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STUDIES ON THE FORAMINIFER SORITES ORBICULUS[1]

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ABSTRACT

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The exclusively epiphytic and sedentary living foraminifer *Sorites orbiculus* (FORSKÅL) has been found in several lagoons and bays on Curaçao (Netherlands Antilles). Only megalospheric specimens were found.

Living *S. orbiculus,* attached to their favourite substratum, the marine phanerogam *Thalassia,* were kept in aquaria for three weeks. Positive phototaxis was observed. Symbiotic algae colour the protoplasm and show its irregular distribution within the test; they also provide a criterion for recognition of living specimens.

Most *S. orbiculus* specimens are enveloped in a pellicle and are encircled by a rim of sediment which is probably a feeding-cyst; both are left behind when the specimen moves away.

INTRODUCTION

Little is known about the biology of living foraminifera. *Sorites orbiculus* (FORSKÅL), a benthonic form living in shallow tropical seawater, has been selected for study. From previous work by HOFKER (1976) and WAGENAAR HUMMELINCK (1977) it is known that this species occurs at easily accessible places on Curaçao. A preliminary collection made by P. van der Wal had furthermore shown that the species lives attached to a substratum, predominantly the marine phanerogam *Thalassia,* so that the living population can be easily separated from a population of empty tests in sediment. I visited Curaçao from June to October 1979 in order to locate the *S. orbiculus* occurrences and to describe these habitats; furthermore living specimens were collected in order to observe, and eventually breed them in the laboratory. The results of the investigations are discussed in this paper. Aspects concerning growth and reproduction will be treated in a separate paper. A short description of the *S. orbiculus* localities on Curaçao is given in the appendix.

ECOLOGICAL ASPECTS OF THE LOCALITIES

The species lives on Curaçao in lagoons and bays that are semi-locked from the free ocean and protected from strong currents and wave action. These localities are always found at the northeastern side of the lagoons and bays, where they are protected against the northeastern trade-wind. Turbulence and wave action is obviously a major limiting factor for the presence of *S. orbiculus.* The communities living at a depth of less than one metre are restricted to quiet water. The number of specimens decreases where the water is more turbulent.

Communities usually cover less than 100 m^2 of a *Thalassia* field. Outside these patches *S. orbiculus* is rare or absent. The boundaries of the communities may be very sharp, for instance over a distance of two metres the frequency can drop from ten specimens to less than one on a *Thalassia* leaf. Sometimes the boundaries are more gradual.

At one locality, the small lagoon near Awa Blancu (Fig. 1), all *S. orbiculus* were attached to the side of the *Thalassia* leaves that faces the sun. This is not the case at other localities where, although usually one side of the leaves contains more specimens than the other, they do not exclusively occur on one side. In the larger lagoons with open connections with the sea, some movements produced by tide runs or swell will

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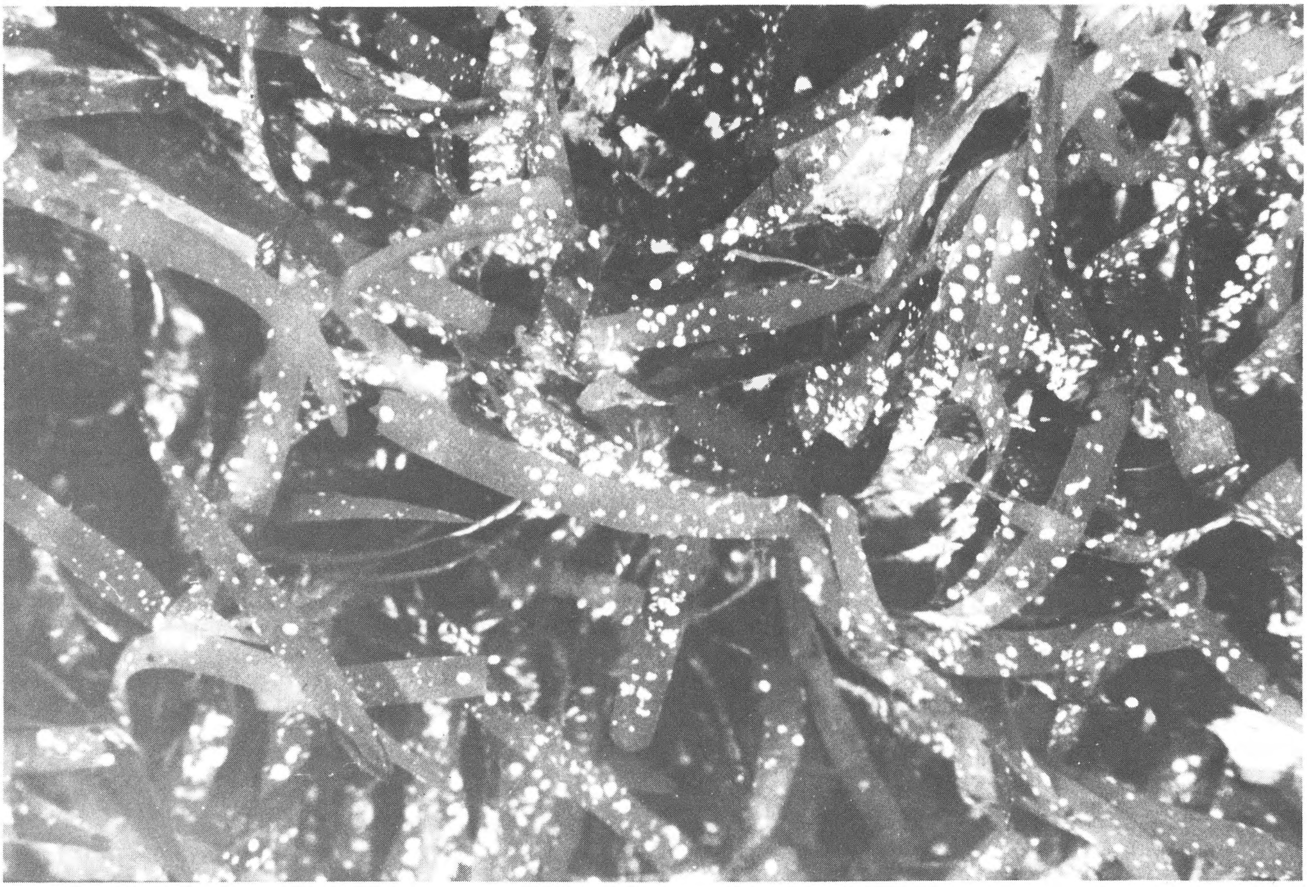

