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Epidermal Nutrition of the Alcyonarian *Heteroxenia fuscescens* (Ehrb.): Absorption of Dissolved Organic Material and Lost Endogenous Photosynthates

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Summary. The trophic strategies were studied of *Heteroxenia fuscescens* living in shallow tropical waters. Structural and physiological adaptations show that particulate food is of less nutritional importance than the uptake of organic material dissolved in the sea, the utilization of assimilates of cytosymbiotic algae (zooxanthellae) and even the symbionts themselves. The external and internal surfaces of the tentacles are enlarged by featherlike pinnules, on the one hand facilitating the epidermal uptake of dissolved organic compounds and on the other offering wellilluminated spaces in which large numbers of zooxanthellae can be 'cultivated'.

Zooxanthellae expelled from gastrodermal cells may be taken up by the mesenteric filaments of the dorsal mesenteries, where they are often decomposed and utilized. The transport of photoassimilates from the gastrodermis to the epidermis through the mesogloea takes place at a low rate. Most of the released assimilates of the symbionts appear in the coelenteron. One fraction of these assimilates is distributed within the gastric channel system and can be taken up by developing stages living there; another fraction reaches the epidermis *extracorporally* via the pharynx and the sea. Thus both the pharynx and the epidermis absorb these photo-assimilates. The epidermal uptake capacity serves two main purposes: (1) active uptake and incorporation of external organic material dissolved in the sea; (2) reabsorption of internal, self-produced organic material, i.e. reduction of the loss of endogenous compounds escaping from the gastric cavity necessarily due to the polyfunctionality of the coelenteron.

Introduction

Several species of marine invertebrates live in mutual symbiosis with unicellular algae. Among these, the cnidarians have been especially well studied with respect to interactions between host organisms and symbionts. The topic has been reviewed by Muscatine (1974), Taylor (1974) and more recently by Trench (1979, including 143 references). Both partners in the symbiosis enjoy unquestioned benefits which have been well documented by Muscatine (1974), Trench (1979) and Thorington and Margulis (1981).

The association is composed of autotrophic and heterotrophic creatures that not only live in intimate physical contact, but whose metabolisms cooperate on a cellular level. Thus, the animal-plant union possesses acquired abilities in an evolutionary sense. The 'hyperorganism' not only results from the combination of the animals' and plants' individual abilities, but cooperation also yields greater efficiency. Especially with regard to the energy supply, the symbiotic relationship achieves a higher degree of independence. In relation to space, primary producers and primary consumers form the shortest possible food chain. In addition to this, one must keep in mind that most symbiotic cnidarian species are also secondary consumers (carnivores, zoophaga) and/or saprotrophs. One can deduce from the metabolic capacities of heterotrophic and autotrophic organisms that intracellular or cyto-symbiosis represents an effective recycling system.

These studies had several goals. The first was to show how zooxanthellae and photo-assimilates are utilized by the host: Do the 'primary consumers' (the alcyonarians) use only photoassimilates, or are the zooxanthellae also exploited by decomposition, i.e. are they used in the same manner in which 'genuine herbivores' in general exploit primary producers? Second, along which paths are substances translocated between symbionts and host tissue? In cnidarians, especially in colonies, these studies are of special interest, since these organisms have only the coelenteron as a distribution system, while the body consists of only two epithelial walls. Generally, all cells are in contact either with water or with the fluid of the coelenteron. This mode of construction facilitates individual cell uptake of dissolved nutrients and/or particulate food and consequently the energy supply is no problem.

Animals and Methods

General remarks About Heteroxenia fuscescens

Colonies of *Heteroxenia fuscescens* consist of a fleshy, mushroomshaped syndete and two types of polyps (autozooids, siphonozooids) as shown in Fig. 1. The colonies are most abundant on shallow inner reefs, e.g. on the coast of Kenya, and their habitat is influenced by the tides. For taxonomical, biological and ecological details see Gohar (1940a, b).

Methods

The colonies were collected, put individually in plastic bags and brought back in tanks with running natural sea water. Conditions of maintenance were: natural light, temperature $26° \pm 2°$ C, and salinity approximately $35‰$ S. Most of the experiments were carried out with autozooids only, since 85%–90% of the total chlorophyll content of the colony is localized in the autozooids. This makes them the most interesting part of the colonies with respect to the production of photo-assimilates. Biochemical stu-

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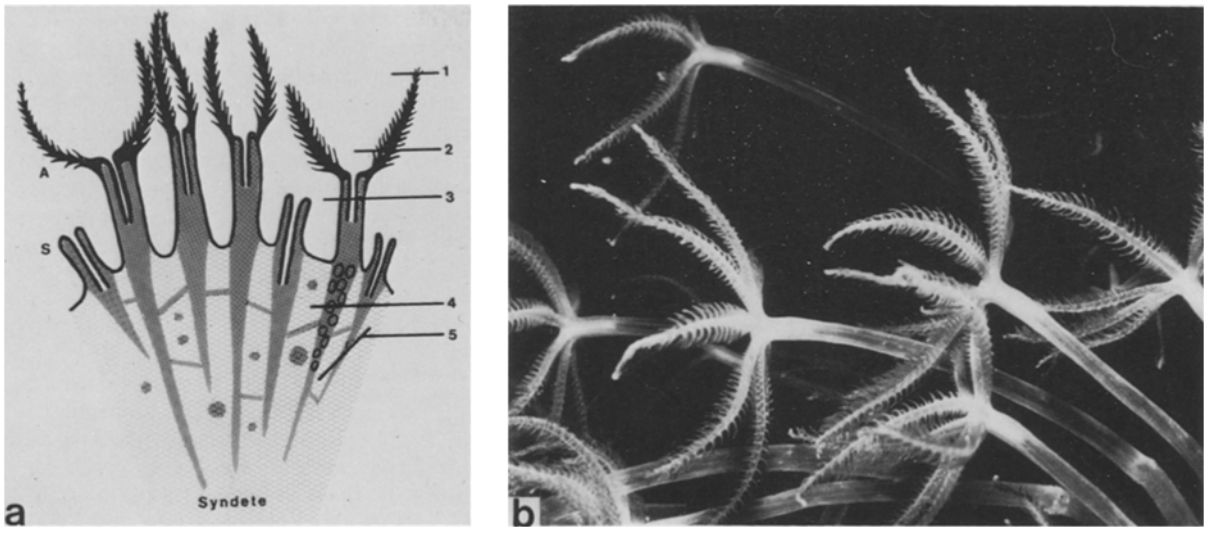

Fig. 1. *Heteroxenia fuscescens.* **a** Scheme of a colony which consists of a fleshy, mushroom-shaped syndete (*S*) and two types of polyps: siphonozooids (*S*) and autozooids (*A*). Nos. 1–5 indicate positions of the histological slices. **b** Approximate size of the extended tentacle crown of the branched autozooids 1.5–2.5 cm

dies show that the rate of dark fixation of ^{14}C-carbonate is 5% of that in the light (Schlichter et al., to be published). Therefore experiments were performed in light, but not in full sunshine. Some primary studies were concerned with the distribution of photo-assimilates through whole colonies.

