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Ecophenotypic variation of the larger foraminifer *Orbitoides apiculata* from the Maastrichtian stratotype

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Abstract

Morphometric analysis of the larger foraminifer *Orbitoides apiculata* Schlumberger from the type Maastrichtian shows that the general evolutionary trend within the genus continued in Maastrichtian times, but that the local evolutionary pattern is not gradual and unidirectional. Specimens from the lower part of the type section on the average have smaller embryons and fewer epi-auxiliary chambers than those from the upper part of the section. Besides, a new phenomenon can be observed: in the latest Maastrichtian the species had developed an asymmetric test, with one thin, superficial lateral layer of the ordinary *Orbitoides* type but with the other layer much thicker and lacking the usual subdivision into lateral chamberlets.

The pattern, however, is not a strictly evolutionary one, but seems to be related to the prevailing environmental conditions. The more advanced populations are only found in debris layers overlying hardgrounds. In the intervals between the hardgrounds, *O. apiculata* is much less abundant and, moreover, has the same morphology as the older, more primitive populations.

A comparison with *O. apiculata* from deposits in southern France, sometimes considered to be slightly younger than the type Maastrichtian, suggests that the development within the Maastrichtian stratotype may be the result of geographic separation.

Introduction

The larger foraminiferal genus *Orbitoides* occurred in the shallow waters bordering the Tethys Ocean from the Late Santonian to the end of the Maastrichtian. During this period it evolved (Fig. 1) from a species with a small embryon with 2 to 4 chambers all within the equatorial plane, without prominent lateral layers and with primary epi-auxiliary chambers only, to a fairly large species (diameter up to almost 2 cm), with the proto- and deuteroconch lying above each other, with a large embryon (up to 1.2 mm), with many additional epi-auxiliary chambers and with pronounced lateral layers (Van Hinte 1965, 1966a, 1966b, 1968; Van Gorsel 1978; Baumfalk & Fortuin 1981; Drooger 1984; Baumfalk & Van Hinte 1985; Drooger & De Klerk 1985; Baumfalk, in press).

Within the frame of a biometric study of the genus *Orbitoides* the type locality of *O. apiculata* Schlumberger 1901 was studied. Our aim was to test wether the evolutionary trend observed within the genus as a whole on a scale of some 18 million years, could be observed also on the much finer scale (less then 1 million years) within the species *O. apiculata* at its type locality. It had already been demonstrated by Baumfalk & Fortuin (1981), Drooger (1984), Drooger & De Klerk (1985) and by

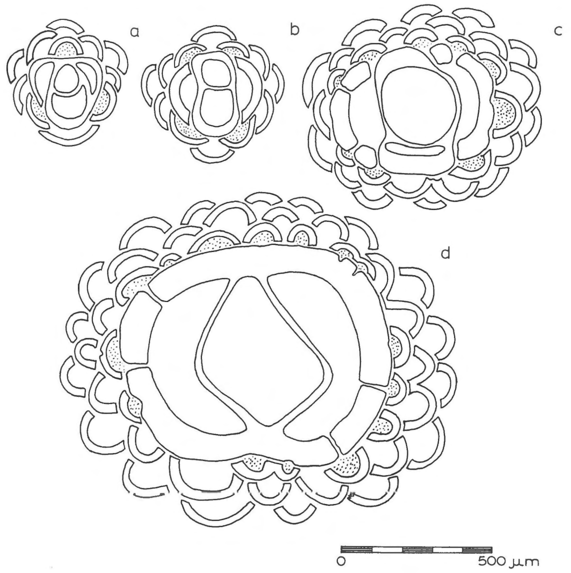

Fig. 1. Line drawings (after scanning electron micrographs) of juvenaria of several members of the *Orbitoides* lineage, showing the large scale evolutionary trend towards a larger embryon, a greater number of epi-auxiliary chambers (shaded) and a shift in the proto/deuteroconch position. (a) *O. douvillei*, Late Santonian – Early Campanian, Belvès, France. (b) *O. media media*, Late Campanian, Aubeterre, France. (c) *O. media 'megaloformis'*, Late Campanian, Aubeterre, France. (c) *O. apiculata*, Maastricht, The Netherlands.

Baumfalk (in press) that the evolution of its predecessor *O. media* (d'Archiac 1837), did not take place gradually, but that the transition of the older type, *O. media media* into the more advanced *O. media 'megaloformis'* occurred in a relatively short period of time. It seemed interesting to compare the pattern observed in the late Campanian *O. media* with the pattern – if any – of late Maastrichtian *O. apiculata.*

The samples from the Maastrichtian type section were collected by Frans Willemsen (deceased in 1982). He left a collection of equatorial thin sections from these samples and of specimens from samples that where collected either in the same quarry or in the direct vicinity of the type locality. Willemsen also left notes concerning samples and his measurements of the sectioned material.

Most samples are from the Maastrichtian type locality the ENCI-quarry in the St. Pietersberg, which is also the type locality of Schlumberger's *O. apiculata.* Another section studied is located in the Blom quarry at Berg, also in the vicinity of Maastricht. Additional material is from single samples collected by others. Most of these are from the Mc/Md boundary, a horizon which is easily identified within the region. The sampling localities are shown in Fig. 2.