Fig. 1
View of a *Thalassia* field in very shallow water near Awa Blancu with numerous attached *Sorites orbiculus* (white spots). For scale: one leaf is about 20 cm long.

occur, which causes the *Thalassia* leaves to move with it, so that both sides are alternatingly exposed to the sun. The little pool near Awa Blancu, however, is closed off from the open ocean and is much smaller than the other localities and therefore more quiet.

A second limiting factor is the absence of a suitable substratum. *S. orbiculus* is exclusively epiphytic, for we did not find one single specimen on the sandy bottom, on corals, stones, shells or rubble. *Thalassia* is by far the most favoured substratum but other plants will also serve, such as *Halimeda, Penicillus, Udotea* and *Syringodium.* When one of these other plants happens to grow next to *Thalassia* one always finds more specimens on the latter. This indicates that there is some ecological difference between these substrata. On *Thalassia* the species lives on fresh green leaves as well as on brown, wilted leaves.

A great diversity of other organisms, such as calcareous algae, foraminifera and arthropods, lives together with *S. orbiculus* on *Thalassia* in varying amounts. In some localities the *Thalassia* leaves and the attached *S. orbiculus* were covered with a thin layer of fine sediment that apparently caused the foraminifer no harm.

S. orbiculus lives from just below the water surface down to a depth of at least four metres. Its presence at greater depth could not be established, as the lagoons and bays where we found the species are not deeper than six metres. In the Gulf of Elat, however, *S. orbiculus* has been found at a depth of 40 metres (REISS, 1977).

The salinity of the seawater at the Curaçao localities ranged from 34-36‰, which is equal or slightly higher than the salinity of oceanic water around Curaçao. The temperature ranged from 29-32.5°C. The water where the species occurs may be clear, but also turbid.

In the sediment under the living communities only empty soritid tests were found. Variations in abundance are clearly due to the ratio between *S. orbiculus* tests production and total sediment production. At Jan Thiel Baai where the species lives on *Halimeda* (which produces an enormous amount of sediment) few soritid tests are found per volume-unit of sediment. On the other hand, underneath *Thalassia* that hardly contributes anything to the sediment, one finds in general relatively many soritid tests (Awa di Oostpunt). Of course, other post-mortem phenomena may change the quantity of soritid tests in the sediment. For example in the small pool southeast of Awa Blancu, where a prolific community of *S. orbiculus* lives on *Thalassia,* surprisingly few tests were present in the sediment underneath. The tests cannot have been transported out of the locked pool; here their scarcity may be due to dissolution.

All growth stages, from two-chambered juveniles to adults in reproduction stage (see KLOOS, 1981), were observed living on *Thalassia* at the same locality. In the sediment all growth stages were found as well, but these were all empty tests.

All living specimens and empty tests belong to the megalospheric generation; not one single microspheric *S. orbiculus* has been found. This implies that embryogenesis is the prevalent mode of reproduction and that gametogenesis does not take place here as far as could be ascertained. This may have different causes:
(1) gametogenesis only takes place in a specific season other than the summer (the time I was there); this possibility is unlikely, as no microspheric *S. orbiculus* were found in the sediment either;
(2) gametogenesis takes place in a different ecological niche, for instance at greater depth, where I have not been able to sample;
(3) embryogenesis is the predominant form of reproduction and accordingly the chance of finding a microspheric specimen is very small.

During the four months of observation (June to October) no important changes were perceived in the size or composition of populations. In other words, no changes due to seasonal influences could be determined.

