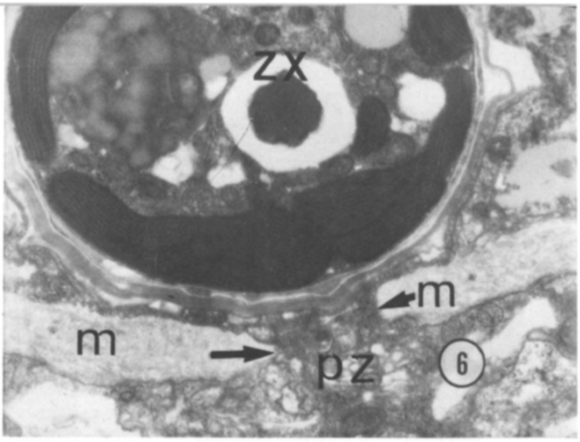
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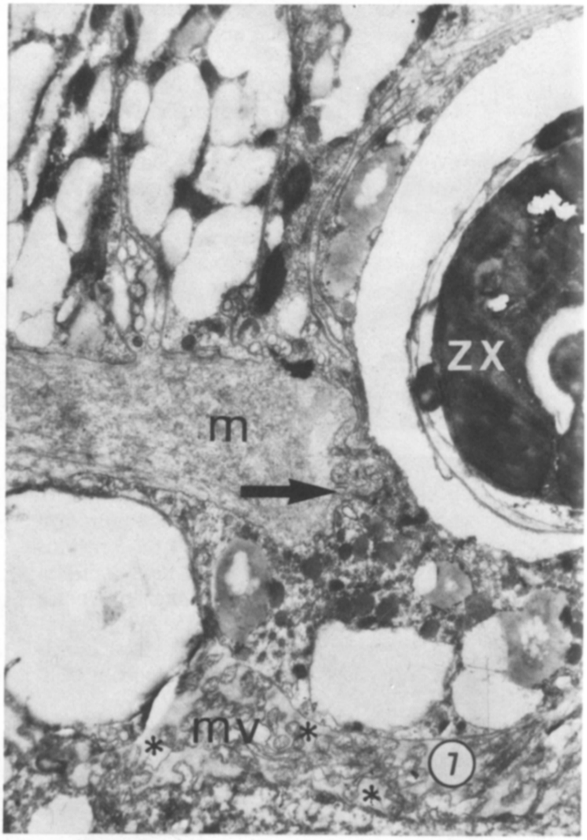
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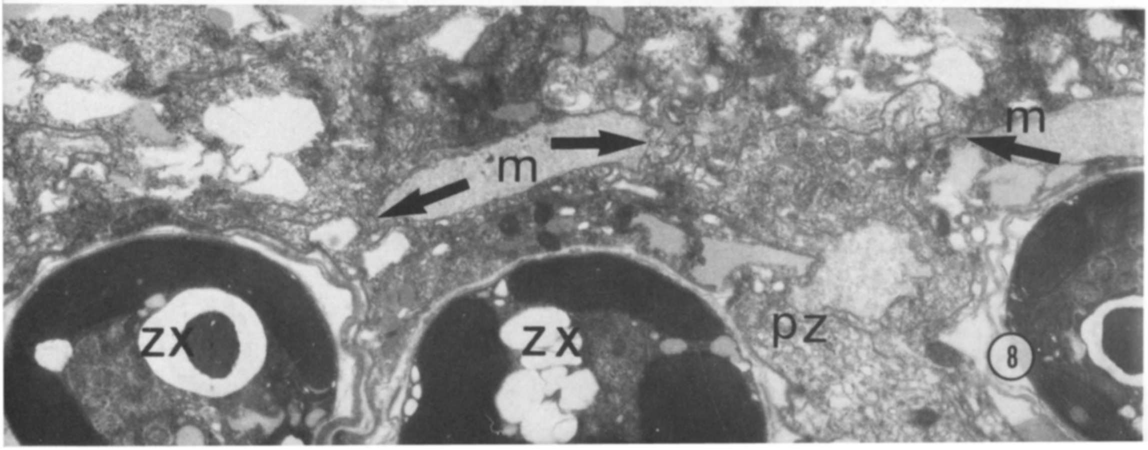
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examined under a binocular dissecting microscope for gonadal development. Material for light microscopy was decalcified in a mixture of equal volumes of formic acid (50%) and sodium citrate (15%) for 20 min. Paraplast (Monoject Scientific) sections 8 μm thick were cut and stained in hematoxylin (Delafield) and eosin. Samples for electron microscopy were fixed in 2·5% glutaraldehyde, buffered with cacodylate, and post-fixed in 2·5 osmium tetraoxide. Subsequently, they were dehydrated with a graded series of ethyl alcohols and embedded in Epon. The sections were stained with both uranyl acetate and lead citrate. The micrographs were studied with Jeol 1200 EX and 1200 CX electron microscopes.

