

UTRECHT MICROPALAEONTOLOGICAL BULLETINS

C. W. DROOGER and J. C. DE KLERK



Project no. 1

THE PUNCTUATION IN THE EVOLUTION OF ORBITOIDES IN THE
CAMPANIAN OF SOUTH-WEST FRANCE

33

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ABSTRACT

For the *Orbitoides* assemblages analyzed from a number of closely sampled sections of Campanian calcarenites in south-west France there is a sudden change in the means of several parameters of the internal embryonic-nepionic stage. The direction of the change is in accordance with the nepionic acceleration principle, known to be valid for all lineages of orbitoidal larger foraminifera. Below and above the level of the morphological break we seem to be dealing with two longer periods without any systematic change in the morphology. In two of the sections the abrupt shift could be narrowed down to a lithostratigraphic distance of about ten centimetres, an interval which is thought to correspond to a time duration of less than a few thousand years.

In none of the sections could any evidence be found that might point to a hiatus in the sedimentation or to a notable change in the open-marine, shallow-water environment. Since the discontinuity was found in sections about 90 km apart (Aubeterre and Meschers) the change must have occurred simultaneously throughout the entire Aquitaine basin. If we take into account that bioturbation must have had an obliterating effect on our data, it seems safe to conclude that the modal morphological change was very large and geologically instantaneous.

Because no comparable change in internal morphology could be detected in the accompanying *Lepidorbitoides* lineage it is thought likely that the fundamental change in the population composition of the *Orbitoides* was an autonomous happening fitting into the evolutionary theory of homeostasis and punctuation. The pulsating pattern in the stasis parts of our data sets is rather weak; phyletic gradualism is still thought to be an acceptable theory to explain the gain of more advanced morphotypes and the loss of conservative ones in our *Orbitoides* sequence.

At the end of our paper it is argued that the concept of sympatric speciation passing through low-frequency bottlenecks in the suites of populations is the one that would fit best to the evolutionary history of the lineages of orbitoidal foraminifera. This model would combine the random character and the directional aspect of evolution, which are expressed in various ways in all better known lineages.

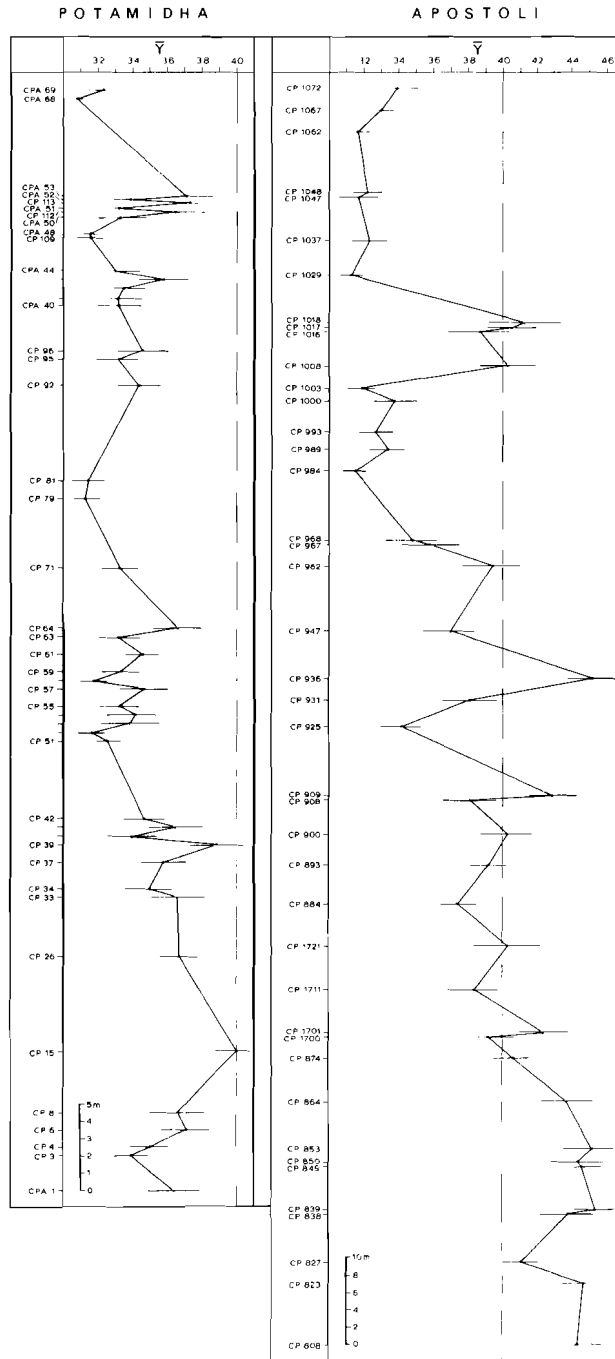


Fig. 1

The pulsation pattern in Miocene Cretan *Planorbulinella* assemblages, expressed in the nepionic configuration parameter \bar{Y} . Sections Apostoli and Potamidha are stratigraphically successive (after M.M. Drooger, D.S.N. Raju and P.H. Döeven, 1979).

Chapter I

INTRODUCTION

In 1975 members of the Utrecht Department of Stratigraphy and Paleontology started an investigation into the accuracy of biostratigraphic correlation methods as part of the I.G.C.P. project no. 1: "Accuracy in time". One of the aims of our research was to reconstruct the detailed course of morphological changes in lineages of orbitoidal larger foraminifera. The evolutionary changes of such groups are assumed to have been unidirectional.

The data on Cretan Miocene *Planorbulinella* (M.M. Drooger et al., 1979) demonstrated for the first time a rather peculiar pattern for the detailed course of the morphometric development in a lineage. We called this pattern pulsating evolution (fig. 1). In the sequence of successive samples statistically significant oscillations were found in the series of mean values for all parameters of the early ontogenetic stage; this initial part of the test is considered to reveal best the development in such a lineage. This "to and fro" pattern seems to be superimposed on the expected overall unidirectional trend, a trend which is in accordance with the evolutionary principle of neponic acceleration, well known from nearly all groups of orbitoidal larger foraminifera.

A similar pattern of pulsations was found in the development of the uniserial *Uvigerina* of the Mediterranean Mio-Pliocene (Thomas, 1980). But this group of foraminifera is not orbitoidal, and the complete evolutionary sequence of these *Uvigerina* finally did not show any net morphological change.

In neither of these two examples could an ecological control be ascertained to explain the pulsations. We must conclude that either there was no such control or that the environmental fluctuations were so small that we are unable to detect their effect from the characteristics of the sediments and the accompanying faunas.

We tried to obtain further confirmation of the pulsating pattern and a better understanding of this phenomenon in other groups of larger foraminifera. For these investigations we needed the regular presence of such a group in fairly long lithostratigraphic sections which could be sampled continuously and in sufficient detail.

The test case elaborated in the present paper deals with part of the *Orbitoides* lineage found in some sections of the Campanian of south-west France,

the deposits of which seemed to be very promising for our purpose on the basis of earlier publications (e.g. Van Hinte, 1966).

The actual field work and sampling were carried out by both authors during several trips to the region in the years 1979–1984, either separately or together. Nearly all the painstaking laboratory work and observations were done by the second author during 1980 and 1981. Additional morphological data were collected by several students of the department. The final manuscript was composed by the first author.

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H. Laagland, G.J. van der Zwaan, P. Marks and J.A. Broekman made critical comments on the manuscript. Mrs. S.M. McNab made linguistic improvements. P. Hoonhout and A. van Doorn prepared the drawings and W.A. den Hartog the plates. The first author took most of the photographs in the field, the second author made those of the thin-sections. Technical assistance with the sample preparation was given by G.J. van 't Veld, G.J. Ittmann and C.W. van de Dood.

Chapter II

ORBITOIDES; HISTORY OF RESEARCH

STRUCTURE AND GENERA

The genus name *Orbitoides*, established by d'Orbigny (1847), has been used in various ways as a standard name for larger foraminifera with a similar build. The adjective *orbitoidal* is still the current term used to denote the chamber arrangement in several unrelated groups of larger foraminifera, in which the skeleton grows in all directions in a so-called median plane by adding many contemporary chambers per growth step.

The family name Orbitoididae has been given a variable scope in the literature. In the widest sense it included a large number of unrelated, Cretaceous and Tertiary, discoidal larger foraminifera of orbitoidal structure (e.g. Neumann, 1972a). Today most authors (e.g. Van Gorsel, 1978) use the family name for only a small number of Late Cretaceous genera, which are considered to belong to a single phylogenetic stock because there are certain morphological peculiarities common to the structure of the early part of their test.

Orbitoides is the main genus of this Cretaceous group. It is characterized by a centrally situated, thick-walled embryo (fig. 2, and plates 2-4), in which commonly more than two primordial chambers can be recognized. The most regular embryo type in early *Orbitoides* species (e.g. in the species *O. tissoti* of most authors) consists of protoconch, deutoconch and two principal auxiliary chambers of equal size (figs. 2-left, 28). In the later species of the genus the regularity of these chambers inside the thick-walled embryo of increasing size declines and it becomes a matter of conjecture how many growth steps are still represented in this early stage; it is commonly supposed that the number remains at three. The evolutionary course of the genus seems to end in forms with very large embryos. In some of these forms a large number of chambers of rather irregular shape is found in the embryo; these cells seem to have calcified their walls simultaneously, if this is the correct interpretation of the embryonic structure of *Orbitoides gensacicus*. The latter species has been made the type species of the genus *Simplorbites* de Gregorio, 1882. The exact relationship between *O. gensacicus* and the more regular, contemporaneous, Late Maastrichtian *O. apiculata* has not yet been established. Recently, Eggink and Baumfalk (1983) gave a satisfactory explanation for the structure of the *Simplorbites*

embryon type, which would consist of a piece of the parental median layer. It remains uncertain whether this peculiar embryogenesis led to genetic separation from *O. apiculata*. If not, the "species" certainly does not deserve to be separated generically.

Our knowledge of the species of the Orbitoididae that must have occurred prior to the morphological level of *Orbitoides tissoti* is incomplete. The earlier species described so far all lack the systems of lateral chambers characteristic for *Orbitoides* s.str. Generic names have been proposed for such earlier forms, amongst which *Schlumbergeria* Silvestri, 1910, has priority over the more commonly used *Monolepidorbis* Astre, 1927. We are inclined to follow the practice of later authors and include all these early species of the family group in *Orbitoides* s.l. The *Omphalocyclus* group of the Old World is the only one that deserves taxonomic separation. It is certainly related to *Orbitoides*, but it cannot yet be tied clearly to the latter's lineage, if one considers its relatively late stratigraphic range (Maastrichtian), the peculiar multiplication of the median layer and the odd structure of its embryo (Jorissen, 1983).

The embryo of *Orbitoides douvillei*, which presumably was the last species without lateral chambers, does strongly remind us of that of *O. tissoti*, but it lacks the conspicuously thickened wall around the four initial chambers, such as we find in all later *Orbitoides* species with lateral chambers.

However, the stratigraphically oldest species of the family, *O. hottingeri*,

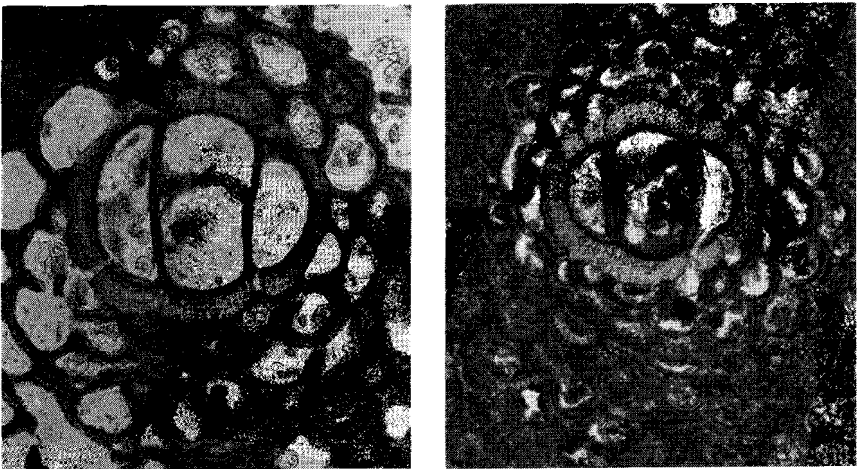


Fig. 2

The thick-walled embryo of two megalospheric *Orbitoides* specimens in median section.

shows an initial stage which is entirely different. The arrangement of its early chambers is strongly reminiscent of that in microspheric specimens of all later *Orbitoides* and *Omphalocyclus* (e.g. Van Hinte, 1966). The chamber arrangement can be described as an irregularly alternating spiral, which means that the single apertural opening of an early chamber is either in the same or in retrovert position relative to the place of the opening of the previous chamber. Extreme, theoretical variants of such growth patterns are regularly spiral at one end and biserial at the other (fig. 3), with a multitude of intermediate types, the number of which may increase exponentially with the number of one-opening chambers in the early part of the test. It must be admitted, however, that on the basis of this hypothesis of random spiral to biserial arrangement, the biserial variants (with 5 or 6 chambers) are distinctly over-represented in our microspheric Campanian *Orbitoides*.

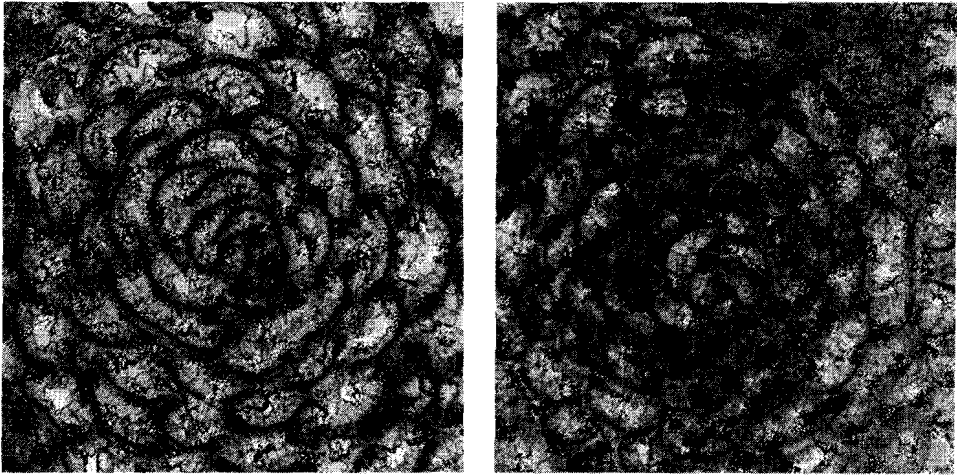


Fig. 3 Median sections of two microspheric *Orbitoides* specimens from Aubeterre, showing a biserial arrangement of the early chambers (left) and a more spiral configuration (right).

The hypothesis seems to apply better to the megalospheric *O. hottingeri* from the Santonian. Van Hinte (1966) found what he called the progressive chamber, i.e. the first chamber with two openings, to range in rank number from 3 to 7 (mean 4.95) in megalospheric individuals of his *O. hottingeri*. Because this progressive chamber may be followed by relapse chambers (with again one opening) in the sense described by Freudenthal (1969) for *Planorbulinella* and *Hellenocyclina*, Van Hinte also recognized an effective chamber, after which there are no more relapses and from which symmetrical spirals are formed that encircle the earlier stages.

Considering these growth patterns of primitive Orbitoididae one may wonder whether the assumption of some *Cibicides*-like ancestor for the group is not more likely than a descentance from a biserial, heterohelicine stock, which is the hypothesis defended by most later authors since the publication of Küpper (1954), a hypothesis strictly based on microspheric specimens of the younger species.

For our purpose there is no need to give a longer introduction to the vast literature on the Orbitoididae; more details can be found in the exhaustive reviews by Neumann (1972b) and Van Gorsel (1978).

BIOMETRICS

Morphometrical research on *Orbitoides* was initiated by Van Hinte (1966). He introduced a large number of parameters on the basis of a well-understood structure of the early ontogenetic stages. Since details on all these parameters are given in chapter IV it is sufficient for the moment to note that Van Hinte built the resulting, numerical classification (1966 and later) on the basis of the means of essentially three of them.

One of these parameters, $(L_i + l_i)$, is based on the dimensions of the four-chambered embryo (fig. 28), the size of which was found to increase considerably in the course of the evolution of the group. The second parameter E pertains to the number of primary peri-embryonic chambers (epi-auxiliary chambers), which are the chambers that have a direct stoloniferous connection with the lumen of the embryo. The mean of this parameter was also found to increase in the course of time. Finally, there is the rank number of the progressive chamber (Pr), which shows a decrease in evolution. This Pr parameter is comparable to the spiral parameter Y, used in many other orbitoidal lineages for the number of early chambers with only one apertural opening; actually, $Pr = Y + 1$.

In 1976 Van Hinte gave a tentative amplification of his earlier 1966 classification; this 1976 species subdivision is repeated in our table 1, given below. The assumed stratigraphic order of the taxonomic units in this table is from top to bottom. The upper four species units are devoid of lateral chambers, the others all belong to *Orbitoides* s.str.

Along this assumed time-bound sequence of species units there is evidently a shift in the relative importance of the three parameters involved. In the early *Monolepidorbis* part of the lineage it is the length of the primordial spiral, expressed in \overline{Pr} , which gives the best opportunity for subdivision. Once we have passed the early *Orbitoides* s.str. stage with the strong unimodal peaks of $E = 4$, the parameter \overline{E} gains in weight. For the distinction

	$\bar{Pr} = \bar{Y} + 1$	\bar{E}	$\overline{(L_i + l_i)} (\mu)$
<i>Orbitoides</i> sp., not known	> 6.0	0	
<i>O. hottingeri</i>	6.0–4.5	0–1.0	
<i>O.</i> sp., not known	4.5–2.5	1.0–2.0	
<i>O. douvillei</i>	2.5–2	2.0–3.9	< 400
<i>O. tissoti</i>	2	3.9–4.0	400–500
<i>O. media</i>	2	4.0–5.5	500–(600)
<i>O.</i> “ <i>megaliformis</i> ”	2	5.5–10.0	(600)–(750)
<i>O.</i> “ <i>gruenbachensis</i> ”	2	10.0–14.0	(750)–1000
<i>O. apiculata</i>	2	> 14.0	> 1000

Table 1. Morphometric delimitation of the *Orbitoides* species, after Van Hinte (1976).

of the early assemblages the embryon size parameter $\overline{(L_i + l_i)}$ may be helpful, although it is always awkward to have such a combination of two parameters in morphometric species delimitations because there may be an undue expansion of the number of intermediate assemblages. We suggest that \bar{E} should be given a stronger weight in classification than $\overline{(L_i + l_i)}$. The necessity of such a hierarchy will become apparent in our final chapter on taxonomy.

Every morphometric system is based partly on unfortunate decisions made by the original author about the species limits. In our example for instance the species limit suggested at $\bar{E} = 4$ is very unpractical, because assemblages with such a mean \bar{E} value are quite common. We do not violate the system if we add for every species unit “larger than” to the lower limits of the ranges in the above \bar{E} and $\overline{(L_i + l_i)}$ scales, so that $\bar{E} = 4$ means that we are still dealing with *O. tissoti*. Actually, this is more in line with Van Hinte’s original morphometric definition (1966) of his species *O. tissoti*.

Otherwise, we think that it is advisable to adhere to the original morphometric subdivision of the first author, unless the limits between his species appear to be utterly untenable. Van Gorsel (1978) suggested that certain limits in the *Orbitoides* classification should be changed, obviously without any compelling reason based on new material. In our opinion it would be unwise to follow this suggestion. Of course it is true that the morphometric limits between adjoining species which bear Linnean names are entirely arbitrary, but giving different positions to one such limit rapidly leads to a new type of confusion about the species names.

The idealized biometrical classification of *Orbitoides* species given above in table 1 has a sound basis – i.e. a sufficient number of assemblages with good relative dating – for only part of the morphology range. For this morphological interval Van Hinte (1966) presented a fairly complete covering

based on ten successive assemblages from a single stratigraphic section in the village of Aubeterre, south-west France. This section is the type section of the Campanian Stage. In this Campanian section \bar{E} was found to increase from 4 to 7.75, $(\bar{L}_i + \bar{l}_i)$ from 431 μ to 616 μ . So we are dealing with the species sequence *O. tissoti*, *O. media* and *O. megaliformis* according to the 1976 classification given above.

Van Hinte's data suggest that the means of the main parameters E and $(L_i + l_i)$ did not evolve jointly along some gradual course. The lowermost part of his section shows a rapid increase in the size of the embryo at a rather stable \bar{E} value close to four. Higher up it is \bar{E} which shows the more rapid increase, whereas the $(\bar{L}_i + \bar{l}_i)$ values increase much more slowly. The smooth line of Van Hinte's figure 8 through the points of the $(\bar{L}_i + \bar{l}_i)$ versus \bar{E} scatter and his table 3 suggest a change in \bar{E} in accordance with the punctuation model of Gould and Eldredge (1972). The pattern was interpreted as such in a repeat-study of the *Orbitoides* from Aubeterre by Baumfalk and Fortuin (1981).

We considered this Aubeterre section with its continuous presence of *Orbitoides* individuals over a sediment thickness of some 40 metres to be very suitable for our detailed analysis of morphometric data at short vertical distances. In the course of the investigation we also analyzed an additional section, situated immediately south of the Plage de Cadet near Meschers on the eastern bank of the Gironde. Both localities are shown in our figure 4.

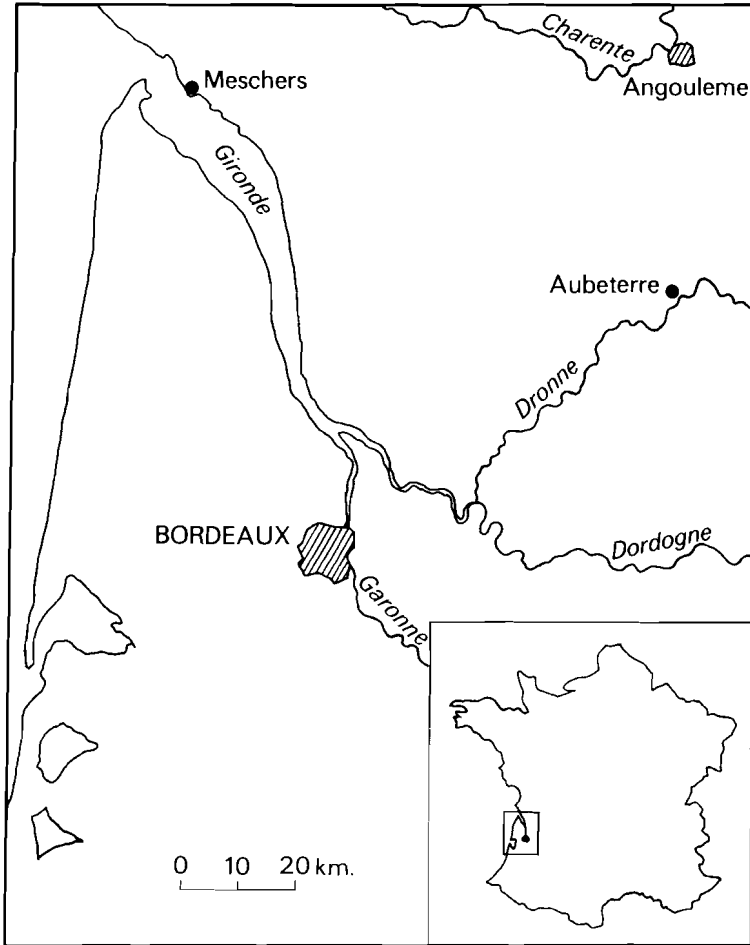


Fig. 4 Schematic map of south-west France showing the location of Aubeterre and Meschers.



Fig. 5 Craie à *Ostrea vesicularis*; coastal section near Meschers.

Chapter III

STRATIGRAPHY OF THE SECTIONS

THE CAMPANIAN STAGE

The section of Aubeterre (département de la Charente) received repeated attention in the literature until eventually it became generally accepted as the stratotype of the Campanian. This stage name was introduced by Coquand in 1857 for his so-called Craie à *Ostrea vesicularis*, this oyster being the characteristic fossil (fig. 5). Already in 1856 he specifically mentioned that the cliffs along the River Dronne near Aubeterre show a complete succession of these calcarenites.

For a long time afterwards most authors followed the entirely different redefinition of the Campanian, introduced by Arnaud (1877). These authors gave the stage name Maastrichtian (or sometimes Dordonian as an equivalent) to all calcareous deposits in SW France in which *Orbitoides* is present. Since this genus starts its continuous range in the lower middle part of the Aubeterre section, the larger, upper part of the type section of the Campanian was transferred to the Maastrichtian. A fair, though not exhaustive review of opinions and arguments is given by Goharian (1971); a clear review of the contents of Coquand's original papers is presented by Van Hinte (1965).

Today the section at Aubeterre is again fully accepted as representing the core of the Campanian Stage of any possible vertical extension (Neumann, 1980). The type section of the Maastrichtian in the SE Netherlands is considered to be distinctly younger and to have no time overlap with the Aubeterre section. Coquand's Dordonian (1857) is considered superfluous; the few metres at the top of the Aubeterre section, which Coquand ascribed to his Dordonian, might well be incorporated in the extended Campanian, because its fauna is not really different from the faunas of the underlying strata, except for the presumed absence of *Ostrea vesicularis* and the abundance of rudists.

THE EXPOSURES OF AUBETERRE

The houses of the village built against and on top of the cliffs and steep hillside above the Dronne nowadays cover a fair part of the earlier exposures (fig. 6). As a consequence it is not really possible to sample one continuous

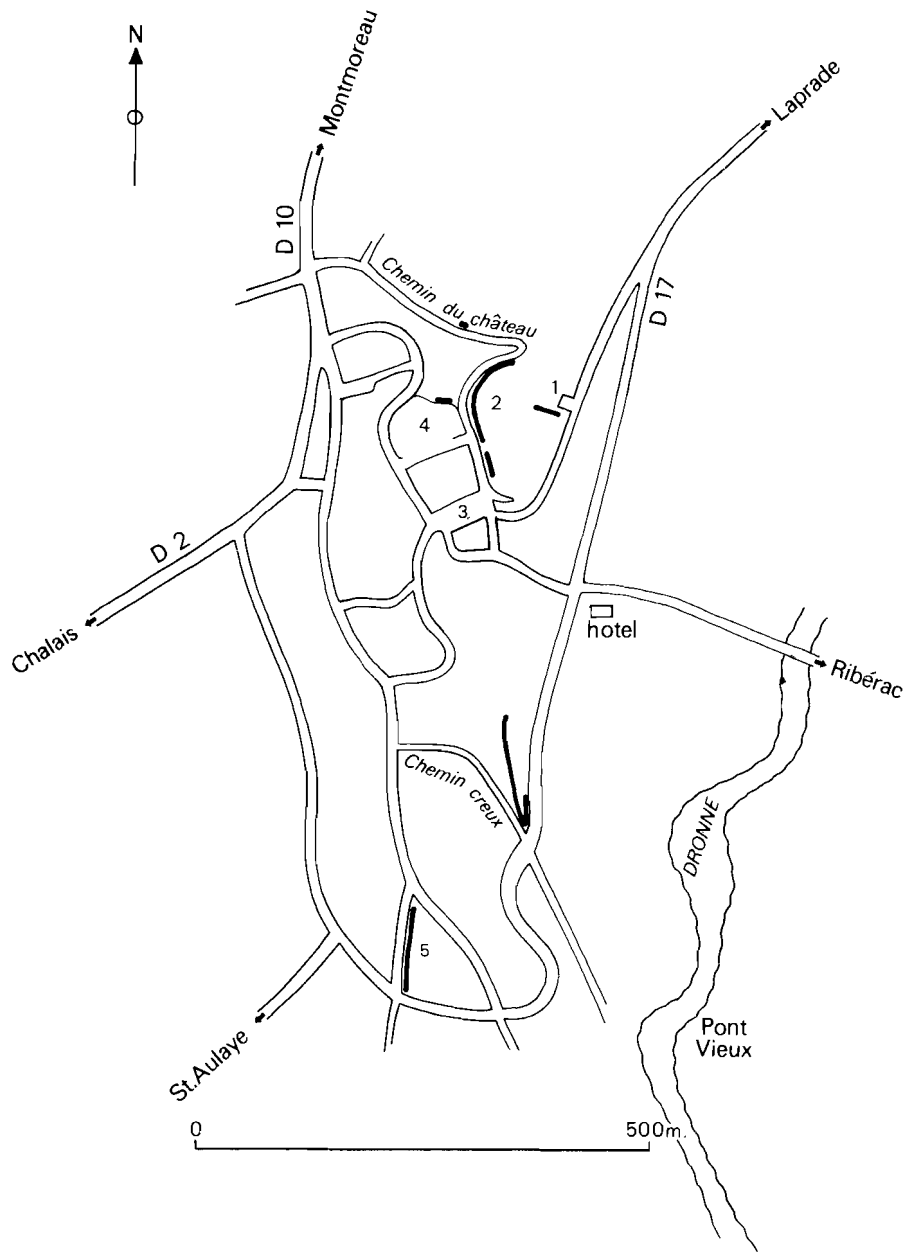


Fig. 6 Schematic map of the village of Aubeterre with the location of the sections. 1 Église Monolithe, 2 castle grounds, 3 Place Trarieux, 4 Champ de Foire, 5 Gendarmerie.

section in a vertical sense. Fortunately the lithostratigraphy of the calcarenites in this small area is sufficiently distinct to permit a reliable correlation in the field. It is especially the thickest oyster bed in the succession that can easily be followed in the surroundings of Aubeterre (fig. 7).

From the large number of smaller exposures a longer one can be composed. We based our investigation on such a composite section and on a few scattered, smaller outcrops in addition (fig. 6).

The lowermost part of the main, composite section can be followed from the cross-roads close to the Dronne and near Hotel Périgord, below the actual village, southwards along the D 17 to the hollow road, called Chemin creux. This "chemin" is the continuation of the ancient road that climbed directly from the site of the Pont Vieux to the centre of the village. Because of the rather poor state of the exposures along the higher part of the Chemin creux we preferred to continue our section through the gardens east of the

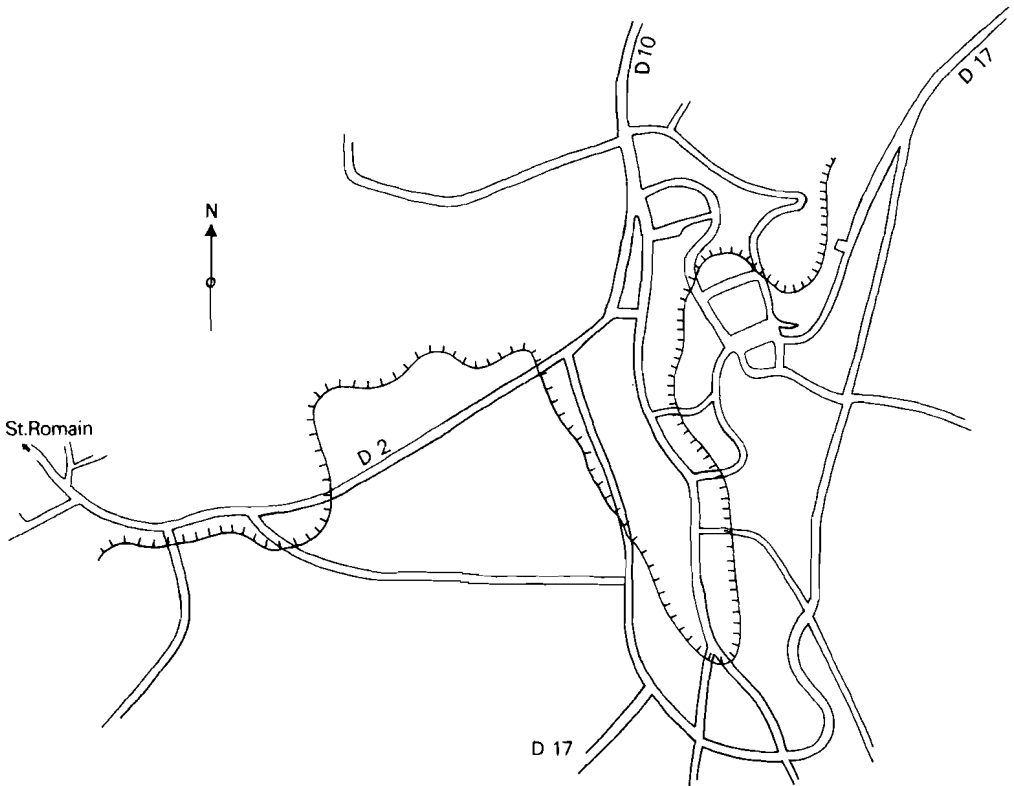


Fig. 7

Contour map of Coquand's unit E (oyster beds) in and west of Aubeterre.

Chemin creux, actually above the roadside outcrops along the D 17 (see fig. 6).

The major and higher part of our section begins at the entrance level of the Église Monolithe (Église souterraine) and up along the cliff through the steep series of small gardens to the lowermost ruins of the former castle, left (south) of and above the former church. The higher portion of this section part is better exposed above the small gardens along the road that runs from the north-east corner of the central square (Place Trarieux) up to the Champ de Foire. From the latter field the section continues upwards along the excavated road (Chemin du Château) leading to the back entrance to the castle grounds.

We sampled at several other places in and near Aubeterre, but only the following exposures will be dealt with in the rest of our paper.

At the time of sampling there was a series of fairly fresh roadside exposures of stratigraphically some eight metres altogether, situated along the road that goes upwards from the D 17, west of the Gendarmerie building (fig. 31).

Outside the actual village of Aubeterre we sampled a section about five metres thick along a country road near Boie de la Roue, some two kilometres north of the village. Since we were on top of the “plateau” we thought we would find a high part of the stratigraphic sequence; according to the *Orbitoides* we appeared to be dealing with an equivalent of the lower part of the village sections.

The lithostratigraphy of these village sections is shown schematically in figure 8. The position of all samples has been entered; only those used for our *Orbitoides* investigation are provided with the field numbers (not all sample numbers are given for the Gendarmerie section).

THE CLASSICAL SECTION

Coquand's descriptions (1856–1857) of the Aubeterre section are purely lithostratigraphic; they appear to be largely correct and we used his subdivision as a suitable basis for our fieldwork.

On the basis of differences in the lithological appearance and in macrofossil contents (many *Ostrea*, or few to none) Coquand distinguished seven superimposed lithostratigraphic units in the calcarenites. He denoted these units from top to bottom by the letters B to H.

His lowermost unit H, situated immediately above the water level of the Dronne would have consisted of dense limestones with silex and without *Ostrea vesicularis*. It would have belonged to the underlying formation,

which he considered to be of Santonian Age. All later authors state that these sediments are no longer exposed; we did not see them either.