OBSERVATIONS IN THE LABORATORY AND DISCUSSION

Every ten days during my stay on Curaçao I took samples at the three most prolific localities: Awa di Oostpunt, Awa Blancu and the small lagoon near Jan Thiel Baai. *Thalassia* with living *S. orbiculus* was sampled by pulling out a number of leaves, which were put into a jar with seawater. Immediately after arrival in the laboratory they were placed in an aquarium with continuously renewed seawater. The sediment underneath the living community was sampled with a shovel in order to obtain a statistically representative sample. The culturing and breeding of *S. orbiculus* was not successful, as after two to three weeks all specimens had died. This was the case both in aquaria and in petri-dishes. All observations on living *S. orbiculus* in the laboratory were therefore done under unnatural (stress-) conditions.

Locomotion and phototaxis

When Thalassia with *S. orbiculus* was placed in an aquarium the first reaction of the soritids to their new habitat could be noted after about two days, when they had moved from the *Thalassia* leaves to the wall of the aquarium. *S. orbiculus* normally lives attached to its substratum, but apparently it can disengage itself and move to the wall of the aquarium. It does not seem likely that soritids can move actively through the water. Perhaps they let themselves be transported passively by the currents from one place to another. In this respect it is important to note that specimens, when detached by hand from *Thalassia,* sank to the bottom of the aquarium which indicates that their specific gravity is higher than that of seawater. A number of times I have seen specimens stuck to the air-water interface; when touched by a pencil these also sank to the bottom. According to observations on *Elphidium incertum* by SHEEHAN & BANNER (1972) surface tension may be used to add buoyance to the organism.

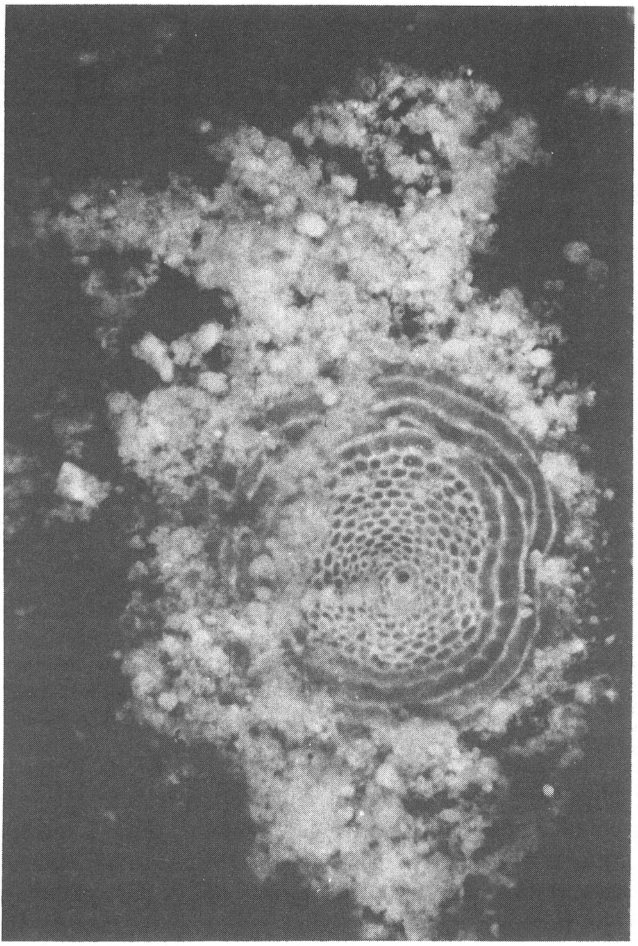

Fig. 2
Sorites orbiculus on a *Thalassia* leaf. This specimen is surrounded by the characteristic sediment fringe; the outer chambers, which are much wider than the preceding ones and of different shape, are the reproduction chambers. 30×.

S. orbiculus can also displace itself actively over a substratum with the aid of pseudopodia. I have observed specimens moving along the aquarium wall in different directions with a speed up to one centimetre an hour. Most specimens settled on the aquarium wall facing the window of the laboratory room. This observation, together with the preferred occurrence on the sun-side of *Thalassia* leaves observed in the field, proves that *S. orbiculus* has positive phototaxis.

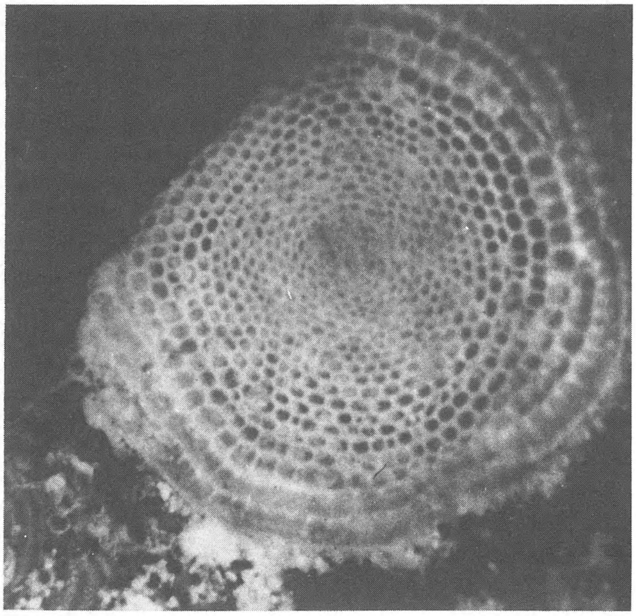

Fig. 3
Sorites orbiculus in situ on a *Thalassia* leaf. The last four chambers, of which the outer two are reproduction chambers, have grown folded around the edge of the leaf indicating that the soritid was immobile when these chambers formed. 30×