Incubation Procedure. Either whole colonies or isolated autozooids were incubated in sterilized natural sea water (SNW) (Sartorius membrane filter 0.45 µm) containing either $NaH^{14}CO_3$ (37 KBq/ml) or a ^{3}H-L-amino acid (200 nmol/l). In complete colonies, autozooids were amputated from the syndete after a period of incubation and fixed in chilled 5% formalin solution or prewashed in pure sea water and frozen. If isolated autozooids were incubated, they were first cut off from the syndete and subsequently transferred into SNW, which was changed several times. After about 20–40 min, the tentacles of the isolated autozooids again began to pulsate rhythmically (60 beats/min), just as they do as colony members. The water was stirred by a gentle air stream so that the pulsating autozooids floated slowly in the beakers. In the same operation the added radioactive compounds were homogeneously mixed, and it was ensured that all autozooids were permanently illuminated during the experiment. After fixed incubation periods autozooids were removed and treated as described above.

Histology and Autoradiography. The formalin-fixed autozooids were rinsed for 24 h in running water, then treated by standard histological methods, including dehydration and embedding in paraplast. The deep-frozen autozooids were lyophilized and directly embedded in paraplast. By the dipping technique, 5 µm sections of the column, the tentacles, the pinnules and the pharynx were coated with Ilford Nuclear Emulsion K2, sections through the syndete being 10 µm thick. After 8 days of exposure (sections of the syndete only 4 days) the slides were developed in Kodak D 19 and stained with hemalum solution.

By the two fixation methods, two substantially different types of autoradiographs are produced. After chemical fixation, the silver grains of the autoradiographs originate chiefly from ^{14}C incorporated into precipitable polymers. After physical fixation soluble ^{14}C-labelled compounds, e.g. photosynthetically produced amino acids, organic acids and sugars are recorded likewise. Radioactivity found outside the histological sections is due to the 'normal' background and to the adsorption of soluble ^{14}C-labelled compounds on the adhesive that glues the sections to the microscope slide.

Electron Microscopy. Tiny pieces from the pinnules and column were pre-fixed in chilled glutaraldehyde/seawater solution for 90 min, then rinsed and postfixed in osmium tetroxide for 60 min. By a standard technique the samples were then dehydrated and embedded in araldite.

Results and Discussion

General Cytological and Histological Remarks on the Organization of Autozooids of Heteroxenia fuscescens

No special microphotographs are presented to illustrate this section; however, references to relevant autoradiographs are given.

Tentacles. A maximum of 8 rows of pinnules (on the average 22 pinnules/row) protrude from the central part (Figs. 1 and 12). Thus, large external and internal surfaces are formed through which exchange processes are facilitated. The surface area of pinnuled tentacles, is 4–5 times greater than that of hypothetical non-pinnuled ones. The epidermis (ectoderm) is weakly developed and looks like a syncytium (Fig. 2). Microvilli are infrequent, i.e. the additional surface enlargement is of no consequence and cilia are absent on the external surface. Some of the physiological functions of these organelles are compensated for by pulsation of the tentacles, e.g. renewing the surrounding water, removing sediment and stirring water layers, which influence exchange processes. Cilia exist in the gastrodermis and nematocysts (atrichous isorhizas) can occasionally be observed in microscopical sections. This may have two consequences; the capture of plankton is almost impossible and *Heteroxenia fuscescens* must possess alternative defense mechanisms. Most probably the high content of terpenoids keeps predators away. In the pinnules, the mesogloea is very weakly developed,

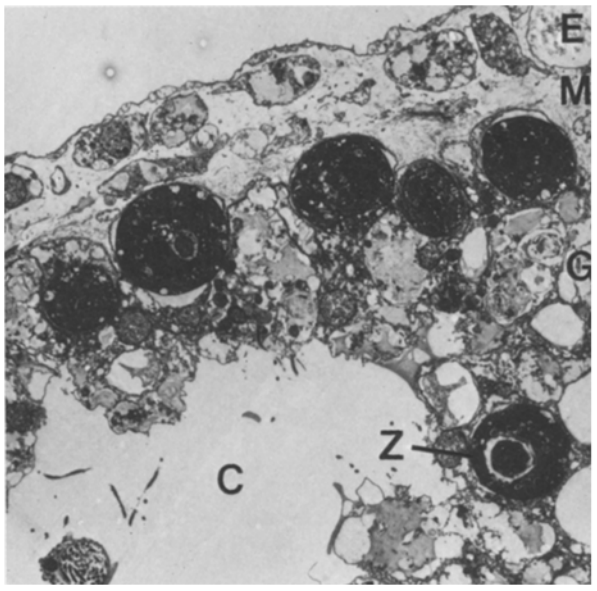

Fig. 2. *Heteroxenia fuscescens.* Electron micrograph of a section through a pinnule. The diameter of the cytosymbiotic algae (*Gymnodinium microadriaticum*) averages 8–10 μm). *E*=epidermis; *M*=mesogloea; *G*=gastrodermis; *Z*=zooxanthellae; *C*=coelenteron; position 1 in Fig. 1a

but in the central part of the tentacle it is well formed (Figs. 2, 3, 12). By far the largest part of the pinnules is formed by the gastrodermis (endoderm), inhabited by innumerable zooxanthellae (*Gymnodinium microadriaticum*) (Figs. 2, 3, 12). The formation of pinnules not only enlarges the external surface, but also much more internal epithelium is produced in which a high number of zooxanthellae can be 'farmed'. The density of zooxanthellae is often so high that the lumen of the pinnules is totally filled (Figs. 3, 8, 12). This suggests that the energy gain that the host can draw from the zooxanthellae is particularly high.

Column. The epidermis, and especially the mesogloea in the body wall, are better formed than in the pinnules (Fig. 4), whereas the gastrodermis is moderately developed and accommodates fewer zooxanthellae. Cilia are present in the gastrodermis, but in the epidermis, as in the epidermis of the pinnules, they are also absent. Large secretory cells can regularly be found in the ectodermal epithelium (Fig. 4c). The columns of the autozooids (and siphonozooids) pass into the syndete.

Mesenteries. Only the two dorsal mesenteries possess mesenteric filaments; on the other six mesenteries these structures are reduced (Fig. 11). The dorsal mesenteric filaments show the familiar organization with a glandular and a flagellated tract. In the welldeveloped mesogloea, granular cells (amoebocytes) are regularly observed (Fig. 11b).

Pharynx. The pharynx consists of closely packed cells of ectodermal origin (Figs. 7, 10). One flagellated siphonoglyph is present, which effects the irrigation of the whole colony in cooperation with siphonozooids and the pulsation of the tentacles.