The overlying 60 metres of calcarenites contain variable quantities of *Ostrea vesicularis* and thus constitute the type section of the Campanian. The five units, named G, F, E, D and C from bottom to top (fig. 8), Coquand called limestones (calcaires), but many later authors use the term chinks. Although the word limestones is often appropriate, we prefer to use

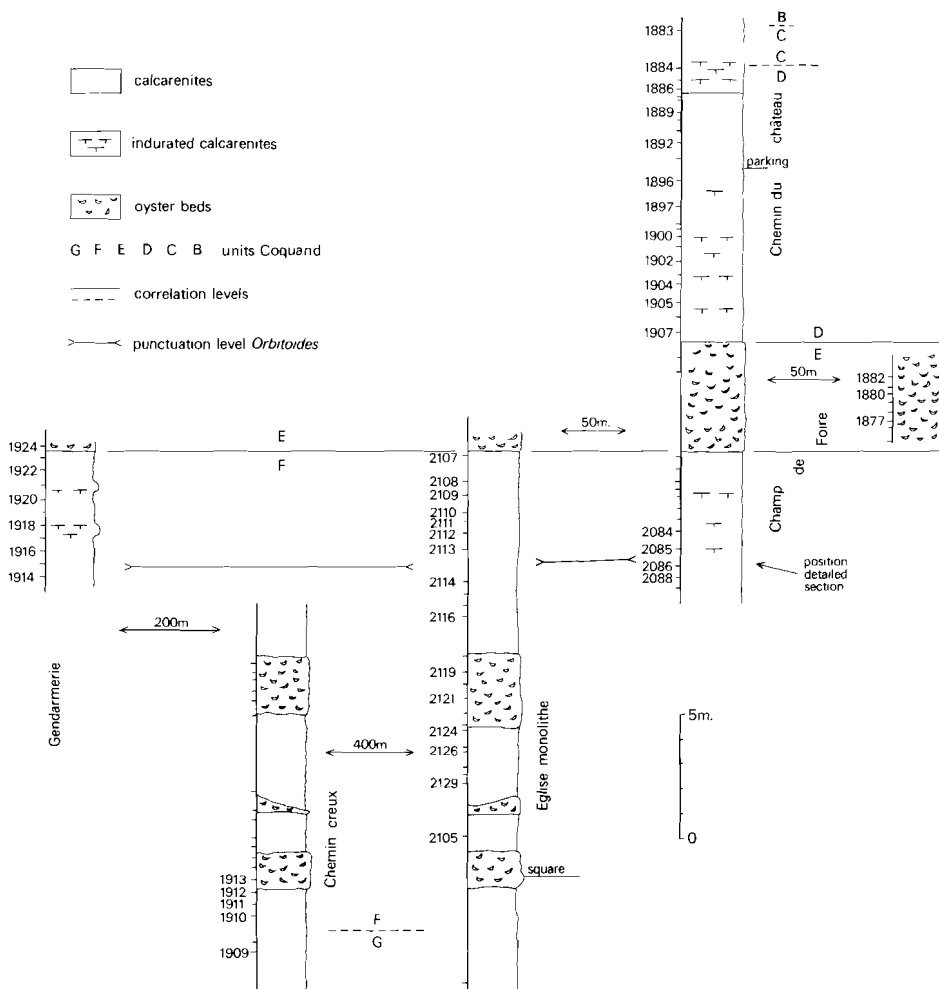


Fig. 8 Schematic lithostratigraphy of the sections in Aubeterre showing Coquand's units G to B, some correlation lines, and the position of our samples.

the term calcarenites, which term is meant to cover all differences in induration, in grain size and in micrite contents.

The lowermost of these five units, G, is more than 25 metres thick, according to Coquand. The lower part of this unit is exposed patchily and we were unable to verify the stated thickness. The unit consists of fairly hard, fine-grained glauconitic limestones. The main macrofossils are large *Ostrea vesicularis* (var. *gigas*), which occur scattered or at irregular levels; the oysters are often partly silicified. Coquand's upper limit for this unit is not very clear. Below the lowermost level of abundant oysters that belongs to the overlying unit F, some ten metres are continuously exposed along the D 17, south of the cross-roads below the village. If we take Coquand's stated thickness of 19 metres for unit F for granted, then the boundary between G and F is a few metres below this lowermost oyster bed. Actually the uppermost one to two metres already strongly resemble the sediments of unit F in lithology and they were found to contain *Orbitoides*. At the Chemin creux these calcarenites show irregular "bedding" with possibly prevailing dips to the south-east. Along the D 2 more northern dips were observed. At

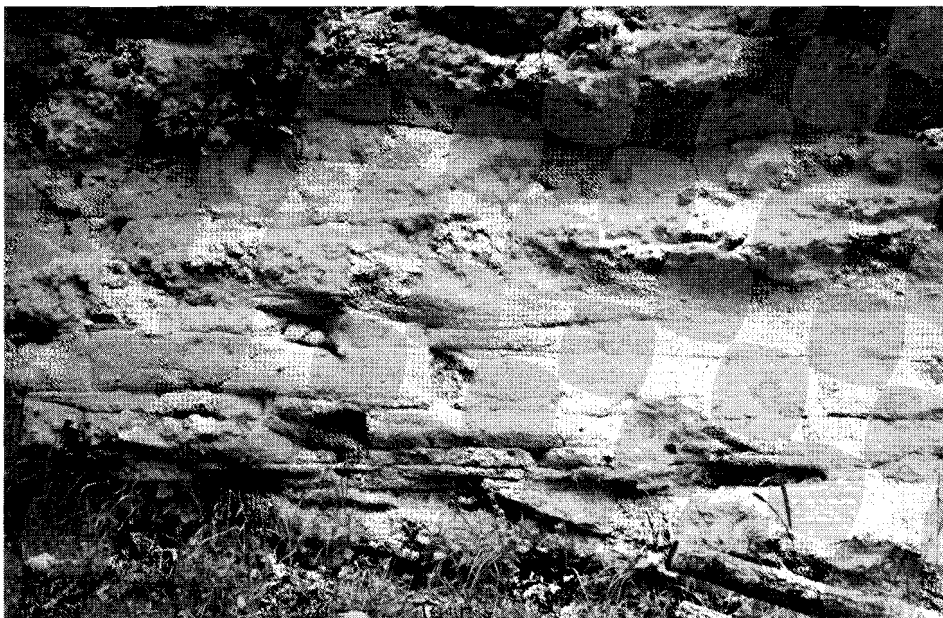


Fig. 9 Irregular bedding in the calcarenites of the lowermost part of Coquand's unit F below the first oyster bed; lower end of the Chemin creux, northern side, Aubeterre.

the lower end of the Chemin creux (fig. 9) we are probably dealing with infillings of shallow depressions or channels.

Anyway we cannot use the beginning of the continuous presence of *Orbitoides* to define the limit between units G and F. These microfossils start their range some eight metres below the lowermost oyster bed. They gradually become more common over these eight metres, whereas the glauconite content slowly diminishes. The lithology of the calcarenites changes to a coarser texture and to whiter colours and the sediments are evidently less indurated. This type of lithology dominates the entire higher part of the Aubeterre section.

Coquand's unit F with a stated thickness of 19 metres consists of fine-grained calcarenites with several interbeds consisting largely of *Ostrea vesicularis*. The *Orbitoides* are common throughout, as they are in the overlying units. The succession in the section above the D 17 and east of the Chemin creux consists from bottom to top of:

- one to 1.5 metres for the lowermost oyster bed,
- 1.75 metres of soft calcarenites,
- 0.1 to 1.0 metre for the second oyster level, which shows considerable, lateral changes in thickness within a few tens of metres,
- 3.5 metres of soft calcarenites,
- 2.5 metres for the third oyster bed of the unit, and
- 8 metres of rather soft calcarenites with concretionary levels, scattered fossils, and locally somewhat enriched in shell debris.

The top of unit F is very distinct; so if Coquand's measurement of 19 metres is correct, he must have included some 1.5 to 2.5 metres below the lowermost oyster bed in his unit F. As far as the lithology is concerned this is quite plausible. This is the part of the section with the channel-infill bedding at the lower end of the Chemin creux. Coquand certainly cannot have used the onset of *Orbitoides* individuals to differentiate his units G and F, because these foraminifera start well below the assumed position of the boundary.

Unit F is the main unit that was quarried in the past for building stones. Also the Église Monolithe was excavated in unit F. With its internal height of 21 metres, this large cave extends into the lowermost part of unit E.

With regard to the investigation of our *Orbitoides* unit F appeared to be the most interesting unit since it contains the punctuation in the *Orbitoides* evolution in the uppermost subunit of eight metres. For this reason a detailed section was sampled below the south-east corner of the Champ de Foire (figs. 33 and 34); it will be discussed in more detail in chapter V.

Unit E of Coquand is formed by the thickest oyster member of the sequence. At the Champ de Foire, both east and north (fig. 10) of this field, we measured a thickness of 4.5 metres. The unit contains numerous *Ostrea vesicularis*, many of them undamaged, dispersed in a finer matrix. The matrix consists of fine-grained calcarenite in which the *Orbitoides* are still

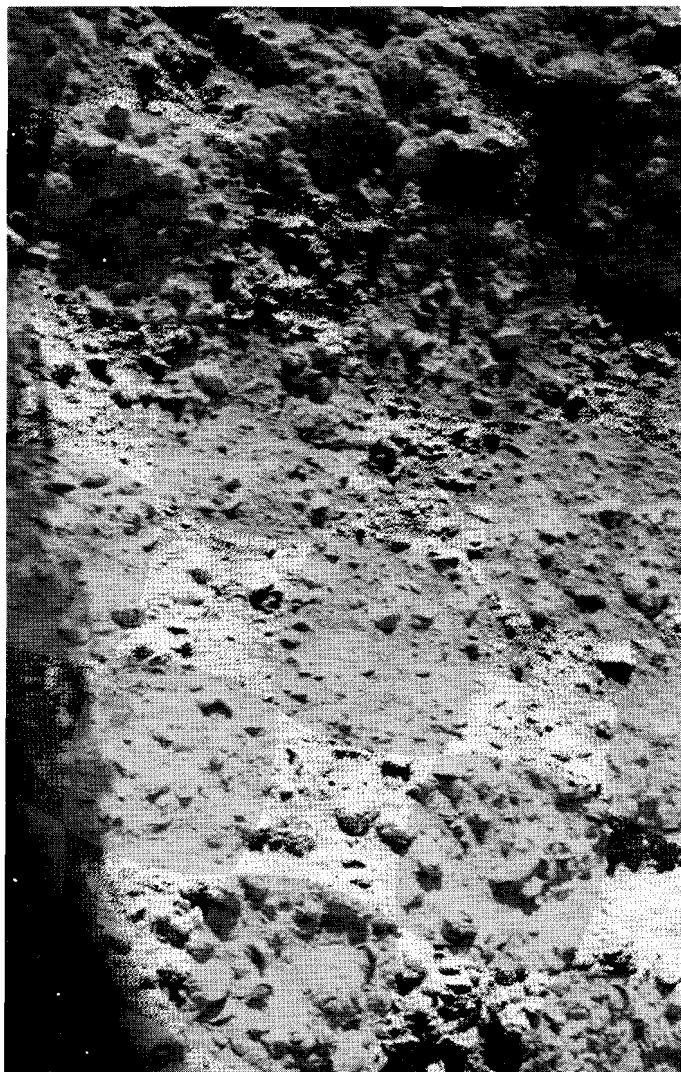


Fig. 10 Oysters and coarse oyster debris in *Orbitoides*-bearing matrix; unit E at the northern side of the Champ de Foire, Aubeterre.

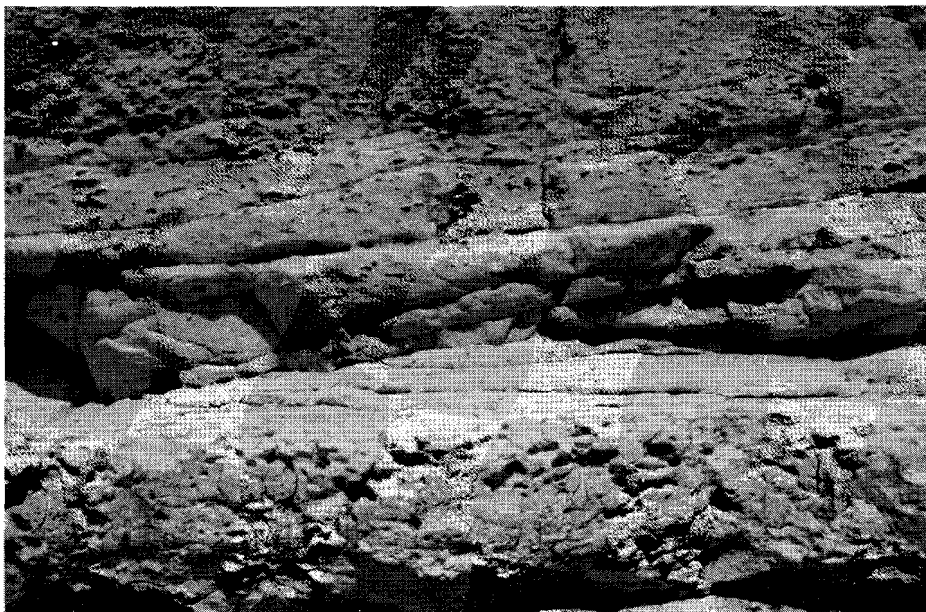


Fig. 11 Channel-infill bedding, distinct in the Campanian *Orbitoides*-bearing calcarenites of the coastal cliffs near Talmont, Gironde (above), of more dubious character in the oyster beds of unit E along the D 2 at Aubeterre (below).



Fig. 12

Irregular concretionary induration in the calcarenites of unit D along the Chemin du Château, Aubeterre.

present in fair numbers. The thickness of the member increases westwards as can be seen in exposures west of the village along the D 2 (figs. 7 and 11), but we were unable to verify whether the 6-metre thickness reported by Coquand is entirely correct. In some exposures an irregular internal stratification seems to be present in these rather massive oyster calcarenites, again reminding us of channel fills (fig. 11, lower part). Admittedly we have some doubt about the real character of these planes. Because they occur rather close to the present surface we may be dealing with pressure planes engendered by some lateral displacement. Such features are very obvious at some other places (e.g. fig. 41). Cleavage below indurated layers has been observed as well (fig. 24).

The overlying units D, C and B of Coquand's description are more difficult to recognize as separate units in today's exposures. Coquand mentioned thicknesses of 8, 2 and "some" metres for these three units, respectively; C is said to be another soft calcarenite full of *Ostrea vesicularis*. A series with altogether a comparable total thickness is fairly well exposed along the lower part of the Chemin du Château, which road leads from the Champ de Foire to a point above the northern entrance to the castle grounds slightly east of the hairpin bend in the road (fig. 6).

The major part of this sequence consists of soft, fine-grained calcarenites with several more or less regular concretionary levels (fig. 12). The scattered oysters diminish in numbers towards the top as do the indurated levels. After measuring some ten metres of such calcarenites with very few oysters we arrived at a distinct "bedding plane", clearly visible above the road level behind the castle grounds (fig. 13). The plane is accentuated by the fact that the softer calcarenite is weathered out below the more indurated overlying limestone. This level can be followed towards the village on both sides above the Chemin du Château, but it loses its distinctness (fig. 13 - below). Above the "bedding plane" we sampled in another two metres of rather hard and coarse grainstone-packstone with a rich macrofauna. The limestone contains a fair number of rudists but again very few oysters. This type of lithology would fit in with the description of Coquand's unit B and our measurements would lead to the same conclusion. Nevertheless we suppose that these more indurated calcarenites represent the top part of his unit D, because the very top of the exposure shows numerous well-preserved oysters again (fig. 13).

Our continuous sampling stopped just below this oyster level, which we think represents the base of Coquand's unit C. Altogether unit D thus would measure 12.5 metres, not eight. Either we overestimated the thickness of the

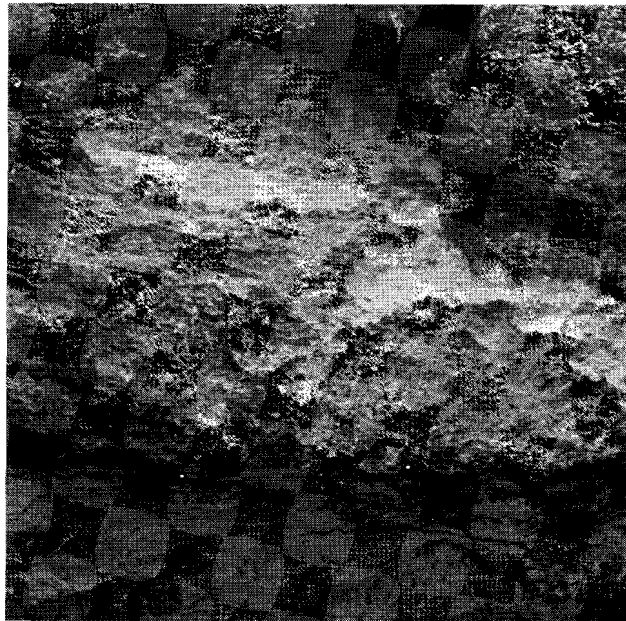
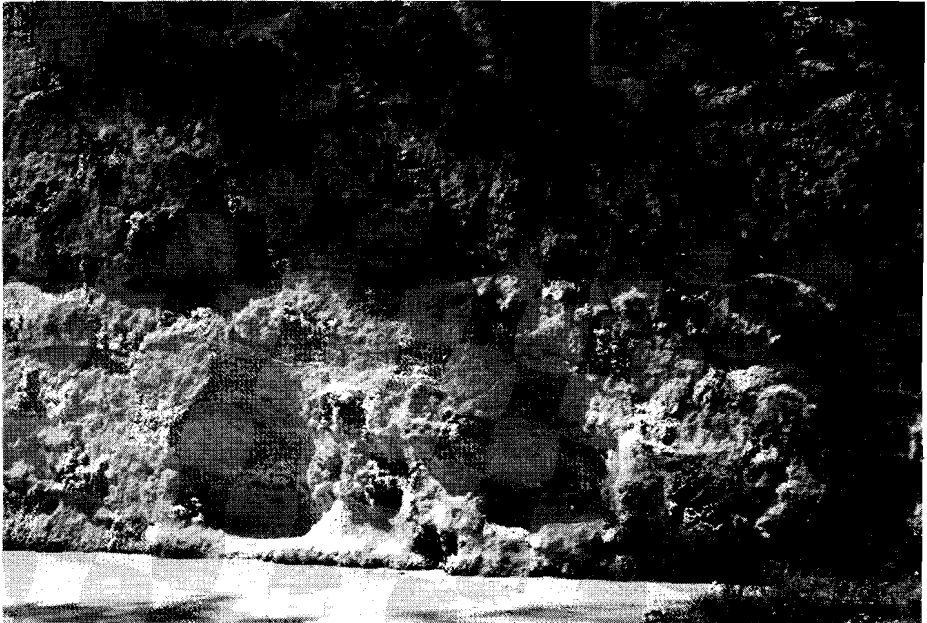


Fig. 13 Above: distinct stratification plane in the top part of Coquand's unit D, close to the hairpin in the Chemin du Château, Aubeterre. Below: the same level (arrow) further down the Chemin du Château. At the top of both exposures a concentration of *Ostrea vesicularis* shells probably marks the base of Coquand's unit C.

unit because of the strong lateral element in our sampling track, or more probably, there are fairly large thickness fluctuations, or a combination of the two.

The fact that we had difficulty in recognizing Coquand's D - C - B succession correctly is fortunately of no importance for our *Orbitoides* investigation.

There are a few small exposures, stratigraphically somewhat higher than the indurated calcarenites shown in figure 13. The only one we used corresponds to our sample FR 1883, taken along the continuation of the Chemin du Château leading from the hairpin to the D 2 (figs. 6 and 8). It corresponds in stratigraphic position with the top of the oyster member C, or more likely, it is still higher, in the basal part of unit B.

Incidentally, Coquand placed this unit B in his uppermost formation, to which he gave the name Dordonian in 1857. Since the *Orbitoides* in the uppermost sample were found to have the same assemblage composition as those in unit D lower down, we tend to follow the general practice of including unit B in the extended Campanian.

THE SECTION NEAR MESCHERS

Orbitoides-rich calcarenites are found exposed at many places along a wide strip that runs parallel to today's NW striking northern limit of Mesozoic outcrops; this limit probably reflects the northeastern margin of the former Aquitaine basin. Longer sections are scarce and at many places the Upper Cretaceous calcarenites are rather coarse and/or strongly recrystallized. In the interior of the Aquitaine basin the outcrops of Aubeterre appear to be of outstanding quality; they probably contain a much higher micrite content than the rocks elsewhere, having been deposited in a kind of depression with rather quiet sedimentation.

Only at the western limit of this outcrop-strip, along the eastern banks of the Gironde (fig. 4), do we find a series of sections of similar or even greater stratigraphic range and with comparatively good preservation. In the literature these exposures are usually referred to as the Royan cliffs after the largest town of the area, but actually they extend from Royan southwards along a series of villages and summer resorts.

We selected for our sampling a vertical section of some 14 metres near the village of Meschers (département de la Gironde), situated some tens of metres south of the southeastern end of the Plage de Cadet. At this northern end of a stretch of cliffs immediately bordering the Gironde, a stairway descends steeply to the first few of a long series of wooden shacks (*carrelets*), from which fishermen hang their nets (fig. 14).

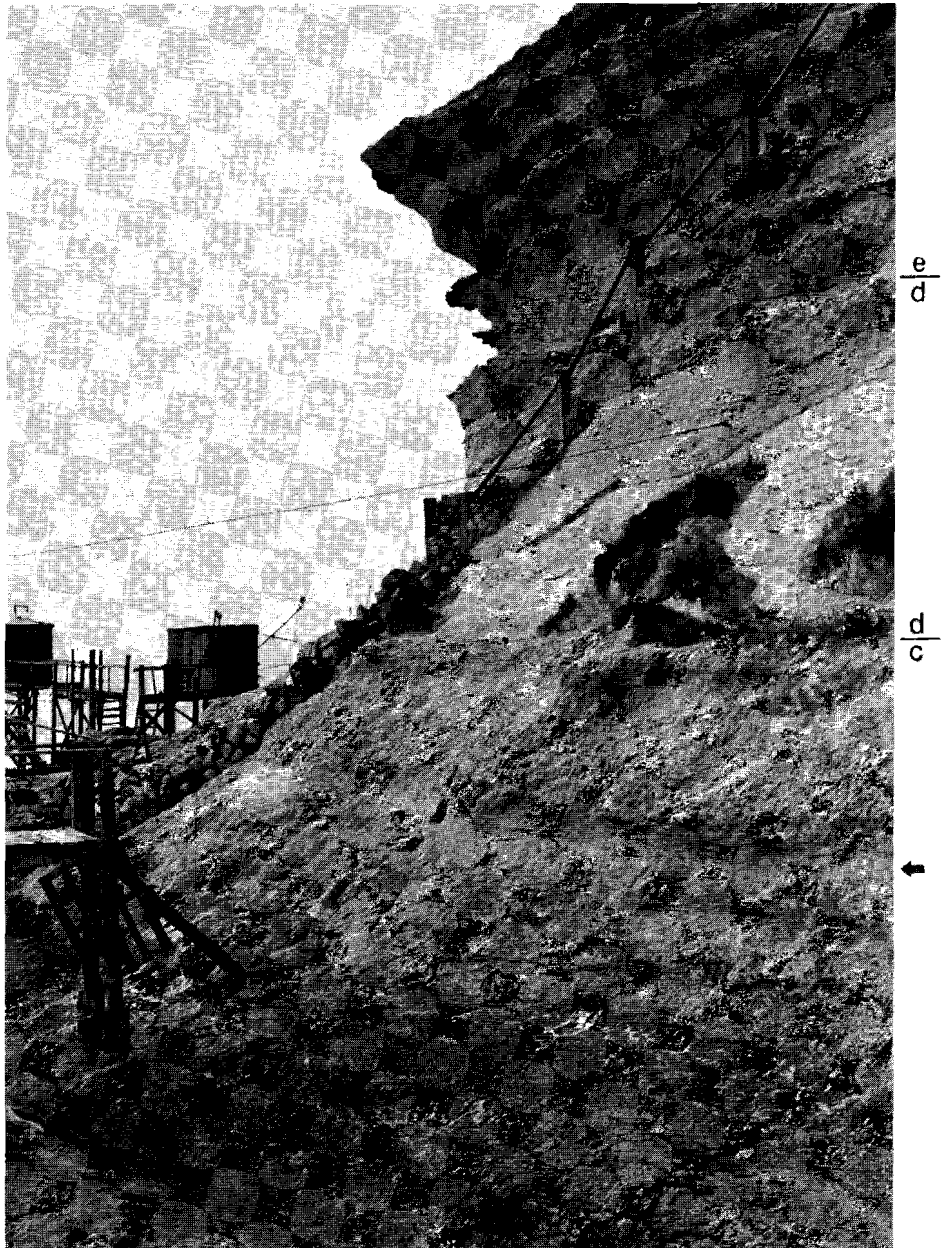


Fig. 14 The stairs going down along our section near the carrelets at the southern end of the Plage de Cadet, Meschers.

The entire section exposed here consists of Craie à *Ostrea vesicularis*, thus corresponding to the Aubeterre sections, called Campanian. Since this section is about 90 km from Aubeterre, it is self-evident that Coquand's lithostratigraphic subdivision of the Charente area is no longer valid here. We used as a reference the description of Vigneaux (1975) in an excursion guide, although this description was originally compiled for a sequence somewhat further south along the cliffs.

Vigneaux distinguished five lithostratigraphic units, which he indicated from bottom to top by the letters a to e. They were distinguished from one another amongst other things on the basis of degree of induration, differences in oyster contents and by the presence or absence of rudists. Units b and c are said to consist of an alternation of coarser and finer calcarenites; this succession with oyster debris and small oysters might be interpreted as consisting of four fining-upward sequences. In the basal part of the individual subunits oysters and their debris would be most numerous; upwards their relative quantity would decrease and very fine clastics would become predominant. Such a description suggests that there were differences in water energy during the deposition, occurring with some kind of rhythmicity. For

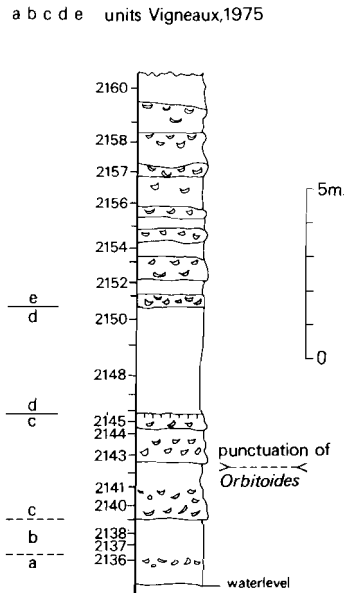


Fig. 15 Schematic lithostratigraphic section of the Campanian calcarenites near the carrelets at the southern end of the Plage de Cadet, Meschers. The approximate position of Vigneaux's units a to e is shown alongside as well as our succession of samples FR 2136 to 2160.

the purpose of our investigation we should not rule out the theoretical possibility that the lower boundary of such single subunits corresponds to an erosive interruption during the deposition. Actually, we are not really convinced of the fining-upward character of the oyster-debris beds. For the upper two grading is very poor, if present at all, whereas the lowermost sub-units are badly exposed, due to the influence of waves and tides.

In our figures 14 and 15 we give the approximate position of these units a to e. To compare our section with Vigneaux' description it was very helpful that the limit between units c and d could be recognized unambiguously; this was not true for the limits lower down in the column. Unit d consists of soft calcarenites, rich in scattered fossils and with a texture very similar to that of the soft calcarenites at Aubeterre. Actual oyster beds of rather variable thickness in the lateral sense occur only in the uppermost unit e (figs. 14 and 16).

Specimens of *Orbitoides* were found throughout the section. The level of greatest importance for our investigation, where a drastic change was found to occur in *Orbitoides* morphology, turned out to be situated in between our samples FR 2141 and FR 2143 (fig. 17). Following our earlier description

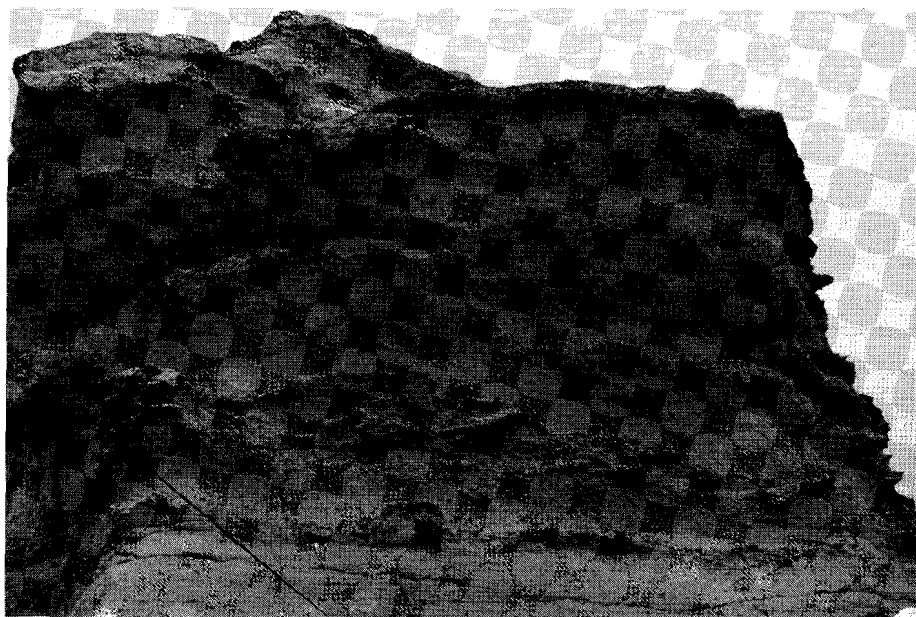


Fig. 16 Irregular oyster beds in the upper part of the Plage de Cadet section near Meschers.



Fig. 17

Part of the section at the southern end of the Plage de Cadet, Meschers, showing the position of our samples FR 2141, 2142 and 2143 and of the white layer between the two uppermost quartz debris beds in *Wignacourt's* unit c

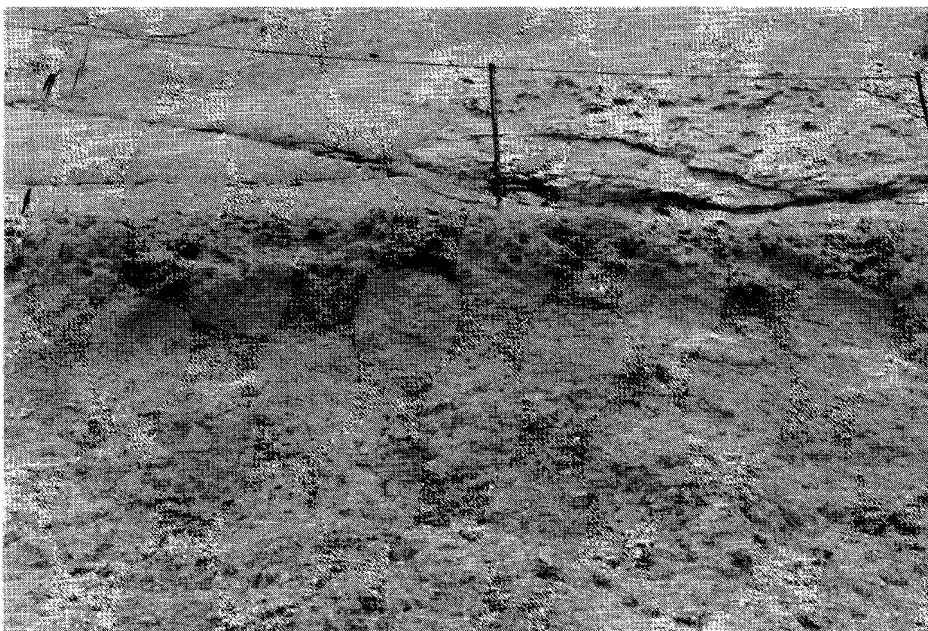


Fig. 18 The uppermost oyster-debris bed of Vigneaux's unit c near the carrelets of the Plage de Cadet, with hardground-like level at the top and complete oysters immediately underneath.

this interval might contain the base of one of the assumed fining-upward sequences, the higher of the two samples having been taken from the uppermost oyster-debris bed of Vigneaux' unit c. Oyster debris is rather evenly scattered in the lower part of this layer; near the top larger and complete oysters start to predominate and the top itself is marked by a surface which resembles a hardground at several places, though not everywhere (fig. 18).

The crucial part of the section was sampled again by the first author in 1982 in more detail. Freshly made exposures across the interval failed to show salient lithological differences that would correspond to the upward fining or to a distinct bedding plane. It must be acknowledged, however, that details of lithology are hard to verify in this lower part of our section, possibly because of the influence of tides and waves in the mouth of the Gironde. At the suspected place of change in *Orbitoides* a veneer of white and fine calcarenites is the most distinct feature; it can be followed from the position of the section in a northward direction along the entire Plage de Cadet (fig. 19). Here, some induration seems to occur underneath, so we also sampled in and



Fig. 19 The Campanian calcarenites of the southern half of the Plage de Cadet and the position of the white layer marked by arrows.



Fig. 20 Units c and d in the middle of the Plage de Cadet. The white layer is indicated by an arrow. Sampling place of FR 2302 and 2303.

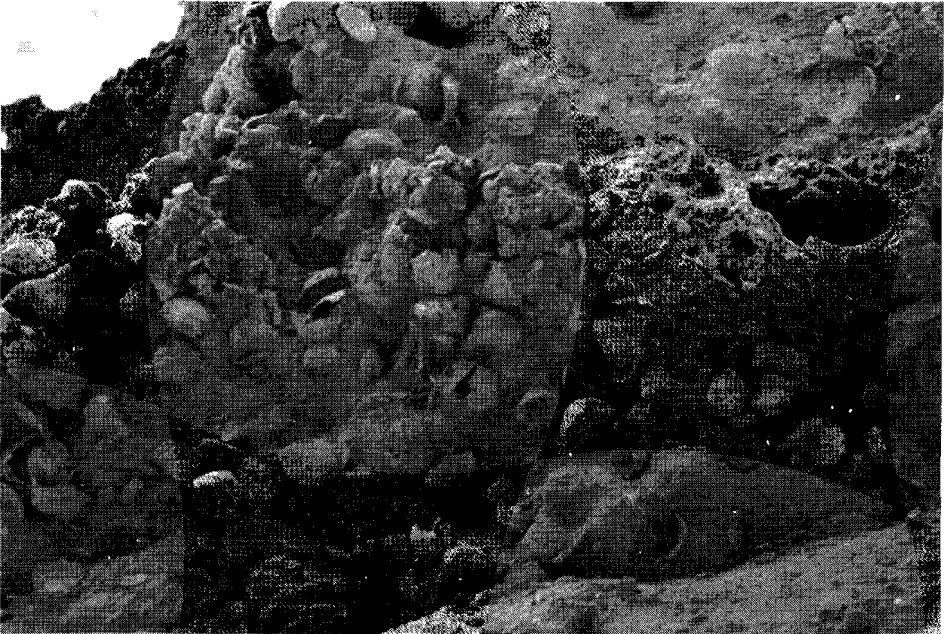
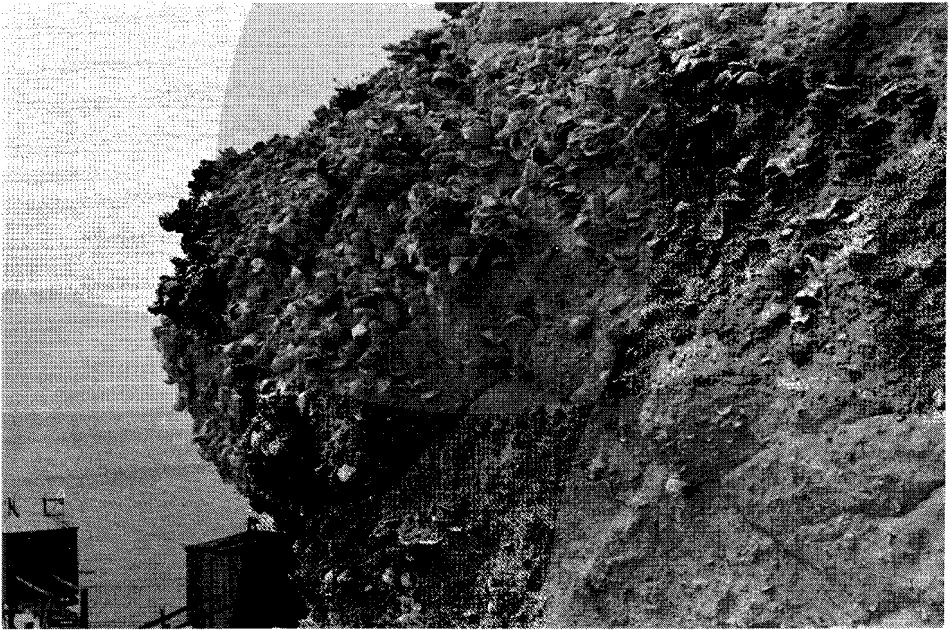


Fig. 21 Well-preserved *Ostrea vesicularis* in one of the oyster beds of unit e in the upper part of the Carrelets section at the southern end of the Plage de Cadet, Meschers.

immediately below the white layer in the middle of the Plage de Cadet (fig. 20).