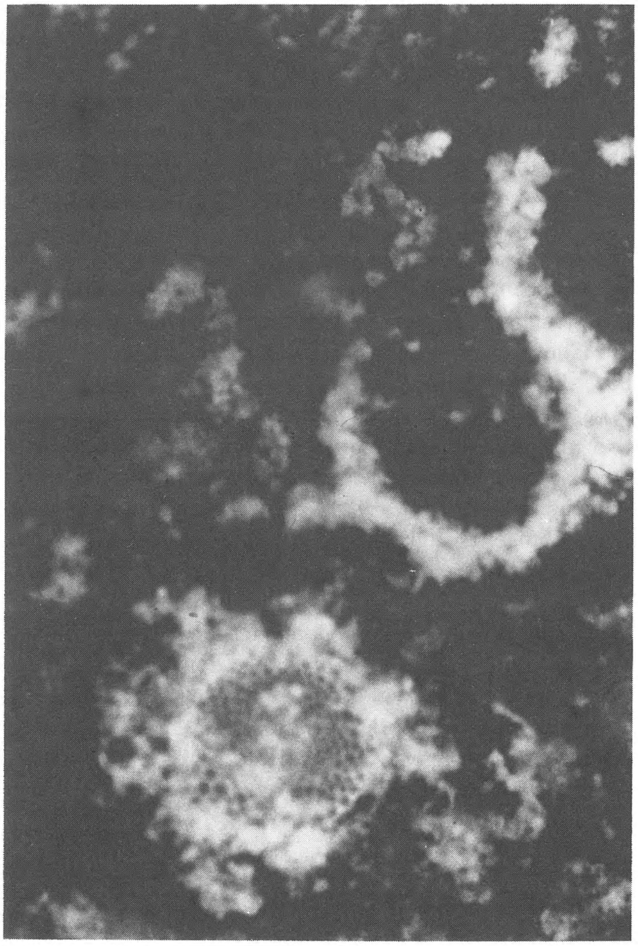

Fig. 4
On the left a living *Sorites orbiculus* with its sediment fringe. On the right a sediment fringe abandoned by a soritid. The circle of sediment is breached showing that the soritid left through the gap. The breached portion of the fringe became detached from the substratum and is seen swung sidewards. 15×

Hottinger, who also investigated this species in the field, could not establish a particular orientation towards the light (HOTTINGER, 1977); perhaps this could be due to the waving of the substrate leaves by water movements. Positive phototaxis has, however, been observed in aquaria in the case of *Amphisorus hemprichii* from Elat by LEE ET AL. (1980). Positive phototaxis is not surprising because *S. orbiculus* houses symbiotic algae which need light for photosynthesis.

Gradually the activity of cultured specimens decreased. The *Thalassia* leaves became brown and alga bloom occurred; next the soritids died and sank to the bottom of the aquarium. In order to find out whether the aquarium cultures suffered from shortage of light I increased the illumination but this did not lengthen their lifetime. Nor was aeration of the water successful. Equipment to control physical and chemical conditions to improve the aquarium environment was not available. An attempt to grow *Thalassia* with rhizomes in an aquarium also failed.

From all samples *Thalassia* leaves were investigated with a stereomicroscope. Within one sample there were leaves with only one or two *S. orbiculus* specimens living on it as well as leaves with more than twenty specimens. Usually there were more soritids on one side of the leaves than on the other. As has already been mentioned, this is thought to be due to positive phototaxis, partially counteracted by the waving motion of the leaves.

The sediment fringe

Almost every *S. orbiculus* specimen is surrounded by a fringe or cloud of sediment grains, held together and glued to the substratum by a mucus-like substance (Figs. 2 and 4). These particles are actively collected by the animal, for I have observed under the microscope how sediment particles were slowly transported and drawn towards the test by pseudopodia. Several authors have found more or less comparable sediment accumulations around other species of foraminifera. These were in most cases associated with the process of chamber-formation: before a new chamber is secreted a so-called 'growing cyst' is constructed in which this chamber is then formed (MYERS, 1940; LE CALVEZ, 1953; SLITER, 1970). For *S. orbiculus,* however, I have found that such a fringe occurs around the majority of specimens and it does not seem likely that they were all in a state of chamber-formation. Moreover, several times I observed the formation of a new chamber (see KLOOS, 1981) and it was never followed by a clearing away of the sediment fringe. The fringe is therefore permanently present and is not restricted to periods of cham-