Results

The oocytes of *L. arboreum* develop along the ventral and lateral mesenteries of the polyp cavities. Their development follows a biannual cycle resulting in the production of mature oocytes with a maximal diameter of 850–1100 μm (Weil, 1990). Each oocyte is attached by a short pedicle to the edge of the mesentery. The oocyte is enveloped by a thin mesogleal layer and by an outer layer of endodermal follicular cells (Fig. 1). The follicular layer is composed of gastrodermal cells with numerous microvilli on their surface, some of which are anastomosed (Fig. 2). Zooxanthellae harbored within membrane-bound vacuoles and ensheathed by a thin layer of cytoplasm were observed within the gastrovascular cavity, adjacent to the follicular cells. Hemidesmosome-like junctions are formed between the microvilli and this cytoplasm (Fig. 2). In addition, many flagella are closely associated with the ensheathed zooxanthellae; most probably they belong to the endoderm of the gastrovascular cavity. The zooxanthella is engulfed by cytoplasmic processes of the follicular cell and gradually is endocytosed (Fig. 3). Oocytes smaller than 100–150 μm in diameter harbor algal cells only in their follicular layer; however, in larger oocytes, zooxanthellae are found also under the mesoglea (Fig. 4).

Notably, some of the symbionts found in the follicular cells disintegrate leaving behind large lipid droplets within the cytoplasm of their host cells (Fig. 4). The surface of the oocyte is densely covered by microvilli which project toward the perioocytic zone, found under the mesoglea (Fig. 5). These microvilli are embedded in a semi-translucent material which extends over their tips. Together with the algae, the perioocytic zone contains cellular debris, e.g, nuclei, cytoplasm and lipid droplets (Fig. 5). During oogenesis zooxanthellae of the follicular cells rest against the underlying mesoglea (Fig. 4). Gaps are opened in the mesoglea adjacent to the algal cells facing this layer (Fig. 6), and zooxan-

Fig. 4. Zooxanthellae (zx) both in follicular cells (fc) and below the underlying mesoglea (m). The follicular cells possess, beside the intact zooxanthellae within vacuoles, gigantic lipid droplets (ld) derived from degradation of symbionts. Inset shows degraded zooxanthellae (zx) within a follicular cell, decomposed into lipid droplets (ld). ×4000; inset ×7800.

Fig. 5. Perioocytic zone (pz) located between the microvilli (mv) of the oocyte (oc) surface and the mesoglea (m). The follicular cells (fc) contain lipid droplets (ld). The perioocytic zone contains zooxanthella (zx) within a vacuole (arrow), nuclei (nu), lipid droplets, and other cellular debris. The microvilli of the oocyte are embedded in semi-translucent material (asterisks). ×5500.

Fig. 6. Zooxanthella within a follicular cell facing an opened gap (arrows) in the underlying mesoglea (m). Cellular debris forces its way through the gap into the perioocytic zone (pz). ×10,000.

Fig. 7. Zooxanthellae (zx) within its vacuole beginning entry through gap (arrow) opened in the mesoglea (m) following the entrance of cellular debris from the follicular host cell. Note the microvilli (mv) of the oocyte (oc) and their semi-translucent coat (asterisks). ×8250.