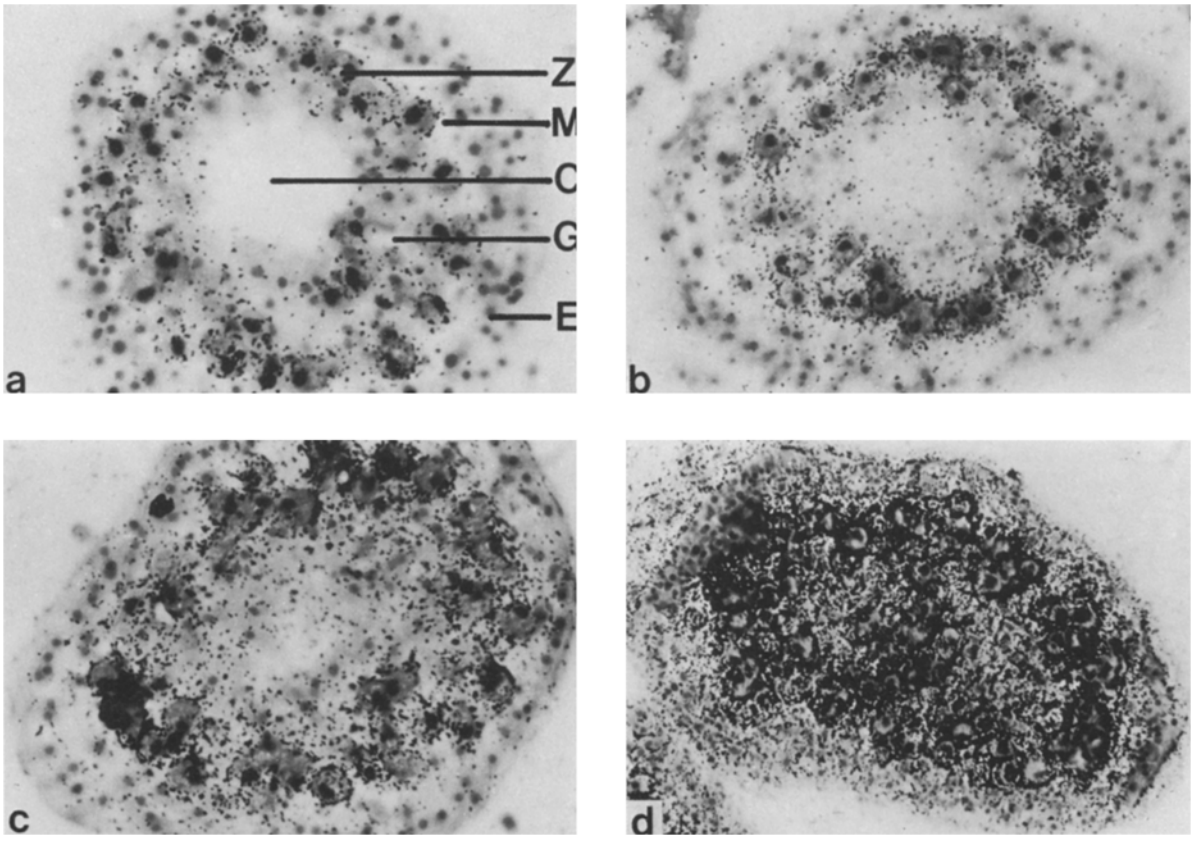

Fig. 3a–d. *Heteroxenia fuscescens.* The time-dependent incorporation of ^{14}C-carbonate into precipitable compounds in tissue of pinnules. After **a** 5 min, **b** 10 min, **c** 30 min and **d** 120 min of incubation; position 1 in Fig. 1a; (see Fig. 2)

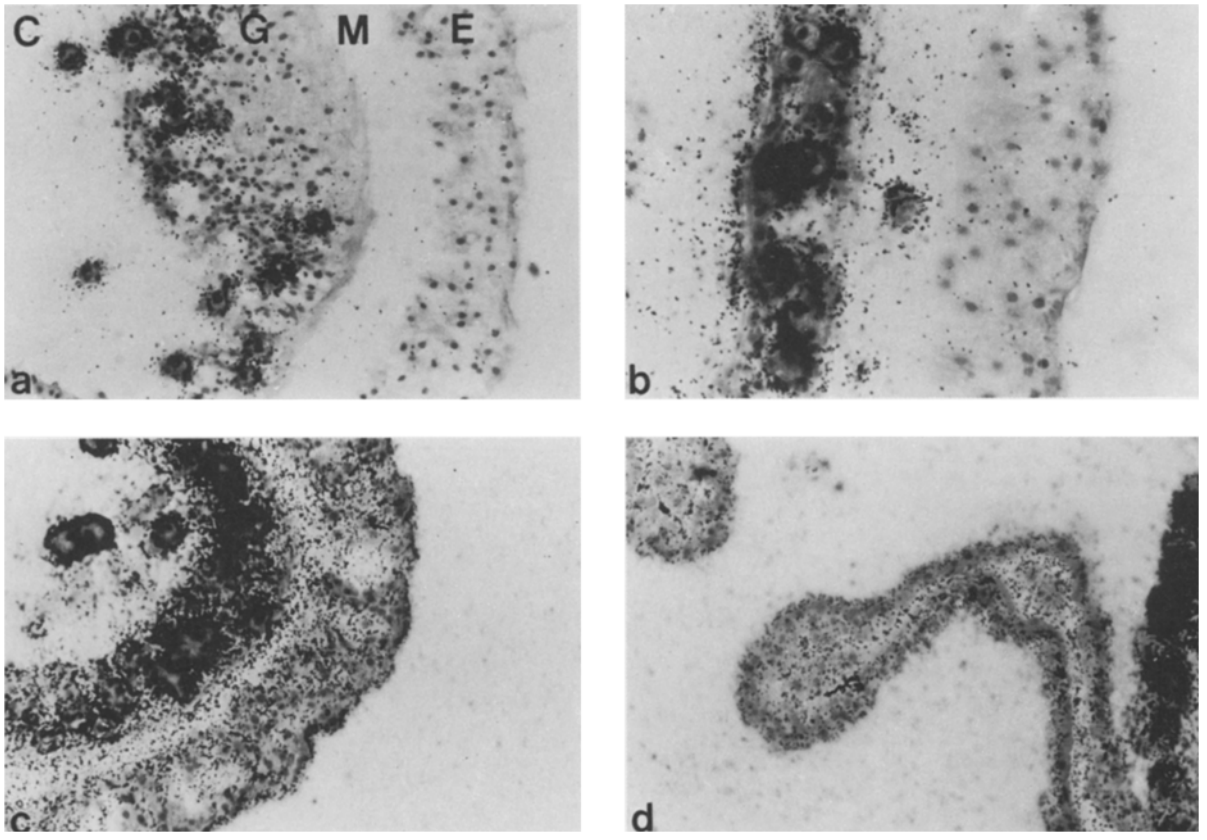

Fig. 4a–d. *Heteroxenia fuscescens.* The time-dependent incorporation of ^{14}C-carbonate into precipitable compounds in tissue of the column of autozooids. After **a** 15 min, **b** 30 min, **c** 180 min and **d** in a lateral mesentery after 240 min of incubation; position 3 in Fig. 1a (see Fig. 2)

Syndete. The mushroom-shaped body of firm consistency contains vertical and horizontal channels by which all individuals of the colony are connected (Fig. 1, 8). At least in the upper part of these gastric channels mesenteries are present, which are not as well-developed as in the autozooids, with the exception of the two dorsal ones (Figs. 11c, d). The vertical gastric channel system is of special interest with regard to viviparity, since it is in these tubes that the developing stages mature (Fig. 9).

The Incorporation of ^{14}C-Carbonate

A few results of the autoradiographic studies are given in Figs. 3–12, in which the time-dependent accumulation and distribution of ^{14}C-labelled compounds are shown. Some of the presented facts are as trivial as expected; but some are noteworthy additions to the knowledge of the biology of alcyonarians.

After only a few minutes of incubation, precipitable radioactive compounds are detectable exclusively in the zooxanthellae lodging in the gastrodermis (Figs. 3, 4). By extending the incubation time, the labelling is much stronger and silver grains can be observed over all body parts. There is no difference between the pinnules and column in the pattern of silver grains with regard to time.

Autoradiographs prepared from chemically and physically fixed material also show the expected results. The density of silver grains in sections prepared from lyophilized tissue is much higher than that in formalin-fixed tissue (Fig. 5), indicating that much photosynthetically produced material remains in the soluble phase.