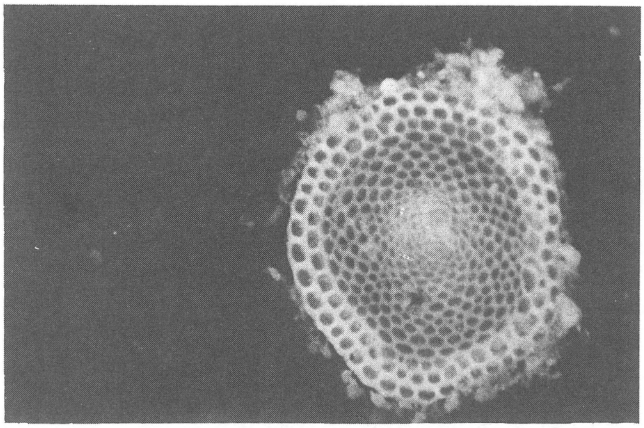

Fig. 5
Sorites orbiculus on *Thalassia* before decalcification. 30×

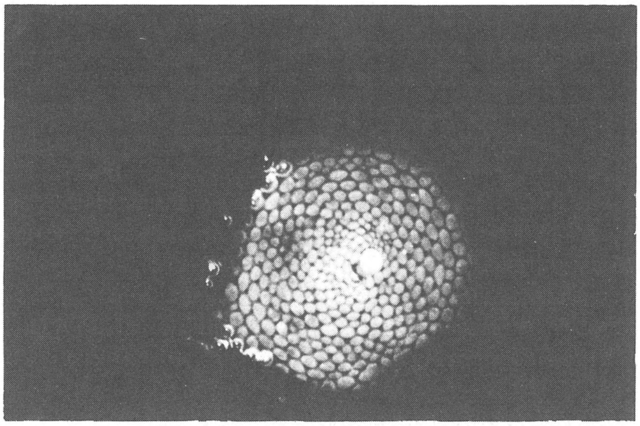

Fig. 6
The same specimen as in Fig. 5, but decalcified in Bouin's fluid showing that the arrangement of the organic substance is left undisturbed by the treatment. 30×

ber-formation. Perhaps it is a 'feeding cyst', as described by JEPPS (1942) and MURRAY (1963) for *Elphidium crispum*, consisting of garbage left behind around the apertural face of the soritid after digestion of algae, diatoms and other micro-organisms from among the particles gathered by the pseudopodia.

The sedentary way of living

S. orbiculus is vagile but may stick to one place during life. Figure 3 shows a specimen that grew around the edge of a *Thalassia* leaf; the growing soritid reached the edge of the leaf but did not move away, so the next four chambers grew folded around it. Other specimens were seen to grow around obstacles such as sand grains forming up to eight indented chambers around them (see KLOOS, 1981). On the other hand I have found sediment rings upon *Thalassia* unoccupied by a soritid (Fig. 4); these are clearly remnants left behind after the specimens had moved elsewhere (see also MURRAY, 1963). Often these rings were breached, a portion having been detached from the substratum and removed or swung aside (Fig. 4). Within the broken circle a pellicle is found which has also been left behind. This pellicle may have been a sheath which covered the soritid when still in place. Such a pellicle has been described by LEUTENEGGER (1977) and can also be compared with the so-called 'Ektoplasmahülle', sensu RÖTTGER (1973), of *Heterostegina depressa.* The function of this pellicle is not understood but may be protective: chamber-formation, for instance, takes place within this pellicle in the case of *Heterostegina depressa* (RÖTTGER, 1973); Röttger indeed observed *H. depressa* to leave its 'Ektoplasmahülle' behind when moving from one place to another.

As already stated above, active movement of *S. orbiculus* has been observed in my aquarium experiments. Thus on one hand active movement is proven by direct observation while, on the other hand, evidence points to the preference for a fixed position. It is concluded that *S. orbiculus* stays in one and the same place for most of its life under stable conditions but that, if these conditions alter and become unfavourable (as in the laboratory), the foraminifer will move in search of a better environment.

Protoplasm distribution and zooxanthellae

Dozens of specimens were investigated more in detail under a microscope with transmitted light. Living soritids were submerged for about fifteen minutes in Bouin's fluid (75 parts picric acid saturated aqueous solution; 25 parts formaldehyde 40%; 5 parts acetic acid) in which the calcareous tests dissolved (Figs. 5 and 6). The non-calcareous parts remained surrounded by some non-calcareous remnants of the sediment fringe (Fig. 7). The organic pellicle may also have been left but could not be distinguished.

The living *S. orbiculus* contains in its protoplasm zooxanthellae, coloured yellowish-brown by symbiotic algae (Figs. 7, 8 and 9). LEUTENEGGER (1977) redefined the terms ectoplasm and endoplasm. The zooxanthellae are restricted to that part of the protoplasm which she names endoplasm. Colouration of the protoplasm is mainly due to the presence of these zooxanthellae so that the endoplasm is recognized by its colour, the ectoplasm being transparent and colourless. Under the microscope the zooxanthellae are well visible in the decalcified specimens. MÜLLER-MERZ & LEE (1976) have found zooxanthellae to be mainly concentrated in what they define as the intermediate chambers of *Sorites marginalis.* The situation is different in *S. orbiculus* and the distribution of zooxanthellae varies from one specimen to another. Usually the major part of the chambers is well stocked with them. They may be absent in the outer chambers, or the inner chambers may lack them. Not seldom are they lacking in an arbitrary segment of the soritid test. The density of zooxanthellae in the protoplasm also varies. Sometimes the chamberlets are closely packed with them and the animal may contain hundreds of thousands of these symbiotic algae;