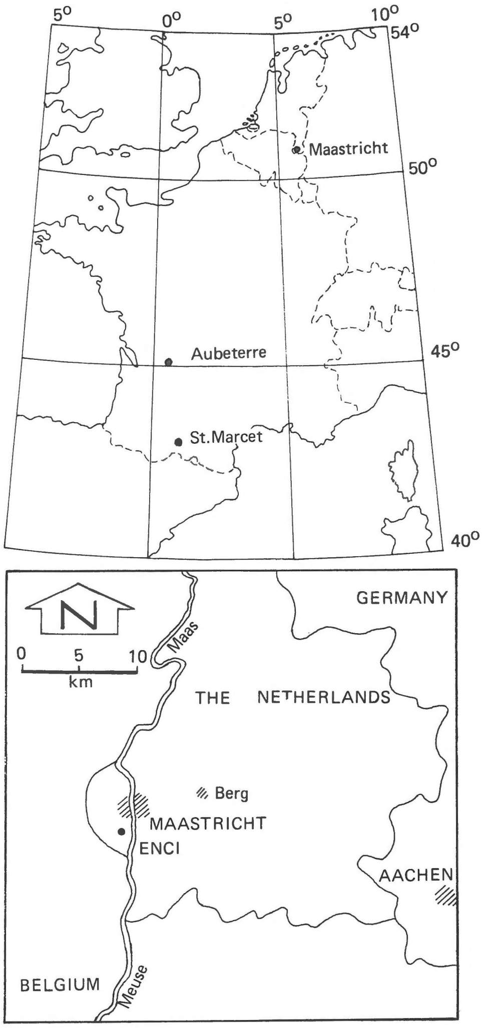

Fig. 2. Locality map.

The sediments of the Upper Maastrichtian at the type locality consist of shallow water deposits (0–40 m (Robaszynski et al. 1985)): white to yellowish coarse bioclastic limestones, with thin layers or lenses of even coarser skeletal debris containing many bryozoan, echinoid and bivalve fragments. The studied part of the Upper Maastrichtian is classically subdivided into the Mc and Md members

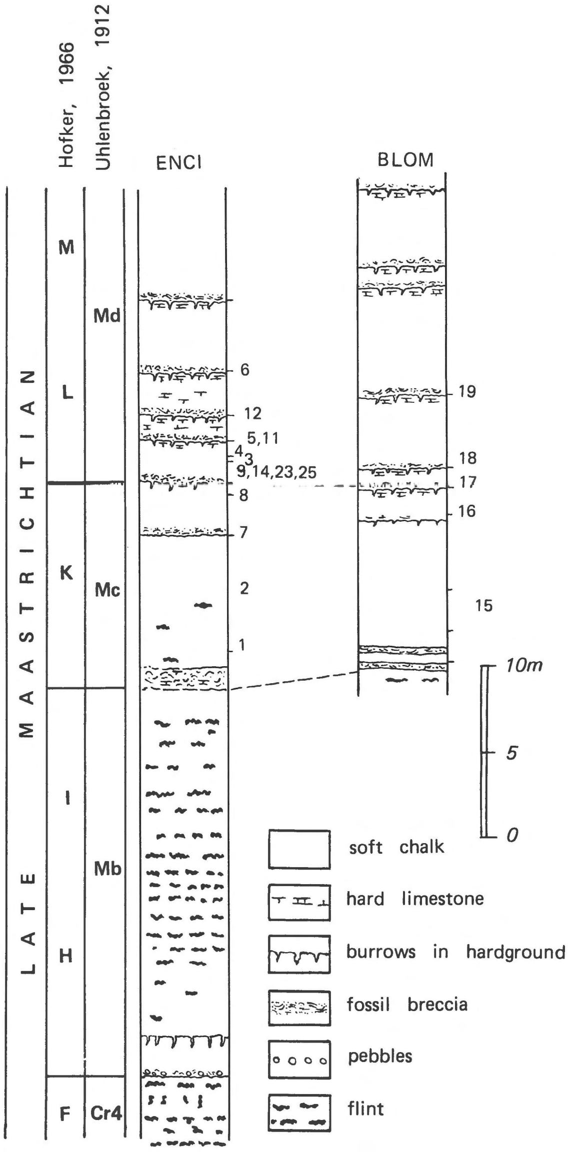

Fig. 3. Schematic stratigraphic columns of both sections in the type Maastrichtian area, with sample positions and zonation of the type Maastrichtian. Second column: foraminiferal zones after Hofker (1966). Third column: subdivisions after Uhlenbroek (1912).

(Uhlenbroek 1905, 1912). The reader is referred to Felder (1975a, b) and Robaszynski et al. (1985) for a more extensive lithological description. The Md member contains several burrowed hardgrounds that are overlain by some decimetres of coarse skeletal debris. The first such hardground (the so-called Caster horizon) marks the transition between the Mc and Md member (Fig. 3).

Materials and methods

Most of the present material consists of equatorial thin sections. However, for some samples (one from the Mc and one from the Md) we also used the method applied by Baumfalk et al. (1982) in the study of *O. media*, in which the specimens are cracked open by means of tweezers. This has the advantage of being much faster and leaves two split halves that can be studied in three dimensions under the scanning electron microscope. The disadvantage of the method is that the fine structure of the test walls can not be observed and, in the case of *O. apiculata*, that the number of epi-auxiliary chambers – which is much greater than in *O. media* – is established with slightly less accuracy that is the case in thin sections.

Apart from the horizontal (equatorial) sections and cracked specimens, some tens of sagittal sections were available (both as thin sections and as centrally broken specimens).

Because of the paucity of *O. apiculata* which is abundant only in a limited number of debris layers, not all samples were treated the same. Most samples were picked for orbitoids under the binocular microscope. Samples 2 and 15 are the collection of all specimens found in a rather large interval with rare *Orbitoides*. Samples were split when *Orbitoides* was very abundant. The stratigraphic position of the samples is indicated in Fig. 3.

The variables measured (smallest and largest outer and inner diameter of the embryon) and counted (number of epi-auxiliary chambers) are indicated in Fig. 4, which also shows some of the variations in size and shape of the embryon. In the case of sagittal sections the thickness of the two lateral layers above and below the embryon and the dimensions of the embryon itself were measured. We also measured the outer diameter of a large number of specimens from two samples with abundant orbitoids.