Fig. 8. Gaps (arrows) in the mesoglea (m) and translocated zooxanthellae (zx) within vacuoles at the perioocytic zone (pz). ×8400.

thellae pass through these gaps from the follicular cell into the perioocytic zone (Fig. 7). Prior to the passage of algae, part of the follicular host cell content is pushed through the mesogleal gap (Figs 6, 7). Hence, cytoplasm with organelles of follicular host cells, infiltrate into the perioocytic zone and lie between the surrounding mesoglea and the microvilli of the oocyte surface (Fig. 5). In immature oocytes, numerous gaps are found along the mesoglea (Fig. 8) and algal symbionts within their vacuoles gradually accumulate at the perioocytic zone (Fig. 9). After the completion of algal entry, the gaps disappear and a continuous layer of mesoglea re-separates the outer follicular cells from the perioocytic zone (Fig. 10). The translocation of symbionts from the follicular cells toward the perioocytic zone is seasonal (see Discussion); nevertheless, throughout oogenesis zooxanthellae reside within the follicular cells. Within the perioocytic zone, zooxanthellae form remarkable sunken areas among the microvilli of the oocyte surface (Fig. 10). At a further stage of oogenesis, a few weeks prior to the commencement of the breeding season of *L. arboreum*, zooxanthellae appear within the periphery of the ooplasm. Algal cells most probably bulge into the ooplasm through the oolema (Fig. 11), and enter into the oocytes, where they accumulate, each within its own vacuole (Fig. 12). In mature oocytes, the follicular cells become much flatter than during the early stages of oogenesis (Fig. 4) in which their height is about 10 μm. At this stage, the microvilli become short and uniformly scattered over the oocyte surface. At late oogenesis they become entangled with a vitelline coat which is replaced by a homogenous substance that flanks the lower side of the mesoglea (Fig. 12). No cellular debris or zooxanthellae are found at this stage within the perioocytic zone, whose volume has, in the interim, diminished.

Discussion

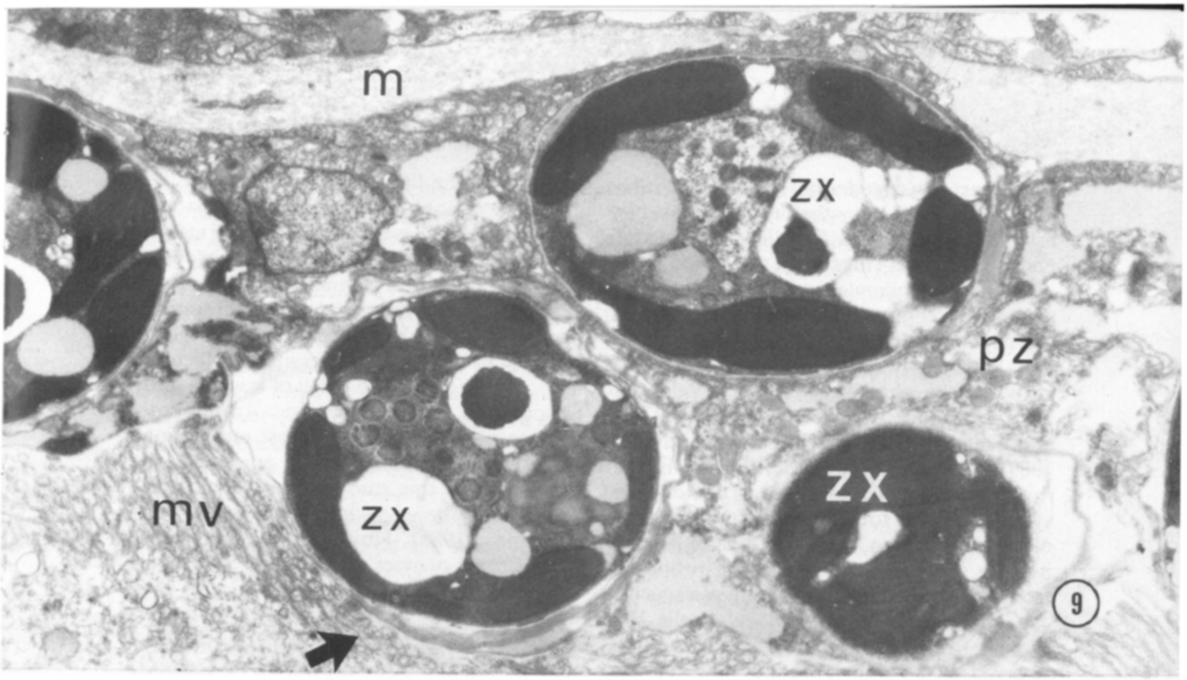
The establishment of a stable symbiosis between an alga and its host has been categorized as a series of stepwise phases, initiated by contact and recognition (Pardy and Muscatine, 1973). In the present study on *Litophyton arboreum*, zooxanthellae within vacuoles were observed to contact the flagella of the follicular cells surrounding oocytes and, subsequently, to be phagocytosed by them (Figs 2, 3). These findings raise an unavoidable question: from where are these algae derived? Schlichter (1982) suggested that in the alcyonacean *Heteroxenia fuscescens*, zooxanthellae are expelled from gastrodermal cells due to either process of regulating their quantity within the host cells, or senility. In addition, these expelled zooxanthellae are phagocytosed exclusively by gastrodermal cells of the mesenterial filaments and used as particulate food. We assume that the observed algal symbionts within the gastrovascular cavity of *L. arboreum* were similarly extruded with their vacuoles while being ensheathed within a