As at Aubeterre, bioturbation must have been quite common during the deposition of the Meschers calcarenites. At some places there are traces of oblique bedding inside the calcarenites, especially in the finer interbeds between the oyster banks of unit e. Orientation of the *Orbitoides* and of shell debris are the main phenomena from which we concluded the obliqueness of the bedding. The oblique bedding seems to show western dips, but is not clear whether we are dealing with foreset bedding or with the infill of channels or hollows. The oysters and occasional rudists in the higher ledges are certainly in situ (fig. 21).

Altogether, the sections near the Plage de Cadet, especially their lower parts, seem to show more traces of water energy and currents than the outcrops near Aubeterre. If the abundance of oyster debris is due to intensive burrowing and not to mechanical demolition, much of this higher-energy argument is invalid, however.

ENVIRONMENTAL ESTIMATES

It is fairly easy to assign the deposits of Aubeterre and Meschers to a general, open-marine environment of warm and shallow waters with insignificant terrigenous input, so that the sediments became predominantly bioclastic. It is much more difficult to give greater precision to the environmental estimate or to explain the differences in lithology along the columns in terms of more detailed habitat composition. For instance, we do not know which were the special conditions that led to the proliferation of oysters, found in situ in some of the beds.

As far as we know, the habitat of Mesozoic pycnodont oysters (Stenzel, 1971; La Barbera, 1981), to which we consider *Ostrea vesicularis* to belong, cannot be compared with that of the Recent Ostreidae. These Mesozoic oysters are often found in reclining position in very fine-grained to muddy sediments, but we must still assume that they needed fairly clean waters because of their filter feeding habits. The rather massive appearance of the most prominent oyster beds in our sections gives the impression that the animals formed a kind of reef, although they do not usually grow fixed to each other. Even the beds with most densely packed oysters (fig. 21) still contain notable quantities of fine to very fine calcareous debris in which the *Orbitoides* are quite frequent.

Another environmental estimate is commonly obtained from the relative

frequencies of the species of smaller benthonic foraminifera. The range charts for the foraminiferal species found by Goharian (1971) at Aubeterre and in other sections of the Campanian in south-west France give the impression of an open-marine environment because of the rather large number of species, which suggests a fair diversity of fauna. Actual counts are needed to estimate the diversity better. Our attempts at species determination were hampered by bad preservation; corrosion, recrystallization and overgrowth usually obliterate the morphological details, especially amongst miliolids and arenaceous forms.

For our detailed set of samples from the section-part below the Champ de Foire in Coquand's unit F we made counts of the perforated foraminifera in the 125–595 μ sieve fractions of the wash residues on the basis of 250 specimens per sample. Because of the chosen size range the specimens of the larger foraminiferal genera are practically excluded from the counts; these mainly belong to *Orbitoides* and *Pseudosiderolites* and to less frequent *Lepidorbitoides*, *Clypeorbis* and *Omphalocyclus*.

Since our primary aim in the counting was to gain insight into the environment we did not spend a great deal of time on correct species determination for all forms we encountered (see chapter VII). Owing to the poor preservation we had to make some admittedly heterogeneous counting groups, such as *Rotalia trochidiformis*, *Gavelinella* cf. *G. bosqueti* and *Cibicides* sp. The quantitative data, expressed in percentages are shown in figure 22.

These percentage data show that there are no real differences in the composition of the faunas of perforate benthonic foraminifera. This fact indi-

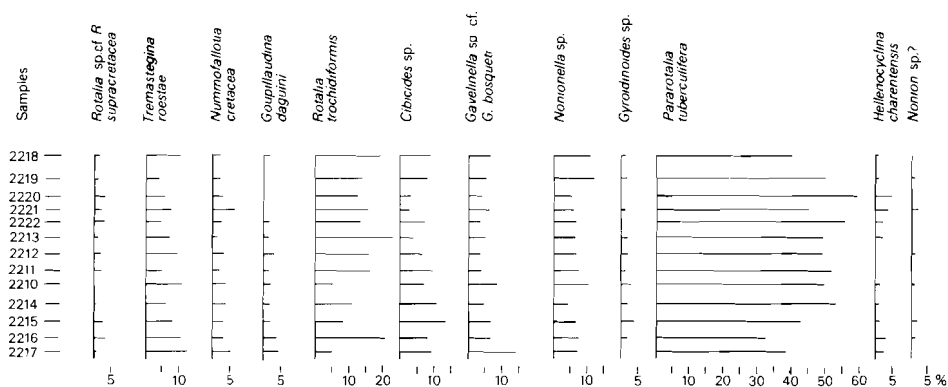


Fig. 22 Percentage values of the most frequent species of benthonic foraminifera in the sample suite of the detailed section below the Champ de Foire, Aubeterre.

cates that our section-part contains no notable changes in environment. A rapid survey of samples from other parts of the Aubeterre calcarenite succession showed that this statement is valid for the entire Coquand series F to B.

The samples FR 2210 and FR 2211 appear to be of special importance for our reconstruction of the history of the *Orbitoides* (see chapter V), and it is especially for this level that we are keen to know whether there could have been an environmental overthrow or a gap in the record. Only *Tremastegina roestae* and *Rotalia trochidiformis* show some difference in relative frequency from FR 2210 to FR 2211, but the calculated percentage values fit in within the ranges observed for the entire set of samples. We can safely conclude that the faunas of these two samples do not reflect markedly different habitats.

Figure 22 also shows that we are not really dealing with a highly diversified fauna, because the associations are dominated by very few taxa. *Pararotalia tuberculifera* constitutes about half of the faunas, while *Rotalia trochidiformis*, *Tremastegina roestae*, *Cibicides* sp., *Nonionella* sp. and *Gavelinella* cf. *G. bosqueti* account for another 40 per cent. These results are not seriously affected by the category "miscellaneous" (i.e. all other, rare species which together never exceed 6%), which was not included in the counts. Whatever index we choose to use the diversity is evidently not as high as we thought it to be from the more qualitative frequency data given in the range charts of Goharian (1971).

The paleoecological interpretation of this rather unbalanced fauna cannot be detailed because there are no connections with the Recent faunas and we did not come across well-documented environmental analyses of similar Cretaceous faunas. Certainly we are dealing with a shallow marine, warm water fauna that lived in the photic zone. Although we cannot assert that any of the species were really epiphytic, it is quite certain that we are dealing with an association living on and in between a well-developed rooted vegetation on a carbonate platform. The large numbers of miliolids and of bryozoans seem to point in the same direction. One might be inclined to assign a lagoonal character to the environment because of the very high numbers of rotaliids and miliolids, but we could easily be dealing with a vast vegetated platform in a wide, open embayment, where excess evaporation caused salinities to be slightly above normal.

Thin-sections were made for all samples of the Champ de Foire section. The sediments appear to range from mudstones to more frequent bioclastic foraminiferal wackestones to packstones. Amongst the foraminifera miliolids as well as simple and more complex arenaceous forms seem to be more fre-

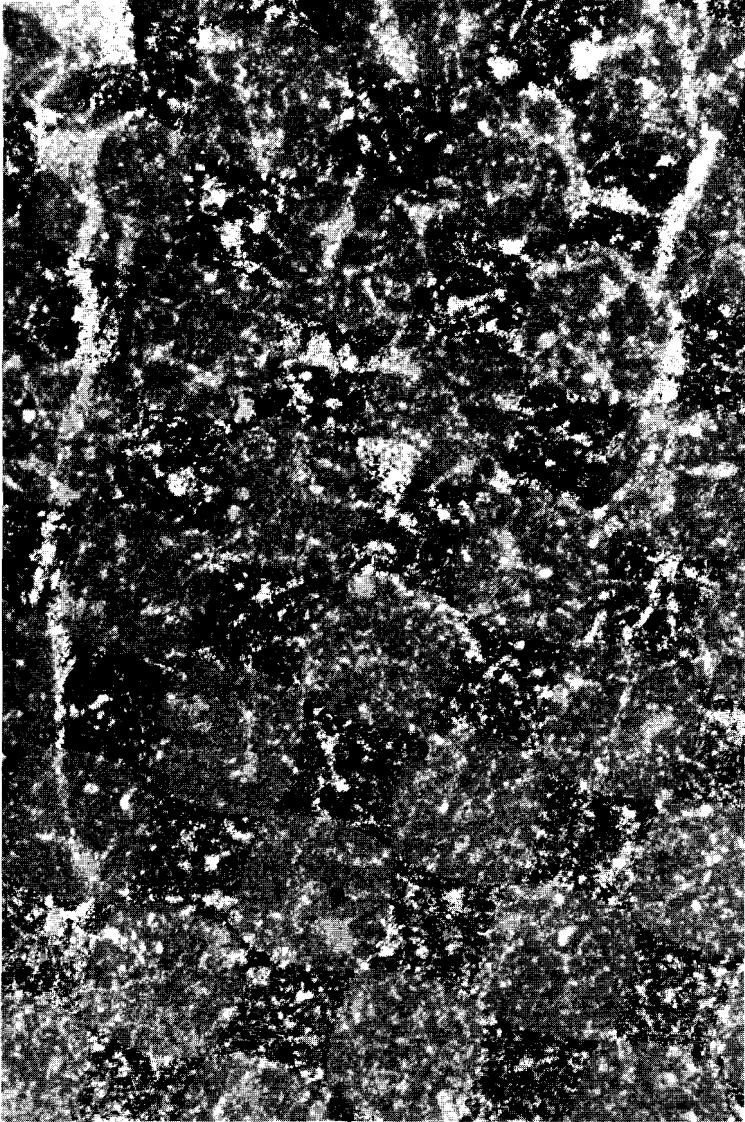


Fig. 22a Mudstone with branching, sparite-filled veins; presumed root-level of marine grasses. Section Champ de Foire, Aubeterre, sample FR 2216. X 100.

quent than we estimated from the wash residues, but perforate species remain to constitute the most numerous elements of the three groups. Amongst the other bioclasts bryozoans and coralline algae are most common as well as pelecypod (mainly oyster) and echinoid fragments. Calcareous worm-tubes occur as well. Particularly because of the abundance of corallines and encrusting bryozoa, this association reminds us of that known from modern seagrass-meadows. A striking difference might be the absence of smaller gastropods in the Cretaceous calcarenites, for these animals are really abundant in recent meadows of *Posidonia*, *Cymadocea* and *Thalassia*. Possibly dissolution played a role; preferential demolition by burrowers and bottom scavengers is difficult to understand.

The various bioclasts are embedded in a variable, but generally high, content of calcareous mud, i.e. of primary micrite. Micritization of the skeletal fragments seems to have been of minor importance. Bioclasts are often mud-filled, foraminifera are occasionally glauconite-filled. Black pigmentation which is probably of early diagenetic origin is especially common in the peripheral parts of bryozoan colonies. Most calcarenites have been modified to some extent by pseudosparitic diagenetic alteration and by secondary solution voids. Some mudstones show a remarkable pattern of minute, more or less branching, elongate voids, partly filled in with sparite. In one section the longer and larger of these veins tend to be parallel (fig. 22a).

The originally high content of carbonate mud may be explained by the baffling action of a dense subaqueous vegetation. Pigmentation of bioclasts due to iron and manganese sulphides points to anaerobic conditions below the sediment-water interface, a phenomenon known from similar Eocene to Recent carbonate muds (Setiawan, 1983; Broekman, 1984). Decomposition of plant-tissue is considered to be responsible for this process. Although the origin of the void-dissected mudstones is puzzling, one wonders whether the parallel veins could be remnants of original root-levels of the vegetation.

Composite mud clasts were observed mainly in the indurated layer of the section we examined in detail; the layer seems to contain somewhat less mud than the less hardened calcarenites. These differences between the indurated and the softer calcarenites are so small, however, that another observer might not reach the same conclusion.

However, a lesser original content of calcareous mud at certain levels may explain the preferential position of the secondary induration in the sequences, which led to the rather irregular concretionary levels; such levels occur especially in Coquand's units F and D (figs. 9 and 34). It should be noted that none of the indurated layers of Aubeterre has a hardground char-

acter. In contrast, there are some strongly cemented layers with a sharp lower boundary. One is found well below the first oyster bed at the lower end of the Chemin creux (fig. 23). Another distinct plane with indurated limestone beds above occurs within the higher part of Coquand's unit D, in the upper part of the composite section (fig. 13). At both places the sharpness of the plane has a very local character and at the Chemin creux the plane shows "pressure-cleavage" in the calcarenites underneath (fig. 24). It is likely therefore that the cementation in these cases is a consequence of rather subrecent diagenesis.

Although oyster beds commonly appear as ledges in the outcrop walls (figs. 16 and 21), their matrix is usually not so strongly cemented. Lower boundaries are frequently more gradual in character than the upper limits. There is no distinct preferential orientation of the oysters, probably because of intensive burrowing during the accumulation of oysters and matrix.

The two "bedding" planes in the Aubeterre section (figs. 13 and 23) are the major indications in the sediments for possible interruptions in the continuous deposition. One can imagine that they correspond to erosional spells



Fig. 23 Sharp lithostratigraphic boundary with indurated calcarenites above, situated stratigraphically more than a metre below the lowermost oyster bed of unit F. Southern side of the lower end of the Chemin creux, Aubeterre. This plane is not distinct in the opposite exposure shown in more detail in figure 9.

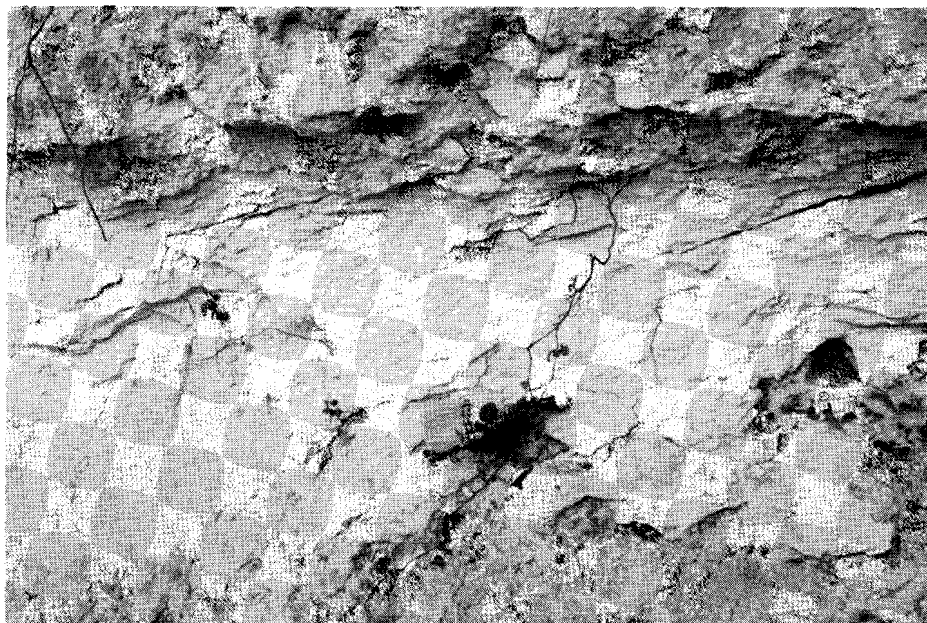


Fig. 24 The sharp lithostratigraphic boundary of figure 23 (above) with detail of the cleavage (below).

of local character, followed by sedimentation of somewhat coarser debris; the latter sedimentation type may be responsible for the later cementation. Otherwise the sequence of calcarenites of Aubeterre seems to witness to more or less continuous sedimentation, although the obvious role of bioturbation must have added to the poor layering.

Sedimentation without any notable interruption was valid for the entire type section of the Campanian. Probably there was no more than a shallowing and acceleration of the sedimentation rate during the transition of the glauconite-rich fine calcareous muds of unit G to the cleaner and somewhat coarser higher units with abundant *Orbitoides*.

The larger foraminifera furnish one more faunistic indication about the relative depth of the environment. The abundance of *Orbitoides* and the scarcity of *Lepidorbitoides* in the Aubeterre calcarenites support the assumption that we are dealing with the shallower part of the photic zone. In this context it is worth mentioning that *Lepidorbitoides* are fairly common only in part of unit F, which is actually the part that corresponds to the detailed section of the Champ de Foire. In the Meschers section the genus is practically absent. Probably the Gironde site was shallower throughout the Campanian.

In addition to the environmental variation along the stratigraphic column we are faced with the remarkable combination of fairly shallow depth (rotaliids predominant. *Orbitoides*, channels or blow-outs (Broekman, 1984); so probably a depth of less than 50 metres) and a high original micrite content of the calcarenites. If we suppose that organic decay and micritization played a subordinate role, it can be assumed that the area was nearly constantly covered by a dense subaqueous vegetation which trapped most of the mud and obstructed the winnowing effect of waves and local currents. Such water movements occasionally caused channelling, but we presume that in the Aubeterre area the infill of such depressions was not affected primarily by sedimentation from horizontal transport but that after each local erosive spell vegetation probably immediately took possession of the depressions again. This might explain why the *Orbitoides* are so well scattered. Bioturbation may have been responsible for the even dispersal in the example of figure 25, but it is less likely to have caused the absence of concentration of the *Orbitoides* in the irregularly bedded calcarenites of the Chemin creux (fig. 26, upper figure). Concentration of larger foraminifera or of shell debris in distinct, thin veneers, which would point to stronger bottom currents, winnowing and the formation of lag deposits, was not found anywhere in the Aubeterre area.

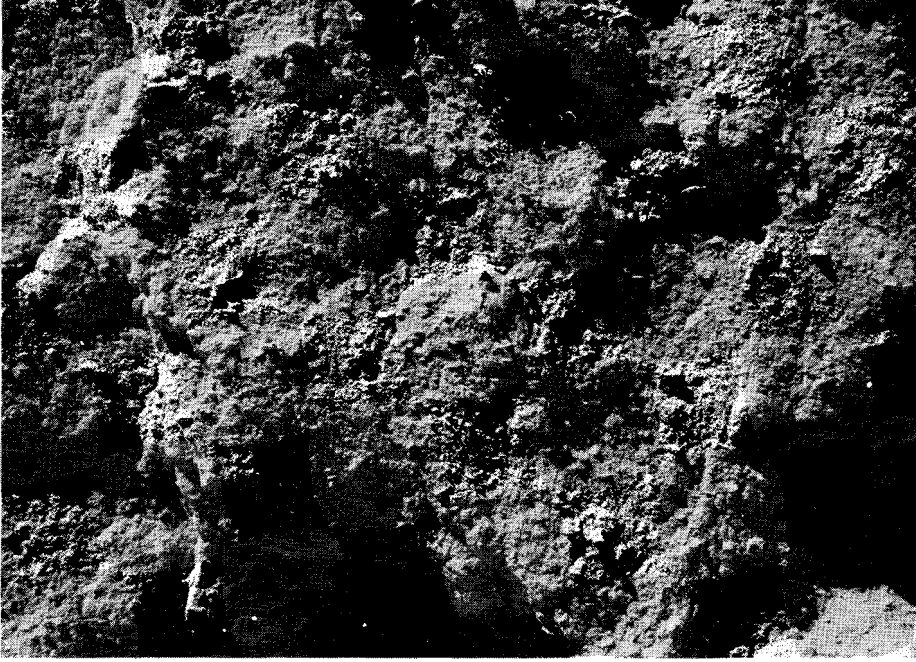


Fig. 25 Scattered *Orbitoides* and shell debris in the calcarenites of the upper part of Coquand's unit D; Chemin du Château, Aubeterre; detail of figure 13 (above).

Possibly we must imagine that the major part of these calcarenites were formed in large, vegetated depressions of the carbonate platform, in which area the somewhat more elevated parts with less constant presence of suspended mud were inhabited by numerous oysters, which thus indeed formed some kind of reefs.

We are well aware that our environmental interpretation is little more than guesswork. We have a general idea, though, in which kind of environment the *Orbitoides* flourished. And apart from two distinct, but local, "bedding" planes in the sequence we have very little evidence that our *Orbitoides* at Aubeterre did not leave an unbroken record of supposedly about one million years (duration estimated from figures 21 and 24 of Wonders, 1980). Since they are continuously present over some 40 metres we can assume that they could have lived in the area without interruption; so we cannot reject the hypothesis that we are dealing all through the time span of the major part of the type section of the Campanian with the development of a local or regional stock.

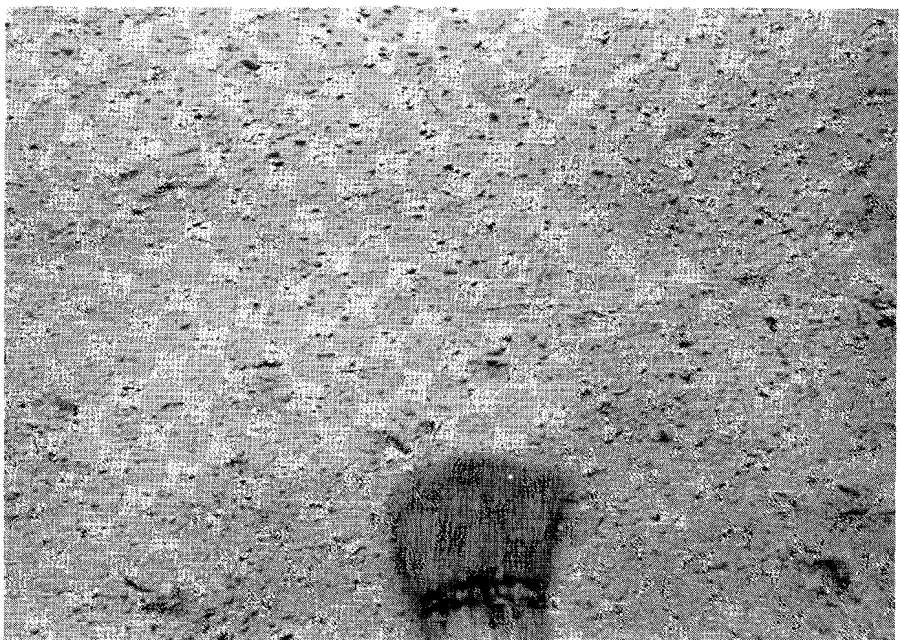


Fig. 26 Evenly disseminated *Orbitoides* individuals and shell debris at two places in the basal part of unit F; lower end of the Chemin creux, Aubeterre.

For our study of evolution of these larger foraminifera the Aubeterre section seems to provide an ideal case history. If we wish to rely on the description of the less well-preserved lower part of the Meschers section, in which oyster debris is much more common, it is possible that at this place currents and winnowing played a more important role. The near-absence of *Lepidorbitoides* in the Meschers section lends independent support to this conclusion of shallower depth.

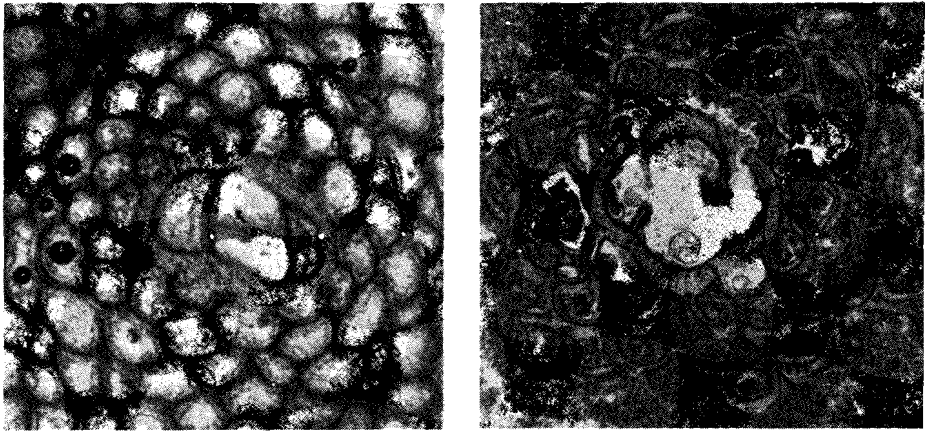


Fig. 27 The dark lining in the walls of embryonic and nepionic chambers in two *Orbitoides* individuals in median section.

Chapter IV

METHODS AND PARAMETERS

Whenever necessary the field samples were crushed before washing and sieving in order to free a sufficient number of larger foraminifera from the adhering sediment. We picked the *Orbitoides* specimens from the > 2 mm and, if necessary, from the 0.5–2.0 mm sieve fractions in order to obtain at least 25 good median sections per sample. We did not measure test diameter and thickness because of the bias involved in our selection procedure. In general, we had the impression that the size of the animals did not show any notable change along the stratigraphical columns.

As far as the thin-sections of the *Orbitoides* individuals are concerned some further bias may result from our selection procedure because we found that individuals with a well-preserved exterior commonly yielded better thin-sections.

Really well-preserved specimens permit reliable observations to be made on the initial stages of the test in half-sections and even after mechanical splitting. However, for recrystallized individuals thin-sections are needed to obtain satisfactory observations. In order to make the type of observations comparable for all samples, thin-sections were made for all specimens. We had to make these sections really thin to be able to observe the dark lining in the lamellar walls of the early chambers (fig. 27). This dark lining is used as a diagnostic feature to distinguish between epi-auxiliary chambers and spiral chambers around the embryo, because often stolons are not visible. The percentage of sectioned specimens per sample, in which all parameters wanted could be measured or counted, varies from 50 to 100; in most samples it is about 80.

The thin-sections were studied under a Leitz microscope with drawing equipment using transmitted light. The embryo and peri-embryonic chambers were drawn with a magnification of 130. Peri-embryonic parameters were established from the drawings; embryonic dimensions were measured directly under the microscope using an ocular micrometer. Precision of the micrometer-scale is $5\ \mu$, which results in a maximum measuring error of $10\ \mu$ for the dimension parameters.

THE PARAMETERS

In his 1966 paper Van Hinte introduced a set of size and configuration

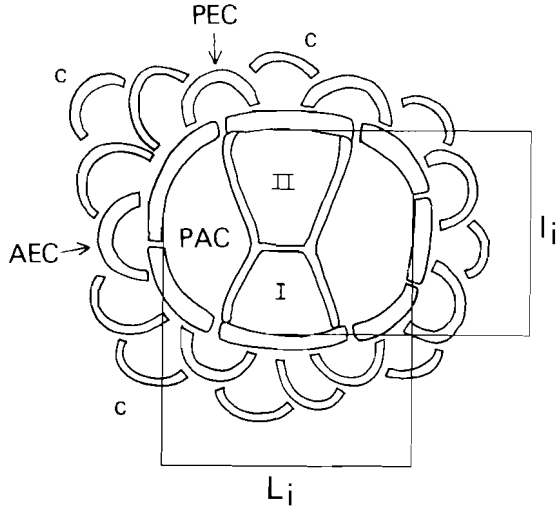


Fig. 28 Schematic drawing of the embryonic-neponic stage of an *Orbitoides* individual in median section. I protoconch, II deuteroconch, PAC principal auxiliary chamber, PEC principal epi-auxiliary chamber, AEC accessory epi-auxiliary chamber, c closing chamber. $E = 7$, $P = 18$.

parameters relating to the four-chambered embryo and to the peri-embryonic chambers. For the sake of comparison we followed his scheme for the most part; see our figure 28 for further information about the parameters.

The largest diameter of the embryo (if not too seriously deformed; see fig. 27-left) was measured in two directions. One (l) is along the line through the centres of the intra-embryonic chambers that are thought to correspond to the original protoconch and deuteroconch; the other (L) is the largest diameter along a line perpendicular to the previously mentioned line, and thus across both principal auxiliary chambers (PAC) that are found incorporated in the embryo. Along both lines we measured the inner (l_i , L_i) and outer (l_o , L_o) diameters. L values are invariably larger than the corresponding l values. Following Van Hinte we used mainly the inner measurements for our further computations. They appeared to be the more reliable ones since they are based on the dark lines at the inner side of the embryonic walls. From these primary measurements we calculated the following parameters:

L_i/l_i as a measure for the sphericity of the embryo. Since l_i is the smaller of the two the ratio values are always larger than unity. In terms of means of the ratio we expect an evolutionary decrease to the value 1; in practice the lower limit for this mean appears to be 1.1.

$(L_i + l_i)$ as a measure for the size of the embryo. The increase of this parameter in the course of time will be dealt with throughout the rest of this paper.

$t = (L_o - L_i + l_o - l_i)/4$ as a measure for the average thickness of the embryonic walls. The large measuring errors relative to the t values play such an important role that we refrain from drawing more than tentative conclusions from the means of this parameter.

The configuration of the peri-embryonic chambers in the oldest *Orbitoides* s.str. species consists basically of four principal epi-auxiliary chambers (PEC), the walls of which originated around blobs of protoplasm that were extruded through the basal stoloniferous openings of both principal auxiliary chambers inside the embryo. Occasionally we found there were only three, and even two, instead of four chambers because the protoplasm from two adjoining stolons had evidently coalesced, or more rarely simply because one of the four chambers seems to be missing. Through the basal stolons of these four epi-auxiliary chambers eight spirals of inter-auxiliary chambers are formed that encircle the embryo, meeting from opposite directions in four closing chambers. In the course of evolution accessory epi-auxiliary chambers (AEC) which also have direct connections with the lumen of the embryo tend to develop on the PAC walls of the embryo. They cause the number of peri-embryonic spirals to increase at the same rate as the number of epi-auxiliary chambers increases. In the final stages of the lineage these spirals tend to consist only of closing chambers in between the epi-auxiliary chambers.

The parameters of the peri-embryonic stage which we used for our investigation are:

E, which is the number of epi-auxiliary chambers: PEC + AEC.

P, which is the total number of peri-embryonic chambers.

E/P, which is used as a measure for the number of growth steps (also called budding steps) until the animal attains the stage of radial growth. E/P values are inversely related with the mean number of budding steps of all peri-embryonic spirals (mC), as calculated by Van Hinte. Calculation of our parameter is less laborious and E/P appears to tell us just as much about the changes in nepionic configuration as does mC.

We did not use any parameter derived from the later median chambers or from the lateral complexes.

With regard to the general concept of nepionic acceleration, E is considered to be the most important parameter in *Orbitoides*. Because E is the expression for the sum of the chambers originating directly from the embry-

on, the \bar{E} values are expected to show an increase upwards in the stratigraphic columns. Furthermore we expect to find a decrease in the mean values of E/P ; this ratio is our measure for the number of budding steps that are required until the animal attains the morphological stage of radial growth. Theoretically \bar{E}/\bar{P} is expected to increase to a maximum of 0.5, which means that there are only closing chambers left in between the epi-auxiliary chambers. The average number of budding steps has then been reduced to five if there are already three such steps in the construction of the embryo. Since the values of P play a role in this E/P ratio, this parameter is of importance too, although it is not clear a priori, whether an increase or a decrease in this total number of peri-embryonic chambers deserves to be called nepionic acceleration. We are of the opinion that neither of the two modes of change can be related to this evolutionary principle.

Actually, the nepionic configuration in our *Orbitoides* associations, expressed in \bar{P} (and in \bar{E}), is considered to be similar to that of the final stages of the evolution in some other orbitoidal lineages (e.g. *Discocyclus*, *Lepidocyclus*), in which the augmentation in the number of peri-embryonic chambers can be interpreted to a large extent as a direct consequence of the overall size increase of the embryo (Drooger, 1974; Fermont, 1982).

In such theoretical constructions of evolution the trend towards greater embryo size is thought to be the primary one, and if the peri-embryonic chambers do not show a proportionately equal size increase, we expect that they had to increase in numbers. If, furthermore, the values of E remained stable, it is P that would show the increase; this is unlikely because it would lead to an evolutionary \bar{E}/\bar{P} course of decreasing values, opposite to the course predicted by the principle of nepionic acceleration. In order to maintain a stable number of budding steps until the animals attain radial growth, we therefore expect that the increase of $(L_1 + l_1)$ will be followed by an increase in both E and P . If it is believed that nepionic acceleration had to continue somehow, we expect the increase in E to be proportionately larger than in P ; as a consequence E/P will tend to attain higher values. This actually appears to be the overall result of what happened in our example of *Orbitoides* evolution, but our detailed record has to show whether this is in fact the precise course which was followed. And moreover, our data set has to provide the evidence to support the theory that nepionic acceleration of the type encountered in *Orbitoides* (belonging to the third phase of nepionic development in the characterization of Drooger, 1984, fig. 2) really followed a primary change in the size of the embryo.

DATA PRESENTATION

Since our story is not constructed in the usual way and does not proceed from individual observations to derived data and conclusions, we shall refer first of all to the various ways in which our data are presented and handled.

In figures 53 and 54 the numerical data on E, P and $(L_i + l_i)$ are compiled in histograms and bar diagrams for the individual samples of the main composite section of Aubeterre and the main section of Meschers, respectively.

For every parameter, we calculated per sample the mean and its standard error. For most sections these data are shown in tables 4 to 8 at the end of the paper. These tables also give the numbers of observations per sample as well as the coefficients of variation for E, P and $(L_i + l_i)$ (tables 4–7 only). Means and their standard errors are presented in the following chapter for all sections in a series of drawings (figs. 29, 30, 32, 36, 37 and 40).

Correlation coefficient values for six (five in table 11) parameter combinations in the separate samples are given in tables 9 to 12. The bivariate scatter plots of figures 44 and 46–52 illustrate the parameter relations for a small number of selected samples.

The graphical presentation per section of the means and their standard errors gave us the general idea about what further statistical treatment we needed for our data sets. The data for the longest section available, i.e. the composite main section of Aubeterre (fig. 29), show that a distinct pulsating pattern with fluctuations of the magnitude observed for *Planorbulinella* (fig. 1), is not present in our *Orbitoides* example. Instead we see a mildly oscillating zigzag course in the mean sequences of all parameters and only a few cases in which the difference between successive samples is on or slightly beyond the verge of statistical significance. In addition, there is one very marked leap or punctuation that can be observed for most of the parameters; the statistical significance of this change hardly needs to be calculated.

For these reasons we did not base our comparisons of individual samples – whether stratigraphically successive or not – on the sum of the three statistical tests used for the *Planorbulinella* data, i.e. an F test and corrected median and Wilcoxon tests. Instead, we applied only the Student's t test, being well aware of the fact that better tests are available, especially for the lower part of the stratigraphic column in which we find very narrow and skewed distributions of E.