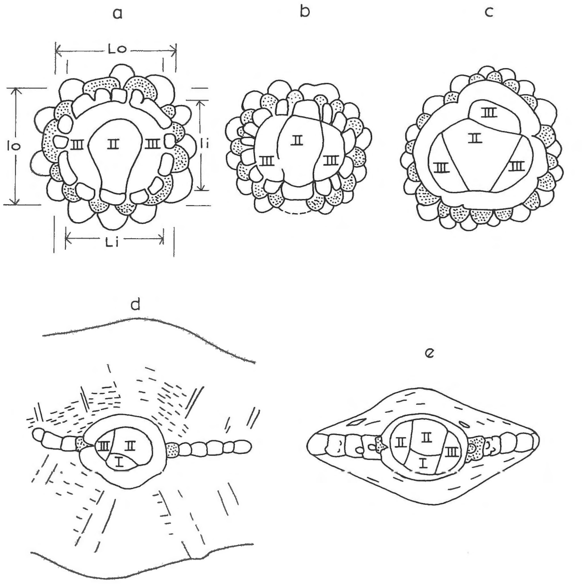

Fig. 4. Camera lucida drawings of sectioned specimens of *O. apiculata.* (a–c) Equatorial sections showing some of the variation in the arrangement of the deutero- (II) and tritoconchs (III). The deuteroconch may touch the embryon wall at one or more spots. The tritoconchs are usually fused. (d–e): sagittal sections. The deuteroconch may be situated partially below the equatorial plane, which may result in a sagittal view as in (d). Usually it lies entirely above the protoconch (I). (a) sample 15, (b) sample 18, (c) sample 17; × 8.5. (d–e) sample 13, × 12.5.

Morphology

Outer morphology

Orbitoides apiculata is lenticular with a more or less symmetric test. One side is usually apiculate, i.e. the slight conical, sometimes slightly concave surface of the test has a central knob, which is provided with radial striae. The surface of the test is covered by fine pustules, which are often arranged in a vermiform pattern of tiny ridges. These ridges are radially arranged, especially near the periphery of the test.

The other side of the test is slightly convex to conical, sometimes almost flat or even concave and in larger specimens usually not clearly apiculate (this in contrast to the juvenile specimens which generally have knobs on both sides). The surface of this side of the test is provided with relatively coarse pustules, arranged in a pattern similar to that on the other side.

Inner morphology

Only the megalospheric generation of *O. apiculata* has been studied in detail. Microspheric specimens were too rare (less than 5%) for a statistical study. The few microspheric specimens that have been examined, however, suggest that the biserial stage may sometimes be shorter than in *O. media.* While in *O. media* the budding number of the progressive chamber is usually around 8, in *O. apiculata* it is around 7, but progressive chambers of a budding stage as low as 3 may be found (Fig. 6F).

In large specimens the equatorial chambers of *O. apiculata* are frequently arranged in concentric zones, similar to growth rings. Within one zone the chambers are of the same size and shape. Zones with small chambers alternate with zones in which the chambers may be much smaller (Fig. 5A). At the periphery there may be a zone with considerably higher and wider chambers interconnected by

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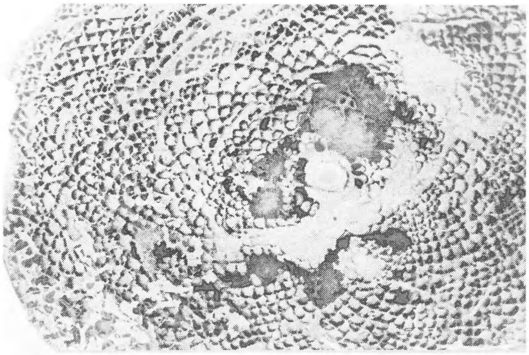
Fig. 5. Scanning electron micrographs of *Orbitoides apiculata*, Late Maastrichtian, Maastricht, The Netherlands. A: Artificial cast of median layer, showing alternation of zones with smaller and zones with larger equatorial chambers. This alternation may reflect seasonal growth. In zones with large equatorial chambers both basal and diagonal stolons occur. Sample 13, × 8. B–F: Embryonic region in equatorial view. Figures 5C and 5D, the apical and abapical part of the same specimen, demonstrate that one of the tritoconchs is partially subdivided by the deuteroconch wall. A thin wall, sometimes partially dissolved, separates proto- and deuteroconch. In the specimens of fig. 5B and 5E the deuteroconch lies completely above the protoconch, whereas in the specimens of figs. 5C–D and 5F, the deuteroconch partially extends below the equatorial plane. The tritoconchs of the specimen of fig. 5E are fused. B: sample 13, × 55. C, D: sample 13, × 50. E: sample 8, × 55. F: sample 13, × 60. G: Sagittally broken specimen. It is more or less symmetric with regard to the median layer, as usual in non-hardground samples. Note the sudden increase in size of the equatorial chambers. Sample 8, × 13. H: Sagittally broken specimen. It is highly asymmetrical, with a thin apical layer of open lateral chamberlets and a thick, compact abapical lateral layer, as usual in the hardground samples in Md. Note the presence of *Talpinella* spec. in the median layer (arrow). Sample 13, × 13.