The Transfer of ^{14}C-Labelled Photosynthates

The most striking conclusions are those drawn from the autoradiographs concerning the distribution of ^{14}C-labelled compounds within the autozooids and colonies. There is conclusive evidence that photo-assimilates from the symbionts rapidly reach all parts of the autozooids and entire colonies, starting from their place of production in the gastrodermis (Figs. 3, 4, 8).

The most spectacular result is that ^{14}C-labelled compounds are detectable on apical epidermis membranes, before transfer of those substances could have taken place through the basal membranes of the epidermis (Fig. 6). The distribution of the silver grains in this particular pattern at a given time means that photo-assimilates are released into the gastric cavities. Depending upon the water currents within the autozooids or colonies, the photo-assimilates are either transported to other parts of the colony within the channel systems or the substances are washed out of the coelenterons (Figs. 6–9). This occurs automatically due to the polyfunctionality of the coelenteron. Compounds washed out, and therefore theoretically lost, can be 'recaptured' and rechanelled through epidermal uptake capacity into the cooperating metabolisms of the animal-plant union. Epidermal absorption of dissolved organic material (DOM) not only makes it possible to utilize natural external DOM from the sea, but also provides a mechanism to reduce the loss of endogenous material to the environment, in this case material originating from the symbionts. In this connection the pharynx, also of ectodermal origin, plays an important role. The in – and outflowing water from the coelenteron permanently provides this epithe-

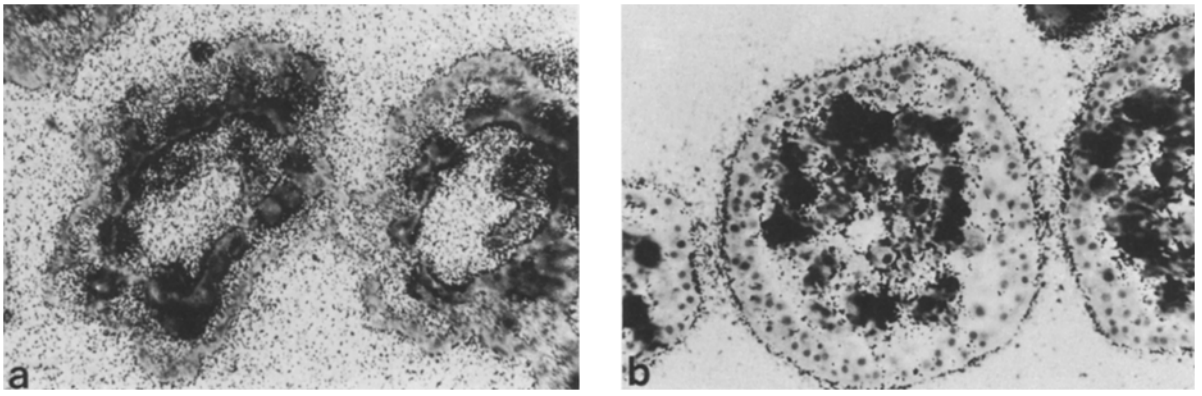

Fig. 5a and b. *Heteroxenia fuscescens.* **a** Autoradiograph from physically fixed pinnules, **b** from chemically fixed pinnules after 60 min of incubation. The tissue samples originate from the same colony. In the first case the amount of silver grains is much greater since all soluble ^{14}C-labelled compounds are also recorded; position 1 in Fig. 1a (see Fig. 2)

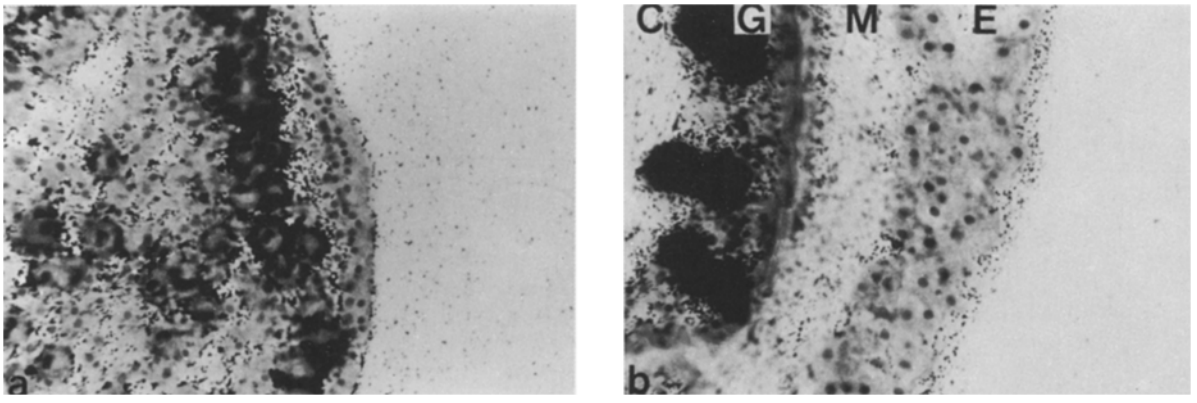

Fig. 6a and b. *Heteroxenia fuscescens.* ^{14}C-labelled compounds already appear on the epidermis, although no assimilate transfer has taken place through the epidermis. The ^{14}C-labelled compounds must have reached the apical epidermal membrane *extracorporally,* i.e. via coelenteron, pharynx and the sea. **a** pinnule after 120 min; **b** column after 180 min; positions 1 and 3 in Fig. 1a; (see Fig. 2)

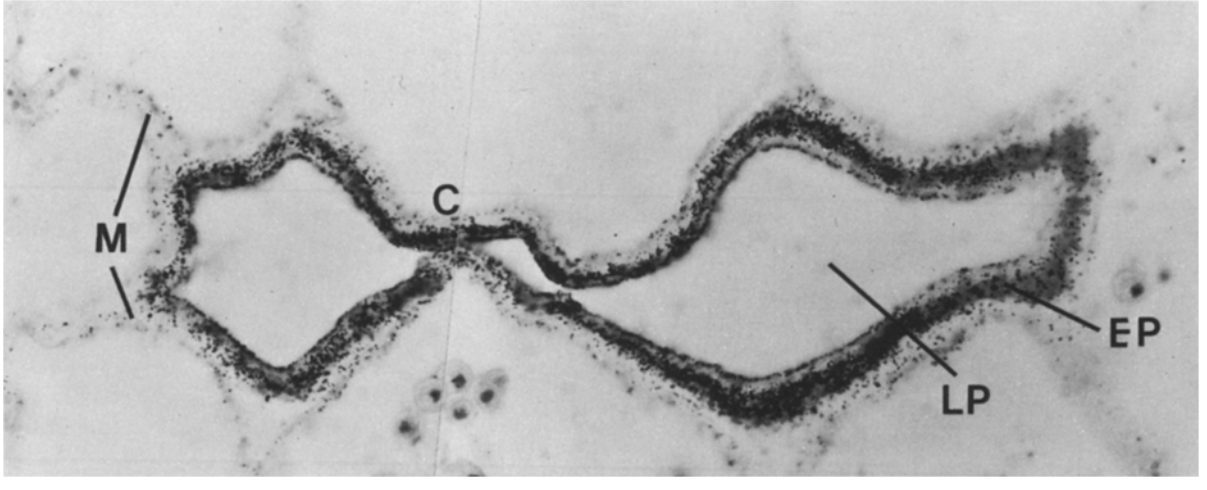

Fig. 7. *Heteroxenia fuscescens.* Autoradiograph of a cross-section through the pharynx. Not only the epidermis, but also the pharynx operates as a 'trap' for dissolved organic substances. In the presented autoradiograph, ^{3}H-L-serine (200 nmol/l) was offered, but photo-assimilates were also absorbed (Fig. 10b); position 3 in Fig. 1a. *M*=mesenteries; *C*=coelenteron; *EP*=epithelium of the pharynx; *LP*=lumen of the pharynx