Since both stratigraphic parts of the Aubeterre section, i.e. below and above the morphometric discontinuity level, when appreciated visually show no more than stasis from the evolutionary point of view, we furthermore calculated so-called grand means (mean of means, not of all individuals to-

gether) to obtain t values for the differences between both parts of the section. We also made an evaluation of the difference between the means of each single sample and the grand means of the suites to which the particular sample belongs.

Although several different types of calculation were carried out which might be regarded as statistical tests for establishing trends for the entire section as well as for its so-called stasis parts, we shall not reproduce them, for the simple reason that visual inspection of the relevant figures already shows that the absence of positive results for these separate section parts of the column is what might be expected from the outset. And the obvious difference between bottom and top of the entire section certainly does not fit to any theory of a fairly gradual trend. The lack of independence of the parameters and the theoretical time series effect (see M.M. Drooger, 1979, 1982) are additional reasons why we will refrain from a lengthy but dubious discussion of trend analyses.

SUBJECTIVITY AND BIAS

Especially when preservation of the morphological structure visible in thin-sections is not good – which is frequently the case in our *Orbitoides* – subjective interpretation may lead to systematic differences in the numerical assessment made by different observers. This is especially true for the observations on the factor E which depend entirely on the correct reconstruction of the curvature of the walls of the peri-embryonic chambers. We became well aware of the marked differences in the numerical expressions of the observations when groups of students were required to analyze the same series of thin-sections.

We did our best to reduce the amount of subjectivity by having nearly all observations made by a single person, the second author. Exception had to be made for the control section of Meschers, for which we entered the numerical data of a single person again (Van Haeringen).

Since the punctuation in *Orbitoides* development is based on a really large difference in \bar{E} , we assume that the subjectivity factor is entirely overruled by the magnitude of the actual change.

Chapter V

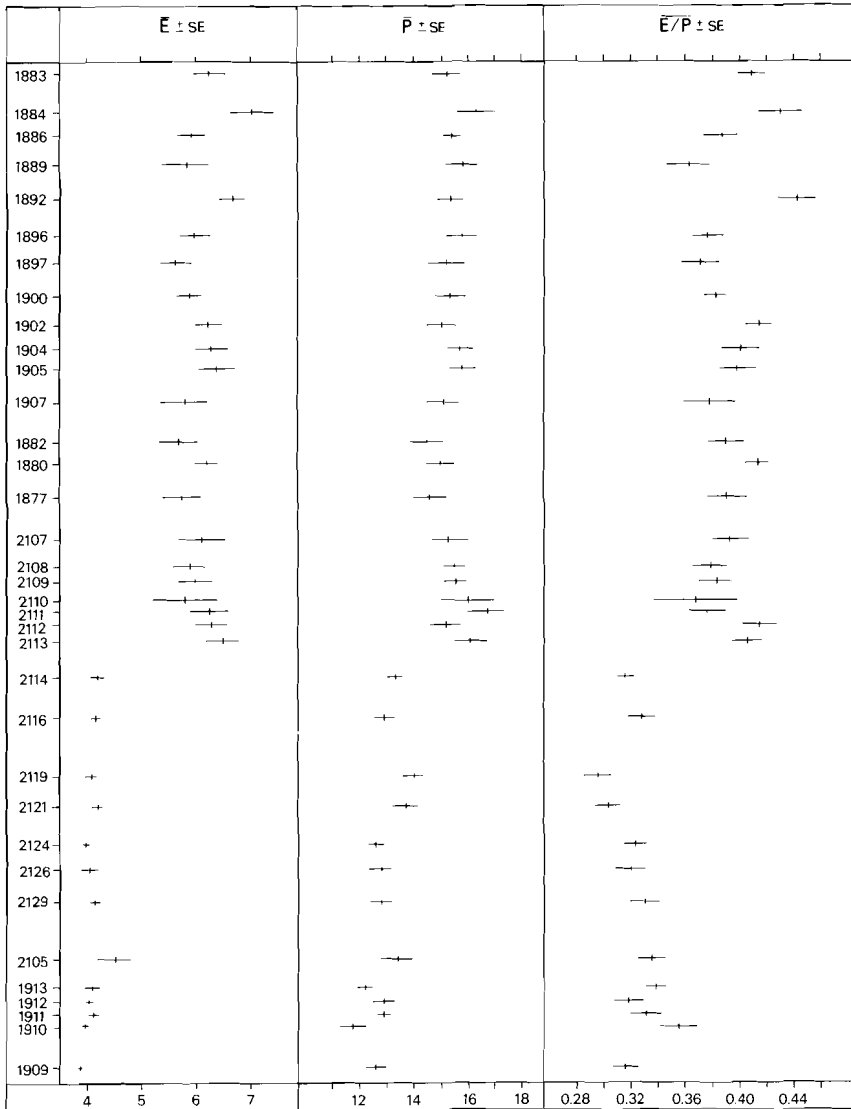
THE BIOMETRICAL DATA

THE MAIN AUBETERRE SECTION

The composite stratigraphic main section of Aubeterre, consisting of the partial sections Chemin creux, Église Monolithe and Chemin du Château (fig. 8), certainly gives the required detail on the basis of the 35 samples we analyzed. Although there were many more samples because our original sample spacing was about 50 cm, the results derived from the 35 shown in figure 29, show that very little new information was to be expected from the data on the samples in between those already analyzed. As a consequence we did not expand our data sets for the stasis parts of this column.

When we compare the lowermost and topmost *Orbitoides*-bearing samples the overall result is in perfect harmony with the principle of nepionic acceleration. \bar{E} is found to increase from less than 4.5 to about 6.5, \bar{P} changes from 12.5 to close to 15.5, and \bar{E}/\bar{P} increases from about 0.32 to values close to 0.42.

Without any further calculation it is obvious from the graphical presentation of the succession of means in figure 29 that there certainly was no consistent trend or sustained change for any of these parameters from bottom to top of the Aubeterre column. The visual impression strongly suggests that there are two different, but successive parts of the section, within each of which there seems to be no trend or net change whatsoever. The rather weakly staggered pattern of the parameter-mean values along both parts of the stratigraphic column is little more than a zigzag line. We might expect such a course to be based on the binomial errors which are normally associated with calculated means of statistical samples taken at different places from a group of populations that had identical morphometrical characteristics. If we consider the \bar{E} values there are a few cases where differences between samples are so large that the null hypothesis of no difference has to be rejected with probabilities of 0.9 to 0.95, but no more (FR 2113-1877, 1892-1889, 1886-1884). Changes are either way and often between samples that are fairly well separated in the stratigraphic column. A similar degree of difference can be noted in some combinations for \bar{P} and for \bar{E}/\bar{P} , but there is no sample combination for which all three parameters jointly show a difference which is on the verge of statistical significance. Furthermore, we certainly cannot claim the observed differences to be of the same order of



magnitude as the clear pulses in the *Planorbulinella* sequence of samples. A weak expression of a random walk, superimposed on a fundamentally stable course is the maximum we can claim for each of the two parts of the stratigraphic column.

In between both parts of the section, in each of which there is a nearly

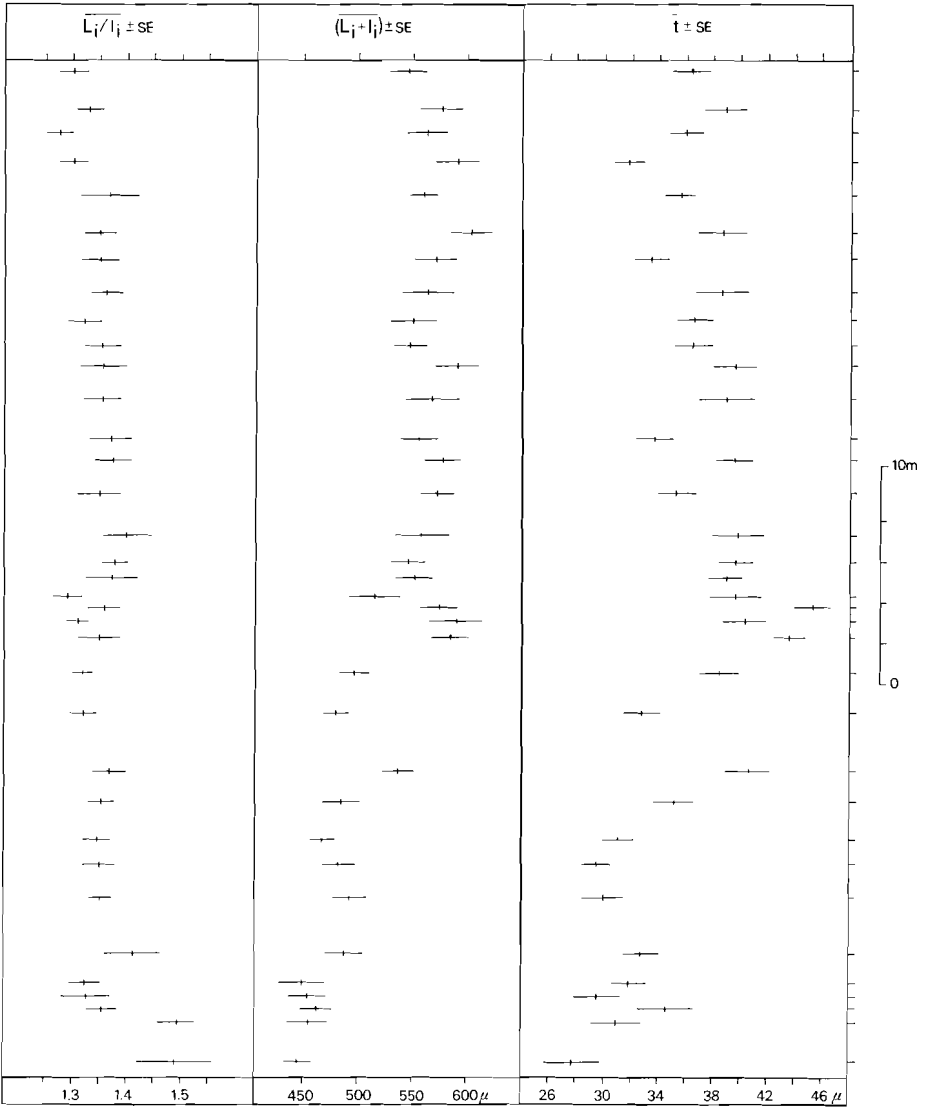


Fig. 29 The sequences of mean values with their standard errors for the internal *Orbitoides* parameters in the samples of the main composite section of Aubeterre.

constant morphology, we observe a sudden, large change in the mean values of all three peri-embryonic parameters. This change is in such a direction that it would substantiate the concept of nepionic acceleration, i.e. it has a direction which is in accordance with the evolutionary course that is commonly believed to be an adaptive response of orbitoidal foraminifera to their

environment. This very large change occurs between samples FR 2114 and FR 2113. These two samples were taken in the Église Monolithe partial section at a stratigraphic distance of 1.30 metres, and from sediments which in the field show no obvious difference in lithology.

In between these samples FR 2114 and FR 2113 we have to accept a major morphological discontinuity or a very rapid change in the suite of means for all three parameters pertaining to the peri-embryonic configuration (E, P, E/P). The leap is of such magnitude that it is undoubtedly the same as the one recognized by Baumfalk and Fortuin (1981) and to be found already in the data of Van Hinte (1966).

With regard to the embryonic features, the succession of mean values of the shape parameter L_i/l_i shows a change from 1.48 in the lowermost two samples to approximately 1.30 in the four highest samples of the Aubeterre section (fig. 29). This change is in accordance with the expected increase in the sphericity of the embryo. Upon closer inspection we see that this effect is due almost entirely to the high values for these lowermost two samples. From FR 1911, the third sample from below, up to the top of the section, $\overline{L_i/l_i}$ values show a zigzag pattern around some kind of stable main course or grand mean. Again the entire section shows no sustained change, but rather a sudden pulse followed by a long period of rather stable morphology. The rather large and significant change in $\overline{L_i/l_i}$ occurs much lower down in the column than the jump in the peri-embryonic features; at the latter level the average of the sphericity parameter remains intact.

The embryo size parameter $(\overline{L_i + l_i})$ also shows a distinct increase from bottom to top in the composite Aubeterre section. We recognize a strong increase between two of the samples, and for this parameter mean the change occurs again between samples FR 2114 and FR 2113, the level at which we also observed the notable changes in \overline{E} , \overline{P} and $\overline{E/P}$. The rest of the pattern of means of $(\overline{L_i + l_i})$ shows some more differences, however. After another two samples above FR 2113 with comparably high values of around 580μ , the $(\overline{L_i + l_i})$ value drops to some 520μ , after which the mean values for the size of the embryo seem to remain on a zigzag course around a possibly stable average population mean of about 560μ . For the samples below the morphological discontinuity at FR 2114-2113 one can calculate a significant positive trend in $(\overline{L_i + l_i})$, which goes from about 450μ to 500μ . On this course there is one notably large positive (and subsequent negative) pulse corresponding to sample FR 2119.

For the entire section the mean wall thickness of the embryo, t , shows a pattern comparable to that of $(\overline{L_i + l_i})$, though more strongly oscillating; both sequences of means show a good positive correlation.

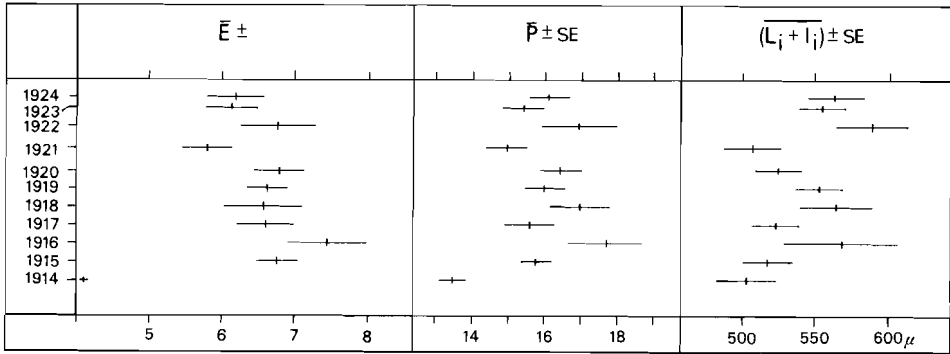
In summary, the composite main section of Aubeterre appears to show one distinct and “rapid” change in the three peri-embryonic parameters and in the size of the embryo; this combination of changes creates the impression of a so-called punctuated equilibrium. The punctuation appears to be superimposed on a fairly stable morphology pattern below and above the discontinuity level. In both parts pulses forward and backward remain at a maximum near the limit of statistical significance, which may make us doubt whether a really pulsating pattern can be recognized in the stasis courses.

In order to evaluate the morphological jump across the punctuation level, we postulated stability above and below the FR 2114-2113 dividing line, and we calculated grand means following the reasoning outlined in the previous chapter. Below the discontinuity level we have 13 means, above there are 22. The resulting means with their standard deviations and standard errors are given in table 2 on page 123. Student’s t-values are given so that the differences can be appreciated.

These t-values show that there is an enormous difference between the grand means of the sample suites below and above the morphometric discontinuity. Only for the sphericity parameter is there no such distinct change, but grand mean calculations are not given in our table because it should be clear from the visual impression in figure 29 that the change across the discontinuity level, if present, has a more gradual character.

Amongst the configuration parameters the difference is evidently most conspicuous in \bar{E} , and it is least impressive in the size parameter $(\bar{L}_i + \bar{l}_i)$. Although the Student’s t-values are caused not only by the difference between the grand means, but also by the degree of variation of the parameters in each part of the column having an influence on SD and SE, it seems fairly safe to conclude that the configuration parameters were the ones which changed most strongly at the punctuation level. Whether this conclusion can be reconciled with the assumption that the configuration had to change because of the size increase of the embryo, will be a matter for discussion in the next chapter.

If we accept the grand mean approach as an acceptable expression of two successive steady-state periods, we can check whether or not all individual means remain inside the expected range of grand mean plus and minus three times the standard deviation. Actually they all do, except one value of $(\bar{L}_i + \bar{l}_i)$ which is just outside (FR 2119). Stasis is evidently predominant in both parts of the Aubeterre stratigraphic column.



THE OTHER AUBETERRE SECTIONS

In and near the village three shorter sections were sampled and their *Orbitoides* analyzed.

The positive pulse or punctuation in \bar{E} , \bar{P} and \bar{E}/\bar{P} was found in two of them. In the section Gendarmerie (table 5) there is only one sample (FR 1914) below the morphometrical discontinuity, but across the estimated 0.50 metres stratigraphical distance to FR 1915 the jump is very distinct (fig. 30), especially in \bar{E} and \bar{E}/\bar{P} . With regard to the embryonic size parameter there is no statistical significance for the increase of the means; differences in the $(\bar{L}_i + \bar{l}_i)$ of successive samples elsewhere in this section are distinctly larger, for instance between the samples FR 1921 and FR 1922 (fig. 30). The exposure of the lowermost part of the section (fig. 31) was too poor for us to verify whether the morphometrical discontinuity could be correlated with any sedimentary phenomenon; at the time of sampling neither here nor at the opposite side of the road did we find any indication for an irregularity in the lithostratigraphic column.

Conspicuous leaps in \bar{E} and \bar{E}/\bar{P} were also found in a short section with only four samples, taken at the lower south-eastern end of the Champ de Foire. The discontinuity occurs between samples FR 2086 and FR 2085 (fig. 8 and table 6) at a stratigraphic distance of 70 cm. The corresponding changes in \bar{P} and in $(\bar{L}_i + \bar{l}_i)$ are less pronounced, but still of statistical significance.

On the basis of the field correlations it is extremely likely that in both these parallel sections we are dealing with exactly the same lithostratigraphic horizon as in the main section in the wall next to the Église Monolithe.

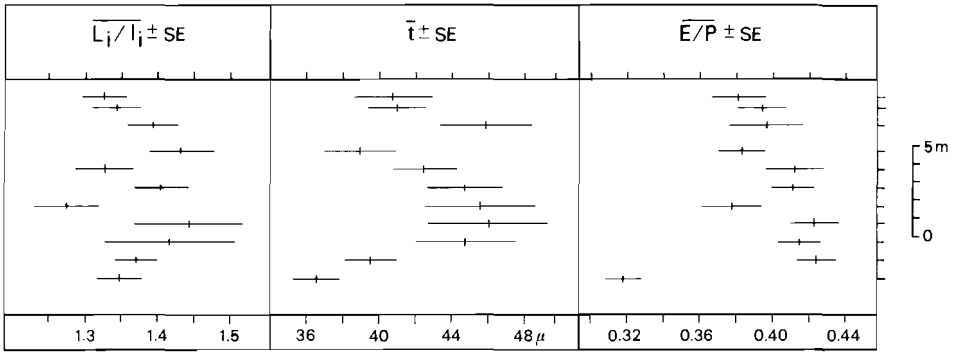


Fig. 30 The sequences of mean values with their standard errors for the internal *Orbitoides* parameters in the samples of the Gendarmerie section of Aubeterre.

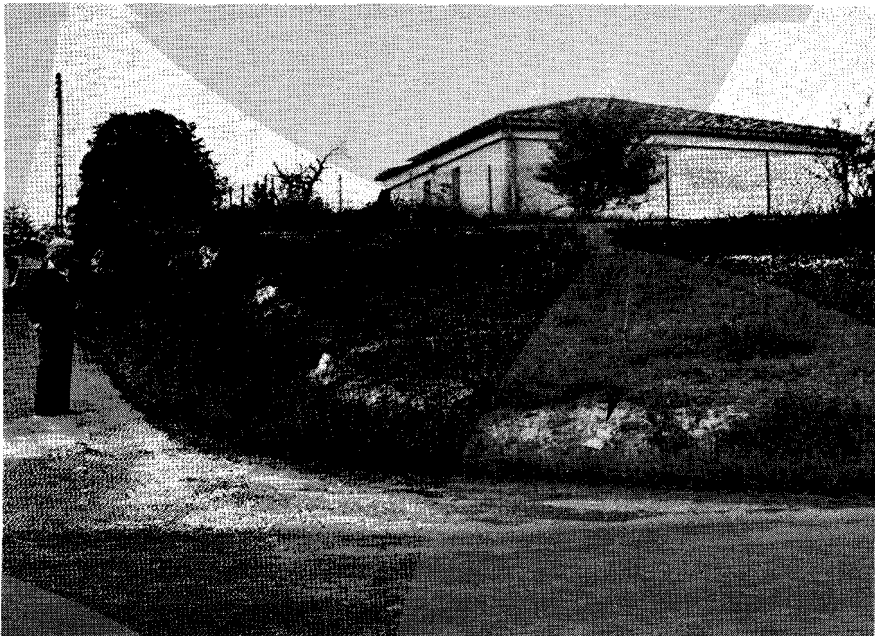


Fig. 31 The lower part of the Gendarmerie section, Aubeterre. The levels of FR 1914 and FR 1915 are indicated by sample bags and arrows. Photograph 1984; since the sampling in 1979 the section has become strongly overgrown.

All eleven samples, analyzed by W. Sikkema from the section we named Boie de la Roue at about 2 km north of the village of Aubeterre, were found to contain the primitive type of *Orbitoides* association. The five metres with oyster levels evidently belong stratigraphically below the morphometric discontinuity level that we observed in the three other sections. The monotonous set of means is shown in figure 32.

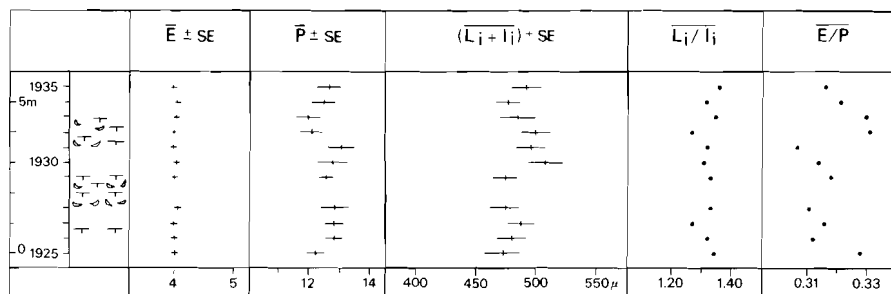


Fig. 32 The sequences of mean values with their standard errors for the internal *Orbitoides* parameters in the samples of the Boie de la Roue section, north of Aubeterre. Lithostratigraphic column schematic.

THE DETAILED SECTION OF THE CHAMP DE FOIRE

The data discussed so far called for still more refined sampling in at least one of the three sections across the stratigraphic interval in which the supposed punctuation had taken place. This sampling was carried out by the second author in the summer of 1981. In the composite main section of Aubeterre the required interval near the Église Monolithe was too poorly exposed for reliable re-sampling to be done in detail. Bad exposure also prevented us from re-sampling the lowermost part of the Gendarmerie section (fig. 31) in a meaningful way.

A very good control section could however be sampled in the wall below the castle grounds in one of the small gardens just below the level of the Champ de Foire (figs. 33–35). This section has the same position as our earlier sample suite FR 2088–2083, in which the morphometric jump was found between FR 2086 and FR 2085 with a stratigraphic distance of 0.70 metres in between.

Thirteen samples were taken practically continuously (fig. 33) over 1.30 metres, each sample corresponding to 10 cm stratigraphic height. Most of the sediment for each sample was taken from the middle part of its 10 cm

interval; so stratigraphically the cores of the successive samples are 10 cm apart. The means in the series FR 2210-2222 are shown in figure 36; the results of the four earlier analyzed samples (FR 2088, 2086-2084) have also been entered in the data record.

In this short section the calcarenites show some differences in induration. There are two somewhat protruding ledges (figs. 33, 34) with irregular, diagenetic and somewhat concretionary hardening. This type of induration is rather common in the entire Aubeterre section, especially in Coquand's units F and D (fig. 12). The ledge in the middle part of the detailed section of the Champ de Foire turned out to be of special importance for the record of our *Orbitoides*. In addition to its more indurated character it shows somewhat more shell debris in its higher part relative to the softer sediment immediately above and below, as well as some scattered oysters. We mentioned already that it seemed to contain less micrite. The lower and upper "surfaces" of this indurated layer of about 40 cm thickness are irregular and rather vague upon closer inspection and they become invisible when the exposure is freshened by chipping off the outer crust.

The result of our counts and measurements on the *Orbitoides* of the 13 samples are shown in figure 36. It appears that we cannot get rid of a sudden large change in mean E value, but now the change occurs between our samples FR 2210 and FR 2211, so at a stratigraphic distance of only 10 cm. These two samples are on either side of the irregular lower surface of the indurated ledge in the middle of the outcrop (figs. 34 and 35).

\bar{E} changes from 4.28 ± 0.10 to 6.05 ± 0.41 . The magnitude of this change

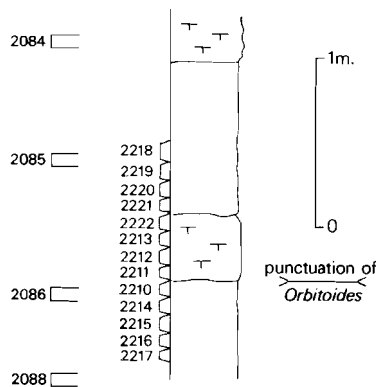


Fig. 33

Schematic lithostratigraphic column of the detailed section below the Champ de Foire, Aubeterre, showing the position of the samples.

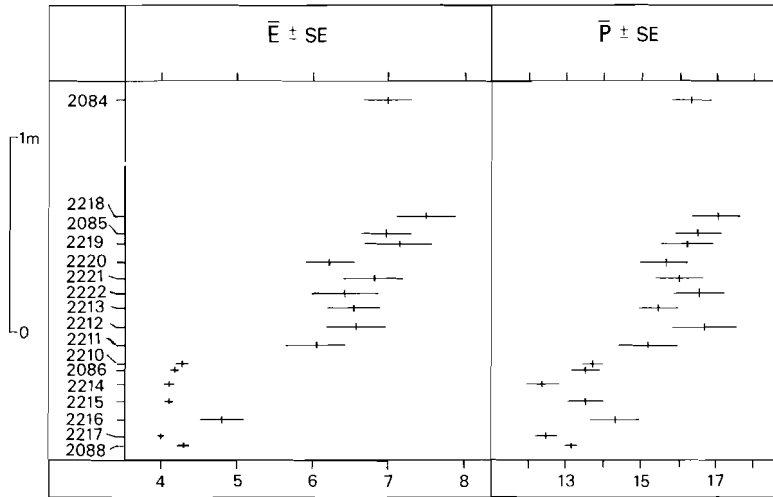


Fig. 34 The detailed section in unit F below the Champ de Foire, Aubeterre, showing the position of samples FR 2210 and 2211 above the garden level (below). The more distant view (above) shows both indurated ledges and surface-parallel planes in the top part of the exposure.

in mean E is of the same order as it was in the three previous examples from parallel sections in Aubeterre, but in the latter three sections we had not ascertained such a small stratigraphic distance between the successive samples. The morphological gap between the critical samples of the earlier series is evidently not filled by a set of intermediate values in our control section. The large change in \bar{E} seems to have been stratigraphically “instantaneous”.



Fig. 35 FR 2210 and FR 2211 at close view.



In between FR 2210 and FR 2211 there is a jump of comparably large magnitude from 0.314 to 0.390 in the values of \bar{E}/\bar{P} , but the corresponding change in \bar{P} seems to fit into a more gradual record of increase, which for the entire series of thirteen samples is 12.44–13.76 / 15.23–16.71. There is certainly a strong increase in \bar{P} at the critical level, but elsewhere in this Champ de Foire section the data suggest oscillations in the \bar{P} values of similar magnitude. Also for $(\bar{L}_i + \bar{l}_i)$ and for the wall thickness \bar{t} the values found in FR 2210 and FR 2211 are not strikingly different from each other. They fit into a more general pattern of fluctuations, which we find superimposed on an overall increase for the entire control section.

Our detailed sampling suite from the Champ de Foire thus appears to show distinct positive trends in all series of parameter means over the entire 1.30 metre interval; only in \bar{E} and \bar{E}/\bar{P} does the change have a very abrupt character over a lithostratigraphic distance of only 10 cm.

THE SECTION OF MESCHERS

The *Orbitoides* of nineteen samples from the original set from Meschers (fig. 15) have been analyzed (fig. 37). Although the Plage de Cadet is at some 90 km distance from Aubeterre, the data from this section on the Gironde show similar details in the sudden change of the morphology, but there are minor differences which require a special explanation.

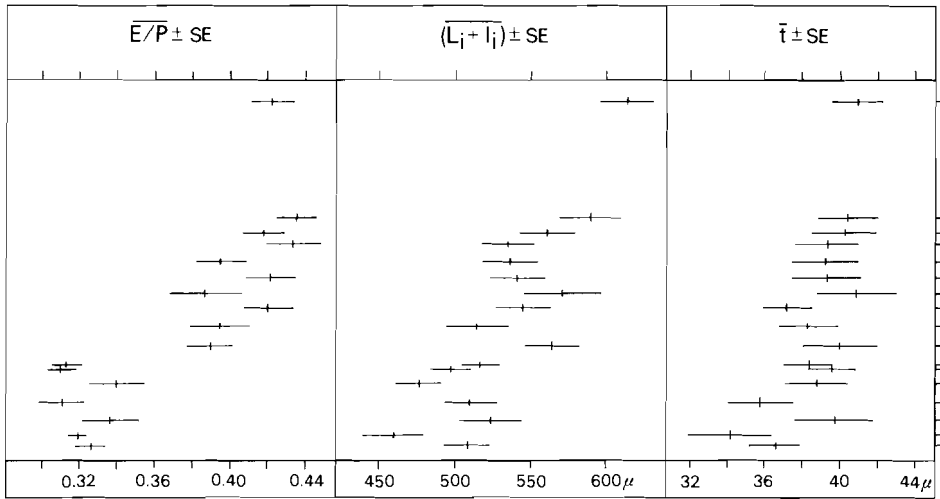


Fig. 36 The sequences of mean values with their standard errors for the internal *Orbitoides* parameters in the samples of the detailed section below the Champ de Foire, Aubeterre.

Most important is that we again found a jump in \bar{E} with comparable direction and magnitude and at about the same place in the morphometric scale. Here the change occurs across a stratigraphic sampling distance of 0.90 metres between samples FR 2141 and FR 2143 (FR 2142 was never analyzed because of too few individuals), taken from sediments of similar lithology: calcarenites with oyster debris (fig. 17). Nevertheless, we felt less certain that there is no sedimentary break in between both samples.

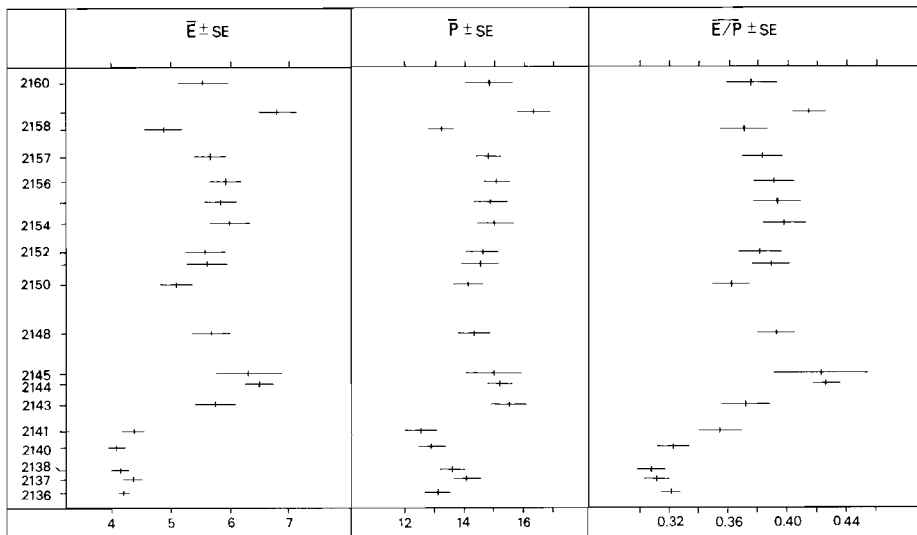
At first sight we get the impression that the leap in \bar{E} from 4.38 to 5.76 is smaller in this Meschers section than it is in the main section of Aubeterre, but if we place the calculated means in series of six successive samples for both sections the sequence of means from Meschers of 4.15–4.09–4.38 / 5.76–6.50–6.33 does not seem to deviate so very strongly from that established in the Aubeterre section: 4.10–4.17–4.20 / 6.52–6.30–6.26. It can be argued that minor differences in sampling spots relative to a presumably short interval of rapid change might be held responsible for the difference in the magnitude of the observed jump. Such reasoning may not be valid, however, and even unrealistic, if the change were really instantaneous everywhere. Alternatively, one could assume that some kind of stronger vertical mixture of sediments reduced the numerical difference across the punctuation level.

A better basis for conclusions can be obtained if we compare from all sections the means of the samples immediately below the discontinuity and

those immediately above. Differences between the sample means below appear to be of no statistical significance; in other words, all topmost assemblages below the discontinuity level could have been derived from the same homogeneous population. This conclusion is not warranted for the samples immediately above the discontinuity. \bar{E} has the largest value (6.75) in the Gendarmerie section at Aubeterre, the smallest is found near the Plage de Cadet (5.76). Applying the Student's t-test to this difference we obtain a t-value of 2.1, from which it is possible to deduce that there is only a five per cent probability that the assemblages from both places could have been drawn from a single homogeneous population.

We can postulate on the basis of this evidence no more than that the \bar{E} value calculated in the Meschers section is low. Furthermore, it can be concluded that the grand mean value of 5.81 found for the \bar{E} in the upper part of this section at the Gironde is the lowest of all.

When we consider this upper sequence of \bar{E} values (fig. 37) we see that the values show a pattern with stronger fluctuations than the pattern we encountered in the Aubeterre sections. There are some values which are very low (FR 2158, FR 2150) showing differences from nearby values lower down in the column which are distinctly significant. We might conclude that



in this sequence of *Orbitoides* populations there are some distinct negative pulses, a conclusion that could not be derived from the Aubeterre data.

These sample means of \bar{E} come so close to the values obtained for the lower series that we start to think of another explanation. If the Meschers site really was shallower during the Campanian and subject to more and stronger current activity than the area of Aubeterre, reworking might account for these low \bar{E} values in the upper part of the Meschers section in these single samples and in the lowermost sample above the discontinuity, as well as for the 5.81 value of the grand mean. Such an explanation is quite plausible, although we must realize that sediments of the lower series should still have been available for reworking after some nine metres of sediment (for FR 2158) had been deposited on top of the interval that contains the morphometric discontinuity.

As far as the other *Orbitoides* parameters in the section of the Plage de Cadet are concerned it appears that the mean \bar{P} values show a pattern strongly resembling that of the \bar{E} values. Again there is a distinct jump between FR 2141 and FR 2143, and an extremely low value for FR 2158, which value is well within the range of \bar{P} found for the lower part of the section.