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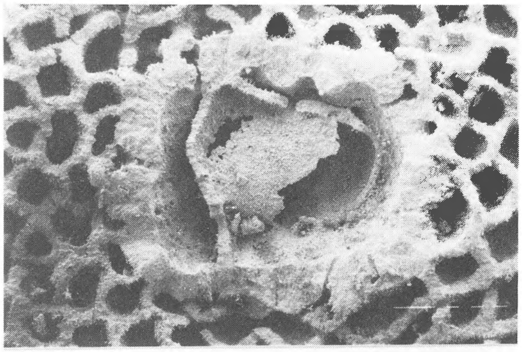

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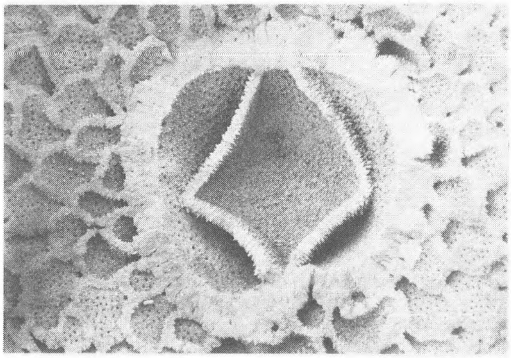

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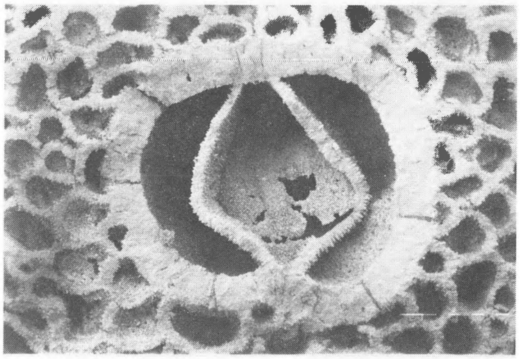

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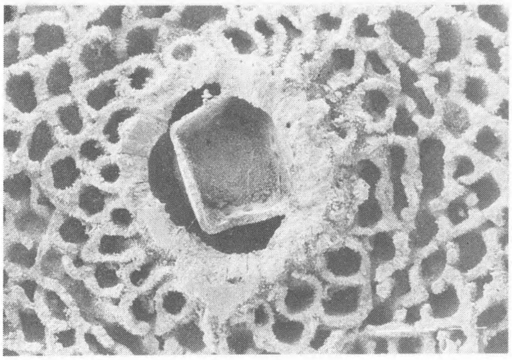

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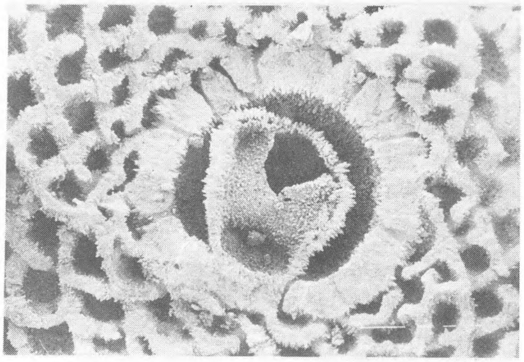

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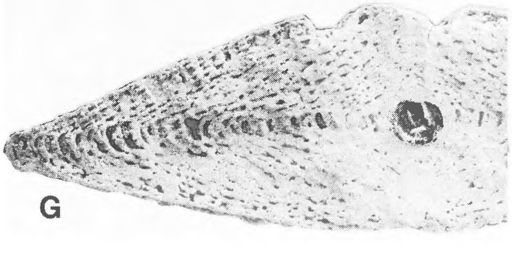

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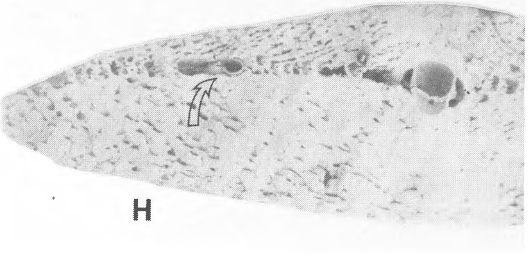

