REPRODUCTION AND LIFE CYCLE OF *Sorites orbiculus* (Forskål), FORAMINIFER

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ABSTRACT

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A sample of megalospheric *Sorites orbiculus* from lagoon Awa di Oostpunt, Curaçao, contains a surprisingly large percentage of adults with brood in the reproduction chambers. Measurements of the initial chambers of a parent do not differ significantly from those of the offspring. This suggests a paratrimorphic life cycle. Two specimens contain undeveloped embryos consisting of protoconch only or of protoconch with incipient flexostyle. It is concluded that protoconch and flexostyle are separate chambers, and that brood formation proceeds with considerable but not perfect synchronism. These protoconchs have thin walls and are perfectly circular in outline; they will be somewhat deformed by the formation of the flexostyle around them after which the wall will be thickened.

The question is raised whether Leutenegger's two plurinucleate specimens with micronuclei could not be diploid megalospheric schizont/gamonts in which case the haploid generation would be reduced to the micronuclei and gametes. The diploidy of such a parent can be tested if the gametes produced by it can fuse *inter se* into viable zygotes.

INTRODUCTION

The material studied forms part of a large mixed sample collected by P. Wagenaar Hummelinck in lagoon Awa di Oostpunt, Curaçao, Netherlands Antilles (see WAGENAAR HUMMELINCK, 1977, p. 51, sample 1666 for location). Date of collection: 22 II 1970 (of importance in case of seasonal cyclicity). Thirty meter from north shore; depth 10-33 cm; *Thalassia* on little sediment upon hard limestone floor; more open arenaceous patches: fields of yellow enteropneusts.

The mixed sample is preserved in formalin. Some small tubes contain larger foraminifera picked from the mixed sample in the Utrecht sorting centre and preserved on alcohol. The sample has been sieved; the coarser fraction contains *Sorites orbiculus, 'Archaias' angulata* and planorbulinids. The finer fraction contains numerous miliolids and some other smaller foraminifera.

Sorites orbiculus is of primary importance for our studies of larger foraminifera: because its ontogeny is characterized by three successive changes; because adults can be recognized by the presence of reproduction chambers; and because one may find specimens with the brood still present in these reproduction chambers.

Normally each individual reproduces only once, after it has attained adult size. We may have found one exception to this (Fig. 1): a specimen (nr. 59) which formed reproduction chambers after the ± 22nd chamber and then continued to grow. Most individuals start making reproduction chambers after the twentieth chamber or thereabouts; but then they reproduce and do not resume growth.

The examination of the sample is still in progress. A first batch of 130 specimens from the tube with picked foraminifera showed: (1) that these are all megalospheric; (2) that a large percentage are adults with brood chambers (the picking has not been aselect); and (3) that a surprisingly large number retained megalospheric embryos in the reproduction chambers.

The number of chambers of all 130 speciments investigated varied between 19 and 29, with an average of 24. The average diameter of the test is 1708 μm. More than half, i.e. 75 specimens, had formed one or more reproduction chambers (maximum number observed: 5), and 34 of these still contained brood! The percentage of specimens with brood

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chambers may perhaps have been greater: these chambers are easily broken off and many individuals may have lost them when the brood was released or afterwards.

The presence of reproduction chambers in the microspheric generation has already been described by earlier authors (see LACROIX, 1941, p. 14). HOFKER (1964, fig. 126; 1976, fig. 131), describing the species under the name *Orbitolites (Amphisorus) hemprichii,* has shown that megalospheric specimens may also have reproduction chambers with megalospheric embryos; such parents, accordingly, are megalospheric schizonts. According to HOFKER (1976, p. 138) such schizonts would be the A1-generation; the A2-generation, recognizable by its smaller chamberlets, would never have reproduction chambers.

Figure 2 shows one of our megalospheric specimens (nr. 14) with the reproduction chambers filled with megalospheric embryos. Figure 3 gives details of the same specimen and figure 4 details of specimen 41a. All embryos pictured consist of protoconch and flexostyle. Each completely fills its brood chamberlet. It is clear that the embryos are released after the flexostyle has been formed and before formation of the next chamber. Figure 5 (detail of figure 4) shows the aperture through which the next chamber will be formed after the release of this embryo. The situation appears to be different in the case of the bi-chambered embryos of microspheric parents pictured by LACROIX (1941, figs. 15, 16) which do not fill the brood chamberlets in which they are situated.