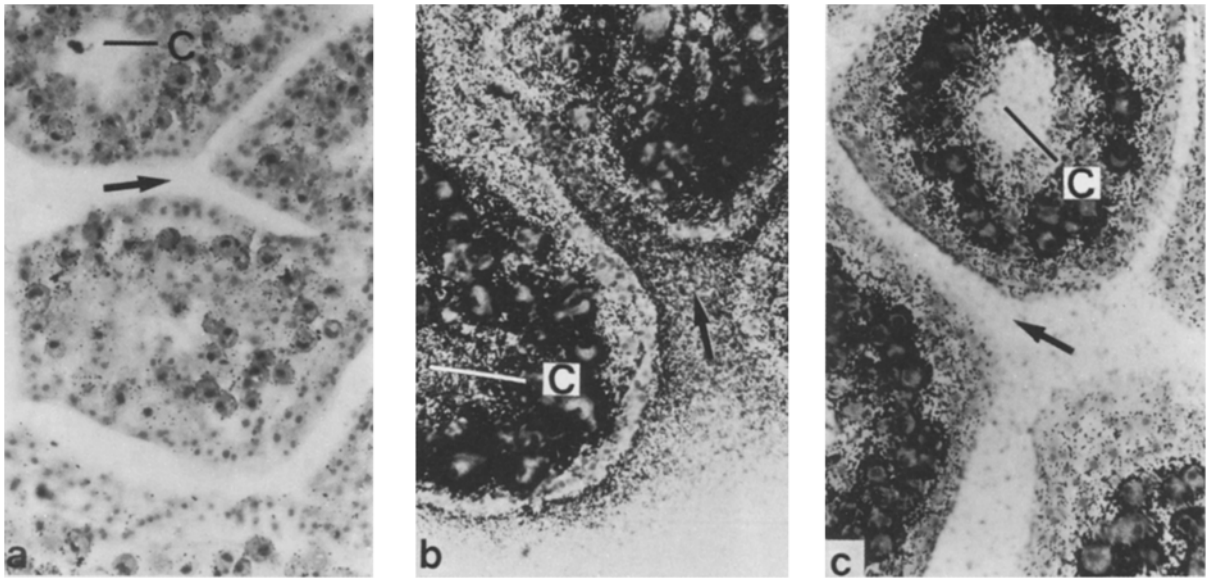

Fig. 8a–c. *Heteroxenia fuscescens.* Release of photo-assimilates. **a** Pinnules after 10 min of incubation. **b** The same colony was incubated for 4 h in a vessel with no outflow. **c** Pinnules from the identical colony, but now after 50 h maintenance in running sea water. Compounds formerly accumulated were washed away; position 1 in Fig. 1a; (see Fig. 2)

lium with organic material (Fig. 7). The possible role of the epidermal mucus in 'trapping' dissolved organic substances is being studied at present.

The provision of epidermal cells with photo-assimilates takes place not only by *extracorporal* transport via the coelenteron, pharnyx and the sea. Compounds are also transferred at lower rates through the mesogloea.

Accumulation of ^{14}C-labelled compounds in the mesenteries and the mesogloea takes place slowly. This is most probably due to the low metabolic demand, since these body regions are permanently supplied with photo-assimilates. In experiments it takes longer before ^{14}C-labelled compounds are utilized and subsequently detectable. Diffusion resistance within this layer is another step that affects the supply.

The Supply of Zooxanthellae Compounds to Autozooids and Colonies

By extending the incubation time of colonies in ^{14}C-carbonate to 4 h, the autoradiographs demonstrate a high content of incorporated ^{14}C-labelled compounds in all parts, including the mesenteries. Under natural conditions, all body parts of the host are continuously supplied with compounds originating from the cytosymbionts (Figs. 3, 4, 8). In the ^{14}C-experiments, the supply process becomes obvious since the time-dependent transfer of ^{14}C-labelled substances begins from the zooxanthellae. During the day, the zooxanthellae continuously produce photo-assimilates, approximately 15% of which are translocated to the host tissue (Schlichter et al., to be published). An unknown amount of assimilates is released into the sea and lost. The autoradiographs also indicate to what extent photo-assimilates are released into the sea. The presented autoradiographs (Figs. 8a–c) originate from sections made from autozooids of a complete colony. After 4 h of incubation, ^{14}C-labelled compounds are aggregated in the gaps between the pinnules and in the coelenteron (Fig. 8b). The same colony was then transferred for 50 h to running sea water (Fig. 8c) after which autozooids were again amputated and prepared. The autoradiograph shows clearly that under those conditions the released assimilates were quickly washed away, also from the coelenteron. This experimental situation does not exist in the biotope. Under natural conditions, therefore, the released photo-assimilates are available for utilization by the epidermis of *Heteroxenia fuscescens* for a longer time. In addition, as former experiments show, the rate of epidermal uptake depends on the concentration of the available substrate (Schlichter 1980). Through the self-created, elevated DOM supply, the epidermal absorption systems work more effectively and the energy profit increases thereby. By the pulsation of the tentacles, the released assimilates also become available to the external surface of the columns of the autozooids, the siphonozooids and the syndete.

An important mechanism for supplying the host with photo-assimilates can be seen. The gastrodermis of the lateral and ventral mesenteries cover the oocytes like a follicle epithelium (Fig. 9). Through this cell layer, organic compounds are transported from the coelenteron into the interior space and to the oocytes. Besides external DOM, the developing stages use photo-assimilates that are produced in the illuminated part of the colony, in the autozooids. It is natural in viviparity that developing stages are nourished by the parental metabolism, but in this particular case the developing stages are also nourished by the symbionts. This topic is being studied at present together with the question of whether the larvae are already infected with zooxanthellae during their differentiation within the syndete. The demonstrated nutrition mechanism for larvae surely applies to all viviparous symbiotic cnidarian species.

The Fate of Zooxanthellae

Zooxanthellae extrude into the coelenteron due either to processes regulating their quantity within gastrodermal cells or to their senility. There are three categories of zooxanthellae each of which undergoes a different fate. The senile ones may be degraded within their vacuoles or they may be decomposed after exocytosis or washed out. After extrusion, the second type is still photosynthetically active and serves as food for organisms