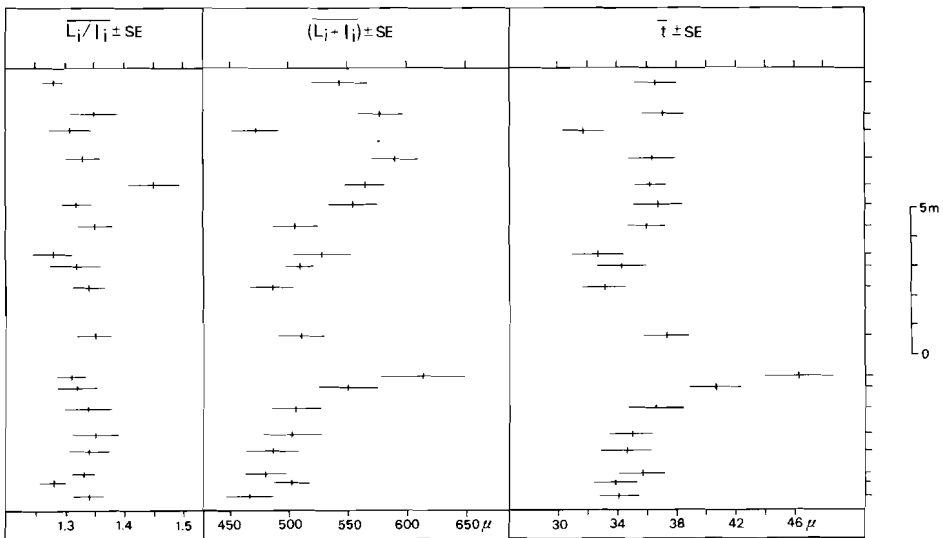


Fig. 37 The sequences of mean values with their standard errors for the internal *Orbitoides* parameters in the samples of the main section near the carrellets at the southern end of the Plage de Cadet, Meschers.

Since \bar{E} and \bar{P} show strong parallelism, we need not be amazed that the \bar{E}/\bar{P} sequence has a more gradual character across the punctuation interval. The increase observed up to approximately FR 2145 is not continued higher up.

The sphericity parameter shows an entirely random pattern throughout. Only the value for FR 2156 is very high without any obvious relation to the other parameter means. The mean size parameter $(\bar{L}_i + \bar{I}_i)$ shows an oscillating upward increase up to the level of FR 2145 followed by a drop and another strongly fluctuating positive pattern of change.

Summarizing the Meschers data, we can point out that there is a distinct jump in \bar{E} and \bar{P} over a vertical distance of 0.90 metres in this section, but this jump is not accompanied by simultaneously occurring strong differences in the sequences of the other parameters means. Both the \bar{E}/\bar{P} and the $(\bar{L}_i + \bar{I}_i)$ changes seem to fit to a rapid, but fairly gradual pattern of change, the maximum of which is found about one metre above the level where the discontinuities in \bar{E} and \bar{P} were observed. The entire section gives the impression of a more irregular data set than those we found at Aubeterre. The possibility that repeated reworking caused the irregularities must be considered seriously, but we realize that such effects cannot be proved. On the other hand, there is no good evidence to support the conclusion that distinct negative pulses occurred in the *Orbitoides* evolution at the Meschers site.

CLOSER SAMPLING AT MESCHERS

The considerable change in *Orbitoides* morphology in the Meschers section might well be related with some depositional hiatus, when we consider one of our earlier guesses about the more turbulent sedimentary conditions in this Gironde area. Samples FR 2141 and FR 2143 were taken from two successive beds, each with abundant oyster debris, separated by a 25 to 40

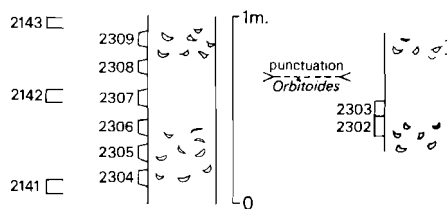


Fig. 38 Schematic lithostratigraphic columns of the detailed sections across the white layer in the middle of the Plage de Cadet (right) and near the carrelets south of this beach (left).

cm white band. In this white layer bryozoans, serpulids and echinoid spines are quite numerous, but larger oyster fragments are virtually lacking. Northwards this white band can be traced all along the Plage de Cadet and beyond to the Plage des Nonnes, but southwards it becomes less distinct. On theoretical grounds one can assume that a break in the sedimentation occurred either at the base or at the top of the white layer.

A first attempt to verify this assumption was made by analyzing a sample taken immediately below the band (FR 2302) from the Plage de Cadet, and a higher one (FR 2303) from the lowermost ten cm of the white band (fig. 20). According to the internal report of C.L. Tielenburg both samples are very similar in morphometrical details; both clearly belong to the lower group of *Orbitoides* assemblages (fig. 38). Morphologically the assemblages of these two samples thus have to be placed below the assumed discontinuity level in *Orbitoides* evolution; so a sedimentary break at the base of the white layer cannot be held responsible for the rapid change in morphology.

As we did for the Aubeterre sections, we then tried to narrow down the stratigraphic distance for the morphological break in the Meschers section to less than 0.90 metres on the basis of a more complete, detailed sample suite between FR 2141 and FR 2143, thus across the entire white layer (figs. 38 and 39). This sampling was carried out by the senior author at the place of the original sample sequence near the carrellets in the summer of 1982. Since the second author had left the department by that time, the analysis had to be carried out by another junior investigator (A. van Haeringen), which fact may have caused some bias in the results when compared with the earlier data sets. For some samples, notably FR 2308, poor preservation may have influenced the result to an additional, unknown extent.

The data in the sequences of means (fig. 40) show a less regular picture than those obtained at Aubeterre (fig. 36). This gives us the opportunity to offer different explanations.

If we wish to find a sudden jump forward, it can be found between samples FR 2307 and FR 2308. Both for \bar{E} and \bar{P} the large difference is clearly of statistical significance. However, if we were to disregard the data of FR 2307, we might come to the conclusion that there was a rapid, but seemingly regular change in the mean values of both these parameters across the entire interval. With regard to the assumption of punctuation FR 2305 and FR 2306 would have too high values for the means of both E and P.

Defending the postulate of a gradual change is even more difficult, however. We may suggest that the low values in FR 2307 are due to stronger reworking of the older stock, just as we argued for some anomalous samples in the upper part of the main Meschers section. The fact that FR 2307 and FR

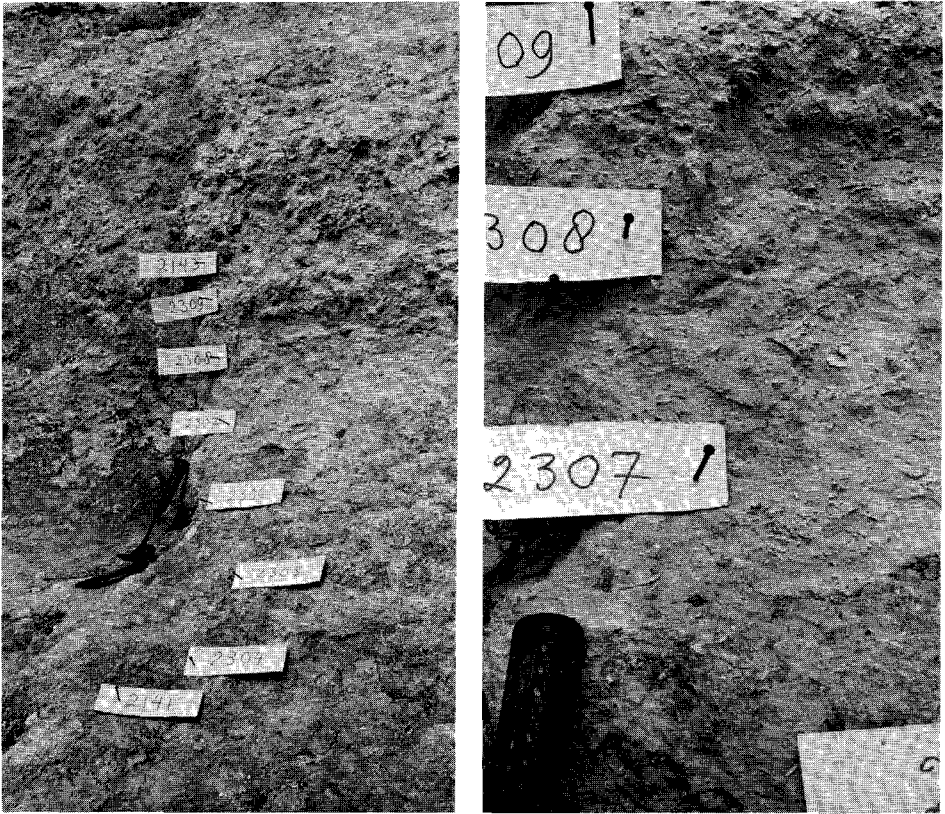
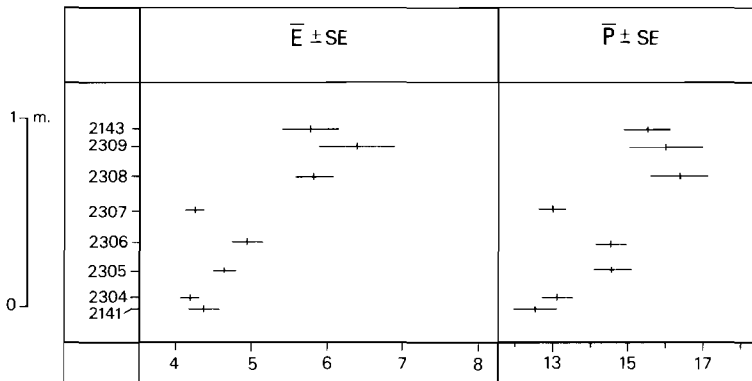


Fig. 39

The detailed section south of the Plage de Cadet, Meschers.



2308 both originate from the so-called white layer without oyster debris seems to contradict this argument.

Possibly the combination of relatively low numbers of observations per sample and the poor state of preservation of especially the Meschers samples which leave too much in the numerical observations dependent on personal appreciation, may account partly for the irregular picture. Actually, in an earlier internal report P. Knijnenburg had calculated an \bar{E} value of 4.48 for FR 2306, a value which would lend better support to the punctuation hypothesis between FR 2307 and FR 2308. If we accept the latter model, the rapid change would again have been across a distance in the column of about 10 cm.

In view of the various restrictions for the interpretation of the irregular data set, it is obvious that we cannot draw too many conclusions from the means of the other parameters (fig. 40). \bar{E}/P shows a very irregular increase, whereas the data on $(\bar{L}_i + \bar{l}_i)$ show no real change at all across the 90 cm interval. Actually, these results strongly resemble those for the longer Meschers section.

Although differences in experience and in the appreciation of the thin-sections of the different observers call for caution in drawing too clear-cut conclusions, our new data still suggest that in Meschers the change in composition of the *Orbitoides* populations might have been just as "instantaneous" as it was in Aubeterre, but the morphological difference seems to be less impressive than it was in the inland sections. Furthermore these data suggest that the jump occurs in the middle of the white band itself, in which we failed to find any lithological peculiarity (figs. 39, 41 and 42).

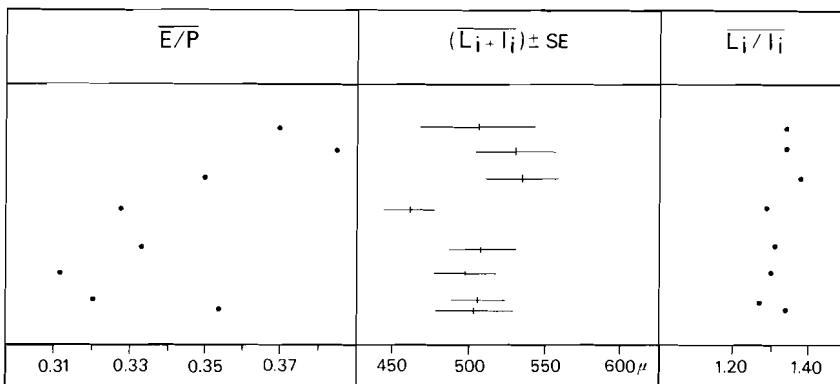


Fig. 40 The sequences of mean values with their standard errors for the internal *Orbitoides* parameters in the samples of the detailed section near the carrellets, south of the Plage de Cadet, Meschers.



Fig. 41 The white layer in the Plage des Nonnes, about one km north of our sections of the Plage de Cadet, showing the irregular increase in coarser shell debris both above and below. The picture shows subrecent pressure-induced planes towards the coast and below the present surface.

Summarizing the data of all our sections, we conclude that the large change in \bar{E} is the most consistent change and that it occurred suddenly and contemporaneously in all three Aubeterre sections, and probably also at exactly the same time level in the section of the cliffs of Meschers. This instantaneous jump in \bar{E} is usually accompanied by a similarly large increase in \bar{E}/P (not in Meschers) and in \bar{P} (not in the control section of the Champ de Foire). The corresponding increase in embryonic size across the critical stratigraphic level seems to be of more gradual character, whereas the sphericity parameter \bar{L}_i/l_i seems to remain unaffected. Some three or four metres above the punctuation level a decreasing trend in embryo size can be observed in both larger sections before the onset of a more static, fluctuating pattern that extends up to the top.

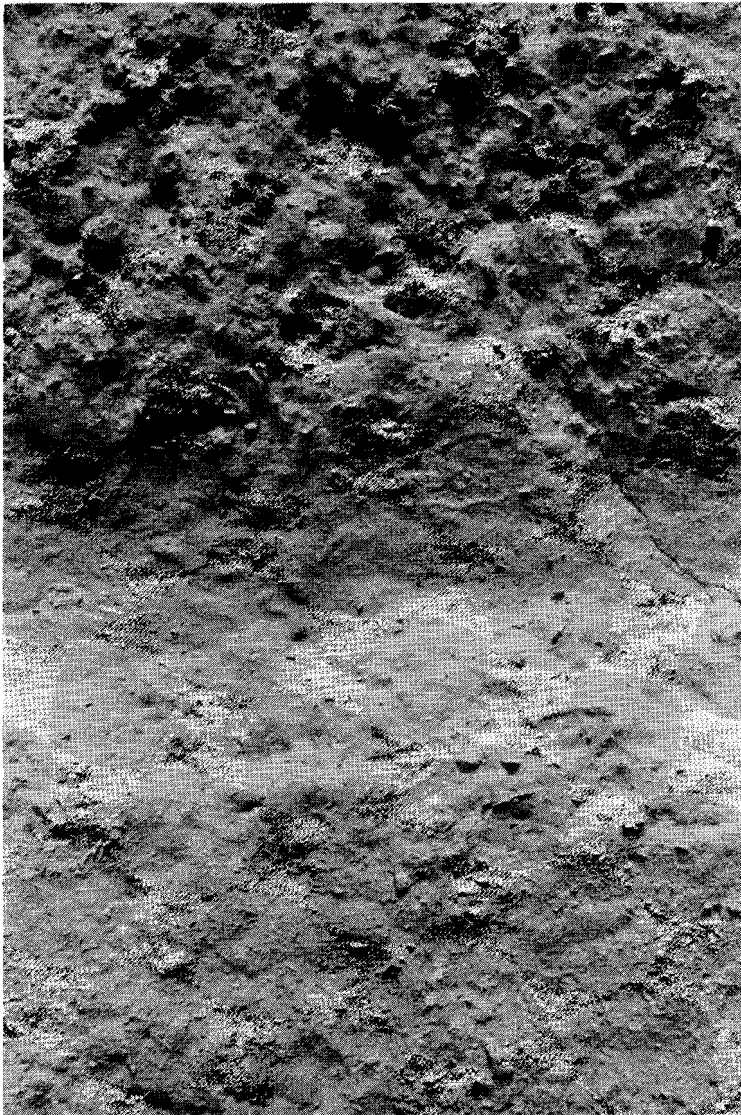


Fig. 42

Detail of figure 41; Plage des Nonnes, Meschers.

Chapter VI

THE PUNCTUATION

Having concluded that the biometric data on the Campanian *Orbitoides* populations of the Aquitaine basin strongly suggest the occurrence of an instantaneous change in their evolution; i.e. a punctuation of an equilibrium, we are obliged to scrutinize all other details of the animals and their environment in order to find an "explanation" for this sudden change in morphology. Obviously the change is most distinct in the nepionic configuration parameter E, which was already considered a priori to be the main yardstick for measuring the level of evolution in this group. The other nepionic parameters P and E/P show the suddenness of the change somewhat less distinctly than E. Surprisingly, there is no corresponding jump in the embryonic acceleration, if we can consider the sphericity parameter L_i/l_i to reflect such a trend. In contrast, the embryo size, expressed in $(L_i + l_i)$, does show a rapid increase across the punctuation level, although there is no clear proof of a real jump between successive samples in our detailed sections; the change usually seems to be more gradual.

THE TIME DURATION OF THE PUNCTUATION

Although we do not feel any need to defend the concept of gradualistic evolution, our first duty must be to check whether the hypothesis of gradual evolution can still be sustained. For instance, a sedimentary break could well have accounted for the observed suddenness of the change in the *Orbitoides* populations. If there were any support for the assumption of a sedimentary hiatus between for instance our samples FR 2210 and FR 2211 from the Champ de Foire detailed section (fig. 35), the jump in morphology might be due to the absence of data corresponding to a missing record of a time span of considerable duration between both samples, during which a sustained morphological change, whether gradual or not, could have taken place.

The first impression we obtain from the lithology of the sediments is that the morphological discontinuity in the *Orbitoides* succession of Aubeterre occurred in a part of the section for which the past deposition was continuous. We are dealing with rather fine, homogeneous calcarenites with a fair number of evenly scattered larger foraminifera, with some shell debris and with occasional complete oysters. If the *Orbitoides* jump coincided with the

top or the base of one of the oyster beds, or with one of the very distinct “bedding” planes in the section (figs. 13 and 23) we would be much more cautious about asserting that continuous sedimentation occurred across such a critical horizon. However, at these more distinct lithostratigraphic boundaries, which might correspond to gaps in the record, the morphology of the *Orbitoides* seems to remain unaffected: e.g. between FR 1912 and FR 1913, between FR 2107 and FR 1877, or between FR 1889 and FR 1886 (fig. 8).

We have seen that in the 1.30 metres of the detailed section near the Champ de Foire the rapid change occurs across the vague lower boundary of a more indurated layer some 40 cm thick (figs. 35 and 43). It is very unlikely that this lithological boundary corresponds to a longer time break than the other ones we mentioned above. If this “bedding plane” in this type of sediment did correspond to a longer period of non-deposition we would expect a hardground underneath, but there is none (fig. 43). If the lower limit of the ledge were the result of erosive processes – a possibility which certainly cannot be ruled out if one recalls the presence of indistinct channel fills and oblique bedding at some other places in the Campanian calcarenites – we would expect a sharper contact and some concentration of fossil debris at



Fig. 43 The indurated ledge (above the large sampling hole) in a garden below the Champ de Foire, Aubeterre, a few metres south of the outcrop of figure 34 (still visible at the left side of the photograph).

the base of the indurated bed as a kind of lag deposit. We found nothing of the kind, either in the Champ de Foire section, or in any of the parallel sections. Only the microfacies analysis of the samples from the Champ de Foire section seems to show a hardly perceptible lesser mud content in the indurated 40 cm and a somewhat higher content of mud clasts and shell debris. These phenomena however are not specifically concentrated at the base of the indurated ledge.

With regard to the detailed section of Meschers we suspected that the somewhat less conspicuous, but still distinct, morphometric change might be situated at the base or at the top of one of the coarser oyster debris beds, but the analysis of the samples showed that it was in fact in the 40 cm thick white layer, in which no lithological discontinuity could be detected (fig. 42).

Evidently there is no proof of a depositional hiatus at the places and level we are looking at, but it must be realized that carbonates are less likely to reveal gaps in their depositional record than are clastic sediments of similar grain size.

If the sedimentation really was continuous and if we consider the likelihood that burrowing and other bioturbation caused a notable vertical mixing of material we can be surprised that the morphological jump still is so sudden. Whatever the extent of the mixing, it evidently did not cause a complete obliteration of the original population differences across the 20 cm of sediment involved in the Champ de Foire section. This may be regarded as another argument supporting the view that the change really was instantaneous.

If we suppose that an average sedimentation rate of 5 cm/10³ years is approximately correct, it is likely that the drastic change in population composition of the *Orbitoides* occurred during a time span of far less than two thousand years, provided sedimentation was indeed continuous. From the geological point of view the morphological overthrow of the *Orbitoides* populations really must have been instantaneous.

A SUDDEN CHANGE IN THE ENVIRONMENT

Since a sedimentary gap in the record is unlikely, we next have to reconsider the possibility that it was an environmental change which caused the sudden shift in *Orbitoides* morphology. In the detailed section of the Champ de Foire the composition of the benthonic foraminiferal faunas (fig. 22) with their large proportions of presumably epiphytic species does not show any notable change across the crucial horizon. The thin-sections of the car-

bonates do not give the impression that there was an abrupt change in microfauna and microfacies across the “bedding” plane between FR 2210 and FR 2211. For several metres below as well as above this horizon we observed that the grain-size distribution of the matrix points to rather low energy conditions. These were probably lower than the energy conditions for most beds higher up and lower down in the Aubeterre column. If energy corresponds to water depth we can assume that the “moment” of our crucial level at Aubeterre was somewhere in the middle of a longer period of somewhat greater depth of deposition at the site.

The presence of such low-energy conditions is confirmed by the relative abundance of *Lepidorbitoides* in the upper part of unit F at Aubeterre, whereas the genus is much less numerous to absent in the lower and upper reaches of the type section of the Campanian. It is generally believed that *Lepidorbitoides* flourished in the photic zone under conditions of lower energy than *Orbitoides*, i.e. at somewhat greater depth (Van Gorsel, 1975; Fermont, 1982).

The relative frequency of *Lepidorbitoides* amongst the larger foraminifera increases across the FR 2210–2211 levels, but the biometric data on *Lepidorbitoides* from the Aubeterre section do not show any notable change (fig. 62).

Although these biometric data on *Lepidorbitoides* (see chapter VII on taxonomy) from our section are relatively scarce – though more numerous than those of Van Gorsel (1975) – they show no deviation in the nepionic configuration and embryonic size parameter values at the critical level in the *Orbitoides* development. There is little more than a zigzag pattern throughout; there may be a slight nepionic acceleration in the section. Although the microfacies types and the relative abundance of *Lepidorbitoides* at Aubeterre indicate a somewhat greater depth, or at any rate lower energy conditions for the Champ de Foire detailed section, these environmental parameters are not specifically linked with the morphology-break in *Orbitoides*; actually they seem to have reigned for quite long periods before and after.

The only argument of general environmental character that might still be put forward to explain the sudden change is that we are dealing with a local maximum of depositional depth, by which some unknown stress was exerted on the *Orbitoides*. Even though the possibility of a threshold condition could be envisaged which caused a sudden morphological change (Drooger, 1983), such an assumption again does not seem to provide an acceptable solution for our observations. In the Meschers section we find the same morphological shift in the *Orbitoides* without obvious lithological change, but here we seem to be dealing with conditions of higher energy and/or shal-

lower depth of deposition throughout. For instance, *Lepidorbitoides* is extremely rare in the entire section of Meschers, and the carbonates in the relevant part of this section show coarser mollusc debris.

Although it is impossible for us to prove that *no* hiatus in the sedimentation record or *no* abrupt environmental change of some kind occurred at the critical level of our various sections, the lack of positive evidence requires that we seriously consider another possible explanation for the overthrow in *Orbitoides* morphology. In other words, we have to investigate whether the latter change could have been brought about by some mechanism inherent in the succession of populations of the animals themselves.

For instance, there might be a link between the configuration and the size parameters. The latter could have been affected by environmental changes too small to be detected from the sediment or the accompanying fauna. Such a link then might become apparent from correlations between these parameters.

SEDIMENTARY MIXTURE AS A CAUSE OF CORRELATION

We thus needed an analysis of the correlations in parameter combinations in single samples as a kind of final attempt to explain the punctuation from a possible influence of the environment.

Before starting to discuss this analysis we have to evaluate the possible role of contamination by reworking. This is particularly important because we suspected that the older group had been added in variable proportions to the assemblages of the higher suite of samples in the Meschers section. Mixture of populations of different composition through reworking would theoretically cause an undue strengthening of positive and negative correlations, which in turn might make us draw incorrect conclusions about the interdependence of parameters and as a consequence about the evolution of our *Orbitoides*. We thought that the coefficient of variation might help us to estimate the influence of reworking.

In tables 4 to 7 we have added the values for this coefficient of variation ($V = \frac{100 \cdot SD}{\bar{X}}$) for the parameters E, P and $(L_i + l_i)$ in the samples of the sections of Aubeterre and of the main section of Meschers. These V values of all three parameters appear to be high and to have a very wide and rather irregular scatter. They are rather high even for assemblages of fossil species.

It is not necessary, however, to conclude that these high values are caused by considerable reworking throughout the columns. For instance, we already said that samples FR 2158 and FR 2150 are distinct examples of heterogeneous assemblages; nevertheless, their V values do not deviate from the

others (table 7). A better explanation for the high V values may be that we are dealing with the asexual generation of the species involved; another explanation for two of the parameters may be that they are based on counts and thus on discontinuous variates.

For the size parameter of the embryo in the Miocene *Planorbulinella* (M.M. Drooger et al., 1979) a V range from 10 to 18 was found in the samples, so our range for the corresponding parameter ($L_i + l_i$) in *Orbitoides* is much larger. When we consider the mean values of V for the various section parts (table 3 on page 123) the difference between *Orbitoides* and *Planorbulinella* seems to be less impressive; these mean values stay at the upper limit of the *Planorbulinella* range.

The histograms of E and P in separate samples (figs. 53 and 54) show the trivial rule that fairly high SD values are responsible for the relatively high V values for these parameters. The variation in V is caused mainly by various irregularities in the rather low and wide frequency distributions. For E the low numerical values of this parameter relative to the wide range is an additional factor causing the high V values, especially above the discontinuity level. The relative rareness of morphotypes other than E = 4 may explain the relatively lower V values for the Aubeterre section below the discontinuity level (table 3). For unknown reasons these other morphotypes seem to be somewhat more frequent in the lower part of the Meschers section, causing the higher V values.

Altogether, the nature of the variation in all three parameters and the seemingly random distribution of irregularities in the V values along the stratigraphic columns do not permit us to draw any conclusion about contamination of the samples by reworking. The V values do not really tell us much about the reliability of the correlation coefficients, the question outlined at the beginning of this subchapter. As will be seen later on, it probably is the near-constant range of parameter values throughout our sections which invalidates this approach. Being unable to estimate the amount of contamination in our individual samples, we are inclined to trust the correlation coefficient values when they are consistent for the majority of the samples.

THE CORRELATION BETWEEN PARAMETERS

Tables 9 and 12 show the correlation coefficient values for six parameter combinations in the individual samples of the main Aubeterre and Meschers sections. Scatter diagrams in figures 44 and 46–50 illustrate these relations for a number of selected samples.

With regard to the characteristics of the embryo there appears to be a

regular, positive correlation between its dimensions and the thickness of the walls (fig. 44). A larger embryo evidently tends to have a thicker wall. This relation suggests that wall thickness had something to do with mechanical strength. This would mean that the megalospheric embryonic stage was free-living for some time before growth continued. Although we actually ob-

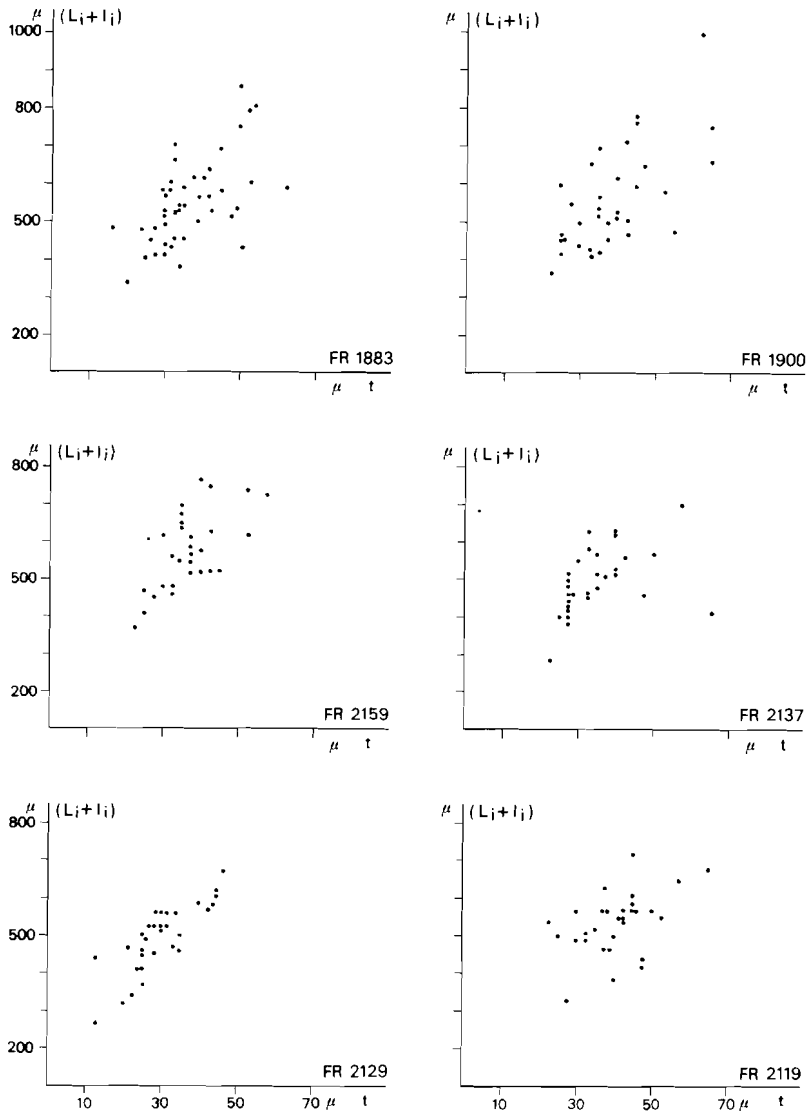


Fig. 44 Scatter diagrams of $(L_i + l_i)$ versus t in six selected samples from Aubeterre and Meschers.

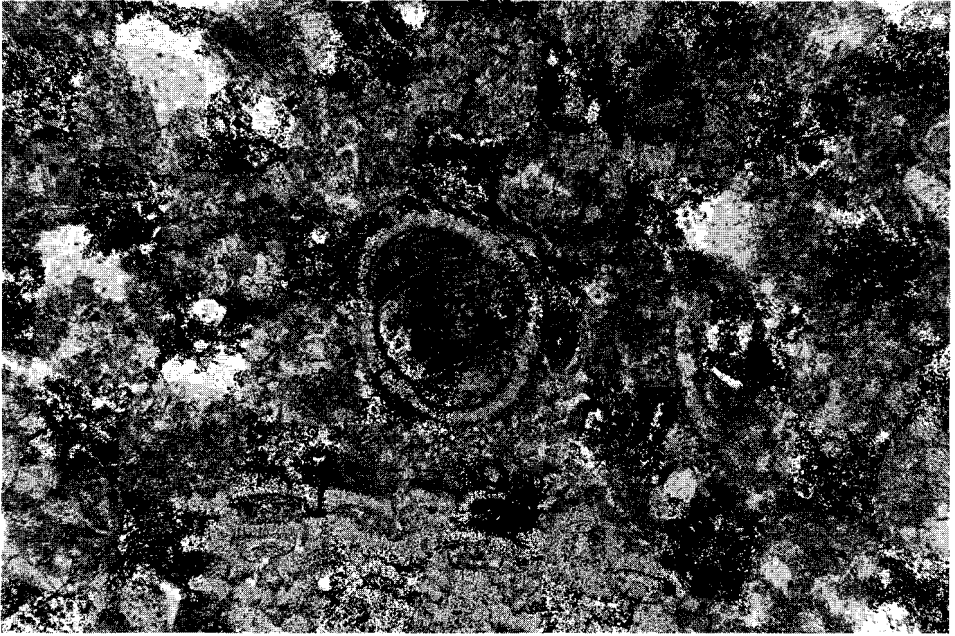


Fig. 45 *Orbitoides*-embryon in whole-rock thin-section, Champ de Foire, Aubeterre.

served an embryo with no more than the vague outline of a few peri-embryonic chambers in one of our whole-rock thin-sections (fig. 45) we shall refrain from speculating further about the possible meaning of the positive ($L_i + l_i$) versus t correlation.

By contrast, there is no consistent significant correlation between the size and the shape of the embryo in individual samples (fig. 46). The long-term change in both parameters (Van Hinte, 1966) is certainly not reflected in the individual populations of our sections. Only in a few samples (e.g. fig. 46, FR 2129) do we see a negative correlation between both parameters, which is the relation in accordance with the overall trends of the means.

The positive correlation between P and ($L_i + l_i$), which is significant in most samples (fig. 47), demonstrates that in the populations the relative size of the peri-embryonic chambers did not fluctuate in proportion to the size of the embryo. The size of the individual peri-embryonic and later chambers evidently remained fairly stable in the course of the evolution of the group.

In many samples there is a significant positive correlation between the parameters E and P of the peri-embryonic constellation (fig. 48). There seems to be some difference between the lower parts of the two sections.

Below the discontinuity level the positive E–P relation is found less regularly at Aubeterre than at Meschers; this is due to the very high relative numbers of the E = 4 morphotype at Aubeterre. By contrast, the E composition is more varied in the lower part of the Meschers section; we already used this

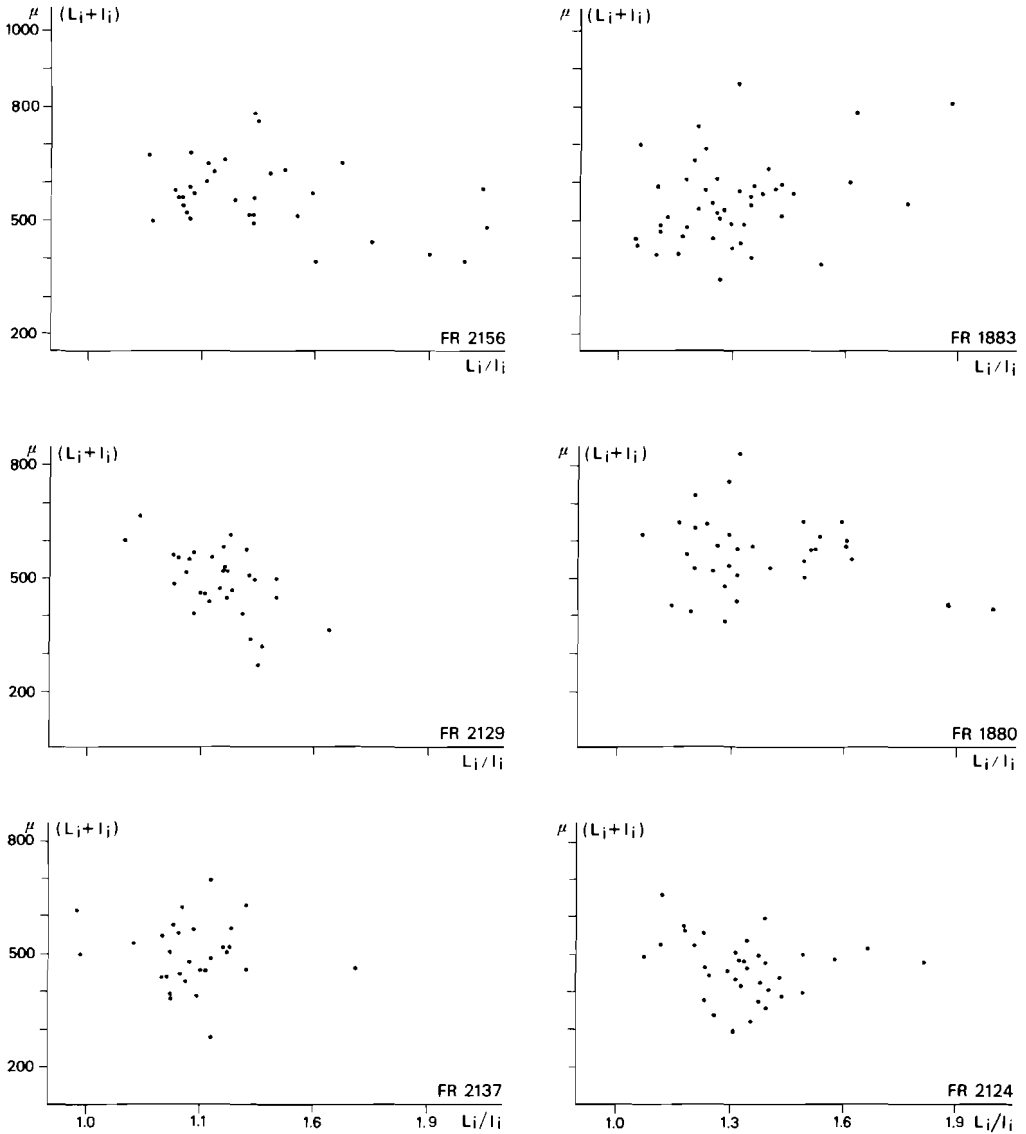


Fig. 46 Scatter diagrams of $(L_i + l_i)$ versus L_i/l_i in six selected samples from Aubeterre and Meschers.

fact to explain the larger V values for E at the latter locality. Actually, only a few $E \neq 4$ variants tend to cause already a significantly positive r-value for a sample (e.g. in fig. 48, FR 2137).