One megalospheric parent (nr. 25b) contains 48 undeveloped embryos which consist only of the protoconch (figure 6). This proves that protoconch and flexostyle are formed separately; they are therefore two separate chambers and not parts of one continuous whole as suggested by KEMNA (1914, p. 9-10) and LACROIX (1940, p. 786-787). It furthermore follows that the process of embryogenesis proceeds with considerable synchronism. This synchronism is not perfect, for 9 out of 48 embryos show an incipient flexostyle. It is noteworthy that these protoconchs are perfectly circular in outline, much more so than the protoconchs of bilocular embryos or those of adult specimens. Their wall, which at this stage is very thin, is apparently still plastic; subsequently a protoconch will be somewhat deformed by the formation of the flexostyle around it, after which its wall will be calcified and thickened. A slightly later development has been observed in specimen 42b (not figured), which contains 7 two-chambered embryos and 27 embryos with protoconchs and an incipient flexostyle in many of them; the outline of these protoconchs is no longer circular but oval.

Table I gives some numerical data.

DISCUSSION

The first problem to be considered is the absence of microspheric specimens in our material. This may be simply due to its scarcity: HOFKER (1976) mentions one microspheric against 190 megalospherics. However, the scarcity in Hofker's material and the lack in ours, could also be due to seasonal cyclicity. Still another possibility could be that the two generations have different ecologic preferences (cf. LEUTENEGGER, 1977a, on *Operculina* and *Heterostegina).*

The life cycle of *Sorites orbiculus* has been supposed to be trimorphic by LACROIX (1941). Lacroix distinguishes a microspheric generation with P: 20-28 μm; and two megalospheric generations, one with P: 20-32 μm, the other with P: 36-43 μm with some outlying measurements at 52, 69, and 84 μm. Lacroix's frequency distributions become intelligible if one assumes his unit of measurement to be approximately 4 micron; intermediate data would then be due to attempts at further precision. The two megalospheric embryos observed by Lacroix in the brood chambers of a

Table I
Numerical data for some of te more numerous broods compared with data for their parents, and for all investigated specimens in which the initial chambers could be measured.
nr = registration number of specimen; P = diameter of protoconch, measured parallel to largest diameter of flexostyle ('deuteroconch'); D = diameter of flexostyle.
The statistics given are: mean, range, standard deviation (unbiased estimate), and coefficient of variation.

nr	P	D	n	$\bar{P}$	range $\bar{P}$	s_P	V_P	$\bar{D}$	range D	s_D	V_D
			adults								
			96	66.0	29.5-108.1	14.9	0.225	146.4	105.7-185.6	18.3	0.125
	parent		broods								
56b	–	–	22	56.0	42.3- 77.8	11.7	0.209	119.4	65.5-152.9	22.6	0.189
41a	74.3	171.4	18	65.0	41.2- 79.2	10.5	0.161	113.2	86.3-139.8	15.2	0.135
14	–	–	24	73.0	46.4-109.2	14.5	0.198	129.8	83.0-161.9	19.1	0.147
18	82.4	163.0	57	75.7	51.3-112.7	11.9	0.158	137.3	100.7-162.2	12.8	0.093
			broods with protoconchs								
25b	95.8	141.7	48	88.8	70.2-105.4	8.4	0.095	–	–	–	–
42b	42.3	105.7	{ 34	92.4	63.9-115.8	11.6	0.126	–	–	–	–
			{ 7	90.8	77.8-103.2	7.6		124.3	85.2-149.9	21.0	

microspheric parent have both P: 28 µm. The group with P: 20-32 µm would therefore be the A1-generation, the other group the A2-generation. Hofker finds additional support for a trimorphic life cycle because of his discovery of the occurrence of megalospheric schizonts. His data are: microspheric generation: P: 16 µm; Al-generation with P: 52-64 µm; A2-generation: P: 70-86 µm with some outlying observations up to 115 µm. Hofker further states: 'Always, when the proloculus of the mother-individual measured about ± 58µ, the embryons had a proloculus with diameter of 86 µ. Obviously the mother-individual belonged to the A1-generation, whereas the embryons were of the A2-generation (see Fig. 161)'. This figure is a frequency distribution with ± 6 µm classes of 172 protoconch diameters. The bimodality which Hofker sees in this frequency distribution is not convincing.

Our measurements give a very different picture: there is no clear difference between the mean diameter of the protoconchs of a brood and that of its parent. It is true that we did not measure the longest diameter of the protoconch but the diameter parallel to the longest diameter of the flexostyle; the protoconch may be somewhat compressed in this direction because of the deformation due to the growth of the flexostyle around it. This accounts for the difference in mean size of the somewhat deformed protoconchs of the bichambered embryos and the greater diameter of the undeformed protoconchs of the undeveloped single-chamber embryos. However, the same method has been applied to bichambered brood and parent, both deformed in the same manner. The conclusion is that our results do not confirm Hofker's statement. On the contrary: if anything, then the initial chambers of a parent tend to be on the large side of the range for the brood; in the two cases where such a comparison can be made for the flexostyle, the parent flexostyle diameter even falls outside the range for the brood. For the protoconch only sample 42b behaves in the manner described by Hofker.