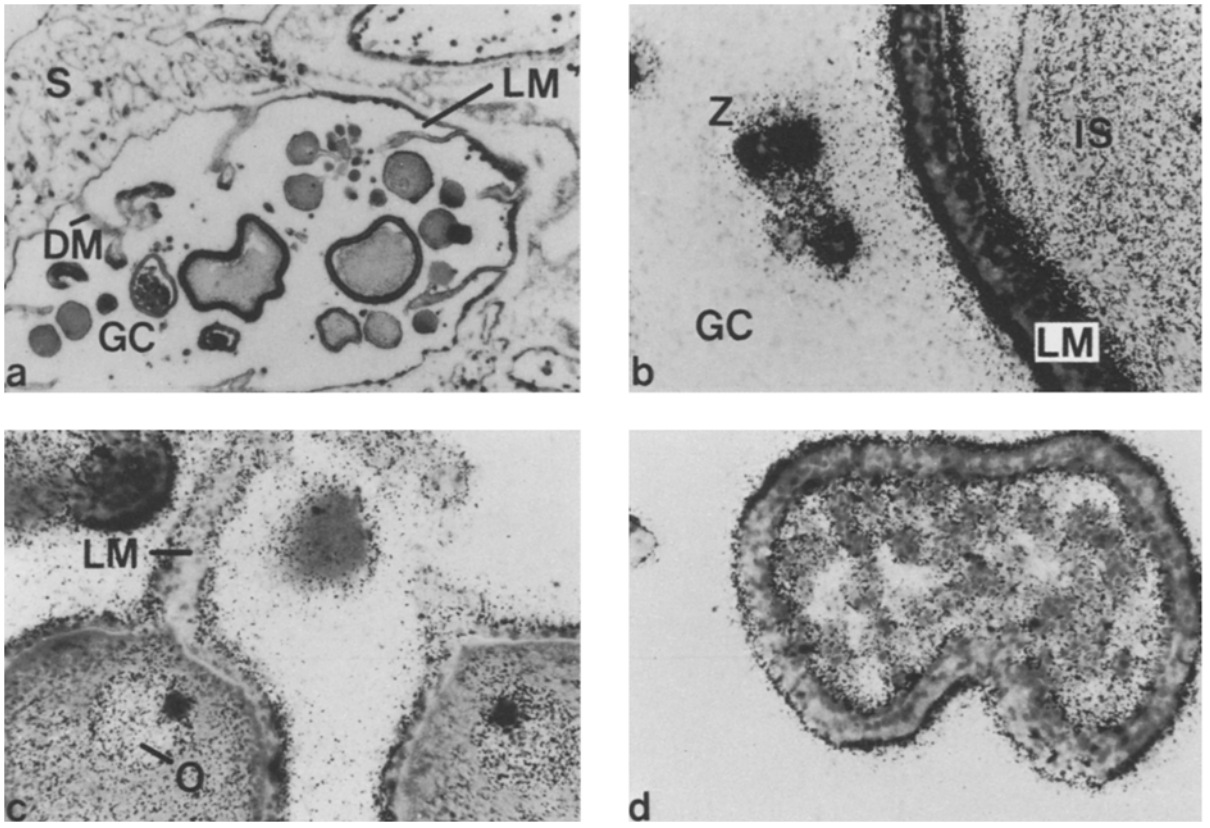

Fig. 9a–d. *Heteroxenia fuscescens.* Cross-section through a syndete (position 4 in Fig. 1a). **a** In the gastric channel developing stages are visible. **b** and **c** Oocytes are covered with gastrodermal tissue similar to a follicle epithelium through which photo-assimilates are translocated from the coelenteron into the interior space. **d** unidentified developing stage. *DM*=dorsal mesentery; *LM*=lateral mesentery; *GC*=gastric channel of the syndete; *IS*=interior space; *S*=syndete; 0=nucleus of the oocyte

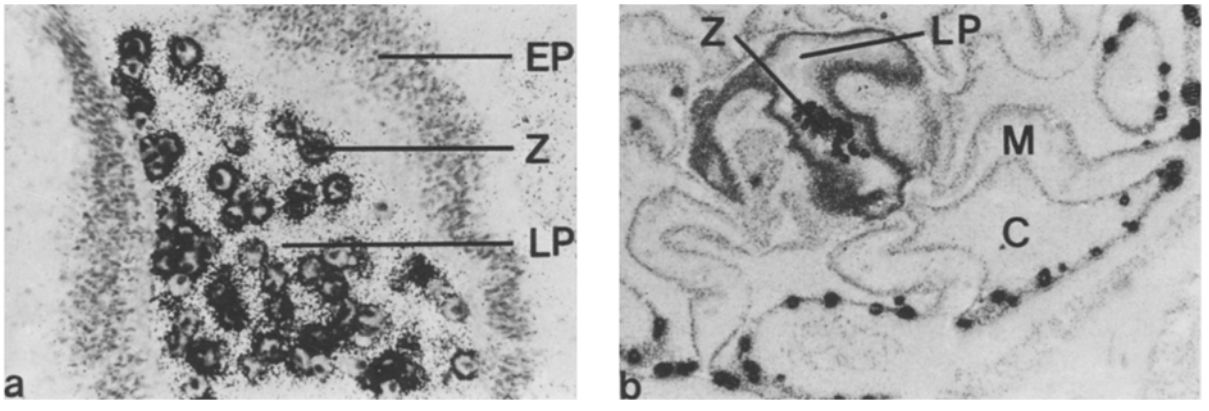

Fig. 10a and b. *Heteroxenia fuscescens.* Zooxanthellae in the pharynx (position 3 in Fig. 1a). During outward transport they release photo-assimilates which can be absorbed by the pharynx. Duration of incubation **a** 120 min, **b** 240 min. *M*=mesenteries; *EP*=epithelium of the pharynx; *Z*=Zooxanthellae; *LP*=lumen of the pharynx (see Fig. 7)

on the reef after being expelled from the coelenteron. During outward transport their released photo-assimilates are utilized by the host (Fig. 10). A third type is used as 'particulate food'. In the literature, the host's utilization of zooxanthellae has been discussed for a long time. Trench (1974), working on the polytrophy of *Zooanthus sociathus,* to my knowledge, first discussed the possibility that zooxanthellae extruded from gastrodermal cells were taken up once more by certain gastrodermal cells of the mesenteries and decomposed there. In the case of *Heteroxenia fuscescens,* expelled zooxanthellae are phagocytized exclusively by gastrodermal cells of the mesenteric filaments of the two dorsal mesenteries (Fig. 11). The autoradiographs clearly show that ^{14}C-labelled material is translocated from the retained zooxanthellae to the host. The further fate of the algae taken up by the filaments of the two dorsal mesenteries is being studied at present.