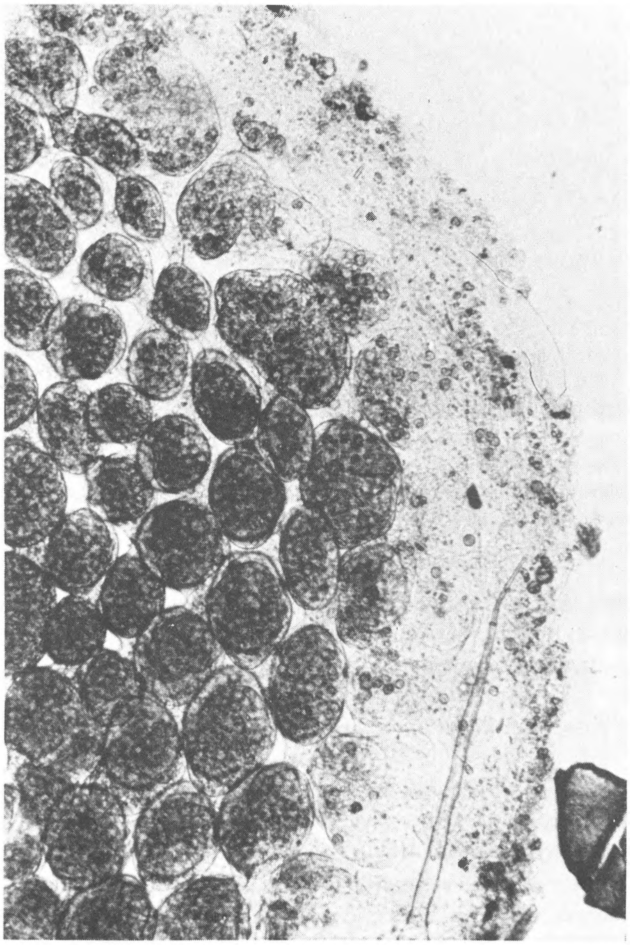

Fig. 7
Detail from the same specimen as Fig. 6 showing the symbiotic algae closely packed in the chamberlets; only the outer chamber is not completely filled by them. The outermost edge consists of non-calcareous particles, remnants of the sediment fringe (at the lower right a sponge needle). 300×

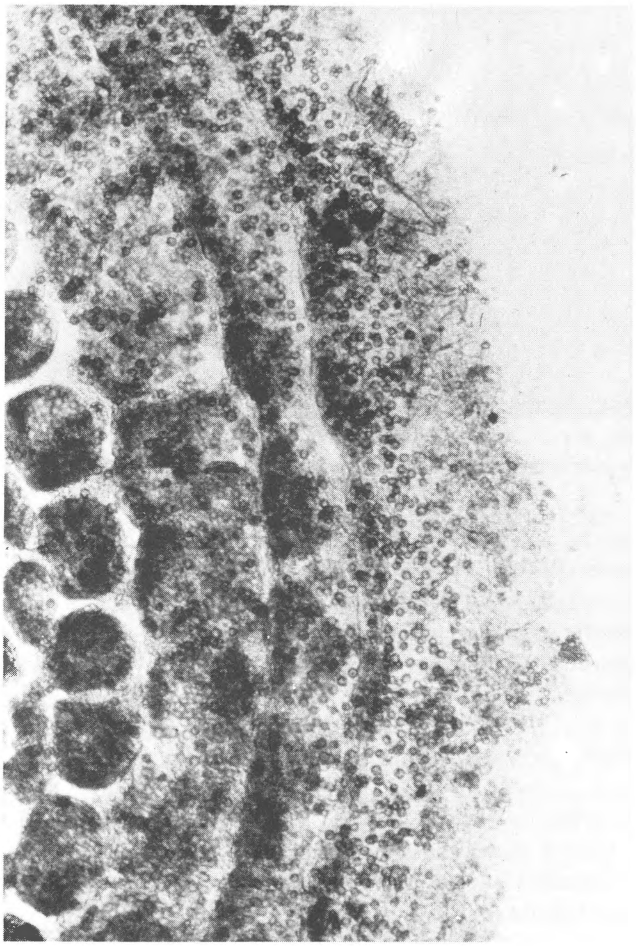

Fig. 8
Edge of a decalcified adult *Sorites orbiculus.* The three outer chambers are imperfectly subdivided into chamberlets. These chambers are also wider than the preceding ones indicating that they are reproduction chambers. Thousands of zooxanthellae can be distinguished, both in the preceding and in the reproduction chambers. 300×

in other cases the entire protoplasm contains but a few hundreds. Protoplasm rich in zooxanthellae has a darker colour than protoplasm containing less of them. Irregularities of the yellowish-brown colouration of living *S. orbiculus* is thus caused by the distribution of zooxanthellae and their density.

Zooxanthellae need light for photosynthesis. *S. orbiculus* is well adapted as a host to its symbionts: the discoid test ensures a maximum exposure towards light and the roof of the test is made of very thin, transparent calcite. Moreover, the animal can increase the light supply by moving towards a more favourable position.