Note furthermore that the standard deviations for the protoconch and for the flexostyle of the 96 adults are not greater than those of a single brood; in the case of bimodality they should be greater. In this connection it is noteworthy that the group of smaller protoconch diameters from the Gulf of Akaba, the A1-generation of Lacroix, appears to be missing in the Caribbean material of Hofker and of us.

Our data are more in agreement with LEUTENEGGER's hypothesis (1977a, b) which assumes a paratrimorphic life cycle for this species. Let us denote the microspheric generation by B, a megalospheric schizont generation by A_s, a megalospheric gamont generation by A_g, and gametes by g, then the normal cycle of alternating generations of foraminifera would be:

$$B - A_g - g - B;$$

a holotrimorphic cycle sensu Hofker would be:

$$B - A_s - A_g - g - B;$$

a paratrimorphic life cycle:

$$B - (o - n)A_s - A_g - g - B.$$

Leutenegger bases his conclusion on the following observations. He observed that the megalospheric specimens studied by him are plurinucleate; he concludes that they must be schizonts and diploid. Two plurinucleate specimens, however, contained different types of nuclei: large intraphasic nuclei, smaller nuclei with electron-dense caryoplasm, and micronuclei which are further differentiated (1977b, p. 21). He considers these micronuclei to be reproductive nuclei formed preparatory to the formation of gametes and accordingly considers these specimens to be haploid gamonts. The presence of vegetative nuclei then is either due to nuclear division directly before gametogenesis, or else these forms would be multinuclear gamonts, which would be contradictory to anything thus far published (LEUTENEGGER, 1977b, p. 30).

The occurrence of megalospheric schizonts and of megalospheric forms with many nuclei has been observed in several species. LE CALVEZ (1950) has been the first to suggest the possibility that such plurinucleate megalospheric schizonts could originate if somehow meiosis were omitted during the schizogony of a microspheric parent; the megalospheric schizont offspring would then be diploid. This is also the hypothesis offered by Leutenegger and appears to be widely accepted (LOEBLICH & TAPPAN, 1964). The assumptions are: that plurinucleate forms are diploid; that gamonts are haploid; and that meiosis takes place prior to the formation of the gamont generation. In all three cycles mentioned, the gamont generation and the gametes would be haploid, all other forms diploid. One would wish to have definite proof of this in every case; there are so many different varieties of life cycle among foraminifera that one should be cautious to extend experience gained from one species to the life cycle of another. Leutenegger's cytologic observations are of great interest, but they are to be supplemented with extensive fieldwork and culture studies.

With regard to Leutenegger's two specimens with different types of nuclei which he considers to be haploid gamonts on the verge of producing gametes, it occurred to us that perhaps these could be megalospheric schizont/gamonts which could generate megalospheric embryos, for instance around the electron-dense nuclei, and gametes from the micronuclei. This would resolve Leutenegger's dilemma. The megalospheric schizont/gamont parent and the megalospheric embryos produced could be diploid, the micronuclei haploid. Meiosis would take place prior to the formation of the micronuclei, and gametes could segregate meiotically into + and - gametes, permitting fusion into viable zygotes. In any case, should a plurinucleate megalospheric parent produce gametes, and should these gametes be able to copulate and to produce viable zygotes, then one would have reason to suppose that the parent was diploid. According to the supposition offered there would not be a haploid A_g generation; the haploid part of the cycle would be reduced to the micronuclei and the gametes. The life cycle then would be:

$$B - (o - n)A_s - A_{sg} - g - B.$$

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PLATE I

Sorites orbiculus from lagoon Awa di Oostpunt, Curaçao, Netherlands Antilles.

Fig. 1
Specimen nr. 59, 40x. Specimen which formed some 3 to 4 reproduction chambers after the ± 22d chamber, then was damaged and subsequently resumed growth. Whether it was able to reproduce before being damaged cannot be said.

Fig. 2
Specimen nr. 14, 40x. Megalospheric parent with up to 4 reproduction chambers still containing ± 50 two-chambered embryos. Size of the initial chambers of the parent similar to that of the brood. The specimen was damaged after the ± 18th chamber.