Fig. 9. Accumulation of translocated zooxanthellae (zx) below the mesoglea (m) at the perioocytic zone (pz) intermingled with cellular debris. Note the sunken area (arrow) among the microvilli (mv) due to presence of zooxanthellae. ×9500.

Fig. 10. Continuous layer of mesoglea (m) re-separates the perioocytic zone (pz) from the follicular cells (fc) after the completion of the zooxanthellae (zx) entry. ×4300.

Fig. 11. Zooxanthella (zx) within the periphery of an oocyte (oc). Arrow indicates the thin ooplasm where the algae most probably bulge into the oocyte from the perioocytic zone, whose basal part is shown, containing microvilli (mv) projection into a vitelline coat (asterisks). ×17,000.

Fig. 12. Follicular cells (fc) and mature oocyte prior to the breeding season. Arrows indicate the basal membrane which lies over the mesoglea (m). The oocyte is covered by oolema (arrowheads) and projected microvilli (mv) entangles with vitelline coat (asterisks). Homogenous substance (hs) flanks the lower surface of the mesoglea. Zooxanthellae (zx) occur both in follicular cells and the ooplasm. ×6000.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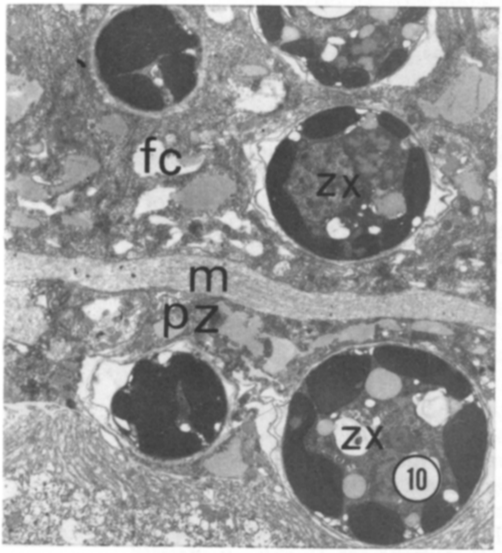
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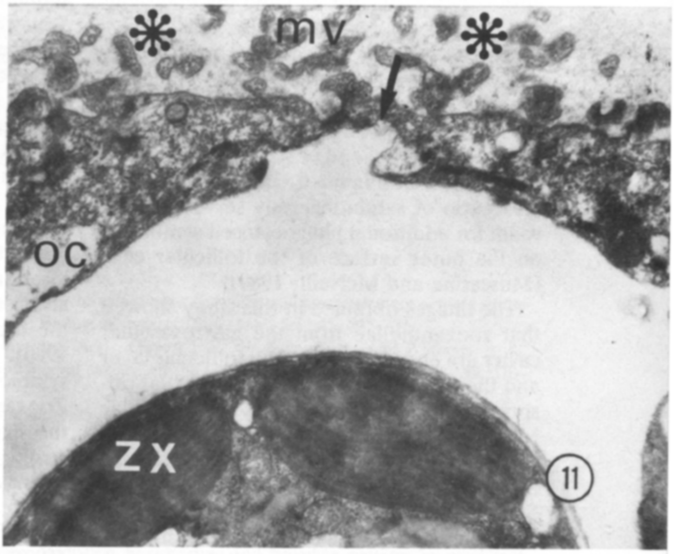
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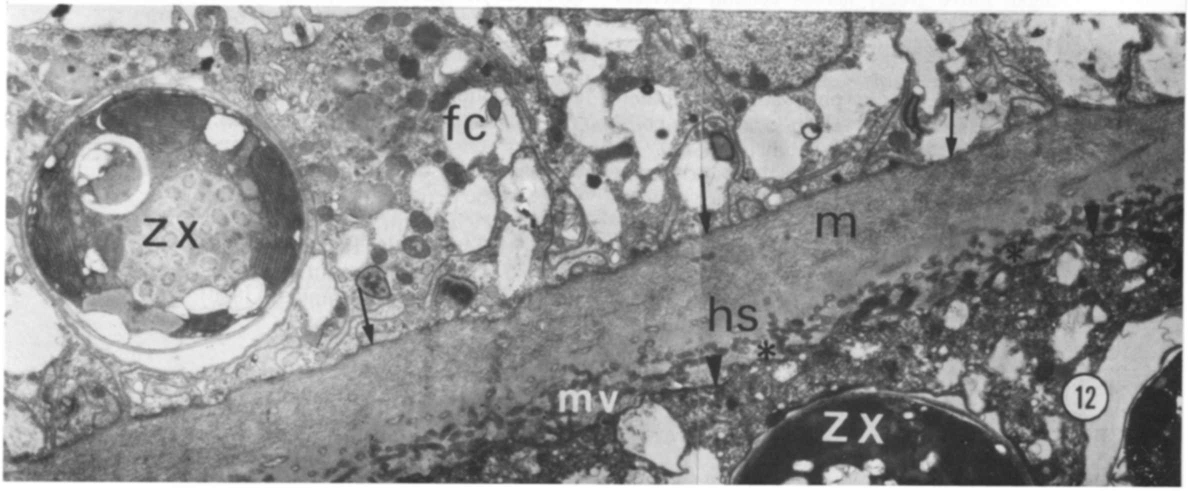
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thin layer of gastrodermal cytoplasm. Such living, non-free zooxanthellae most probably are propelled by the flagellae of adjacent endodermal cells (Figs 2, 3), and taken once more by the follicular cells. Subsequently, some of these symbionts are used to infect the developing oocytes. It should be noted that live, newly-freed symbiotic algae are known to be phagocytosed by endodermal host cells, and to establish symbiosis (Fitt and Trench, 1983; Muscatine and McNeill, 1989). However, the present study is the first indication of the presence of non-free symbiotic algae, found within extruded vacuoles and cytoplasm, in the gastrovascular cavity of a symbiotic cnidarian. The proposed fate of these zooxanthellae requires a specific cue for recognition by the follicular cells. We propose that in *L. arboreum* such recognition is manifested through contact between the ensheathed zooxanthellae and the microvilli of the surface of the follicular cells. Phagocytosed senile symbiotic algae may be degraded (Fig. 5), as suggested by Schlichter (1982). Other types of zooxanthellae, which are still photosynthetically active, invariably move to the basal end of the follicular cell as also shown in Figure 5. This intracellular relocation of symbionts may serve to leave room for additional phagocytosed symbionts on the outer surface of the follicular cells (Muscatine and McNeill, 1989).