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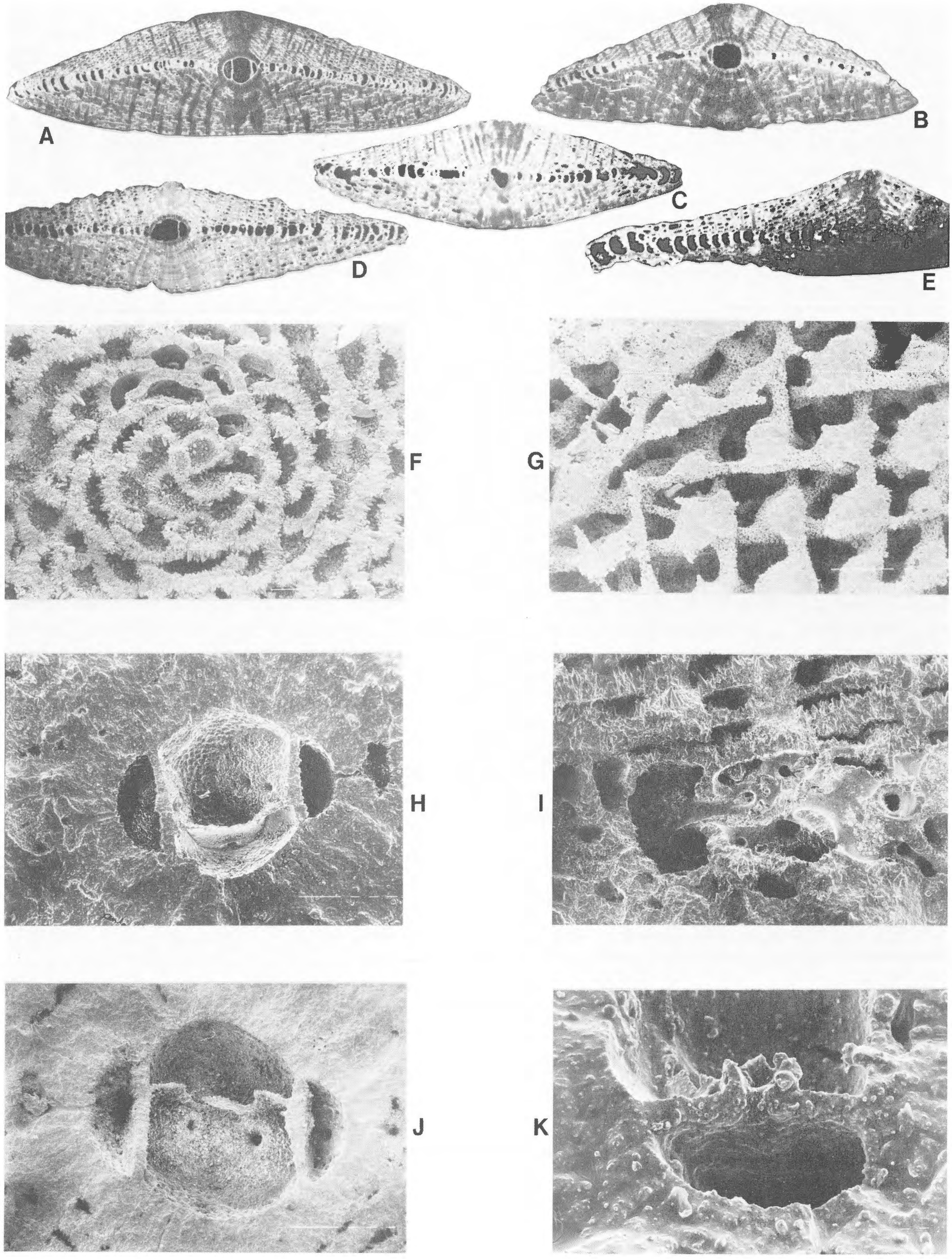
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Fig. 6. Orbitoides apiculata, Late Maastrichtian, Maastricht, The Netherlands. A–E: micrographs of sagittal thin sections. A–B: Asymmetric specimens from hardground sample, showing growth bands in the massive, abapical lateral layers. Sample 13, × 10. C–D: Specimens from non-hardground sample. The abapical lateral layer is thinner and less massive than in the specimens of figs. 6A and B. Note the subdivision of large equatorial chambers at the periphery in 6C. Sample 8, × 10. E: Detail of microspheric specimen with extremely large peripheral equatorial chambers. Sample 8, × 10. F–K: Scanning electron micrographs. F: Initial portion of microspheric specimen. Progressive chamber belongs to budding stage 3. Sample 13, × 90. G: Artificial cast of stolon system in median layer. Both basal and diagonal stolons are present. Stolon levels in one direction are continuous for only a few buddings. Sample 13, × 105. H: Oblique view of embryon of sagittally broken specimen, showing excentrical stolon between proto- and deuteroconch and some stolons between the deuteroconch and tritoconchs. Sample 13, × 75. I: Detail of stolons between equatorial chambers (sagittally broken specimen). The central main stolon is a smooth, 'streamlined' feature provided with a clear collar. Above and below it small additional stolons are present. Sample 13, × 110. J: Other half of same specimen as in fig. 6H. with two more stolons to the tritoconchs. Sample 13, × 80. K: Detail of stolon between deutero- and tritoconch with an inwardly directed collar (sagittally broken specimen). Sample 13, × 150.

a large number of stolons. If present, the transition from the zones with ordinary equatorial chambers to the peripheral zone is often quite abrupt. Sometimes the chambers in this zone are situated partially above each other, forming a multiple equatorial layer comparable to the chamber arrangement in *Omphalocyclus* (Fig. 5G, 6C). The zones in the equatorial layer correspond to what seem to be growth rings in the lateral layers (Fig. 6A and B).

The equatorial chambers show at their base (where they are attached to the previous chambers), or slightly above it, a series of stolons. The number of these stolons is associated with the height of the chambers.

Van Gorsel (1975, 1978) noted that in *L. socialis* the type of stolons that connect chambers of the same, previous and subsequent budding stage, varies with distance from the centre. Near the embryon chamber a simple four stolon system with basal stolons only is observed. Further toward the periphery the basal stolons shift their position from the suture to slightly above the base, whereas chambers near the periphery have both basal and diagonal stolons.

The stolon system in *O. apiculata* is directly comparable to that of *Lepidorbitoides socialis.* Both a simple four stolon system and a six stolon system with diagonal and basal stolons may occur in the same specimen. Which system is present at a certain budding stage, does not so much depend, however, on the distance from the centre, but rather on the average size of the equatorial chambers in a zone. In a series of rings with large chambers basal and diagonal stolons can be observed (Fig. 6G). As in *L. socialis* (Van Gorsel 1975) the two diagonal stolons leading to a chamber occupy different levels: stolons of one diagonal direction run above stolons of the other direction. In contrast to the *Lepidorbitoides* specimens figured by Van Gorsel (1975), the system is less regular, and the two stolon directions may switch levels after a few buddings.

The main stolons are surrounded by an outwardly pointing collar, which becomes very pronounced in the equatorial chambers of the peripheral zone of large specimens. Within a chamber, the outgoing stolon appears as a smooth, 'streamlined', raised area of the chamber wall (Fig. 6I). The number of diagonal stolons in one chamber again varies with the size of the chambers. In the very high chambers in the peripheral zone many stolons may occur above each other. In the central zones there are usually 1–3 stolons above each other, only one of which is provided with a clear collar.