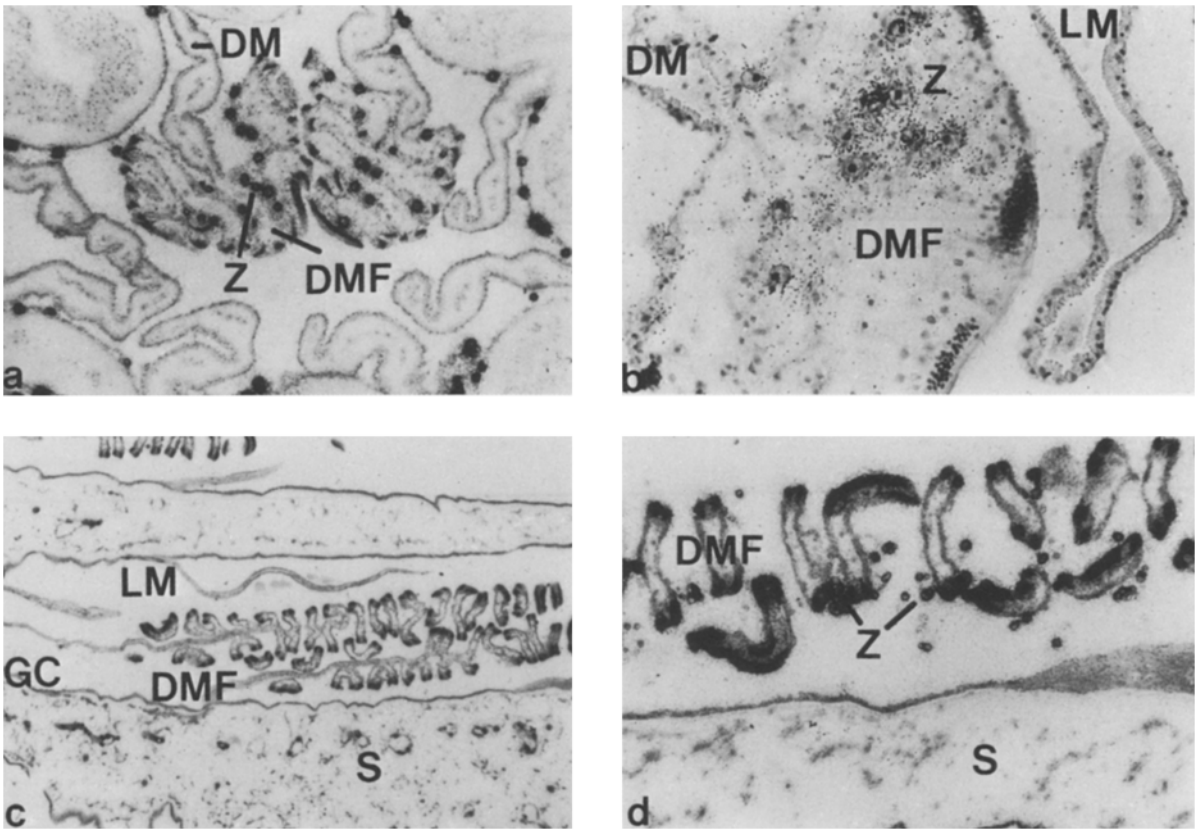

Fig. 11a–d. *Heteroxenia fuscescens.* Expelled zooxanthellae are taken up by the filaments of the two dorsal mesenteries, where they are most probably decomposed (position 3 in Fig. 1a). *DM*=dorsal mesentery; *DMF*=dorsal mesenteric filament; *LM*=lateral mesentery with amoebocytes; *Z*=zooxanthellae; *GC*=gastric channel; *S*=syndete. **a** and **b** Cross-sections through an autozooid. **c** and **d** Longitudinal sections through the syndete (position 5 in Fig. 1a)

The Feeding Strategies of Heteroxenia fuscescens

The results of the autoradiographic studies, together with those from experiments concerning the importance of DOM for nutrition (Schlichter, in press) and biochemical investigations of the metabolism (Schlichter et al., to be published), give the following picture of the nutrition of *Heteroxenia fuscescens.* Included in these considerations are structural and physiological adaptations, which may be important in connection with polytrophic feeding strategies. In this discussion special emphasis is placed on two aspects: (1) with which energy sources (kinds of nourishment) can the metabolism be fuelled and (2) which part of the colonies or individual specimens profits most from nutrients of different origin?

Particulate Food. Gohar's observation (1940a, b) was experimentally confirmed that food particles of visible size, e.g. crustacean larvae, were never swallowed by autozooids. The possibility of utilizing microplankton still remains, but several facts speak against it: the external epidermis does not bear any cilia, a prerequisite for filter feeding; nematocysts are scarce and those present are tiny and appear unsuitable for capturing planktonic organisms; the mesenteric filaments of the lateral and ventral mesenteries are totally absent; only the two dorsal mesenteries possess well-developed mesenteric filaments, i.e. only they are qualified for decomposing particulate food. One may conclude that the uptake of *external* particulate food seems to be of little importance for the nutrition of *Heteroxenia fuscescens* with one notable exception – the utilization of self-produced particulate food, the zooxanthellae.

Absorption of Dissolved Organic Compounds. The energy profit which can be drawn from absorption of DOM is at least equivalent to the energy demand (Schlichter, in press), i.e. the trophic advantage from DOM uptake is great. Especially those tissues (epidermis, pharynx) in contact with permanently renewed water have the highest gain (Fig. 12). The transfer of absorbed DOM through the mesogloea takes place at a low rate. However, organic substances washed from the coelenteron are 'recaptured' due to epidermal uptake capacity (Fig. 6).

There are two methods of utilizing cytosymbiotic algae. The first is the degradation of zooxanthellae. The decomposition of the algae takes place in the mesenteric filament of the dorsal mesenteries (Fig. 11). Dissolved compounds liberated through the decomposition process are either washed out of the gastric cavity or are transported through the gastric channel system in the syndete. The second involves photo-assimilates. Cytosymbiotic algae as their free-living relatives 'voluntarily' release photo-assimilates. The first stage of the release occurs in the vacuoles in which they live, from which the assimilates are transported through membranes and the cytoplasm of the host cells to the coelenteron. During transport the compounds can be used directly by the gastrodermal cells. Assimilates pass at a much lower rate through the mesogloea to the epidermis; in the coelenteron assimilates are used by the gastrodermal mesenteries where zooxanthellae never live (Fig. 11). The assimilates

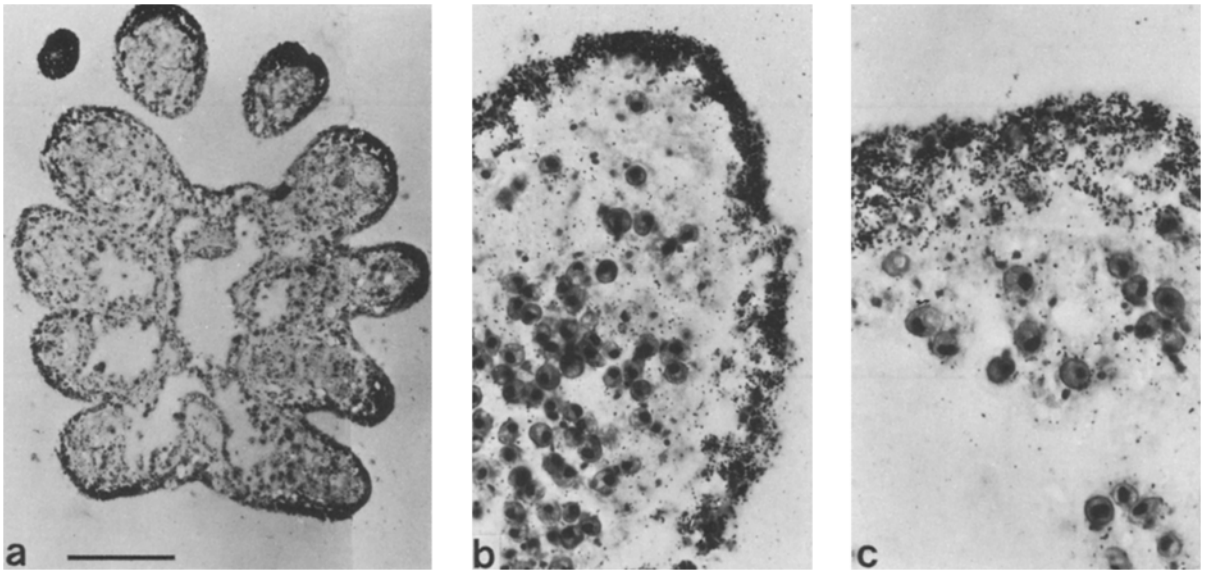

Fig. 12a–c. *Heteroxenia fuscescens.* Uptake of dissolved amino acids through tentacle tissue. The autozooids were incubated for 30 min in 200 nmol/l ^{3}H-L-Lysine. **a** Cross section through a tentacle (position 2 in Fig. 1a). **b** and **c** Detail in higher magnification. Absorption takes place through apical epidermal membranes and the absorbed compounds stay mainly in the epidermis; compare with Figs. 3 and 4

are also necessarily washed out of the coelenteron and thus become available for uptake by the pharyngeal epithelium (Fig. 7), or other epidermal parts of the colony (see above).