The same line of reasoning can be used to explain the positive correlation between E and the size of the embryo (fig. 49). This correlation is more

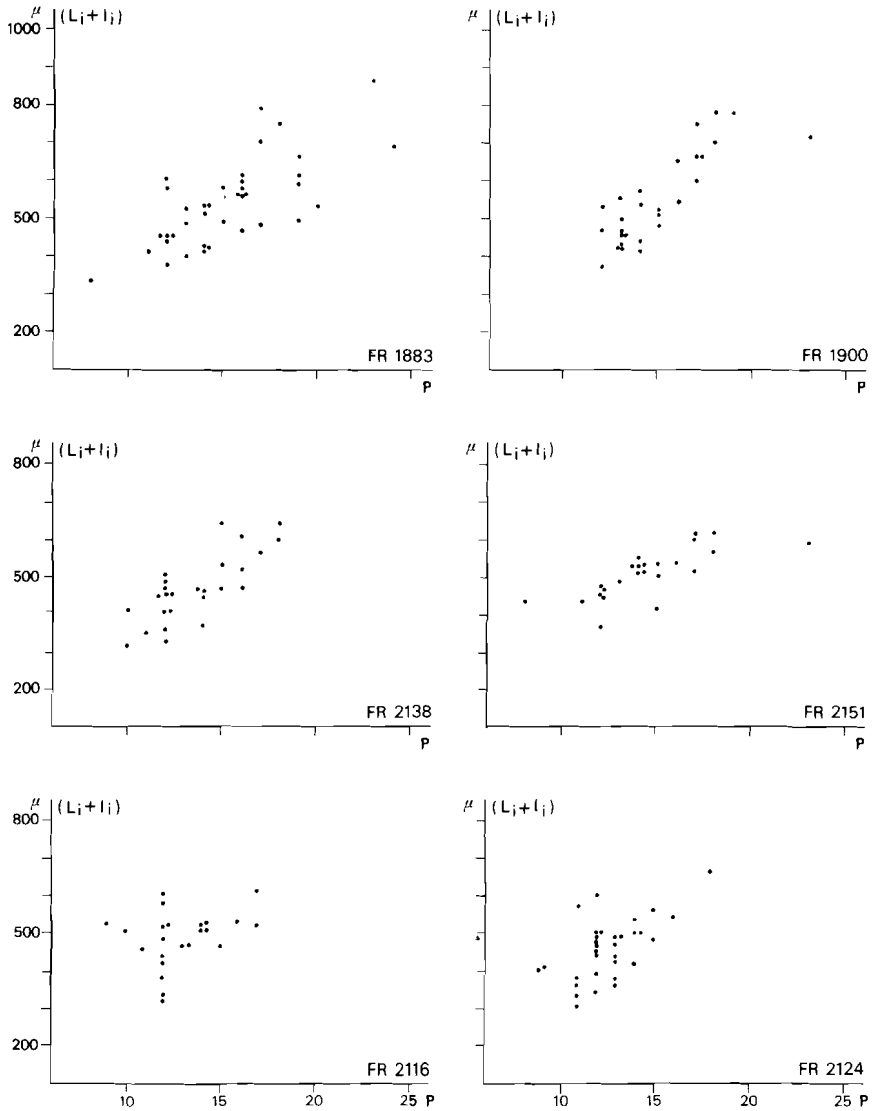


Fig. 47 Scatter diagrams of P versus $(L_i + l_i)$ in six selected samples from Aubeterre and Meschers.

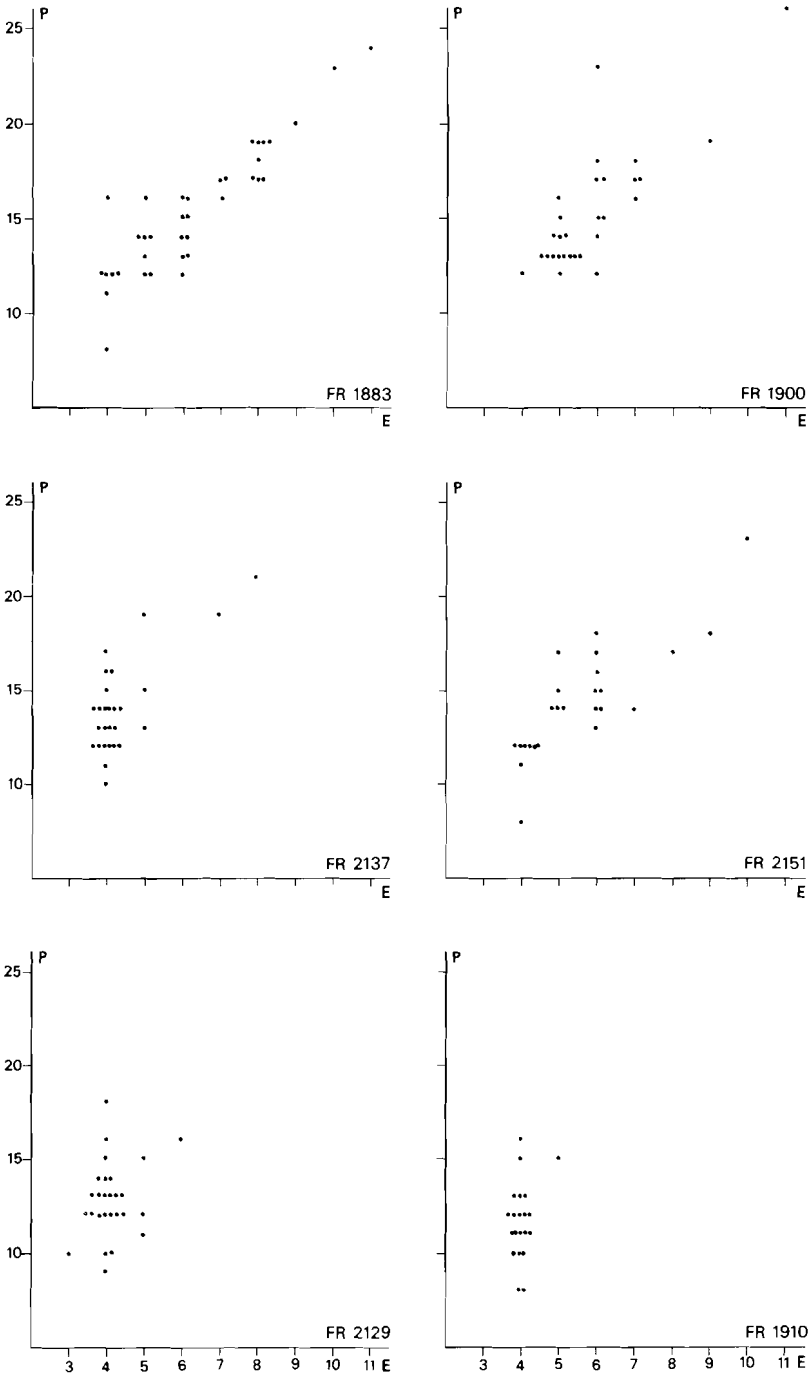


Fig. 48 Scatter diagrams of E versus P in six selected samples from Aubeterre and Meschers.

regularly significant throughout the entire Meschers section, whereas at Aubeterre significance is less frequent in the lower part. Regarding P and $(L_i + l_i)$ there is not such a strong difference between the two sections. The total number of peri-embryonic chambers is evidently positively correlated with the size of the embryo, irrespective of the values of E . When in a sam-

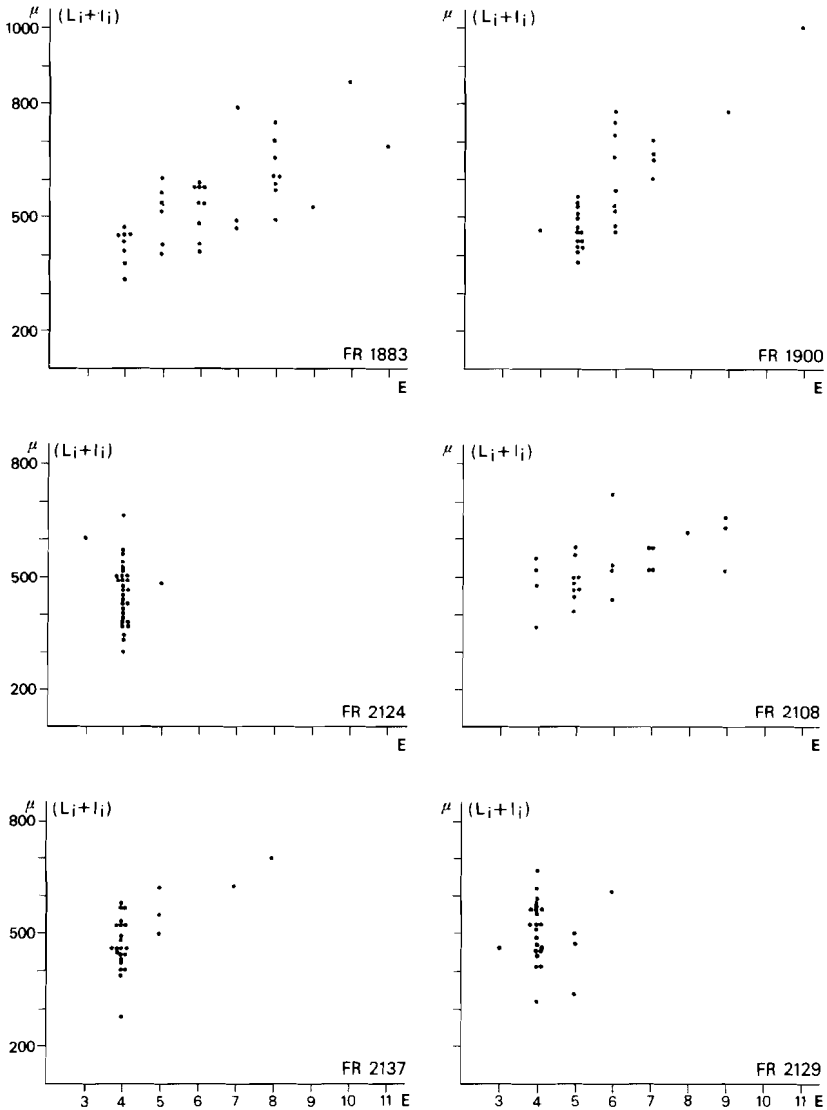


Fig. 49 Scatter diagrams of E versus $(L_i + l_i)$ in six selected samples from Aubeterre and Meschers.

ple E has predominantly the value four, it is the increase in the number of inter-auxiliary chambers which accounts for the stability in the correlation of P with the embryonic size parameter.

This partial difference in the behaviour of E and P explains why the E/P versus $(L_i + l_i)$ correlation coefficient tends to be negative below the discon-

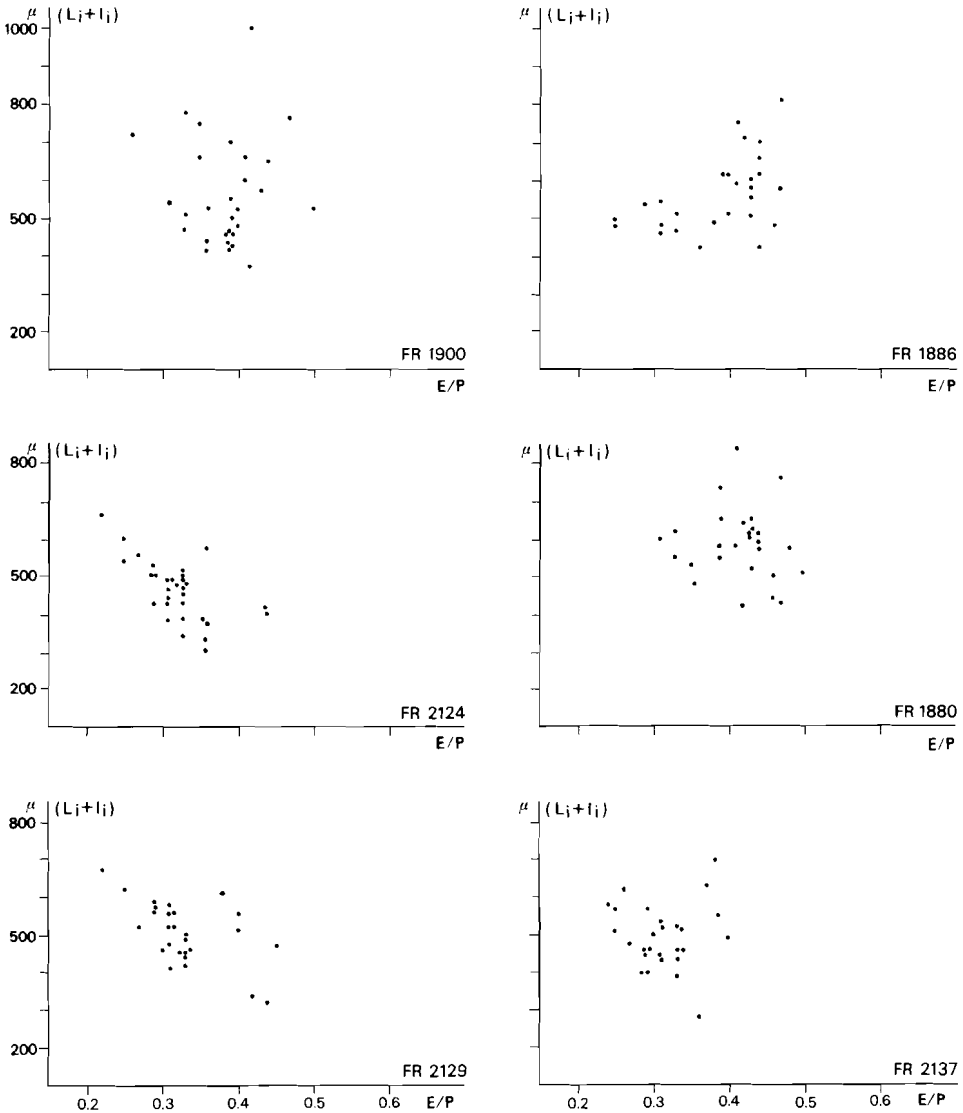


Fig. 50 Scatter diagrams of E/P versus $(L_i + l_i)$ in six selected samples from Aubeterre and Meschers.

tinuity level, especially at Aubeterre (fig. 50, FR 2124 and FR 2129), whereas above this level E may respond better to a larger embryo than P. It is the latter relation which accounts for the occasional significantly positive r-values (fig. 50, FR 1886). For most samples, however, E/P seems to be the peri-embryonic parameter, which is most independent of the actual size of the embryo (in fig. 50: FR 2137, FR 1900 and FR 1880).

The main conclusion from these intra-sample correlation coefficient values is that there is commonly an unmistakable, positive correlation between the directly counted peri-embryonic configuration parameters (i.e. E and P) and the size of the embryo. If we wish to appreciate or measure the evolution level of *Orbitoides* assemblages primarily on the basis of the configuration characteristic E, we must be aware of the possibility that there may also be an influence of the environment on the configuration of the nepiont via the size of the embryo.

EMBRYON SIZE AND DEPTH OF THE HABITAT

During the last ten years it has been argued on several occasions that the size of the megalospheric embryo of certain species of larger foraminifera can change with changing external factors that probably are somehow related to the depth of the habitat. The original postulate was based on the Oligo-Miocene group of the Miogypsinidae (Drooger and Raju, 1973), and subsequently the theory was checked with reference to some living species along their depth gradients. Confirmation of the hypothesis seems to be found in *Operculina* (Fermont, 1977) and at some places in *Heterostegina* (Biekart et al., 1985), whereas no distinct depth-related morphocline in embryonic size could be ascertained in either of the two *Planorbulinella* species present in the Gulf of Aqaba (Thomas, 1977).

The changes observed in *Operculina* and *Heterostegina* consist of a size increase of the embryo from very shallow waters down to a depth of about 80 metres; according to Fermont et al. (1983) the embryo size of the *Operculina* species would decrease again below 80 metres. The latter authors linked the largest embryo size along the depth-related morphocline to maximum density of the species, i.e. to a living optimum in the habitat range; they interpreted this relation in terms of productivity.

At the moment we do not yet know whether such depth-linked morphoclines have a general validity for larger foraminifera – they probably have not – ; we are only starting to obtain some background knowledge on the embryogenetic processes that accounted for such differences. We can speculate that the differences are brought about by a corresponding morphocline

in size of the parental test at the moment of embryogenesis*, or that the relative proportion of gamont- and schizont-derived megalospheres changes with depth (Hottinger, 1983). Evidence to support the latter hypothesis seems to be forthcoming from the detailed analysis of Biekart et al. (1985) of cultures of megalospheric *Heterostegina* derived from various depths near Hawaii.

If for our *Orbitoides* individuals we accept the hypothesis that the embryo size could have become greater with increasing depth of the habitat, at least in the shallower part of their depth range, this might "explain" the change we observed in the middle part of the Aubeterre section because here we already postulated some depth increase on other grounds. Because of the positive correlations in the samples the increase in $(L_i + l_i)$ could have led to the increase in \bar{E} and in the mean values of the other peri-embryonic parameters. If we were allowed to make a direct comparison of our *Orbitoides* with the *Operculina* of the Gulf of Aqaba-Elat (Fermont, 1977), the increase of $(L_i + l_i)$ would reflect a depth increase of the order of 50 metres, which is quite a plausible estimate.

However, several objections may be raised against this suggestion of an ecophenotypic response to explain the size increase of the embryo of the *Orbitoides* in our sections.

Firstly, changes in embryo size following a depth gradient are thought to be determined ecologically and thus should be reversible when depth decreases again. It is very unlikely that depositional depth remained the same at such greater depth for all the higher parts of the Aubeterre calcarenites to account for the larger embryo throughout this part of the stratigraphic column. The lithology of these upper beds with for instance more rudists suggests that shallower depths returned, but the embryo retained its larger size. And in Meschers too we find the increase in $(L_i + l_i)$, and here there is not the slightest evidence for a corresponding deepening.

Secondly, one can imagine that a change that was primarily an ecophenotypic response of the animals to details of their environment subsequently became somehow genetically fixed in the later populations. However, we would then expect the evolutionary change in the $(L_i + l_i)$ versus \bar{E} pattern to follow the direction of the regression lines in the $(L_i + l_i) - \bar{E}$ relation of the individual samples. Such a parallelism has been observed, for instance, in the evolutionary development of the *Planolinderina* lineage (Raju and Drooger, 1978; Drooger, 1983).

The plotting of all available $\bar{E} - (L_i + l_i)$ combination data (figs. 51 and 52,

*) On the basis of random collections of 50 specimens per sample we found no mean-size difference between the *Orbitoides* of the Gendarmerie samples FR 1914 and FR 1915 (data G.J. van 't Veld).

but especially fig. 60) shows that we obtain two distinct clusters with a few stray points in between which lie in the open space that is caused mainly by the jump in \bar{E} values. Correlation is very poor in each of these clusters. These scatter diagrams suggest a vertical trend followed by a horizontal one (fig. 51), directions which had already been given by Van Hinte (1966) on the basis of much fewer data in his figure 3. In our figure 60 these directions are horizontal and vertical, respectively. These directions parallel to the coordinate axes deviate from those in the $(L_i + l_i)$ versus E scatters whenever E has a sufficiently large variation (fig. 49). We thus can conclude that evolution followed its own path, a path which was different from the assumed, environment-controlled morphocline.

However, when we reconsider the actual successions of the mean combinations in the separate sections, we must acknowledge that the lines of central tendency we think we recognize in both clusters of mean values, i.e. vertical and horizontal, have little to do with evolution. There is no time sequence in the order of the points in either of the clusters; nothing directional actually happens in the two separate parts of the stratigraphic columns. The scatters

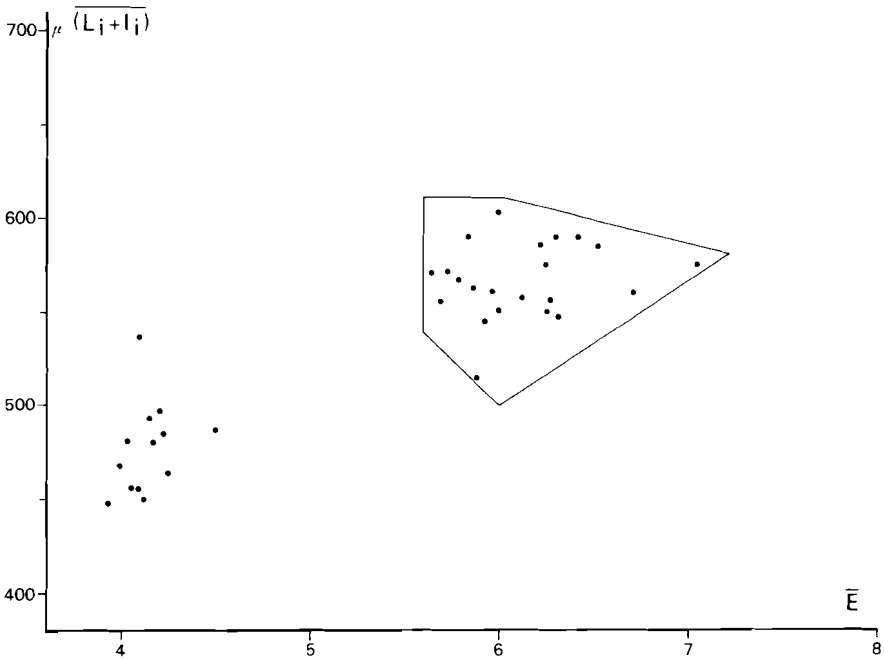


Fig. 51 Scatter diagram of \bar{E} versus $\overline{(L_i + l_i)}$ for all 35 samples analyzed from the main composite section of Aubeterre.

with their vertical and horizontal trends reflect a random variation of the mean combinations around some kind of grand mean. Below the discontinuity it is $(\overline{L_i + l_i})$ which has the wider scatter of the two, above the discontinuity more variation is found in \overline{E} .

Evolution can only be recognized in the shift in position of the entire clusters, and the direction of this shift would indeed be conformable with the regression direction in individual samples. The few stray points in between seem to strengthen this picture of evolution, but when we consider these points separately we feel less certain about the validity of this argument. One of the samples is from the Champ de Foire control section and its position is not really so certain because of the very large standard error of the \overline{E} value. Two others from the upper part of the Meschers section had already been singled out before as possible, negative pulses, but more probably as mixtures of populations due to reworking. Several more samples from the upper part of the Meschers section are seen to plot towards the gap in the record; this position may indicate that reworking at our site near the Gironde

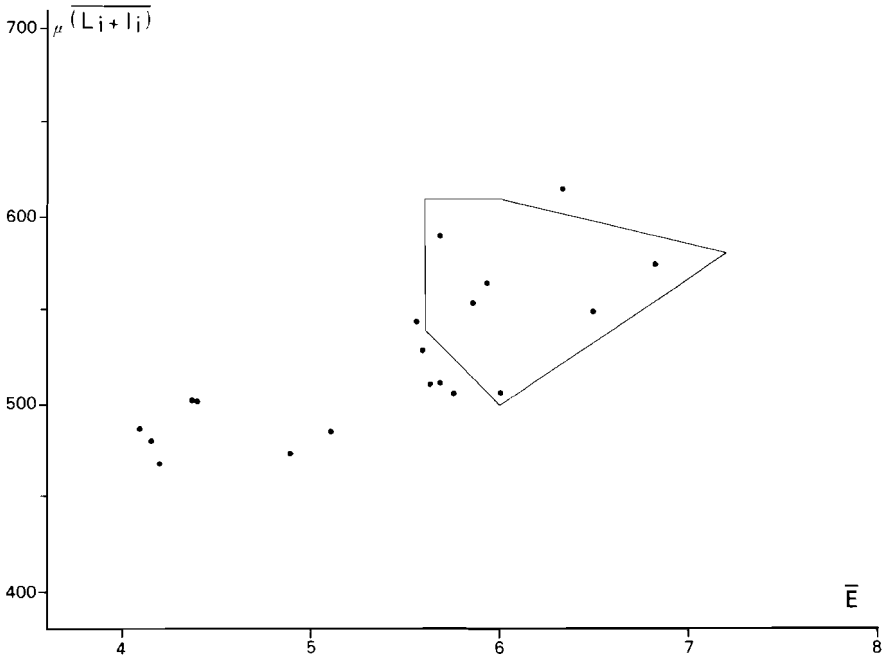


Fig. 52 Scatter diagram of \overline{E} versus $(\overline{L_i + l_i})$ for the 19 samples analyzed from the carrellets section near the Plage de Cadet, Meschers. The scatter periphery of the upper group of samples at Aubeterre (fig. 51) is repeated to demonstrate the wider scatter of the samples in the Meschers section.

was indeed rather common, much more than it was at Aubeterre (figs. 51 and 52).

The conclusion that the evolutionary jump would parallel an assumed, environment-linked morphocline, but that variation in the stasis parts of the column would not, seems rather odd. We would have expected a reversed relation in the interdependence, with the stasis differences being primarily linked to the intra-population variation pattern.

As a consequence, we are inclined to reject the assumption that some environmental control of the morphology of our *Orbitoides* was responsible for a strong change in embryo size and that this change was automatically followed by a jump in \bar{E} and in the other peri-embryonic parameter means because of intra-population correlation.

There is yet another objection to the theory that there was a correlation-based environmental control of the evolutionary leap. The jump in \bar{E} and in the other configuration parameters appears to be much more sudden and numerically distinctly more impressive than the change in embryo size. The $(L_i + \bar{l}_i)$ data from the Champ de Foire detailed section provide no reason for rejecting the hypothesis of a fairly gradual, though rapid, size increase of the embryo across the critical level. Such a gradualism cannot be defended for the means of the configuration parameters, however.

One final suggestion which might still save the idea of some environmental control on the *Orbitoides* evolution is that there was a threshold value of $(L_i + \bar{l}_i)$ which it was necessary to exceed for a sudden change in \bar{E} . Recently it has been pointed out that sudden changes in embryo size, sometimes though not regularly accompanied by a similar large change in nepionic configuration, must have occurred in several other groups of fossil larger foraminifera (Drooger, 1983). Although rather speculative, these changes were linked with a change in depth and in vegetation. However, it was argued that in these cases the larger embryos occurred at shallower depths; this conclusion is clearly opposed to our idea of a deepening trend at Aubeterre. The Meschers section provides no evidence in support of such a type of environmental change either.

Just as in our discussion about the possibility of a sedimentary break, we find it impossible to disprove that some environmental change played a role in the rapid change in *Orbitoides* morphology, but we are unable to find irrefutable arguments to support such a hypothesis.

THE AUTONOMOUS DEVELOPMENT OF ORBITOIDES

Having found no clear evidence that the morphological changes in our

Orbitoides were somehow caused or triggered by changes in the environment, we are obliged to find some explanation that relies entirely on current evolutionary theories. The strong shift in the peri-embryonic configuration, or rather in the average configuration, appears to have been an autonomous evolutionary happening in accordance with the theory of punctuated equilibria in between two periods of homeostasis, as advanced by Gould and Eldredge (1972 and later). In other words we are dealing with the sudden introduction of a more highly specialized stock from elsewhere at those places in the Aquitaine basin where we gathered our data. According to theory this new stock rapidly took over the entire habitat array from the earlier populations because it was better adapted to the overall environment, which itself had not changed fundamentally.

Following the current concept of the punctuation mechanism there should have been some small population in marginal isolation, which went through the rapid change. Such a marginal population sequence might have been situated in some smaller area of the Aquitaine basin itself, but it is just as likely that it lived and evolved in some other basin. Such a theory based on peripheral isolation is hard to prove or disprove, because it is not feasible to search for such a marginal population, especially if it has to be looked for in a remote corner of the Aquitaine basin. We would stand a better chance of finding supporting evidence by carrying out similar detailed investigations on *Orbitoides* in other basins. If another basin were to contain a more gradual sequence of populations missing in the Aquitaine, then we might explain the punctuation by assuming differences in the rates of the parallel evolutionary changes and the subsequent migration of a more advanced stock to the area in south-west France.

Of course the current theory of marginal isolation of a suite of small populations cannot be checked in the fossil record, but in addition one may wonder – also on theoretical grounds – whether such a theory of punctuation to explain the speeding up of genetic changes can be defended for our microfossils.

For one thing, populations of billions of individuals of such organisms as a standing stock in the parental habitat areas at each time level seem to form an extra difficulty to be overcome by the small group of assumedly better equipped invaders, unless we accept that these newcomers were genetically isolated already and were really much better adapted to the general environment.

Furthermore, we may wonder whether the concept of genetic drift, which plays the important role in the punctuation theory, is really valid for our larger foraminifera. After all, it has to be remembered that our observations

pertain to the megalospheric individuals of all these species, and that these individuals are the products of asexual reproduction. It can be suggested that we replace the term genetic drift by something like clonal drift, which would mean the numerical rise and fall of specific clones owing to the chance effects or adaptive response in the small marginal populations. Although we do not know for sure whether clones maintain a certain embryonic or nepionic configuration type in successive asexual generations (but see Kloos, 1984) there seems to be no point in preferring the term clonal drift for our larger foraminifera. As in the example of the Cretan Miocene *Planorbulinella* microspheric specimens are quite common; the suite of French *Orbitoides* populations evidently contained a fair number of such individuals (up to 5 per cent of all the *Orbitoides* per sample), so genetic control of the changes, if deemed necessary for our explanation, could well have been exerted all the time.

PHYLETIC GRADUALISM

Before continuing our search for the best explanation for the punctuation we shall first consider some other details of the morphological changes in our *Orbitoides*. Just as for other groups of orbitoidal larger foraminifera we suppose that configuration parameters rank higher than size parameters in the hierarchy of morphological characteristics when we wish to demonstrate the directional evolution. Although in this respect \bar{E}/P would theoretically have the highest qualification value, we think that the changes in \bar{E} give the best yardstick for measuring the sudden evolutionary change in the nepionic configuration. So we shall first make a closer inspection of the variation in \bar{E} .

From the bar diagrams of \bar{E} in the main sections (figs. 53 and 54) and also from the corresponding values of the coefficient of variation in tables 4 and 7, we see a sudden change in the shape of the frequency distributions and a considerable increase in the V values at the discontinuity level, especially in the Aubeterre section. These phenomena are caused by the strong reduction in relative numbers of the morphotype $E = 4$, whereas there is an increase in the relative numbers of the morphotypes $E = 6$, $E = 7$, $E = 8$ and $E = 9$. Yet, we cannot say that there is a sudden introduction of all these morphotypes more advanced than $E = 5$. The observations on the lower samples, below the discontinuity level in both sections, show that all these morphotypes $E = 6$ to $E = 9$ had been observed sporadically in these lower parts of the columns. Such variants evidently already existed in the populations for a long time before they suddenly became more numerous. The jump in \bar{E} is therefore caused by a sudden and extreme alteration of the frequency distribution within the range of an already existing set of adjoining variants.

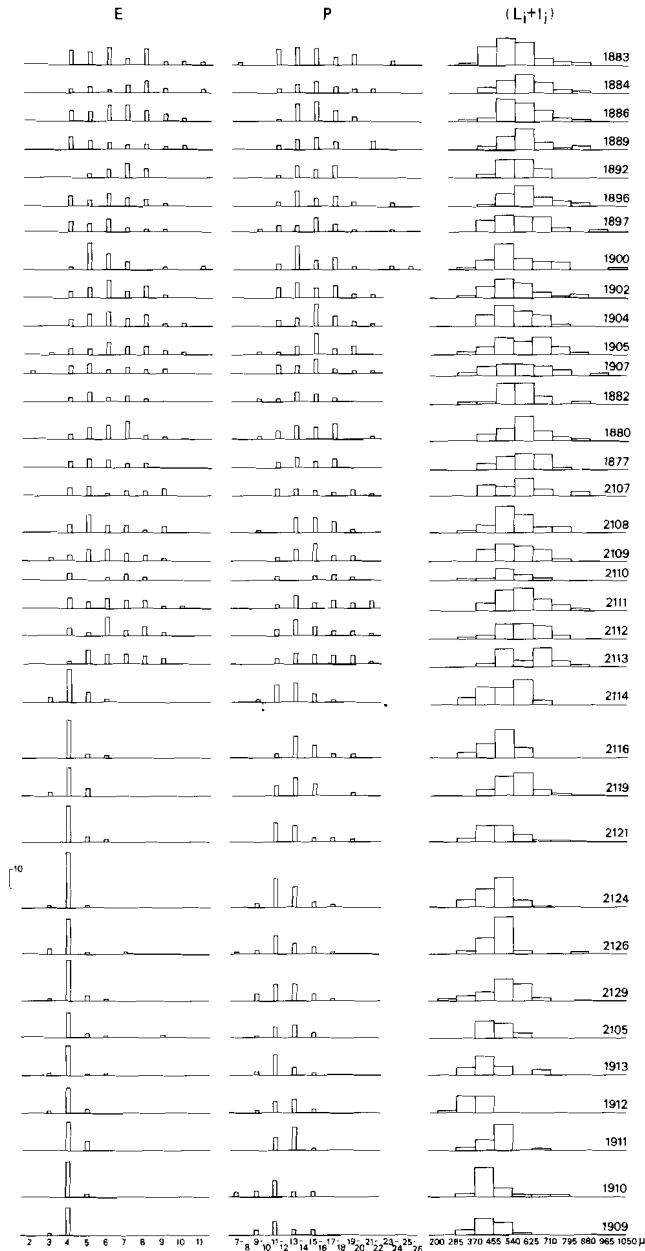


Fig. 53

Frequency distributions of E, P and $(L_1 + l_1)$ in the samples of the main composite section of Aubeterre.