In principle, the embryonal apparatus of the macrospheric specimens consists of 4 chambers. The protoconch is approximately hemispherical and situated below the equatorial plane. It is therefore seldom visible in equatorial thin section. An excentrically situated stolon forms the connection between the proto- and the deuteroconch (Fig. 6H). The stolon is provided with a collar. The very thin wall between proto- and deuteroconch is usually flat or somewhat depressed in the direction of the protoconch. Part of the deuteroconch may lie beside the protoconch (as in more advanced specimens of *O. media*), although in most specimens it is situated completely above the protoconch (Fig. 5B-F). Proximally, i.e. near the aperture of the protoconch, the deuteroconch is attached to the embryonal wall at the level of the equatorial layer. To the distal side in the equatorial plane, the deuteroconch may lie free from the embryonal wall or it may make contact with it at one or more spots. The deuteroconch is usually angular in horizontal section. A number of stolons just above the suture with the protoconch connect the deuteroconch with the tritoconchs. They are surrounded by a low collar (Fig. 6H and K). The occurrence of more than two stolons in the deuteroconch, is a phenomenon not yet observed in *O. media* and may be comparable with the introduction of extra stolons in the tritoconchs of *O. media 'megaloformis'*. In most specimens the tritoconchs appear to be fused, forming one large chamber partially surrounding the proto/deuteroconch constellation. This is true even when the deuteroconch is in contact with the embryon wall at more then one site. This is in sharp contrast to the tritoconchs in *O. media*, where the tritoconchs are always completely separated from each other by the proto- and deuteroconch.

Statistical results

The sample means and standard deviations of the measured and counted variables in equatorial section are summarized in Table I. In Table II the correlation coefficients between the variables are presented. Of course, the size variables are strongly correlated, but also the number of epiauxiliary chambers appears to be directly proportional with embryon size, a fact also observed in more advanced specimens of *O. media* (Baumfalk in press) and in *Lepidorbitoides minor* and *L. socialis* (Van Gorsel 1974). The development of a greater number of epauxiliary chambers and trend toward a larger embryon cannot be independent, as was postulated by Van Gorsel (1975) in the case of *Lepidorbitoides*. This is demonstrated by the strong correlation of the two variables, but especially by the fact that the relapse observed in two Md

Table I. sample means and standard deviations of measured variables

smp	n	$\overline{\mathrm{Lo}}$	σLo	$\overline{\mathrm{lo}}$	σlo	$\overline{\mathrm{Li}}$	σLi	$\overline{\mathrm{li}}$	σli	$\overline{\mathrm{E}}$	σE
1	17	523.6	65.3	409.1	41.0	470-1	53.0	346.2	34.3	13.2	2.1
2	14	500.4	87.0	386.9	64.6	440.6	84.6	315.7	75.5	12.0	2.6
3	18	511.3	88.5	412.2	70.5	437.7	82.0	326.3	64.2	12.8	2.7
4	33	549.6	115.1	436.3	87.3	475.3	100.2	353.4	81.3	13.0	2.8
5	47	705.5	123.0	553.6	95.7	614.0	92.2	452.8	77.6	14.9	2.6
6	9	634.4	98.4	511.1	83.4	565.0	102.4	439.7	93.8	15.1	2.8
7	16	557.4	119.9	416.2	81.0	503.6	119.9	357.9	94.0	12.3	2.7
8	38	542.5	78.3	431.1	66.0	490.0	78.0	369.3	67.6	13.3	2.6
9	30	768.6	120.9	601.0	89.5	690.6	88.7	519.9	70.6	15.5	3.1
12	18	748.5	174.8	577.3	116.3	686.4	143.6	512.9	92.2	18.6	3.2
13	33	671.5	95.0	530.6	73.7	594.6	93.2	453.2	73.1	15.9	2.6
14	35	714.8	99.3	560.8	80.0	640.8	96.0	482.0	76.4	15.6	2.8
15	20	509.7	95.1	398.7	68.7	458.1	99.0	336.9	81.8	11.7	2.4
16	14	589.8	196.3	454.9	146.1	510.0	135.5	367.4	94.8	12.4	3.0
17	22	691.7	84.8	542.7	69.6	611.7	101.8	455.8	81.8	15.7	2.1
18	48	668.5	104.6	520.2	79.3	591.4	98.5	432.5	75.0	14.2	2.4
19	12	691.8	134.7	557.3	112.1	619.7	116.7	473.0	90.6	17.6	3.3
20	25	666.2	86.2	517.3	70.1	602.0	108.4	448.9	98.5	15.4	3.2
23	22	716.0	128.7	553.1	105.0	666.5	116.4	490.4	84.2	14.6	2.2
25	20	755.4	109.4	572.6	84.9	678.7	87.6	479.1	72.0	15.6	1.9

smp: sample number, n: number of specimens, Lo: largest outer diameter, lo: smallest outer diameter, Li: largest inner diameter, li: smallest inner diameter, E: number of epiauxiliary chambers.

Table II. correlation matrix of measured variables

Lo	lo	Li	li	E	
Lo	1.00				
lo	0.97	1.00			
Li	0.88	0.83	1.00		
li	0.81	0.80	0.96	1.00	
E	0.62	0.59	0.69	0.69	1.00

Lo: largest outer diameter, lo: smallest outer diameter, Li: largest inner diameter; li: smallest inner diameter, E: number of epiauxiliary chambers.

sample is on both characters.

A principal component analysis reveals that more than 95% of the total variance is accounted for by the first two eigenvectors. The first eigenvector mainly reflects embryon size and related number of epi-auxiliary chambers, whereas the second eigenvector represents the 'shape' of the embryon. The sample means of the vector I loadings are graphed in fig. 7 against the stratigraphic column. It shows that most Md samples have on the average a larger embryon and a greater number of epi-auxiliary chambers than the Mc samples, but that two Md samples cannot be discerned from the more primitive Mc populations.