The images obtained in this study showed that zooxanthellae from the gastrovascular cavity are endocytosed by the follicular layer and then translocated into future sexual offspring. The movement of zooxanthellae requires the breakdown of dissolution of histological barriers that must be crossed by the algae prior to being taken up by the ooplasm. Such processes have recently been demonstrated in *Hydra viridissima*, whose chlorella algae move freely across cellular barriers (Campbell, 1990). In contrast, symbionts in *L. arboreum* are translocated while encased within vacuoles and host cell cytoplasm. Similarly, among scyphozoans, zooxanthellae have been observed in 'wandering cells' within the mesoglea (Ludwig, 1969), or moving from endoderm to the mesoglea in amoeboid cells (Colley and Trench, 1985). Trench (1987) observed the passage of cytoplasm processes which bore algae through the mesoglea that separates the egg from the endodermal tissue. The present study reveals, for the first time, open gaps in the mesoglea prior to the translocation of zooxanthellae (Figs 6–9). The detailed mechanism by which such dissolution of mesoglea occurs should be examined further. It appears that the first step of gap formation may result in the presence of zooxanthellae adjacent to the basal membrane of follicular host cells (Fig. 4). The entry of oocytes into mesoglea of the sea anenome *Actinia fragecea* is carried out by a process resembling amoeboid movement, and is analogous to the results of this study, since cytoplasmic processes are being pushed into the mesoglea (Larkman, 1983). However, in contrast to the entry of oocytes, the present study indicates puncture of the whole width of the mesogleal layer including the basal membrane of the follicular cells. A unique feature is the accumulation of translocated zooxanthellae along with cytoplasm, nuclei, mitochondria and other cellular debris at the perioocytic zone (Figs 5–7). This stage was observed in oocytes only during December-March in 1989 and 1990. Later, prior to the breeding season (April-June), the oocytes possessed neither the perioocytic algal accumulation nor the cellular debris. These results suggest a seasonal translocation of zooxanthellae from the follicular layer toward the perioocytic zone. Final translocation of the symbionts into the oocytes is also seasonal and commences at the start of the breeding season in July-August (Weil, 1990). Some stony corals also incorporate symbionts into their eggs prior to maturation. Zooxanthellae usually are incorporated into the eggs of *Porites* and *Montipora* a few weeks prior to maturation, while in *Montipora digitata* the symbionts appear in eggs as late as 24 hr before spawning (Harrison and Wallace, 1990). Recently, Glynn *et al.* (1991) described numerous zooxanthellae in mature unfertilized oocytes of *Pocillopora damicornis*. Therefore, it seems that algal acquisition by oocytes is seasonal and occurs at maturation, a stage at which they are 'ready' to incorporate the symbionts.

Algal cells vary in their location in the ooplasm. In *L. arboreum*, zooxanthellae are found in the periphery of the mature oocyte, while in *P. damicornis* they occur near the nuclei (Glynn *et al.*, 1991), and in *H. viridissima* symbionts are scattered throughout the whole ooplasm (Campbell, 1990). The significance of such differences should be explored further. The absence of zooxanthellae in the eggs of most studied symbiotic anthozoans (Babcock *et al.*, 1986; Alino and Coll, 1989; Klainman, 1990; Harrison and Wallace, 1990) may indicate the lack of ability to recognize the symbionts, incorporate them and consequently establish symbiosis. Even among those species whose eggs possess symbionts, this property is acquired at a rather advanced oogenic stage (see above).

In summary, entry of zooxanthellae into the oocytes of *L. arboreum* involves an elaborate ultrastructural pathway. At all stages of the process, symbionts are translocated while residing within vacuoles, which most probably inhibit lysosomal fusion (Fitt and Trench, 1988). Extruded symbiotic algae found within vacuoles and surrounded by a cytoplasmic sheath are phagocytosed by the follicular cells of young oocytes. Subsequently, gaps open in the underlying mesoglea, and zooxanthellae within vacuoles are translocated along with follicular cytoplasm into the perioocytic zone, where the symbionts accumulate, suspended within cellular debris. Prior to the breeding season, the symbiont bulges through the oolema into the periphery of the mature oocyte. Such early uptake of symbionts by sexual progeny at the oocyte stage is very rare among symbiotic cnidarians. We propose that this feature indicates a highly specialized mode of interaction between symbiont and host. The significance of the developmental stage at which symbionts are acquired, requires further studies.

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