Depth adaptation in Amphistegina: change in lamellar thickness

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Using specimens of *Amphistegina lessonii, A. lobifera*, and *A. papillosa* from the Gulf of Elat, changes in shell shape with depth observed in previous studies can be quantitatively accounted for by a corresponding trend in thickness of secondary laminae.

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Introduction

In recent years, several authors have published observations regarding changes in test shape with depth in symbiont-bearing foraminifera (e.g. Hottinger and Dreher, 1974; Larsen, 1976; Hottinger, 1977; Larsen and Drooger, 1977). Using *Amphistegina* from the Gulf of Elat, Larsen and Drooger (op.cit.) demonstrated that the relationship between shell diameter and shell thickness changes through ontogeny at a given depth while for each size class the relationship shows a morphocline in populations from different depths. In Elat, the hydrographic conditions are unique since virtually no thermocline nor other cline exists in the water body (Klinker et al 1977); the only physical factor changing with depth is the amount and composition of light. This led Larsen (1976) to suggest that the increase in surface to volume with increasing depth observed in *Amphistegina* shells may be causally linked to the light gradient. In laboratory culture experiments, Hallock (in prep) found that *Amphistegina* grown at reduced light levels developed an increase in surface to volume ratio like that observed in nature by Larsen, indicating that the intraspecific variation in test shape is not genetic.

Hottinger (1977) reported on morphologic modifications in nummulitid shells with depth. He pointed out that in shallower environments, the shells are involute and thick, whereas they become evolute and thin in deeper waters. He further noted that there must be a relationship also to thickness of the secondary lamellae reflected by the solidity of the shell.

The above observations suggest that changes in surface to volume have structural implications within the foraminiferal shell. The purpose of this study was to determine if the depth associated trends in test shape are the result of corresponding trends in the thickness of the lamellae from which the test is constructed.

Materials and methods

Material used in this study originated from the same set of samples studied by Larsen (1976) and Larsen and Drooger (1977). Specimens to be examined for lamellarity were prepared according to the techniques already published in several articles (e.g. Hansen and Lykke-Andersen, 1976). The sections were studied and photographed in Cambridge MK.IIa and 180 scanning electron microscopes housed in the Geological Institute of the University of Copenhagen. They were coated with 200Å gold using a Polaron sputter device. Overlapping mosaics of enlargements of approximately 2000x were prepared of the areas of interest. Thus, thicknesses of individual secondary lamellae could be measured to the nearest 0.25 µm. Secondary lamellae were measured in the umbilical regions of both the spiral and umbilical sides in vertical sections through the proloculus.

In preparations of the kind used in this study,

the boundaries between secondary lamellae are generally distinct. However, in a few cases, measurements were difficult due to the existence of primary lamination (*sensu* Hansen et al 1969). The primary laminae are not continuous and cannot be followed. Therefore, when lamels were measured, the boundaries were traced not only on the high magnification photographs, but also on corresponding lower magnification pictures whereby primary laminae were identified.

Observations

The structure of the group of foraminifera usually contained in the family Asterigerinidae was described in some detail by Hansen and Reiss (1972). They demonstrated that members of this family basically follow an identical scheme regarding both morphology and structure. All members were found to construct their chambers of two layers of calcite separated by an organic layer. With the addition of a new chamber, the outer calcareous layer forms a continuous sheet of material covering all exposed ontogenetically younger shell parts. In addition, the new chamber is subdivided by a partitional wall constructed of the double inner calcareous layer with an additional inpush termed the »gutter« constructed of the inner as well as the outer calcareous layer separated by the organic median layer.

The genus *Amphistegina* is separated from the genus *Asterigerina* and associated forms by the partly involute arrangement of the chambers on the spiral side. With the addition of new chambers and thereby deposition of secondary lamellae, the maximum number of secondary lamellae deposited on any chamber wall in the final whorl

Table 1.