Recognition of living specimens

Many investigators have problems with the distinction between dead and living specimens of foraminifera (ARNOLD, 1974). The unreliability of the rose-Bengal technique of Walton, for instance, is well known. Fortunately the living *S. orbiculus* can be distinguished simply by the presence of the symbiotic algae. The yellowish-brown colouration is easily observed even in the field with a magnifying glass. Dead soritids do not contain zooxanthellae and are usually bright white. In this way it could be established that most of the specimens on *Thalassia* are alive (Fig. 10). Some empty (white) tests are found as well, but in most cases these were shells of soritids that had recently reproduced as shown by remnants of reproduction chambers. These were always easily removed from the *Thalassia* leaves with a fine brush. Living specimens on the other hand were much more difficult to dislodge in this manner. After death or reproduction *S. orbiculus* tests will not stay attached to the substratum for long, but become detached and sink to the bottom just as the dead specimens of the aquarium experiments did.

As a consequence of the epiphytic life, only white empty

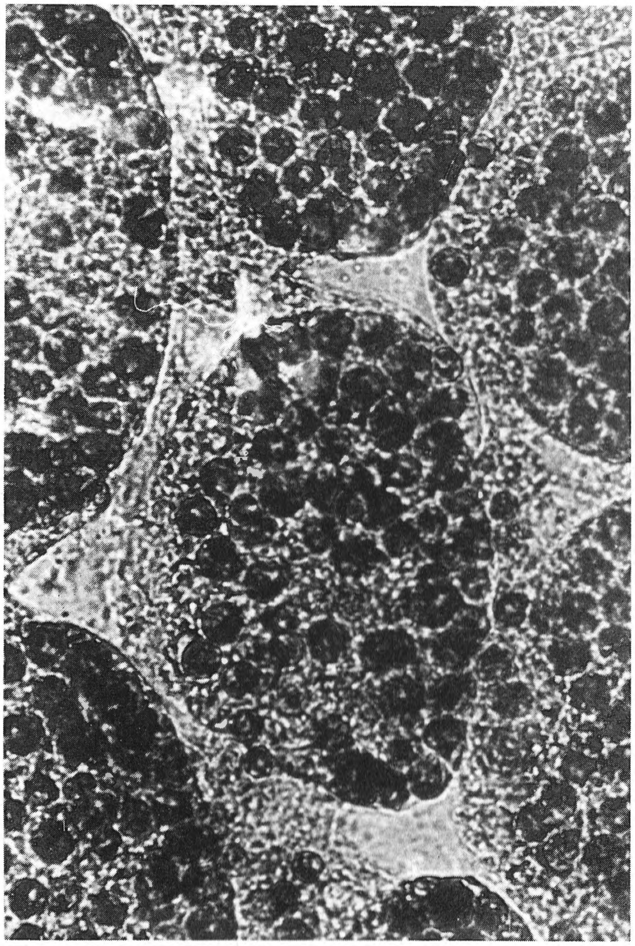

Fig. 9
Detail of a decalcified *Sorites orbiculus* showing some chamberlets containing numerous zooxanthellae (dark spots). 3000×

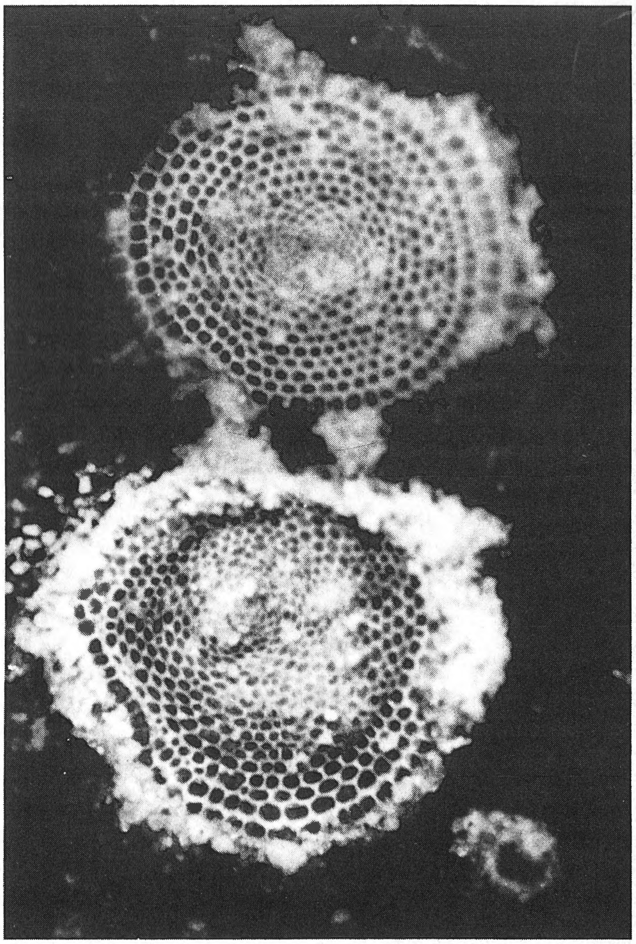

Fig. 10
Two specimens of *Sorites orbiculus* on a *Thalassia* leaf. The lower one is a living specimen, dark coloured by protoplasm with zooxanthellae and surrounded by a sediment fringe. The specimen on the top is an empty test of a soritid that has reproduced. The outer (reproduction) chambers are for the greater part broken off and the sediment fringe is no longer complete. This test will soon loose its adhesion on the *Thalassia* and sink to the bottom. Note the pale colour of this test. 30×

tests were found in the sediment. Nor did freshly sampled sediment, placed in an aquarium, show any activity of soritids. However, a sediment population of empty tests is not to be regarded as a thanatocoenosis, for many of these are tests discarded after reproduction. Their inhabitants did not die, but participated in the continuation of the stream of life.