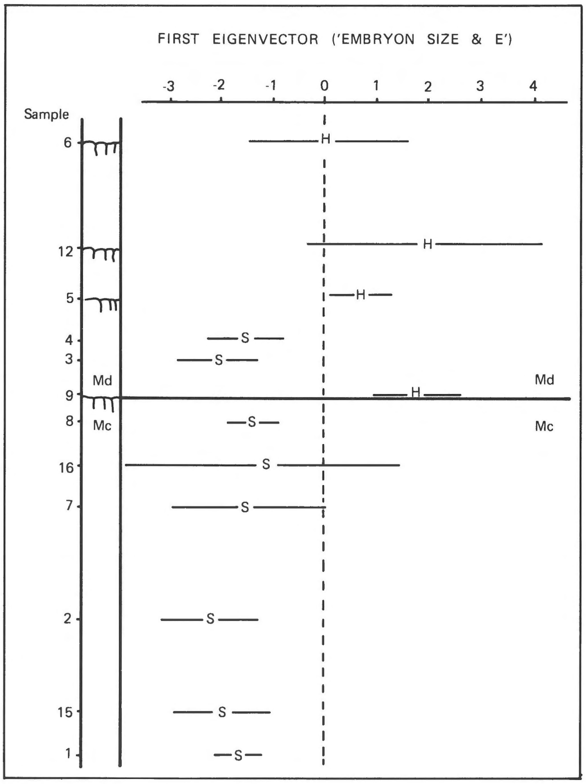

Fig. 7. Plot of sample means (and their 90% confidence intervals) of the loadings on the first principal component. The first eigenvector reflects embryon size and number of epi-auxiliary chambers. Samples taken directly above hardgrounds are indicated by H, the rest by S. Note that the two non-hardground samples from the Md fall within the same range as the Mc samples. Only one sample for each stratigraphic position is shown.

If we look at a bivariate scatter (Fig. 8) of sample means (Lo/E) it appears that two clusters of samples exist, one with a mean number of epiauxiliary chambers around 12.5 and mean Lo around 0.550 mm, and one with mean E around 15 and mean Lo around 0.700 mm.

Although most of the samples of cluster I are from the Mc, two samples in that cluster were collected in the Md of the Maastrichtian sections. The other cluster contains samples from the Md only. No stratigraphic ordering of the samples is visible within each cluster. The clustering coincides, however, with the facies of the sediments from which the samples were taken. Cluster I only contains samples collected in the intervals between the burrowed hardgrounds, whereas cluster II consists of those collected in the orbitoid rich fossil breccia immediately overlying each hardground.

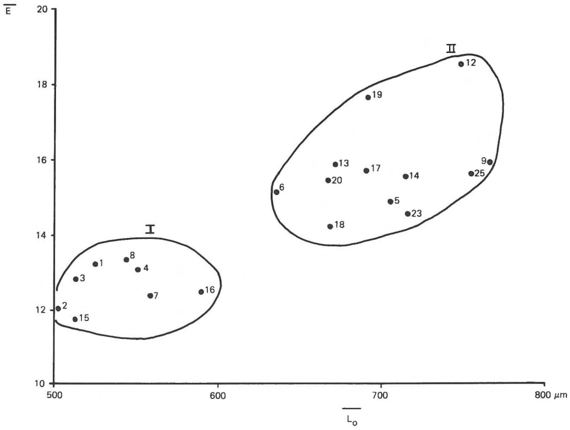

Fig. 8. Bivariate scatter of sample means (Largest outer diameter (Lo) versus number of epi-auxiliary chambers (E)). Samples fall within two clusters. Cluster I contains all non-hardground samples, cluster II all hardground samples.

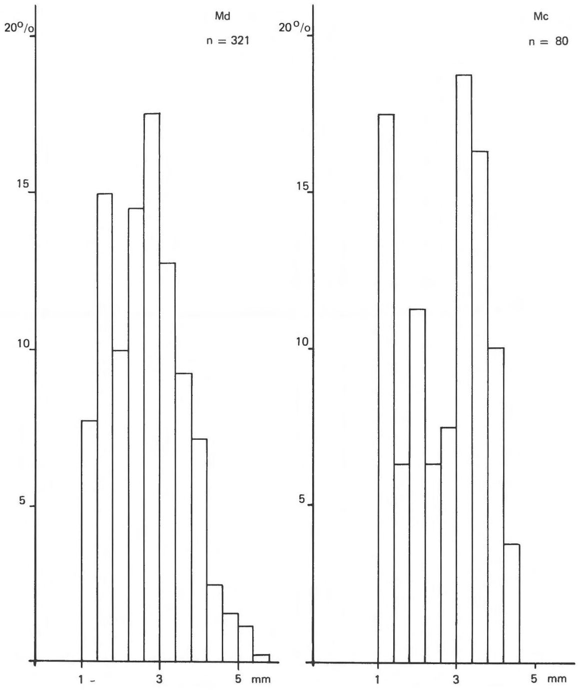

Fig. 9. Histograms showing overall test size distribution of two selected samples, just below and above the Mc/Md boundary. Both distributions are bimodal, with a relatively large number of juvenile specimens.

Figure 9 shows the distributions of the overall test size of two typical samples from the Mc and Md. It seems that both distributions are at least bimodal with a relatively large number of juvenile specimens. Although mean test size of a sample is a variable that is easily influenced by differential transportation, the general congruence of the two distributions suggests that sorting cannot have played a major role and that the observed differences should be considered to reflect the original situation, i.e. the Md specimens have on the average a larger test.

A comparison between the sagittal sections of specimens from the same samples shows that the largest difference between the two populations lies in the asymmetry of the test (Fig. 5G-H, 6A-D). While the Mc specimens are more or less symmetric (mean ratio between the upper and lower lateral layer in the Mc sample around 0.8), the Md specimens are almost without exception clearly asymmetric (mean ratio around 0.3). The significance of this phenomenon will be discussed below.