In order to increase the metabolic profit by the transfer of photo-assimilates it is advantageous to maintain a great number of zooxanthellae within the body. The formation of the pinnules seems to serve this purpose. One may speculate that special strains (ecotypes) of *Gymnodinium microadriaticum* evolutionarily best adapted to mutual cooperation were 'domesticated' by natural selection.

For *Heteroxenia fuscescens,* as well as for other cnidarians under study (Schlichter 1973, 1980), one has the impression (Figs. 3, 4, 12) that the epidermis is supplied by the uptake of DOM, which originates from different sources. The gastrodermis is supplied by assimilates or by uptake of decomposed zooxanthellae. The provision of the mesogloea takes place by transfer of compounds from both epithelia, most probably only by diffusion. However one should be careful not to look too narrowly at the described conditions.

Multifarious evolutionary advantages result for the autotrophic and the heterotrophic partners in mutual cooperation. A detailed description of possible advantages for symbionts and hosts is given by Muscatine and Porter (1977) and a few aspects are discussed here. First, a reliable and stable supply of nourishment for both partners is guaranteed. Second, the algae live protected within the host in a stable microecosystem under constant conditions, which probably provides the only possibility for growth of populations of unicellular algae. In habitats with a poor supply of particulate food such as tropical reefs, dense free-living algal populations would soon be extinct. Third, the nutritional strategies of (sessile) cnidarians seem to be an optimal answer to the specific nutritional situation. Through DOM absorption and the utilization of photo-assimilates, energy is permanently available and all metabolic processes, including reproduction, are supported continuously. Thus the organisms are to a large extent independent of the particulate food supply. Obtaining particulate food can be problematic for sessile organisms and particulate food is not always available. In a symbiosis of animals and plants this insecurity is avoided. The hosts (the primary consumers) normally use only those compounds released voluntarily from the symbionts (the primary producers). The secretion of photo-assimilates is on the one hand due to general physiological and structural properties of unicellular algae; on the other hand, it cannot be excluded that the symbionts are stimulated by the host to increase the release of photo-assimilates (Trench 1971; Muscatine et al. 1972). The substances released and transported through the pharynx are not lost, for the hosts are equipped with very effective epidermal systems for uptake of dissolved organic compounds.

Generalizations

The nutritional strategies listed above are valid for *Heteroxenia fuscescens;* however, each cnidarian species has its individual set of adaptations for feeding which may include, omit or add to those described. Carnivorous species capture particulate food which is decomposed in the gastric cavity and taken up by endocytosis. DOM liberated by this process in the coelenteron is also absorbed by tissue of ectodermal origin (pharynx, epidermis). The following mechanism is an additional way of producing DOM. The captured prey is pre-orally degraded by 'skin digestion', i.e. epidermal enzymes liberate DOM from the prey during transport to the pharynx and this DOM is directly used by the epidermis. In the case of aposymbiotic species the contribution of zooxanthellae is inapplicable. For the few fresh water species of cnidarians, the uptake of DOM seems to be of no importance.

The outlined scheme (Fig. 13) for the cnidarian's energy supply may appear complicated at the first glance, but when one is familiar with the structural and physiological organization of these organisms, with their behaviour and the trophic sources available under natural conditions, the schema makes sense. It can be surmised that the gastrodermis is either supplied by endocytosis of particulate food or by compounds originating from zooxanthellae. The epidermis takes up DOM either of external origin, thus utilizing an inexhaustible energy source – the sea

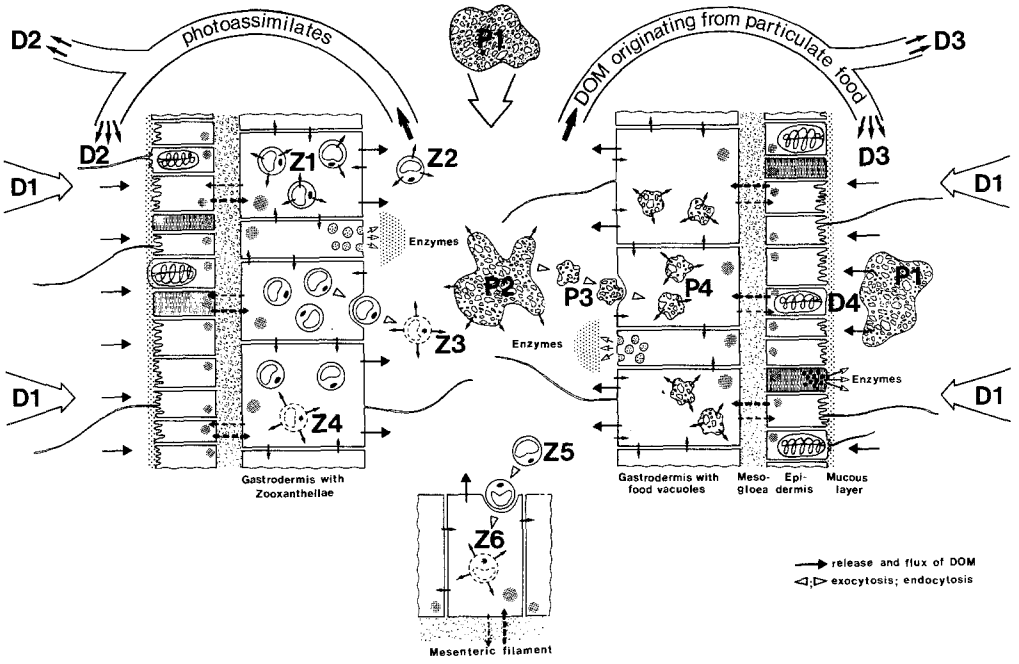

Fig. 13. Polytrophy of symbiotic cnidarians. The scheme shows different possibilities of nutrition by which the metabolism can be supported. Left part: the contribution of zooxanthellae. Right part: the contribution of particulate food. The structures are not drawn to scale. Explanation of the abbreviations: D1 = naturally occurring DOM in the sea; D2 = photo-assimilates released from zooxanthellae into the coelenteron; D3 = DOM liberated by digestion of zooxanthellae or particulate food; D4 = DOM liberated from particulate food by "skin digestion"; P1 = particulate food; P2 = decomposition of particulate food in the coelenteron; P3 = endocytosis of food particles; P4 = digestion of food particles within food vacuoles; Z1 = release of photo-assimilates by zooxanthellae within gastrodermal cells; Z2 = release of photo-assimilates by zooxanthellae in the coelenteron; Z3 = lysis of zooxanthellae in the coelenteron; Z4 = lysis of zooxanthellae within gastrodermal cells; Z5 = uptake of expelled zooxanthellae by cells of mesenteric filaments; Z6 = degradation of zooxanthellae within cells of mesenteric filaments

– or DOM of internal origin, which necessarily leaves the coelenteron due to the polyfunctionality of the gastric cavity. The outflowing DOM derives either from ingested particulate food or from released photo-assimilates or products of zooxanthellae degradation. The epidermal uptake capacity of marine invertebrates seems to serve two main purposes: (1) utilization of external DOM, e.g. DOM produced by phytoplankton, decay of carcasses (2) reduction of the loss of internally produced DOM which generally escapes from the gastric systems or the bodies in the case of higher invertebrates (Gomme 1981).

As mentioned in the introduction, the cooperation between cytosymbionts and hosts is very complex. In the future the back-transfer of metabolites from the host to the symbionts also needs to be studied in more detail.

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