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APPENDIX

From June 20th until October 17th 1979 all favourable bays and lagoons on Curaçao were investigated on the presence of *S. orbiculus.* Actually it was found only in a few of them, and the localities are described below.

Awa di Oostpunt

Awa di Oostpunt is an open lagoon with an inlet of about 150 m width. Great parts of the bottom were covered with *Thalassia* meadows, but only in one place *S. orbiculus* was found on it. There, however, it was present in great numbers. This place is located about 100 m southwest of a triangulation point (D.P.1/3.4). The bottom consists of a one decimetre thick layer of silty carbonate sediment resting on karstic coral-limestone. Water depth was about 40 cm. At the time of my visits the *Thalassia* did not look very flourishing; many leaves were brownish, and very often covered with a layer of fine mud. The soritids were found between this mud and partly covered by it. The temperature of the water was measured at three occasions (10/8; 27/9; 16/10); the mean temperature was 32°C. The salinity was also determined three times (10/8; 27/9; 8/10) using a T-C Refractometer (catalog 10419, Am. Optical. Corp., Keen, N.H., U.S.A.). The mean salinity was 34‰, which is normal for ocean water around the Netherlands Antilles.

At the back of Awa di Oostpunt *Syringodium* leaves were found floating on the water, but no growing *Syringodium* was observed, so it is apparently living in the deeper part of the lagoon. A few soritids, however, were found on these needle-thin leaves growing wrapped around them.

Awa Blancu

This is a somewhat smaller lagoon, a few kilometres west of Awa di Oostpunt. It has an inlet of about 50 m width and a few decimetres depth. In the shallow parts at the northeastern side of Awa Blancu (down to a depth of 1 m) much *Thalassia* was growing as well as *Udotea. S. orbiculus* was found on both plants, but it was much more common on *Thalassia.* The sediment underlying the plants consisted mainly of *Halimeda* fragments, but living specimens of this calcareous alga were not found at this point. *Thalassia* also grew in the shallow part at the southwestern side of the lagoon, but no soritids were living there. Much *Thalassia* also grew in the deeper part of the lagoon, down to a depth of four metres and a few soritids were found on it. The *Thalassia* plants growing at shallow depth were brownish in colour like those in Awa di Oostpunt, whereas the deeper growing *Thalassia* looked freshly green. The leaves were covered with mud. Salinity and temperature were measured at the same dates as in Awa di Oostpunt; the mean values were respectively 34‰ and 30°C.

A remarkably prolific locality was found in one of the small pools southwest of Awa Blancu. It has a surface of about 100 m^2 and a depth of about 60 cm; this pool is not in direct contact with the open ocean. The bottom was for the greater part overgrown with *Thalassia.* Even from as far as five metres distance one could easily see the white spotted green leaves, the spots representing *S. orbiculus* (Fig. 1). Especially in the most northeastern part abundant specimens were living on the *Thalassia,* up to dozens per leaf. Remarkable as well was the fact that all *S. orbiculus* specimens were situated on the upper side of the leaves, that is the side turned towards the light. Salinity of the water in the pool was 35.5‰ and the temperature was 31.6°C.

Jan Thiel Baai

At the west side of Jan Thiel Baai two small lagoons are located which are in open connection with the ocean. In the smaller of these two, the easternmost one, *Thalassia* was abundant with subordinate *Halimeda. S. orbiculus* was especially prolific in the most easterly part of this lagoon. It was found both on *Thalassia* and *Halimeda* but appeared to prefer *Thalassia.* The bottom consisted mainly of *Halimeda* fragments. Depth was about 50 cm, salinity 34‰ and temperature 29°C.

In the somewhat larger lagoon, *Thalassia, Halimeda* and also *Penicillus* grew side by side. *S. orbiculus* lived on all three plants but on *Penicillus* it was restricted to the stalks. The number of soritids decreased westwards in this lagoon.

Fuikbaai

There is a small beach in Fuikbaai, where the water is quiet and shallow. *Thalassia* grew at a depth of about one metre on a strongly bioturbated sandy bottom. A few soritids were found on it.

Barbara Beach

This touristic beach is situated at the mouth of Spaanse Water. On the sandy bottom at a depth of a few decimetres a *Thalassia* meadow was found and, in spite of the people wading through it, some *S. orbiculus* were present.

Spaanse Water

This is a large bay surrounded by private houses and oil tanks. On two places, sheltered from the trade-wind, small *Thalassia* fields were found at shallow depth on which a few soritids were living.