Species	Depth (m)	$\bar{D}$ (µm)	$\bar{D}/T$	Number chambers	Lamellar thickness (µm) spiral X	spiral SD	umbilical X	umbilical SD
A. lobifera	5	1000	1.57	29	7.3	5.5	10.5	7.5
		890	1.63	22	7.6	6.1	9.4	7.5
		1050	1.79	24	7.6	3.9	11.5	4.4
	45	1100	1.88	37	4.9	3.0	9.3	5.0
		1250	1.96	34	6.0	2.6	9.0	4.8
		1244	2.08	29	5.8	2.5	7.8	4.0
A. lessonii	5	1165	1.99	36	4.8	2.1	7.9	2.8
		1148	2.07	30	6.1	3.6	9.1	5.3
		1174	1.98	40	4.2	1.8	8.4	3.8
	38	1056	2.29	36	4.2	2.2	6.7	3.6
		869	2.17	30	4.7	2.5	6.9	3.8
		1044	2.23	33	4.5	2.2	7.0	3.9
	64	900	2.24	32	3.3	1.9	6.4	3.8
		929	2.42	29	3.8	2.2	7.0	3.9
		850	2.41	24	4.5	1.4	5.7	3.0
A. papillosa	45	958	2.56	48	3.3	1.8	3.3	1.8
		983	2.60	42	2.7	1.6	3.6	1.9
		1100	2.27	49	3.6	1.7	3.8	2.1
	70	980	2.87	44	3.2	1.5	3.3	1.8
		919	3.12	44	1.9	1.1	3.0	0.8
		960	2.87	37	2.3	1.0	2.9	1.2
	90	939	3.65	49	2.1	1.1	2.3	1.0
		904	4.37	40	1.3	0.6	2.0	1.0
		905	3.70	43	1.9	1.1	2.4	1.1
A. bicirculata	45	1350	3.41	33	3.4	1.6	4.7	2.2
		1140	2.78	32	3.9	2.5	5.6	2.7
		1357	2.84	39	4.7	2.2	5.6	2.3

Table 1. Diameter ($\bar{D}$), shape index ($\bar{D}/T$), number of chambers and mean lamellar thickness for four species of Amphistegina from the Gulf of Elat.

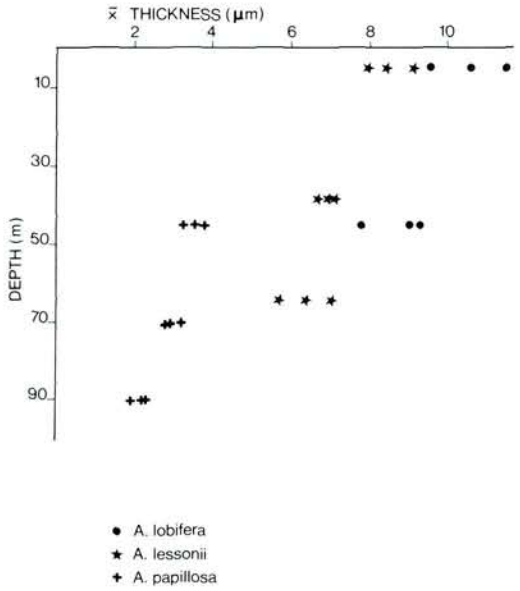

Figure 1. Mean lamellar thickness of the umbilical side (umbilical region) versus depth for three species of Amphistegina.

corresponds to the number of chambers exposed. By contrast, the umbilical regions receive secondary lamellae from all chambers deposited through ontogeny since coiling is partially evolute. Accordingly, since test shape as defined in previous studies is expressed as shell diameter relative to shell thickness as measured from one umbilicus to the other, any constant change in lamel thickness between individuals will have a cumulative effect on the measurements carried out in the umbilical region, but to a lesser degree in the diameter.

Since the techniques applied are rather time consuming, representative specimens were selected. Larsen and Drooger (1977) tabulated size-specific shape indices (ratio of diameter/thickness) with depth for a series of *Amphistegina* spp. from Elat. For the present study individuals of approximately median shape index from four depths were selected from the material studied by Larsen and Drooger. For each species, three specimens were picked for each depth, all with diameters in the range 850–1357 µm (table 1).

The mean values of lamellar thickness from the umbilical regions of the umbilical and spiral sides respectively are shown in fig. 1 and 2. In the sections thickness of both the primary chamber walls and the secondary lamellae increased during ontogeny (figs. 3, 4). In addition, some variation occurred in the thickness of single laminae, hence, average lamel thickness is recorded.

Discussion

From the results presented above, it is evident that all three species investigated show a tenden-

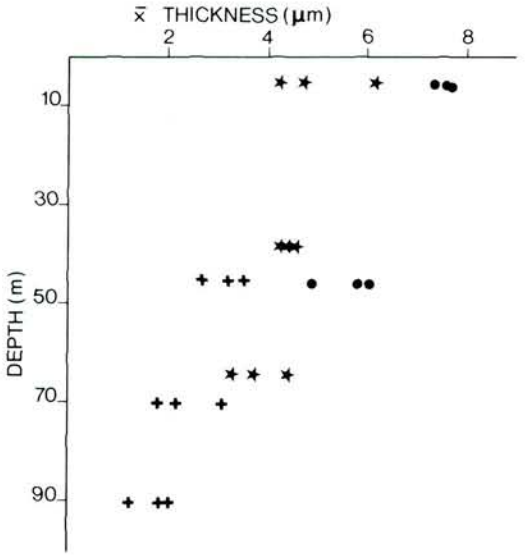

Figure 2. Mean lamellar thickness of the spiral side (umbilical region) versus depth for three species of Amphistegina. Legend like in Fig. 1.