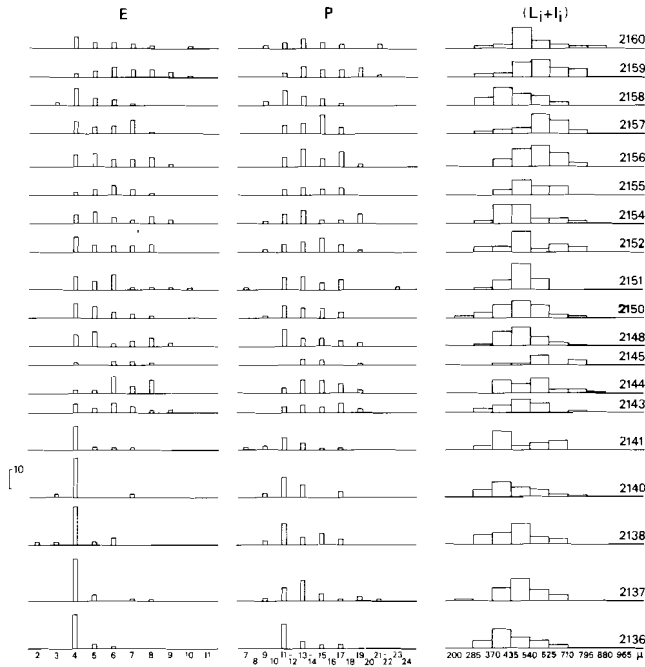


Fig. 54 Frequency distributions of E, P and $(L_j + I_j)$ in the samples of the Meschers section.

Apart from the rapid evolutionary change because of the sudden leap in average peri-embryonic configuration at one specific level in our sections, we acknowledge that progress in the sense of nepionic acceleration seems to have been a very slow process in the *Orbitoides* of our sections, especially if we concentrate on the role of the more extreme variants (fig. 55). The figures show that the introduction of further, progressive morphotypes (i.e., $E = 10$, $E = 11$) in our counts seems to reflect an extremely slow process in the higher parts of the Aubeterre and Meschers sections. However, this statement of slow progress may be exaggerated if one considers the assumed duration of roughly one million years for the entire *Orbitoides* range in Aubeterre. A similar remark of very slow change can be made with regard to the loss of old, conservative morphotypes ($E = 3$, $E = 4$), which actually did not take place at all for the four variant.

We cannot escape from the impression that “better” morphotypes had little or no adaptive value. Or maybe it is more correct to say that the more advanced morphotypes were unable to increase in relative numbers in the huge populations during the periods of stable *Orbitoides* morphology.

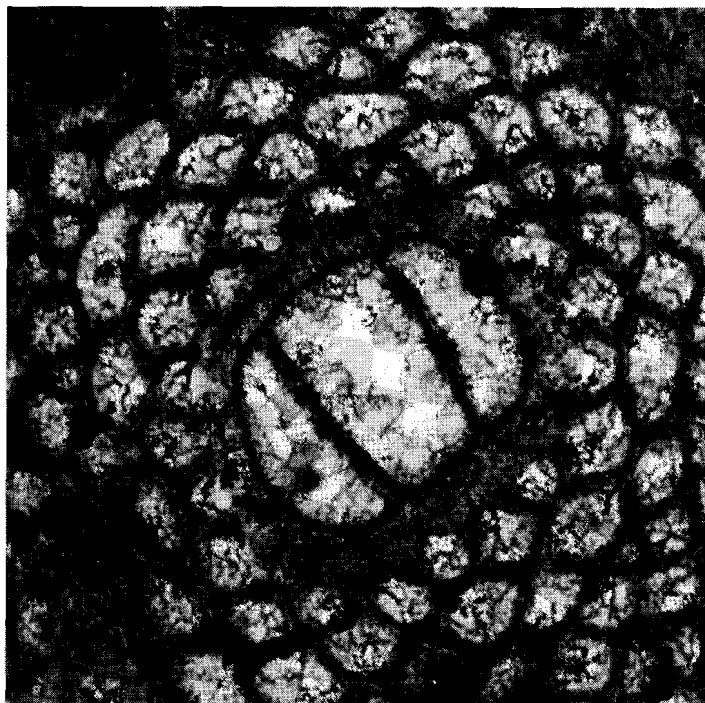


Fig. 55 Progressive *Orbitoides*-variant with an E value of 9 or 10.

The changes along the stratigraphic columns in the variation range of the E morphotypes indicate that the discontinuity level that we concluded from the means does not play a prominent role; across this level the range remains practically the same. With respect to the gain of new morphotypes and the loss of old ones, we might very well appreciate the sequence of morphotype ranges to be a fairly good reflection of the concept of phyletic gradualism. This remark is equally valid for parameter P. In figure 53 we observe the successive entries of four larger-value classes, irregularly distributed along the column, but the topmost sample shows that nothing was lost at the lower-value side of the frequency distributions.

A similar conclusion, namely slow changes of the morphotype ranges could be drawn also with regard to the Y variants in the *Planorbulinella* example (M.M. Drooger et al., 1979). Here too, practically nothing new seems to have been added and nearly nothing has been lost in the sequences of samples from the Cretan Miocene sections. Concerning the range of the variants involved the lineage of *Planorbulinella* seems to show an extremely slow change. As in the case of *Orbitoides*, the large changes which strike

the eye, are based entirely on rapid shifts in the mean values, and thus on sudden changes in the frequency distributions of the variants within a near-constant range.

If we assume that the morphological range is a good reflection of the genetic variation in the populations, we are inclined to believe that the qualitative composition of the hereditary pool of *Orbitoides* and of *Planorbulinella* did not really change across these punctuation levels. And the concept of “splendid” marginal isolation to explain the punctuations does not seem to apply for our examples.

THE PULSATION PATTERN

Although the sudden change in \bar{E} and in other parameter means in *Orbitoides* is striking because it is rather extreme and the only one in our sequences of data, the picture reminds us of the sudden changes in *Planorbulinella*. However, in the latter lineage example there were repeated changes – but dispersed over a longer period of 3 to 4 mA – involving both directions. In *Planorbulinella* the repeated changes, called pulses, expressed in mean values for the nepionic configuration parameters Y and (Y + R), were caused by modal shifts to and fro in the frequency distribution of the adjoining morphotypes. The *Planorbulinella* type of succession of means with many statistically significant setbacks and leaps forward – to which the name pulsating evolution has been given – is much less distinct in our *Orbitoides*, or at least it is much less impressive.

In part of the evolutionary sequence of our *Orbitoides* the absence of real pulses is not at all surprising. In the \bar{E} sequence from the lower parts of the sections the frequency distribution of E, apart from being narrow, is so strongly dominated by the single variant E = 4 that we cannot expect significant deviations from the grand mean. The rare deviations that do occur (e.g. FR 2306 from Meschers) might well be due to chance effects in a small sample. The high value in FR 2306 might even be ascribed to accidental sampling from a large unnoticed burrow filled by material from above.

However, above the morphological discontinuity level setbacks might well be possible because of the width of the variation and the absence of any strong dominance of single morphotypes. In practice the visual setbacks in \bar{E} appear to attain no more than a low significance level.

If we consider the possible setbacks only, then we can recognize a small number of cases in the Aubeterre sections for which a level of $\alpha = 0.10$ to $\alpha = 0.05$ can be ascertained, but the samples corresponding to these comparisons are frequently at quite a considerable stratigraphic distance from one

another (fig. 29). In the Meschers section there are a number of “pulses” of comparable magnitude in the upper part of the section, but here the magnitude is much greater for two of the samples, FR 2150 and FR 2158. In these two samples \bar{E} has unmistakably too low values relative to the adjoining samples, even much lower ($\alpha < 0.01$) than one of the lowermost \bar{E} values in the series of means immediately above the discontinuity level (FR 2144). These two samples also have aberrant positions in figures 52 and 60. In the latter figures they are situated in the morphological gap between the two major clusters that correspond to the groups of lower and upper samples of all sections.

However, we are reluctant to conclude from these two examples that large-scale setbacks in the \bar{E} means did occur in our *Orbitoides*. In our opinion the influence of a sedimentary admixture of individuals from the lower group must be taken seriously, i.e. reworking may have helped to account for these anomalous mean values. It is easy to imagine that during the time of deposition of the upper series, sediment and fossils of the lower series were eroded elsewhere (supposedly further eastwards) and were subsequently redeposited in the Meschers area. Reworking seems to offer a reasonable explanation for these two “negative pulses”, notwithstanding the fact that the samples involved were taken at fairly large stratigraphic distances above the discontinuity level, at four and nine metres, respectively.

Although *Orbitoides* appears to differ from *Planorbulinella* with respect to the relative magnitude of the pulses, except for the single one corresponding to the very large jump forward, both groups are similar in another though negative aspect. For *Planorbulinella* too we were unable to conclude that some ecological factor could be held responsible for the sudden changes. If this conclusion leads us to reject any environmental influence, we can only assume that a chance factor caused the pulsating or punctuated pattern.

So we now start to ascribe the observed evolutionary courses in both these lineages to the effects of chance, a process which has been given various names in the literature (see M.M. Drooger, 1982). The term best known to paleontologists is the random walk in the sense used by Raup (1977). For every population the frequency composition of its variants would be the result of that of the immediately preceding population plus the chance result of a random change. Over a longer period the latter combination of factors contains a time series effect. Such random shifts are not distinct in the stasis parts of the *Orbitoides* example, but they are repeatedly present in the *Planorbulinella* lineage. Although we do not find indisputable, strong negative pulses in *Orbitoides* but only a notably large step forward, we see no

obvious reason why the various pulses of *Planorbulinella* over 3–4 mA and the single punctuation in *Orbitoides* in 1 mA should be of different character. We therefore need not look for different evolutionary mechanisms for both lineages.

If numerical deviations are sufficiently distinct because of magnitude or duration, one might expect them to be recognizable in the successions of means over longer geographic distances, i.e. they might have a certain value in stratigraphic correlations. The expectation that such a correlation value may be present has been expressed earlier for the example of the *Mio-gypsinoïdes* sequence described from the Kutch area of India (Drooger and Raju, 1978); in the *Planorbulinella* example such an application value could not be substantiated, however. The theory seems to find additional support in the *Orbitoides* example. In addition to the feeble oscillation pattern and the single strong leap in peri-embryonic configuration – which was also recognized at a distance of 90 km – the sections show yet another regularity, but it is impossible to check it statistically.

Following the great change from FR 2210 to FR 2211 the various parameter means in the detailed section of the Champ de Foire seem to follow a course of further increase in the next higher metre of the section; for $(\bar{L}_i + \bar{l}_i)$ this trend seems to have commenced already in an irregular fashion below the discontinuity level. It is true that such trends are less clear in the other sections; this, however, may be a consequence of the wider sample spacing. Nevertheless, there are indications for a similar behaviour in the sections of Meschers and Gendarmerie. In all these sections we see a return to lower values again at some two to five metres above the discontinuity level. Above this level we recognize an irregularly staggered pattern throughout the higher parts of the sections around some seemingly stable grand mean. Although of no statistical significance, it looks as if – after the rapid progressive change – the stabilization of the populations caused an initial retreat before the course became really stable again.

Since we think we recognize this pattern both in Aubeterre and in Meschers, we might conclude that it was valid for the entire Aquitaine basin. If so, it can be concluded that populations were fairly similar over considerable horizontal distances in each time slice, in other words that geographic clines in morphology were negligible.

Such a conclusion needs some further consideration, however. If correct, we expect the frequency distributions of parameters for Aubeterre and Meschers to be almost the same, both below the punctuation level and above. In the earlier discussions on parameter means and V values we

argued, however, that the Meschers assemblages below this level showed a more advanced character than their counterparts of Aubeterre. On the basis of the total frequency distributions (figs. 56–58) we performed a series of χ^2 tests.

As far as the lower parts of the sections are concerned it appears that the relatively larger number of $E > 6$ observations at Meschers does not lead to a rejection at an $\alpha \leq 0.1$ level of the hypothesis that the assemblages from Meschers and Aubeterre could have been derived from population groups with the same frequency distribution. In other words, a horizontal morphocline cannot be substantiated for the overall population composition below the discontinuity level. The same results followed from the tests on the P and $(L_1 + l_1)$ distributions.

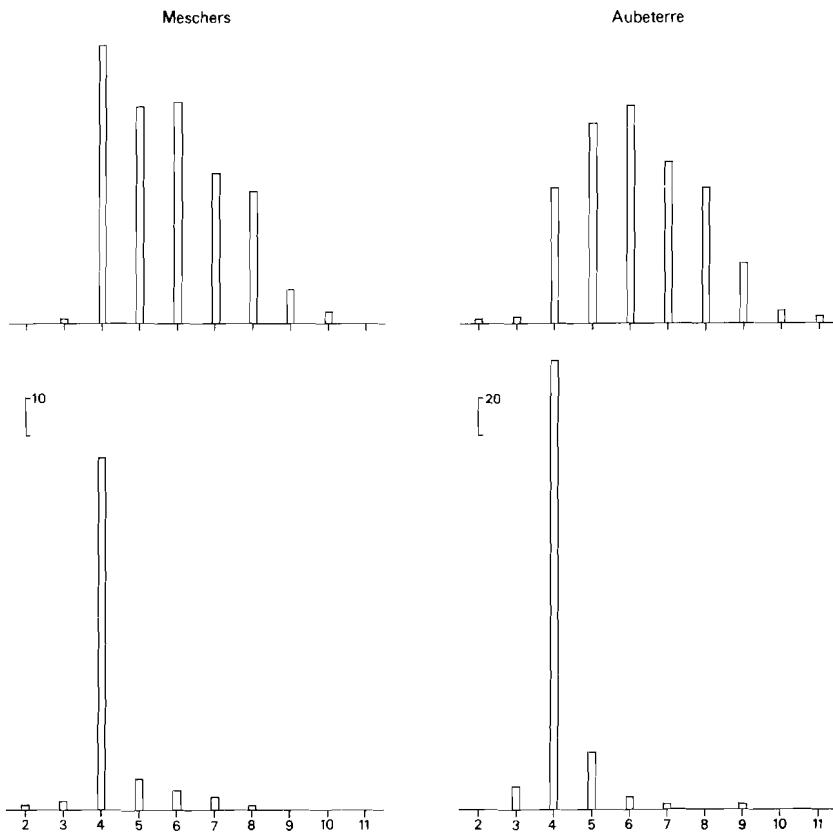


Fig. 56 Composite frequency distributions of E below and above the *Orbitoides* discontinuity level in the main sections of Aubeterre (right) and Meschers (left).

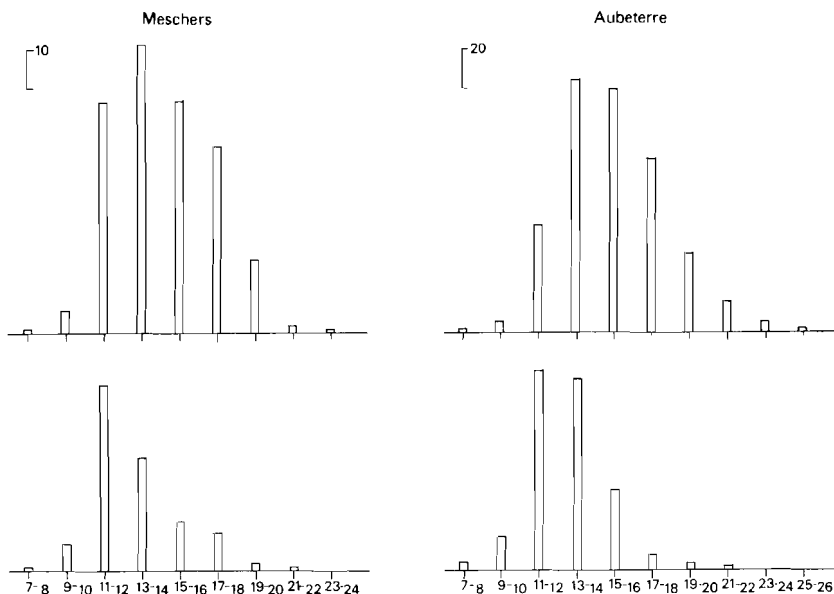


Fig. 57 Composite frequency distributions of P below and above the *Orbitoides* discontinuity level in the main sections of Aubeterre (right) and Meschers (left).

Above the discontinuity level and for all three parameters the χ^2 tests suggest a rejection of the null hypothesis at a probability level smaller than 0.01. At Aubeterre E, P and $(L_i + l_i)$ tend to be larger than at Meschers. Stronger reworking of older deposits at the Gironde site is considered to be a more likely explanation for this difference than the assumption of a geographic morphocline or the presence of negative pulses at the Meschers site only.

PULSATING EVOLUTION VERSUS DIRECTIONAL CHANGE

The total picture of the evolution of our *Orbitoides* is still puzzling. On the one hand we have two prolonged periods of near-stability in morphology, during which nothing seems to have changed across all kinds of local environmental fluctuations such as for instance those of the special biotopes reflected in the oyster beds. This picture resembles that of the middle course of a random walk. On the other hand we have seen the “big leap forwards”, probably basin-wide, without there being any obvious reason in the environment for such a drastic change. This looks like a punctuation of the “classical” type or like an isolated positive pulse. The mechanism underlying both remains enigmatic.

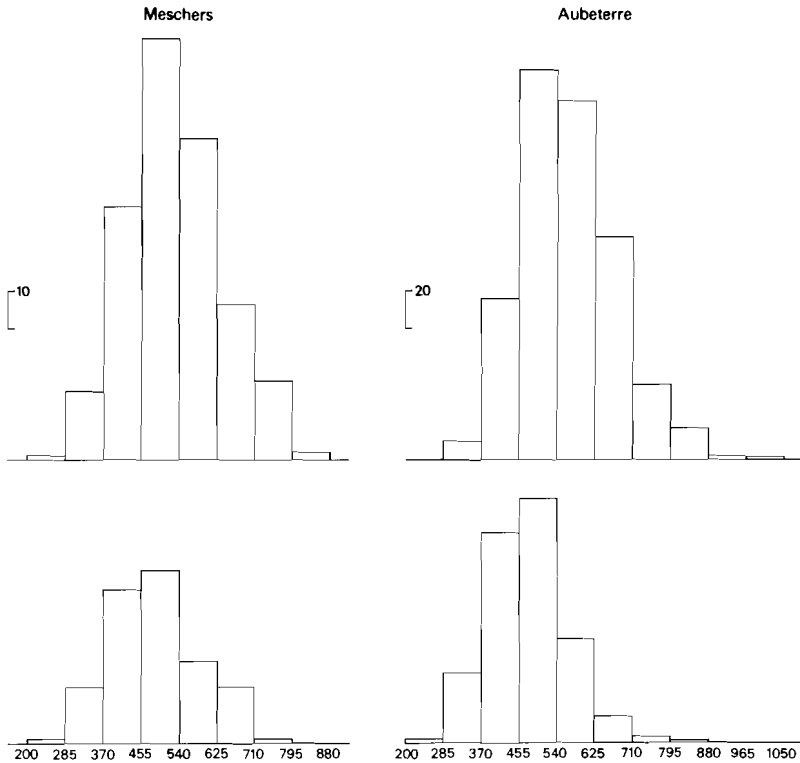


Fig. 58 Composite frequency distributions of $(L_1 + l_1)$ below and above the *Orbitoides* discontinuity level in the main sections of Aubeterre (right) and Meschers (left).

If we ascribe the punctuations or pulses to a chance factor we are still confronted with the fact that the final result of the evolution in all lineages of the orbitoidal larger foraminifera, also in *Orbitoides*, is directional in accordance with the so-called principle of nepionic acceleration. As a consequence the random walk model cannot be held solely responsible for the evolution in all these lineages of larger foraminifera; it has to be rejected on simple statistical grounds (M.M. Drooger et al., 1979). We evidently have to explain a chance overprint on an overall direction of change, or a specific direction superimposed on a large number of random walks.

The direction of the changes towards the ultimate result of the lineages may well be explained as advantageous for the groups, i.e. as an adaptive response of the organisms to their environment. This adaptation has been variously translated as a trend to better radial symmetry, or expressed more properly, as a trend to a more rapid attainment of radial growth by the indi-

viduals during the time range of the lineages involved. If the actual course of the evolution in these orbitoidal lineages were the general result of some kind of delicate balance between an overall urge to embryonic-nepionic acceleration and the chance factor responsible for either the pulsating overprint or the basic course, we would expect each lineage to show its own morphological peculiarities. Those of *Orbitoides* with its four-chambered, thick-walled type of embryo are quite unique and are not found in any of the other lineages.

With regard to the controversy mentioned in the title of this subchapter we again raise the question of whether or not a (i.e. our) punctuation can be regarded as an isolated pulse. It can be argued that punctuations are sudden evolutionary "advances", whereas the pulsating pattern also contains sudden shifts backwards against the direction of overall "progressive" change. In order to avoid misunderstanding we state here that the terms advanced and progressive are meant to correspond to changes which are in line with the direction of nepionic acceleration or embryonic acceleration in the orbitoidal foraminifera.

With regard to nepionic acceleration, so far we have only a few well-documented examples of punctuation, or rather of changes that look like punctuations. And it can be doubted whether such punctuations always led to more advanced forms. In the example of Indian *Miogypsinoides* (Drooger and Raju, 1978; Drooger, 1983) the postulated punctuation from *M. bermudezi* to *M. complanatus* leads to more primitive forms in the sense of nepionic acceleration and this change seems to have a world-wide value because it is known to have occurred in India and in Central America. But in the species suite of *Planolinderina* (Drooger, 1983) and in the later part of the French *Lepidorbitoides* lineage (Verhallen et al., 1984) there are other possible punctuations which do have a "forward" direction.

As far as direction is concerned it thus seems acceptable to consider pulses and punctuations as evolutionary phenomena of the same type. They should fit in with a single explanation to account for the seemingly random directional effect of such changes. The explanation must be still more complex, however, because the final results of evolution in all kinds of lineages of orbitoidal foraminifera are clearly directional. So it is safe to assume that, in addition there was some adaptive response which led to better radial growth and to parallelism of the lineages. As far as the successions of means are concerned, sustained changes seem to be unlikely, because we find directionless or more or less stable courses interrupted by rapid pulses of change; the net effect of all pulses together yields the final directional result for each lineage.

Whether we call the rapid change a pulse or a punctuation the effect seems

to be that in a geologically very short time interval a radical change occurred in the frequency distribution of an existing range of morphotype variation. There need not be any conspicuous addition of new morphotypes or loss of older morphotypes. In our *Orbitoides* and *Planorbulinella* examples the latter types of change generally seem to have had imperceptibly low rates, which are not specifically linked to the short periods of the pulses. Once a new and more advanced morphotype has been introduced, there is no rapid frequency increase in the populations. During the periods when the lineage is relatively stable such new types seem to be unable to expand in relative numbers. This apparent stability during the major parts of the history of the lineages seems to fit in with the evolutionary theory based on large populations. Such large populations are easy to imagine in the year-to-year stock of foraminiferal species. And the pulses thus lead us to assume that genetic drift played a role to account for the random direction of change in very small populations.

Theory therefore requires that very small populations be inserted in the history of the group to bring about the rapid morphological changes of the pulses. One wonders, however, whether the concept of geographic separation and isolation of marginal populations is a realistic approach for understanding of the mechanism in foraminifera. In contrast with many higher organisms a sequence of enormous non-isolated populations was probably left in the larger parental habitats to continue along successive generations. The more evolved small group will have found it hard to eliminate this large stable group when it returned to this larger realm after it had undergone a forward change during the period of "advantageous" isolation. If, for instance, such marginal *Orbitoides* populations of an original $\bar{E} = 4$ composition had rapidly attained a $\bar{E} = 6$ stage, the joining of both groups afterwards would have led to renewed genetic exchange and probably the suppression of the characteristics of the small group of newcomers. These immigrants were hardly in a better position to dominate the enormous parental stock that had stayed "at home" than were the occasional variants in the continuous suite of large populations. Actually, the phenotypic composition – and probably also the genetic variation – of parental and marginal groups appears to be the same in our examples; the groups differ only in modal character of the frequency distributions. And if the advanced morphotypes were unable to increase in relative numbers in the large populations, it seems unlikely that they expanded after the re-introduction of the more advanced, but still small marginal group.

It is therefore more plausible to assume that the entire stock in a certain area, e.g. our *Orbitoides* in the Aquitaine basin, went through a minimum-frequency crisis. The necessary radical shifts in morphotypic (and genetic) composition then could have taken place in the succession of ensuing small populations. If such a frequency bottleneck could cause a random change in the composition of the variant frequencies one would understand why the corresponding pulses can be "forward" as well as "backward".

Nevertheless, this purely random result does not explain why the sum of all successive pulses led to the final evolutionary result in all lineages of orbitoidal foraminifera. How do we conceive the fact that the advantageous direction scored better in the end, if the pulses towards a more conservative composition stood an equal chance of continuing in the ensuing populations after each frequency bottleneck had been passed? Many random walks could not have led to the similar ultimate results; for statistical reasons the apparent parallelism of many random walks must be rejected.

A purely hypothetical solution to this problem has been proposed by the first author (1984). If we assume that there was a strong frequency drop in the parental stock in a certain area and, as an extra condition, that in some cases we are left not with a single small population but with for instance two such small populations, geographically well-separated from each other in the original realm, we can postulate that either both residual populations rapidly changed in different ways or one changed and the other did not. One sequence may have become more conservative, while the other remained stable or showed an advance. Furthermore we assume that after an adequate separation time both small stocks came together again, blended and expanded in numbers. If we assume that the difference in the adaptive value of both groups of approximately equal size had grown sufficiently large, it is conceivable that the more advanced group of the two had a better chance of achieving dominance in the following generations than the more conservative group. In this model we thus avoid the problem of a small, advanced group of individuals that has to gain dominance over a very large more conservative group.

In other words, during the period of low frequency one suite of small residual populations would have an equal chance for setback or advance, in addition to the possibility of remaining stable. In the rare cases where there were two, or more, residual population suites that managed to pass the low-frequency bottleneck period, there would be near-equal chances for stability or advance for the ultimate combination that continued after this period, but there was a smaller probability for the backward direction.

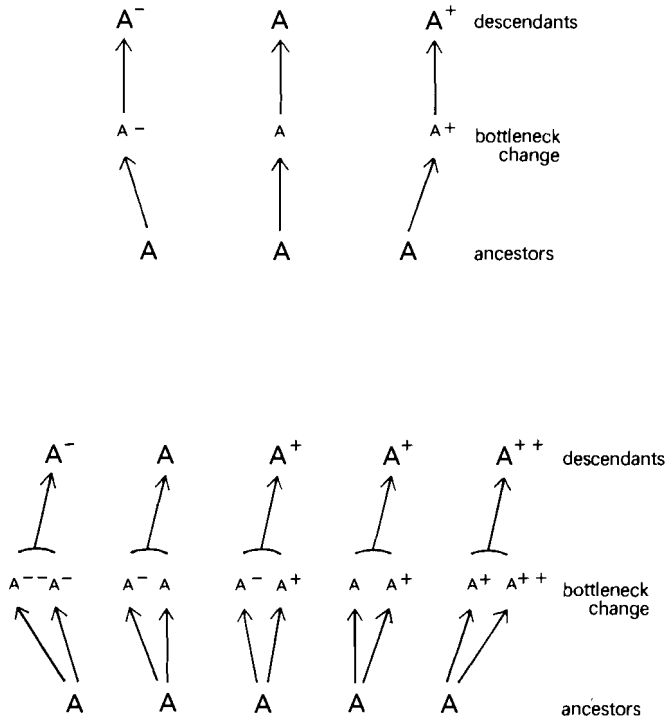


Fig. 59 Lineage evolution based on the assumption of low-frequency bottlenecks leading to completely random (above) and directional (below) effects. A is the morphotypic or genotypic mode or mean in the populations. + and - stand for "forward" and "backward" change, respectively (after Drooger, 1984).

This purely hypothetical model of frequency bottlenecks (fig. 59) might explain both the random walk character of pulsating evolution and the ultimate adaptive direction we find in all orbitoidal lineages.

Although in the discussions we concentrated on the *Orbitoides* and *Planorbulinella* examples, we do not wish to imply that pulses and punctuations could not have coincided with notably large changes in the morphotype ranges of the populations. Actually, the examples of the sudden changes in *Miogypsinoides* and in *Planolinderina* in the Indian Oligocene (Drooger and Raju, 1978; Raju and Drooger, 1978), mentioned earlier, both show that a fair number of new variants were introduced at the level where the respective means show their jump. Such examples might very well be attributed to allopatric speciation as specified in the punctuation model of Gould and Eldredge, but again evolutionary progress is evidently not the

only possible result. It appears that the change in *Miogypsinoides* is in a direction opposite to that expected from the principle of nepionic acceleration.

The question that remains concerns the mechanism that could have temporarily reduced the huge populations of the foraminiferal species to such very small groups of individuals, which could be affected by the random factor. Again we may think of external environmental influences, but actually we are only able to recognize very general changes in the environment of our fossils. Therefore it is not surprising that the role of an environmental change at the moment of the pulses so far has escaped our attention.

One can imagine that during the long successions of generations the species occasionally suffered from bacterial diseases or from parasite blooms, or that such phenomena affected their floral nutrients or their symbionts. Such factors might have caused mass-mortality during a period of one or a few years, causing the bottlenecks in population size, and in extreme cases even regional extinction of the entire species may have followed. It is logical that such disasters only affected certain species, but left others untouched. There are several examples where one species shows a rapid change, whereas an accompanying one does not (Drooger, 1983); our story of *Orbitoides* and *Lepidorbitoides* at Aubeterre is yet another example. But of course it is still possible that several groups were affected at the same time. Our bottleneck theory does not rule out the possibility of identical behaviour of two or more species during low-frequency bottleneck periods, but we still think that the data available suggest that the effects on one species in a fauna are more frequent than the reduction in the numbers of several species at the same time.

It is true that data on Recent foraminifera provide as yet little proof of such frequency reductions, but the observations of Zohary et al. (1980) on *Amphisorus hemprichii* in the Gulf of Áqaba have pointed out that the size of populations of larger foraminiferal species may vary strongly from year to year. This example makes us realize that the processes we postulated need not be entirely hypothetical.

It is doubtful whether the actual numbers of individuals per small number of years of for instance *Orbitoides* in our sections can ever be determined to support our theory. If we assume that 5 cm of sediment in Aubeterre correspond to a thousand years, we can say that our samples contain a mixture of some two thousand generations because of our sampling technique. It thus is impossible to recognize a low-frequency spell of a few up to a hundred generations. If we were to try to sample in much greater lithostratigraphic detail, our efforts would be thwarted by the much coarser effect of bioturbation.

At the end of this chapter, it has to be acknowledged that the explanation we propose for the pulses and punctuations in the lineages of our larger foraminifera can be criticized on the grounds that it cannot be checked. However, with regard to the possibility of control our explanation is just as good or as bad as any other proposed so far.

Chapter VII

TAXONOMIC NOTES

We shall refer to only some of the taxa mentioned in the previous chapters. Some numerical data on *Orbitoides* and *Lepidorbitoides* will be discussed which were not really needed in the earlier chapters, but which have a bearing on species determination. We refrain from figuring the smaller benthic species because their poor state of preservation prevented us from making good photographs.

Genus *Orbitoides* d'Orbigny, 1847

We intend to follow the biometric definition of the *Orbitoides* species given by Van Hinte (1966, 1976), because in such a system the species units that are recognized are considered to be closest to the concept of "natural" biological species. Although the original subdivision in such a lineage may be based on too optimistic a concept of gradualism and irreversibility in evolution, it provides a sharply defined morphometric delimitation of the taxonomic units.

In figure 60 we repeat the scatters of the means of E versus $(L_i + l_i)$. We have drawn vertical and horizontal lines corresponding to the limits between the successive species involved. The species units of *Orbitoides* were defined on the basis of these parameters. The figure clearly demonstrates that a biometric subdivision of the assemblages belonging to a lineage, which is based on two independent characteristics, may easily lead to the awkward result that too many samples fall outside the fields delimited for the taxonomic units.

Actually, the majority of our assemblages are outside the ranges of the successive biometrically defined species *O. tissoti*, *O. media* and *O. megaliformis*. The tentative definition that Van Hinte (1976) gave for the $(\overline{L_i + l_i})$ limits of his species appears to be rather unfortunate as far as our French data are concerned. This is also true for part of Van Hinte's own 1966 data on *O. megaliformis*. The scatter of his mean-points along the periphery of our own cluster might very well be due to inevitable, systematic differences in the measuring and counting done by different investigators, but nonetheless most of the 1966 assemblages from the upper part of the Aubeterre section have too low $(\overline{L_i + l_i})$ values for the limit Van Hinte suggested himself.

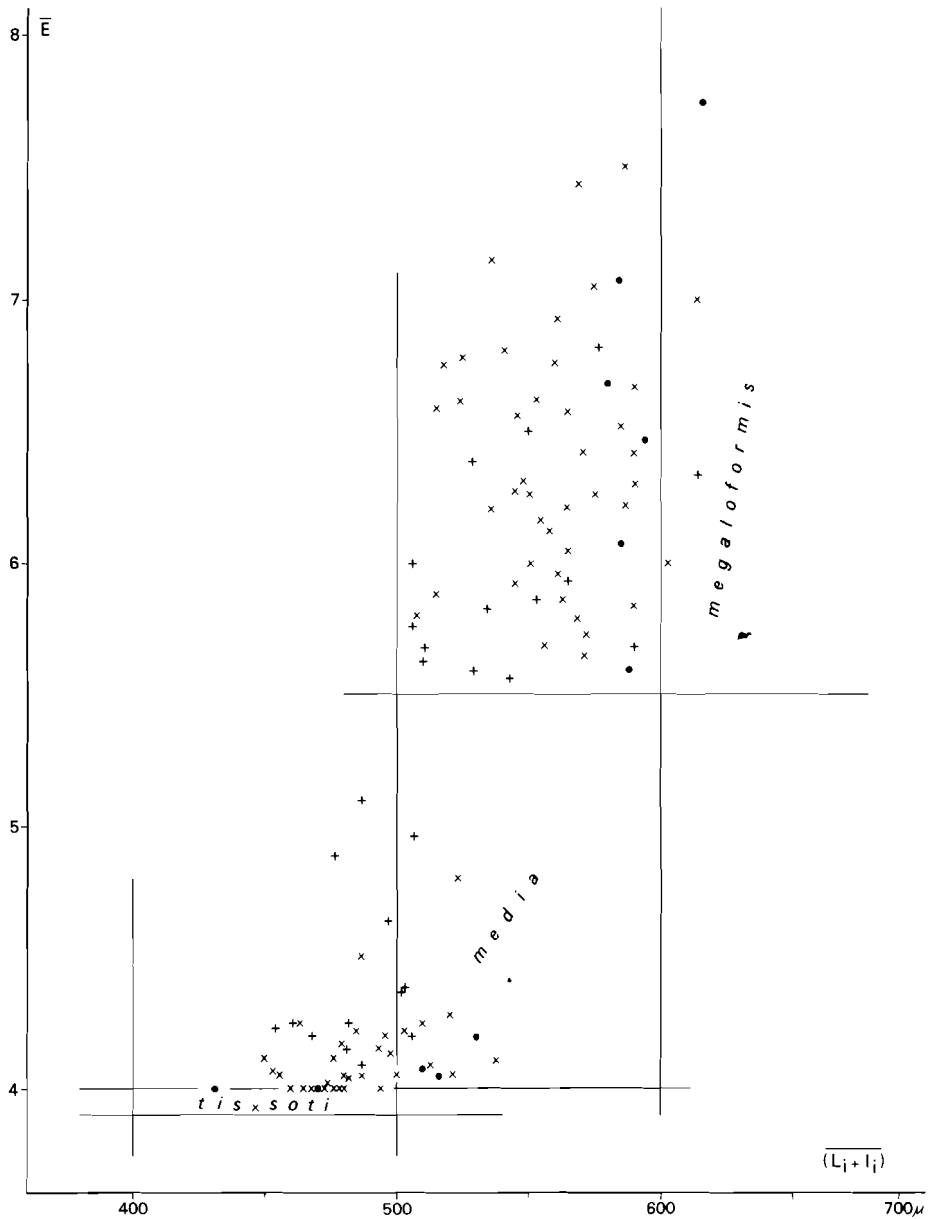


Fig. 60 Scatter diagram of \bar{E} versus $(L_j + l_j)$ for all analyzed samples from Aubeterre and Meschers. The morphometric species limits, proposed for *O. tissoti*, *O. media* and *O. megaliformis*, have been entered as horizontal and vertical lines. x Aubeterre, + Meschers, • data from Aubeterre given by Van Hinte (1966).