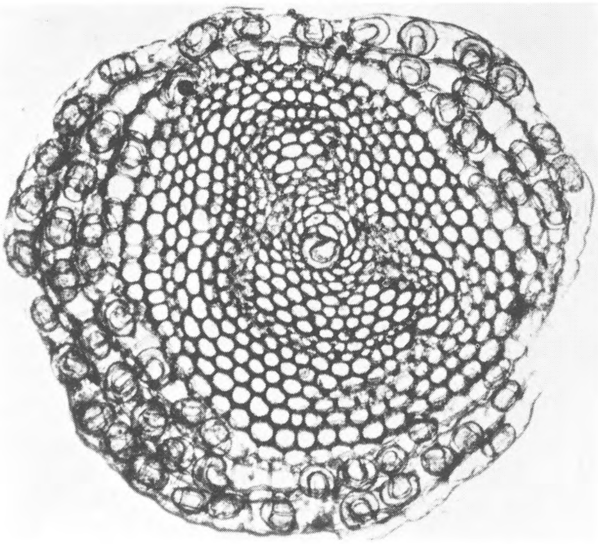
Fig. 3
Detail of figure 2, 150x. Two-chambered embryos completely filling chamberlets of the reproduction chambers.

Fig. 4
Specimen nr. 41a, 135x. Detail of reproduction chambers with two-chambered embryos. The parent still contained ± 43 embryos, but may have produced up to ± 160 embryos in all.

Fig. 5
Detail of figure 4, 410x. Two-chambered embryo; note aperture of flexostyle through which next chamber will be formed after the release of this embryo from parent.

Fig. 6
Specimen nr. 25b, 135x. Four reproduction chambers with thin-walled undeveloped embryos, consisting of protoconch only. Note circular outline; compare shape and wall thickness with those of the two-chambered embryos of figure 4 (same magnification).

1



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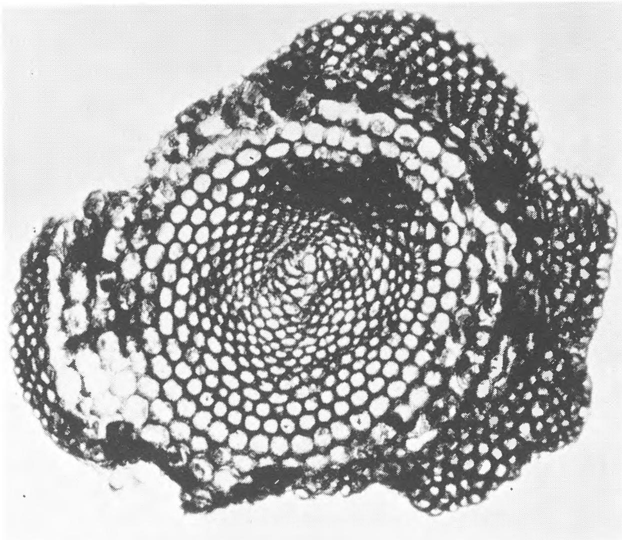

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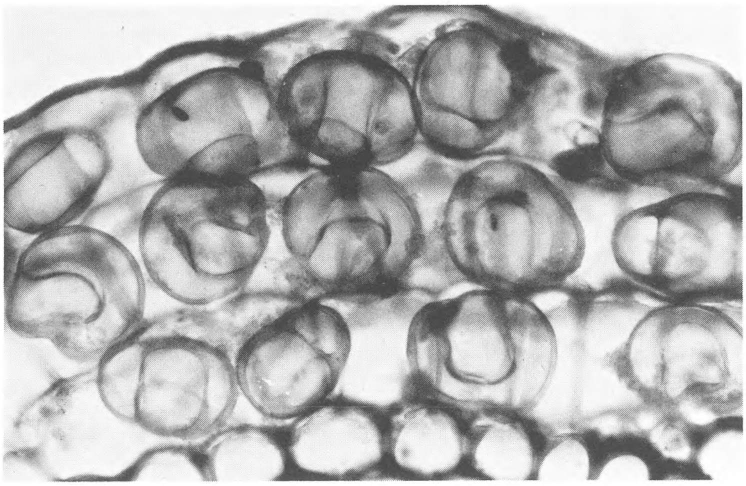

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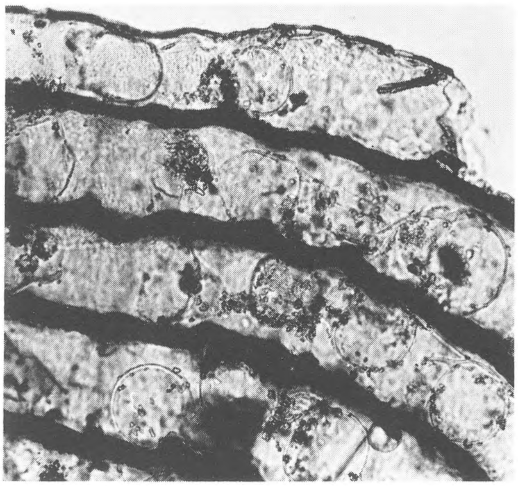

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