Only a few sagittal sections from the non hardground samples of the Md are available, but they also show the 'standard orbitoidal' symmetry in the lateral layers, comparable to the Mc specimens.

Within the equatorial layer of large number of specimens, both from the Mc and from the Md, the traces and/or the test of *Talpinella* sp. can be observed (Fig. 5H). The close association of this boring, and perhaps parasitic foraminifer, with members of the genus *Orbitoides* is discussed by Baumfalk et al. (1982) and Baumfalk & Nijholt (1984).

Discussion and conclusions

It seems plausible that the observed differences in the orbitoid populations from the hardground and non-hardground facies are phenotypic and directly related to the ruling environmental conditions. If true, the environmental conditions leading to the formation of burrowed hardgrounds did not yet occur during the deposition of the Mc, and consequently populations with the larger number of epiauxiliary chambers and larger embryos, did not occur until the beginning of the Md deposition.

It should be noted that the trend toward larger embryons and a larger number of epiauxiliary chambers observed during the Maastrichtian, is a continuation of a tendency that started in Santonian times. Therefore, the observed morphologic changes in the Maastrichtian, though also connected to environmental factors, cannot be evaluated but in the perspective of the long term evolutionary trend within the genus *Orbitoides*.

The fact that in this case the link with environmental changes can be shown to be likely, may shed light upon the evolutionary mechanism at work during some 20 million years. In the case of *O. media* it could be demonstrated that no gradual evolutionary trend is present on the scale of a few million years, but that on the contrary one sudden and rapid change in the otherwise static morphology of the orbitoid population took place in the late Campanian, marking the transition from *Orbitoides media media* to *O. m. 'megaloformis'* (Baumfalk & Fortuin 1981; Drooger 1984; Drooger

& De Klerk 1985; Baumfalk in press). In a typological sense some specimens of the *'megaloformis'*-populations could well be considered as *O. apiculata*.

In the Maastrichtian deposits it is clear that the general trend continued, but that it takes some time to cause the old genotype to disappear and the new to become fixed. When conditions returned to those prevailing during the Mc deposition, the orbitoid population apparently was still able to readapt rapidly to that environment and to return to its former composition. The Cretaceous/Tertiary boundary events prevented the stasis phase of the new *apiculata* type, since the entire orbitoid group was extinguished.

Orbitoides apiculata occurs in the Mc and Md of the Upper Maastrichtian, but is only locally abundant, especially around the Mc/Md boundary. It seems that the frequency of *O. apiculata* is environmentally induced, probably by water depth: where *O. apiculata* (together with *Omphalocyclus*) is abundant, *Lepidorbitoides minor* is rare and vice versa (see also Van Gorsel 1975).

A kind of parallelism can be observed if the evolutionary pattern of *Lepidorbitoides* and *Orbitoides* from the type Maastrichtian is compared with the development of these genera in southern France (St. Marcet and Gensac).

Van Gorsel (1975) studied the evolution of *Lepidorbitoides* in both regions and postulated that *Lepidorbitoides socialis* occurring in the southern France localities is the successor of *L. minor* from the Maastrichtian type locality. An argument in favour of this hypothesis is that in the same localities where *L. socialis* occurs, one also finds *O. gensacicus*, which Van Gorsel considered as the final stage of the *Orbitoides* lineage. He therefore assumed that the late Maastrichtian deposits of southern France are slightly younger than the orbitoid bearing strata of the type Maastrichtian, but he also remarked that this assumption will be hard to prove. *Orbitoides gensacicus*, however, occurs together with *O. apiculata.* It is probably a deviant offshoot of the *Orbitoides* lineage (Eggink & Baumfalk 1983) and not the last phase of the Santonian to Maastrichtian trend in the genus *Orbitoides*. Moreover, *O. apiculata* from southern France has a mean number of epiauxiliary chambers of around 12 and a mean embryon size of around 600 μm (Baumfalk, unpublished observations). This stage of development corresponds to the Mc- rather than to the more advanced Md populations of the type Maastrichtian, although they are not morphologically identical. The differentiation in the apical and abapical lateral layers of the test is virtually absent (similar to *O. media*) in the southern France samples. Mac Gillavry's (1955) opinion, that the two *Lepidorbitoides* species evolved independently remains therefore valid. Geographical separation triggered both the development of the exceptional *O. gensacicus* as well as the speciation event leading to *L. socialis* in the south. The same can be said for *O. apiculata* in the north.

The differentiation in an apical and abapical lateral layer is more developed in the Md samples than in the older samples. This might be considered an argument in favour of the hypothesis that the *O. apiculata* populations in southern France (which are even more symmetric than the Mc specimens in the type Maastrichtian) are older than the type Maastrichtian ones. The alternative explanation that this is a feature unique to the Maastricht localities, evolved in relative geographic isolation at the northernmost boundary of the *Orbitoides* distributional area, is preferred.

The biologic significance of the asymmetry may lie in the anchorage function a thick and massive abapical lateral layer would perform under high energy conditions. It should be noted that the debris layers overlying the hardgrounds indeed reflect higher energy environments. Whether this asymmetry is only ecophenotypic or is an expression of a new mutant gene remains questionable, but asymmetry has not been observed in Campanian *O. media* populations derived from similar high energy deposits, which suggests evolutionary change raher than pure ecophenotypic variation.

When conditions returned to those prevailing during the Mc formation, the population returned to its old morphologcal range with on the average a slightly smaller embryon, fewer epiauxiliary chambers and symmetric test. Perhaps the evolutionary pattern observed in the *Orbitoides*-lineage as a whole can be explained in similar terms. Only when a new environment (and corresponding selection pressure) lasted for a rather long time, a new trait became fixed and the old genotype was lost.

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