Figure 3. Polished and etched vertical section through the proloculus of A. lessonii. 70 x.

cy towards reduction in thickness of the secondary laminae with depth. The magnitude of the thickness reduction is quantitatively sufficient to account for the changes in test shape observed by Larsen and Drooger (1977).

And, just as the phenotypic variability demonstrates a change in test shape within the single species, a general genotypic trend with depth is also evident in the species of *Amphistegina* studied (fig. 5). This interspecific trend with depth is evident both with regard to lamellar thickness and to the resultant test shape (surface to volume relationship).

Hallock (in prep) found that, on a western Pacific reef, *A. lessonii* produced about 0.2 mg carbonate per individual while *A. lobifera* produced about 0.5 mg per individual. Both species grew to maturity in approximately the same length of time, though *A. lobifera* attained larger overall size, both shell diameter and shell thickness. The differences in both size and carbonate productivity per individual are easily understood in light of the lamellar thickness differences between the two species.

Also using *Amphistegina* from the Gulf of Elat, Hansen and Buchardt (1977) and Buchardt and Hansen (1977) demonstrated a gradual reduction in ^{18}O depletion with depth. This depletion was suggested to be intimately connected with the decreasing amounts of light and thereby smaller amounts of fractionation by symbiont activity agreeing well with a recent study by Erez (1978). These authors also showed that at the lower limits of existence of symbiont-bearing Amphisterina (120 m in Elat), the deeper dwelling species approach the ^{18}O depletion values as found in non-symbiont carrying *Bolivina* spp.

It seems that the shallow dwelling forms (*A. lobifera* and *A. lessonii*) have higher requirements for symbiont activity than the two deeper dwelling forms (*A. papillosa* and *A. bicirculata*). The two latter forms apparently can exist at very low symbiont activity levels near their maximum depths of occurrence since, in accordance with the oxygen isotope values, their skeletal carbonate production is almost unaffected by symbiotic fractionation.

Since carbonate production is enhanced by

Figure 4. Detail of Fig. 3 showing the secondary lamellae of the spiral side. The pitted lines represent lamel boundaries. 1265 x.

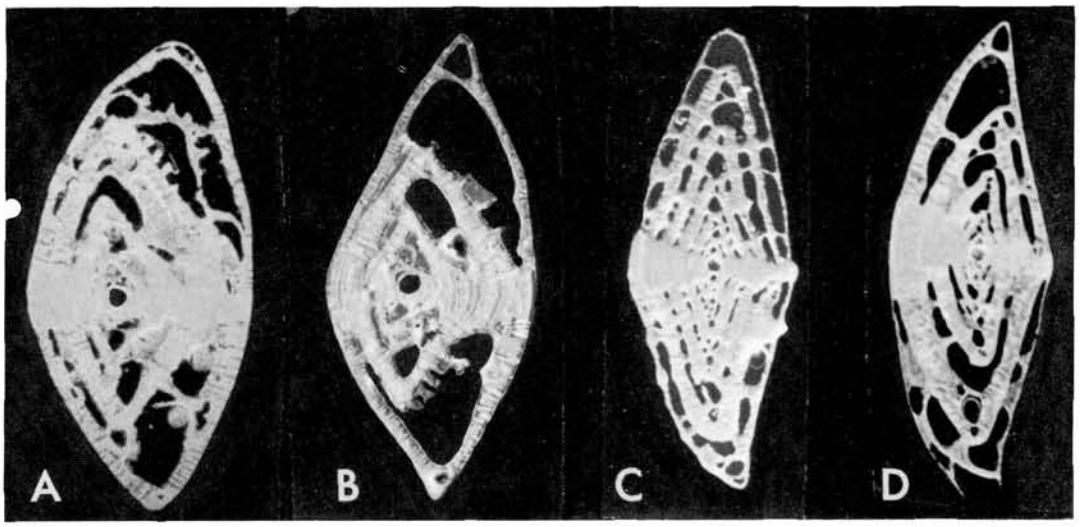

Figure 5. Vertical sections of A. lobifera (A), 48 x x; A. lessonii (B), 53 x; A. papillosa (C), 63 x; A. bicirculata (D), 44 x.

symbiotic activity in a number of marine invertebrates (Pearse and Muscatine, 1971), it is not surprising that decreased symbiont activity in *Amphistegina* with increased depth as demonstrated by the oxygen isotope values is at the same time manifested in decreased thickness of the lamellae and thereby in the reduced amount of carbonate secreted at each chamber-forming instar.

Variation in lamellar thickness as related to depth of occurrence is a potential tool for paleobathymetric interpretation. It would appear to be a more refined indicator of relative depth of habitat within the photic zone than gross morphology *per se*.

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H. Egelund drew the figures.

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Dansk Sammendrag

Ændringer i skalform med dybde hos tre arter af foraminiferslægten *Amphistegina* fra Elat Bugten, Israel kan kvantitativt forklares ved en tilsvarende udvikling af de sekundære lameller i skallerne.

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