We do not intend to alter the biometric limits between the species, but we propose to use only the \bar{E} scale for the purpose of classification.

Orbitoides tissoti Schlumberger

Orbitoides tissoti Schlumberger, 1902, Bull. Soc. géol. France, ser. 4, vol. 2, p. 259, pl. 8, figs. 21–25.

This species was originally described typologically from Algeria. Following the definition of an upper \bar{E} limit up to and including the value four, part of our assemblages from the lower parts of the Aubeterre and Meschers sections can be assigned to this species. Actually, these few assemblages are so close to the limit with *O. media* that the distinction of *O. tissoti* as a separate species is rather meaningless in our material from south-west France.

Orbitoides media (d'Archiac)

Plate 2

Orbitolites media d'Archiac, 1837, Mém. Soc. géol. France, vol. 2, no. 7.

Orbitoides media (d'Archiac), Schlumberger, 1901, Bull. Soc. géol. France, ser. 4, vol. 1, p. 464, pl. 7, figs. 1–7.

Again we are not certain whether the original localities of d'Archiac and Schlumberger really contain *O. media* in the biometric sense Van Hinte had given to this species, but we consider the name to be a suitable label for his species unit.

The means of the majority of our samples taken below the *Orbitoides* discontinuity level in our sections are found scattered in the lowermost part of the \bar{E} range of this species, defined from larger than four to 5.5. The 500 μ lower limit for $(\bar{L}_j + \bar{l}_j)$, given as an additional condition to the definition of this species, appears to be of no use, since most of our assemblages have mean embryon size values below this limit. In our sections the upper part of the \bar{E} range of *O. media* remains empty, except for the few samples which in one way or another seem to be unreliable since they are believed to reflect heterogeneous "populations".

Orbitoides megaliformis Papp and Küpper

Plates 3, 4

Orbitoides media (d'Archiac) subsp. *megaliformis* Papp and Küpper, 1953, Sitzungsber. Österr. Akad. Wiss. Wien, math.-naturw. Kl., vol. 162, p. 74, pl. 1, figs. 8, 9.

Our assemblages from above the *Orbitoides* discontinuity level fill the lower part of the range of this species unit from $\bar{E} = 5.5$ to approximately $\bar{E} = 7.5$. Nearly all of them are plotted too low in the scatter diagram relative

to the tentative lower limit of 600μ suggested for the size of the embryo. Just as in the case of the *O. media* assemblages, there is no clear time order for the details of the successions of \bar{E} values in the sections.

Genus *Lepidorbitoides* Silvestri, 1907

For the biometric subdivision of this genus into species units we follow the classification of Van Gorsel (1975).

Lepidorbitoides campaniensis Van Gorsel

Plate 5

Lepidorbitoides campaniensis Van Gorsel, 1973, Proc. Kon. Ned. Akad. Wetensch., ser. B, vol. 76, p. 263–269, pl. 1, figs. 1, 2, 4, pl. 2, figs. 1, 3, 4, pl. 3, figs. 3, 4.

The type locality of this species is at Aubeterre in an exposure along the higher part of the Chemin creux, presumably in the higher part of the F unit of Coquand. The *Orbitoides* from this locality were not included in our investigation.

According to the original description of the species the nepionic arrangement is predominantly biserial. The biometric delimitation, given by Van Gorsel in 1975, is based on the average number of uni-apertural chambers in the initial spiral of the test ($2.1 > \bar{Y} > 1.5$), while \bar{d}_{II}/\bar{d}_I , the ratio of the means of the diameters of the embryonic chambers is between 1.2 and 1.4.

In our Aubeterre sections we found *Lepidorbitoides* specimens to be most common in the upper part of unit F up to the oyster beds of unit E, with frequencies of up to 50% relative to those of *Orbitoides*. In unit E the genus is nearly absent. With a few exceptions (FR 2121 lower down, FR 1904 and FR 1905 higher up) the genus is rare to absent in the rest of the column. The section part with high relative frequencies corresponds lithostratigraphically to the type level of *L. campaniensis* in the Chemin creux.

The internal features of 72 specimens from seven samples were analyzed, using the parameters proposed by Van Gorsel (1975) and shown in our figure 61:

d_I = diameter of protoconch,

d_{II} = diameter of deutoconch; both largest dimensions of the embryonic chambers were measured in μ , and perpendicular to the medio-embryonic line.

Y = the number of uni-apertural chambers of the original nepionic spiral; there were invariably two such chambers, i.e. the protoconch and the deutoconch.

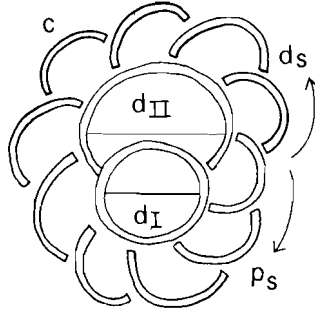


Fig. 61 Schematic drawing of the embryonic-nepionic stage in median section for an individual of *Lepidorbitoides campaniensis* Van Gorsel. d_I diameter protoconch, d_{II} diameter deutoconch, p_s protoconchal nepionic spiral, d_s deutoconchal nepionic spiral, c closing chamber.

p_s and d_s , numbers of spiral chambers around the protoconch and deutoconch, respectively; both embryonic chambers are included in each of the counts, the closing chamber is not.

The means and their standard errors for the seven investigated samples are shown in figure 62. These mean values compare very well with those given by Van Gorsel for his *L. campaniensis*, with the exception of \bar{Y} . We found Y to be 2 for all 72 specimens, whereas Van Gorsel observed this biserial ar-

	$\bar{d}_I \pm SE$	$\bar{d}_{II} \pm SE$	$\bar{p}_s \pm SE$	$\bar{d}_s \pm SE$
1905	+	+	+	+
2111	—	—	+	+
2084	—	—	+	+
2085	—	—	+	+
2086	—	—	—	—
2087	—	—	—	—
2121	+	—	—	—
	70 90 110 μ	90 110 130 150 μ	7.0 8.0 9.0 10.0	5.0 6.0 7.0

Fig. 62 The sequences of mean values with their standard errors for the embryonic and nepionic parameters of *Lepidorbitoides campaniensis* Van Gorsel in seven samples of the Aubeterre section. The *Orbitoides*-discontinuity level in the section is indicated by a horizontal line.

rangement of the nepionic chambers in 80% of his 14 specimens, 20% being quadriserial, so their Y is 1.

d_I and d_{II} show a positive correlation in most samples, which is significant ($\alpha < 0.01$) in three of the samples; p_s and d_s tend to have a negative correlation, which is logical but is significant at the same level in only one of the samples.

Our data compiled in figure 62 furthermore show that the *Orbitoides* discontinuity between samples FR 2086 and FR 2085 is not reflected in any of the *Lepidorbitoides* parameters; we are dealing with *L. campaniensis* throughout. The pattern fluctuates for all parameter means, but we cannot conclude much more than that, considering the low numbers of observations and the irregular spacing of the samples. The uppermost sample suggests that there is a size increase of the embryo.

Hellenocyclina charentensis Freudenthal

Hellenocyclina charentensis Freudenthal, 1969, Utrecht Micropal. Bull. 1, p. 134, pl. 11, figs. 2–14, pl. 14, fig. 5.

This species was originally described from the Aubeterre section. No further biometric study was made of our material, but there is little doubt that we are dealing with specimens with a moderately long nepionic spiral. Goharian (1971, p. 26) argued that the species should be transferred to the genus *Planorbulina*, but we consider his arguments to be invalid because they are based on a misunderstanding of orbitoidal growth.

Nummofallotia cretacea (Schlumberger)

Pl. 1, figs. 3, 4

Nonionina cretacea Schlumberger, 1900, Bull. Soc. géol. France, ser. 3, vol. 27, p. 460.

In the wash residues we found only halves. Complete specimens are quite common in the whole-rock thin-sections (plate 1). The splitting must be due to the washing procedure, whereas hydrodynamic energy and bioturbation during the sedimentation evidently had insufficient effect to cause the meridional parting.

Goupillaudina daguini Marie

Goupillaudina daguini Marie, 1958, Bull. Soc. géol. France, ser. 6, vol. 7, p. 861, pl. 1, figs. A–D, pl. 2.

The umbilical region of our specimens is smooth and in transverse sections no pillars are seen. We are still not certain whether *Daviesina primitiva* Hof-

ker (1959) is the same species; it looks quite similar and it has been described from the Upper Cretaceous of the northern Aquitaine basin.

Gavelinella sp. cf. *G. bosqueti* (Reuss)

cf. *Rosalina bosqueti* Reuss, 1862, Sitzungsber. K. Akad. Wiss. Wien, math.-naturw. Kl., vol. 44, p. 316, pl. 3, fig. 1.

Considerable variation is found in our assemblages with respect to the acuteness of the periphery, the flatness of the ventral side and the width of the umbilicus. Poor preservation inhibits a more certain species determination. The specimens figured as *Cibicides bosqueti* by Hofker (1959) and Villain (1977) seem to be different from ours.

Cibicides sp.

Many specimens in our assemblages placed in this counting group are probably synonymous with *Gavelinopsis voltziana* (d'Orbigny) as described and figured by Hofker (1959) and Villain (1977), but they do not correspond with the original.

Nonionella sp.

Although rather frequent in our samples we could not find a suitable name for this slightly trochoid form with five inflated chambers in the final whorl and a depressed umbilicus on either side. Possibly our forms are conspecific with the group of *Gavelinella* (cf.) *danica* (Brotzen) of authors.

Nonion sp.

Our specimens are too indistinct for specific determination. The general characteristics are: test biconvex, planispiral, involute; periphery rounded; about ten chambers in the final whorl; sutures slightly curved, indistinct, not depressed; glassy umbilical fillings; aperture indistinct.

Gyroidinoides sp.

Our specimens resemble *Gyroidina depressa* (Alth) as described and depicted by Visser (1951, p. 270, pl. 8, fig. 12).

Rotalia trochidiformis (Lamarck)

Rotalia trochidiformis (Lamarck), Davies, 1932, Trans. Roy. Soc. Edinburgh, vol. 57, p. 416, pl. 2, figs. 8, 10–15, pl. 3, figs. 1, 3–13, pl. 4, figs. 3–6, 9–11.

This counting group shows a wide variation in our material with respect to the degree of convexity of the ventral side, the number of chambers (5–12) in the final whorl and the complexity of the rotaliid structures of the ventral side. Much of this variation parallels the growth sequence of individuals, as depicted by Davies. Other species described in the literature, such as *Rotalia saxorum* d'Orbigny, may have been incorporated in our group, but we have been unable to make a clear division into more than one species.

Rotalia sp. cf. *R. parasupracretacea* (Hofker)

cf. *Rosalina parasupracretacea* Hofker, 1959, p. 284, fig. 66.

The general shape of our specimens agrees well with Hofker's figures, but other characteristics are rather obscure. Because of the pustulous umbilical mass we are inclined to place our specimens in the genus *Rotalia*, but this assignment may be unwarranted.

Pararotalia tuberculifera (Reuss)

Rotalia tuberculifera Reuss, 1862, Sitzungsber. K. Akad. Wiss. Wien, math.-naturw. Kl., vol. 44, p. 313, pl. 2, fig. 2.

We assume that our forms are primitive ancestors of this species, which is especially frequent in the Maastrichtian and the Lower Paleocene. This is the most common species in our samples, occasionally making up over fifty per cent of the entire benthonic foraminiferal fauna. In the final whorl of adult specimens we observed 6 to 8 chambers, i.e. less than the ten shown in Reuss' figure. The periphery is acute, lobate with a short spine to each chamber. There is a distinct umbilical knob and an areal "aperture".

Tremastegina roestae (Visser)

Cibicides roestae Visser, 1951, Leidse Geol. Meded., vol. 16, p. 291, pl. 6, fig. 9.

Although we followed the practice of later authors (e.g. Villain, 1977) and placed this species in the genus *Tremastegina* we are not so sure whether it is not a true rotaliid (pl. 1, fig. 1). Its placing in *Lockhartia* (Hofker, 1955, Natuurhist. Maandblad, vol. 44, p. 4) seems unjustified, however.

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	\bar{E}	SD	SE	\bar{P}	SD	SE
upper (1883–2113)	6.13	0.35	0.08	15.48	0.52	0.11
lower (2114–1909)	4.14	0.14	0.04	12.91	0.59	0.17
Student's t	22.47			12.60		
	$\bar{E/P}$	SD	SE	$\overline{(L_i + l_i)}$	SD	SE
upper (1883–2113)	0.394	0.021	0.004	566	19.9	4.3
lower (2114–1909)	0.325	0.015	0.004	477	18.2	6.8
Student's t	12.20			8.0		

Table 2. Grand means with their standard deviations and standard errors of \bar{E} , \bar{P} , $\bar{E/P}$ and $\overline{(L_i + l_i)}$ for the upper and lower groups of samples in the Aubeterre main section. An estimate of the significance of the differences is expressed by means of the Student's t-values.

	N		E		P		$(L_i + l_i)$	
	Aub.	Mes.	Aub.	Mes.	Aub.	Mes.	Aub.	Mes.
upper	22	14	25.2	25.7	17.2	16.9	18.7	19.1
lower	13	5	12.8	18.5	14.2	17.1	17.5	20.9

Table 3. Mean V-values for E, P and $(L_i + l_i)$ calculated separately for the samples above and below the morphometric discontinuity level in the main sections of Aubeterre and Meschers. N is the number of samples.

Table 4. Means with their standard errors for six internal *Orbitoides* parameters in the samples of the Aubeterre main section. V-values are added for E, P and ($L_1 + I_1$). The numbers of nepionic and embryonic observations are given separately.

Sample	\bar{E}	$\pm SE$	V	\bar{P}	$\pm SE$	V	$\bar{E/P}$	$\pm SE$	n	$(L_1 + I_1)$	$\pm SE$	V	\bar{L}_1/I_1	$\pm SE$	\bar{t}	$\pm SE$	n
FR 1883	6.27	.30	28.8	15.24	.55	22.0	.409	.010	37	545	17.0	20.9	1.30	.027	36.4	1.5	45
FR 1884	7.05	.42	26.1	16.26	.68	18.3	.431	.016	19	575	19.1	19.4	1.33	.025	38.9	1.6	34
FR 1886	5.96	.27	23.5	15.33	.36	12.1	.387	.013	27	561	17.9	18.3	1.28	.027	36.0	1.3	33
FR 1889	5.84	.43	31.9	15.84	.63	17.4	.363	.016	19	590	19.1	16.8	1.30	.028	31.8	1.2	27
FR 1892	6.76	.24	14.3	15.41	.47	12.6	.442	.015	17	560	13.3	12.3	1.37	.054	35.6	1.1	27
FR 1896	6.00	.32	25.2	15.82	.63	18.6	.377	.012	22	603	20.4	18.2	1.35	.029	38.7	1.8	29
FR 1897	5.65	.31	24.5	15.25	.68	20.0	.372	.013	20	571	20.6	20.7	1.35	.036	33.5	1.3	33
FR 1900	5.86	.26	24.0	15.34	.60	21.2	.383	.009	29	563	23.1	23.9	1.36	.029	38.6	2.0	34
FR 1902	6.26	.27	22.4	15.07	.53	18.4	.414	.009	27	550	21.1	21.4	1.32	.032	36.6	1.4	31
FR 1904	6.31	.31	25.3	15.69	.47	15.2	.401	.014	26	548	15.6	16.1	1.35	.035	36.5	1.5	32
FR 1905	6.42	.37	27.9	15.83	.51	15.8	.399	.014	24	590	19.8	19.9	1.36	.047	39.6	1.6	35
FR 1907	5.79	.44	32.9	15.05	.61	17.6	.378	.019	19	568	25.8	23.6	1.36	.035	39.0	2.0	27
FR 1882	5.69	.35	22.0	14.46	.65	16.1	.393	.013	13	556	17.3	16.8	1.37	.041	33.7	1.4	29
FR 1880	6.22	.23	19.6	15.07	.50	17.3	.413	.009	27	587	17.1	16.5	1.38	.034	39.8	1.4	32
FR 1877	5.73	.34	23.3	14.60	.56	14.8	.391	.015	15	572	15.7	14.3	1.35	.039	35.3	1.5	27
FR 2107	6.12	.46	31.1	15.29	.72	19.4	.393	.014	17	558	24.2	21.7	1.40	.045	39.9	2.0	25
FR 2108	5.92	.32	26.7	15.52	.44	14.2	.379	.013	25	545	15.2	16.5	1.38	.025	39.7	1.4	35
FR 2109	6.00	.31	24.6	15.52	.44	13.7	.383	.013	23	551	17.3	17.2	1.37	.048	39.0	1.3	30
FR 2110	5.88	.58	28.0	16.00	.98	17.4	.368	.031	8	515	26.2	17.6	1.29	.031	39.6	2.0	12
FR 2111	6.26	.36	27.8	16.65	.71	20.4	.376	.014	23	575	17.2	18.2	1.36	.031	45.3	1.4	37
FR 2112	6.30	.32	22.5	15.20	.64	18.9	.415	.013	20	590	26.5	22.9	1.31	.022	40.4	1.7	26
FR 2113	6.52	.30	22.6	16.08	.56	17.3	.405	.011	25	585	17.5	17.2	1.35	.038	43.8	1.2	33
FR 2114	4.20	.13	15.4	13.32	.34	12.6	.316	.007	25	496	14.8	18.2	1.32	.020	38.5	1.5	37
FR 2116	4.17	.10	11.8	12.91	.42	15.5	.328	.010	23	480	13.6	15.5	1.32	.025	32.8	1.4	30
FR 2119	4.10	.12	13.2	14.00	.38	12.4	.295	.010	21	538	15.0	15.3	1.37	.029	40.6	1.7	30
FR 2121	4.22	.11	12.3	13.65	.46	16.2	.314	.010	23	485	17.2	18.1	1.35	.024	35.2	1.6	26
FR 2124	4.00	.05	6.5	12.61	.33	14.7	.323	.008	31	468	13.5	17.1	1.35	.025	31.1	1.2	35
FR 2126	4.04	.15	18.6	12.79	.43	16.3	.320	.012	24	482	16.3	18.2	1.35	.029	29.5	1.1	29

FR 2129	4.15	.10	12.9	12.81	.39	15.9	.330	.011	27	493	16.3	18.4	1.35	.020	30.0	1.6	31
FR 2105	4.50	.29	27.7	13.39	.59	18.7	.335	.011	18	487	17.8	16.8	1.41	.050	32.8	1.4	21
FR 1913	4.11	.14	14.2	12.17	.33	11.4	.339	.008	18	450	21.2	22.1	1.33	.031	31.9	1.4	22
FR 1912	4.06	.11	10.9	12.88	.40	12.3	.319	.011	16	454	17.2	16.5	1.33	.046	29.6	1.8	19
FR 1911	4.25	.10	10.5	12.95	.22	7.7	.331	.011	20	463	15.5	16.1	1.36	.031	34.7	2.1	23
FR 1910	4.05	.05	5.5	11.75	.47	17.9	.355	.014	20	456	18.7	20.9	1.50	.035	31.0	1.9	26
FR 1909	3.93	.07	6.6	12.60	.41	12.7	.316	.009	15	447	13.7	13.7	1.49	.070	27.8	2.1	20
Sample	\bar{E}	$\pm SE$	V	\bar{P}	$\pm SE$	V	$\bar{E/P}$	$\pm SE$	n	$(L_i + l_i) \pm SE$	V	$\bar{L}_i/l_i \pm SE$	\bar{t}	$\pm SE$	n		

Table 4. (continued)

Sample	\bar{E}	$\pm SE$	V	\bar{P}	$\pm SE$	V	$\bar{E/P}$	$\pm SE$	n	$\overline{(L_i + I_i)}$	$\pm SE$	V	$\overline{L_i/I_i}$	$\pm SE$	\bar{t}	$\pm SE$	n
FR 1924	6.21	.39	30.8	16.13	.61	18.5	.382	.015	24	565	19.2	18.0	1.33	.032	40.8	2.2	28
FR 1923	6.16	.35	25.0	15.47	.60	16.9	.395	.014	19	555	18.3	18.4	1.34	.034	41.0	1.6	31
FR 1922	6.67	.53	32.0	17.00	1.05	25.5	.399	.021	17	590	24.1	20.4	1.40	.036	45.9	2.5	25
FR 1921	5.80	.34	26.0	15.00	.61	18.2	.384	.013	20	508	20.2	19.5	1.44	.043	39.0	2.0	24
FR 1920	6.78	.36	22.4	16.44	.65	16.7	.413	.016	18	525	16.2	14.5	1.33	.039	42.5	1.8	22
FR 1919	6.62	.31	25.0	16.03	.56	18.7	.412	.012	29	553	17.3	19.0	1.41	.038	44.8	2.1	37
FR 1918	6.58	.54	35.6	17.05	.84	21.5	.378	.017	19	565	24.4	20.7	1.28	.047	45.6	3.1	23
FR 1917	6.61	.39	28.4	15.57	.72	22.2	.424	.014	23	524	16.2	15.8	1.44	.079	46.1	3.3	26
FR 1916	7.44	.57	32.3	17.72	1.05	25.1	.415	.012	18	569	40.1	29.9	1.42	.093	44.8	2.8	18
FR 1915	6.75	.28	23.5	15.81	.44	15.8	.425	.011	32	518	17.2	18.8	1.37	.028	39.6	1.5	32
FR 1914	4.22	.09	10.0	13.48	.39	13.8	.318	.010	23	503	17.5	17.7	1.35	.033	36.6	1.3	26

Table 5. Means with their standard errors for six internal *Orbitoides* parameters in the samples of the Gendarmerie section, Aubeterre. V-values are added for E, P and $(L_i + I_i)$. The numbers of nepionic and embryonic observations are given separately.

Sample	\bar{E}	SE	V	\bar{P}	SE	V	$\overline{E/P}$	SE	n	$\overline{(L_i + l_i)}$	SE	V	\bar{t}	SE	n
FR 2218	7.50	.40	23.9	17.05	.63	16.5	.436	.011	20	587	20.2	17.9	40.5	1.6	27
FR 2219	7.15	.46	28.8	16.20	.72	19.9	.435	.015	20	536	18.6	18.4	39.3	1.7	28
FR 2220	6.23	.36	27.1	15.64	.67	20.1	.397	.014	22	536	18.7	18.8	39.3	1.8	29
FR 2221	6.81	.39	26.2	16.05	.68	19.4	.422	.014	21	541	19.0	19.2	39.4	1.8	30
FR 2222	6.43	.45	26.2	16.57	.68	15.4	.387	.020	14	571	26.8	17.6	40.9	2.1	14
FR 2213	6.56	.34	25.9	15.48	.54	17.5	.420	.013	25	546	17.2	17.3	37.3	1.3	30
FR 2212	6.59	.40	25.0	16.71	.87	21.5	.395	.016	17	515	21.4	18.6	38.3	1.6	20
FR 2211	6.05	.41	31.8	15.23	.78	24.0	.390	.012	22	565	18.0	17.7	40.0	2.0	31
FR 2210	4.28	.10	12.6	13.76	.29	11.4	.314	.008	29	520	12.3	13.6	38.4	1.3	33
FR 2214	4.11	.08	8.3	12.44	.47	16.0	.340	.015	18	476	15.3	16.7	38.8	1.7	27
FR 2215	4.09	.06	6.9	13.59	.49	16.9	.311	.012	22	513	17.5	16.7	35.8	1.7	24
FR 2216	4.80	.29	27.2	14.35	.65	20.3	.337	.015	20	523	21.1	18.9	39.7	2.1	22
FR 2217	4.00	.00	0	12.50	.27	6.1	.320	.005	8	460	20.7	13.5	34.2	2.2	9

Sample	\bar{E}	SE	V	\bar{P}	SE	V	$\overline{E/P}$	SE	n	$\overline{(L_i + l_i)}$	SE	V	\bar{t}	SE	n
FR 2084	7.00	.36	24.7	16.43	.60	17.5	.422	.012	23	614	19.3	16.9	41.0	1.4	29
FR 2085	6.93	.35	26.7	16.45	.69	22.1	.417	.011	28	561	20.0	19.2	40.3	1.8	29
FR 2086	4.13	.07	8.3	13.58	.41	14.8	.310	.009	24	498	14.2	14.5	39.6	1.3	26
FR 2088	4.25	.11	12.7	13.17	.13	4.9	.325	.008	24	510	15.1	14.8	36.6	1.4	25

Table 6. Means with their standard errors for five internal *Orbitoides* parameters in the detailed section below the Champ de Foire, Aubeterre. V-values are added for E, P and $(L_i + l_i)$. The numbers of nepionic and embryonic observations are given separately.

Sample	\bar{E}	\pm SE	V	\bar{P}	\pm SE	V	$\bar{E/P}$	\pm SE	n	$(\bar{L}_i + l_i)$	\pm SE	V	\bar{L}_i/l_i	\pm SE	\bar{t}	\pm SE	n
FR 2160	5.56	.438	31.5	14.8	.81	21.9	.3766	.0175	16	543	24.3	21.0	1.28	.018	36.6	1.50	22
FR 2159	6.82	.358	24.6	16.3	.60	17.3	.4147	.0118	22	577	19.4	18.1	1.35	.043	37.1	1.51	29
FR 2158	4.89	.323	28.8	13.2	.47	15.5	.3704	.0169	19	473	19.2	20.7	1.36	.034	31.7	1.42	26
FR 2157	5.68	.282	23.3	14.8	.43	13.6	.3827	.0143	22	590	20.0	17.0	1.33	.030	36.4	1.60	25
FR 2156	5.93	.302	26.5	15.1	.43	14.8	.3909	.0142	27	565	16.3	16.6	1.45	.046	36.3	1.02	33
FR 2155	5.86	.312	19.9	14.9	.57	14.3	.3936	.0174	14	554	19.3	16.0	1.32	.027	36.8	1.61	21
FR 2154	6.00	.366	28.6	15.0	.67	21.0	.3981	.0150	22	506	18.9	19.8	1.35	.030	36.0	1.33	28
FR 2152	5.59	.330	27.7	14.6	.54	17.4	.3820	.0151	22	529	25.5	24.6	1.28	.034	32.7	1.79	26
FR 2151	5.63	.329	28.7	14.5	.61	20.6	.3888	.0128	24	510	12.3	12.3	1.32	.045	34.3	1.70	26
FR 2150	5.10	.270	23.7	14.1	.51	16.2	.3618	.0132	20	487	20.1	22.6	1.34	.027	33.2	1.50	30
FR 2148	5.68	.351	29.0	14.3	.56	18.4	.3930	.0134	22	411	18.9	19.2	1.35	.030	37.3	1.59	27
FR 2145	6.33	.558	21.6	15.0	.93	15.2	.4230	.0317	6	614	36.6	18.9	1.31	.026	46.3	2.27	10
FR 2144	6.50	.255	19.2	15.2	.43	14.8	.4265	.0106	24	550	24.2	22.0	1.32	.034	40.6	1.78	25
FR 2143	5.76	.369	26.4	15.5	.59	15.7	.3714	.0178	17	506	21.5	18.5	1.34	.039	36.6	1.81	19
FR 2141	4.38	.221	20.2	12.5	.57	18.2	.3544	.0146	16	503	24.2	23.1	1.35	.041	35.0	1.45	23
FR 2140	4.09	.140	16.4	12.9	.45	16.7	.3225	.0109	23	487	23.1	23.2	1.34	.033	34.6	1.70	24
FR 2138	4.15	.164	20.5	13.6	.45	16.9	.3082	.0100	26	481	17.5	19.6	1.33	.019	35.7	1.65	29
FR 2137	4.37	.186	22.1	14.1	.49	18.1	.3114	.0083	27	502	16.3	17.5	1.28	.022	33.9	1.52	29
FR 2136	4.20	.120	13.1	13.1	.44	15.4	.3215	.0064	21	468	19.3	21.0	1.34	.026	34.1	1.45	26

Table 7. Means with their standard errors for six internal *Orbitoides* parameters in the carapets section at the southern end of the Plage de Cadet, Meschers. V-values are added for E, P and $(L_i + l_i)$. The numbers of nepionic and embryonic observations are given separately.

Sample	\bar{E}	$\pm SE$	\bar{P}	$\pm SE$	$\bar{E/P}$	$\overline{(L_i + \bar{I}_i)}$	$\pm SE$	$\overline{L_i/I_i}$	$\pm SE$	n
FR 2309	6.39	.51	16.1	1.03	.385	529	27	1.34	.05	18
FR 2308	5.83	.29	16.4	.79	.350	534	24	1.38	.05	24
FR 2307	4.25	.10	13.0	.36	.327	461	17	1.29	.04	20
FR 2306	4.96	.18	14.5	.37	.333	507	23	1.31	.04	25
FR 2305	4.64	.16	14.6	.39	.311	497	19	1.30	.03	25
FR 2304	4.20	.10	13.1	.40	.319	506	17	1.27	.03	18
FR 2303	4.23	.08	12.9	.29	.328	454	23	1.34	.04	21
FR 2302	4.25	.17	12.6	.32	.327	482	16	1.32	.02	24

Table 8. Means for five internal *Orbitoides* parameters with standard errors for four of them in the samples from the detailed sections of the Plage de Cadet, Meschers. The column with n-values refers to both nepionic and embryonic data.

Sample	E – (L _i + l _i)	E – P	E/P – (L _i + l _i)	P – (L _i + l _i)	L _i /l _i – (L _i + l _i)	t – (L _i + l _i)	n
FR 1883	.7126	.8883	.2944	.7158	.1661	.5286	37
FR 1884	.8667	.8083	.5791	.7727	.3644	.5981	19
FR 1886	.7546	.6989	.5076	.7011	–.3466	.5751	27
FR 1889	.7975	.8499	.5261	.8437	.4201	.5085	19
FR 1892	.2767	.4203	–.3558	.7437	–.1500	.4261	17
FR 1896	.6858	.8255	.1751	.8482	–.2650	.6823	22
FR 1897	.6432	.7705	.1084	.6672	.2970	.5568	20
FR 1900	.8349	.8062	.0554	.8923	.1143	.6706	29
FR 1902	.6640	.8847	.2419	.6788	.0036	.6976	27
FR 1904	.7265	.7114	.3992	.7444	–.0230	.5739	26
FR 1905	.7815	.8619	.6323	.7834	.0118	.6747	24
FR 1907	.8442	.8270	.5972	.8498	.0348	.6721	19
FR 1882	.8278	.8244	.3984	.7915	.4299	.5381	13
FR 1880	.4278	.8435	–.1009	.5348	–.2104	.3538	27
FR 1877	.4819	.7517	.1650	.6071	.0140	.5627	15
FR 2107	.6389	.9336	.5110	.6447	.1123	.6833	17
FR 2108	.5572	.7559	.2597	.7221	–.3653	.6220	25
FR 2109	.6010	.7804	.4999	.5293	.0439	.3349	23
FR 2110	.8116	.5012	.5394	.6398	–.1326	.3253	8
FR 2112	.6115	.8233	.2276	.5549	–.4237	.7179	20
FR 2113	.5750	.7506	.2319	.5644	.3711	.2733	25
FR 2114	.5933	.6700	–.0266	.7244	.2311	.4788	25
FR 2116	.2855	.4794	–.0145	.2758	.2720	.5741	23
FR 2119	.0370	.3214	–.3980	.5154	–.1039	.3234	21
FR 2121	.4871	.4265	–.4257	.8067	–.0762	.4481	23
FR 2124	–.1907	.2087	–.6257	.5967	.1964	.7552	31
FR 2126	.1691	.5059	–.3397	.5453	.0742	.5330	24
FR 2129	.0447	.3089	–.5878	.6811	–.5330	.8074	27
FR 2105	.8118	.8574	.4991	.7222	.1508	.7299	18
FR 1913	.5755	.7054	.0754	.5842	–.3763	.4864	18
FR 1912	.7133	.3917	.2212	.4222	–.0456	.6265	16
FR 1911	.1123	–.2076	–.1224	.3658	–.4491	.6687	20
FR 1910	–.0256	.3644	–.0558	.2248	.0302	.4353	20
FR 1909	.1469	.4511	–.4598	.5159	–.2990	.0769	15

Table 9. Correlation coefficient values for six parameter combinations in the samples from the main composite Aubeterre section. Significance levels $\alpha < 0.01$ bold, $\alpha < 0.05$ italics. n is the number of nepionic observations.

Sample	E — (L _i + l _i)	E—P	E/P — (L _i + l _i)	P — (L _i + l _i)	L _i /l _i — (L _i + l _i)	t — (L _i + l _i)	n
FR 1924	.6006	.7658	.3690	.5942	-.1063	.5999	24
FR 1923	.6541	.8247	.3735	.6593	.0903	.5582	19
FR 1922	.7547	.7064	.2513	.8314	.0773	.7429	17
FR 1921	.6610	.8427	.2443	.7431	.0700	.5308	20
FR 1920	.2142	.6853	-.2133	.4484	.4615	.1529	18
FR 1919	.6707	.7796	.2478	.7377	.1799	.7434	29
FR 1918	.7010	.8720	.4275	.7801	-.3072	.7970	19
FR 1917	.6476	.8294	.1323	.7250	.1812	.4305	23
FR 1916	.8195	.9447	.3192	.8700	-.0249	.7333	18
FR 1915	.4213	.8194	-.0443	.6319	-.1454	.8340	32
FR 1914	.3439	.1515	-.4000	.6781	.1480	.5460	23

Table 10. Correlation coefficient values for six parameter combinations in the samples from the Gendarmerie section, Aubeterre. Significance levels $\alpha < 0.01$ bold, $\alpha < 0.05$ italics. n is the number of nepionic observations.

Sample	E — (L _i + l _i)	E—P	E/P — (L _i + l _i)	P — (L _i + l _i)	t — (L _i + l _i)	*ne	nn
FR 2218	.6145	.9369	.4593	.6178	.7156	27	20
FR 2219	.7870	.8998	.4695	.8216	.7899	28	20
FR 2220	.5805	.7581	.2864	.5123	.7815	29	22
FR 2221	.8128	.8486	.6345	.6633	.6394	30	21
FR 2222	.6215	.6903	.2143	.7699	.5879	14	14
FR 2213	.6960	.8667	.4795	.6494	.3719	30	25
FR 2212	.3618	.8041	-.3268	.6654	.4027	20	17
FR 2211	.7154	.9201	.5222	.6667	.6600	31	22
FR 2210	.0839	.1691	-.3094	.5356	.5217	33	29
FR 2214	.3413	.4633	-.5314	.6651	.6444	27	18
FR 2215	.1475	.0575	-.5948	.6637	.5663	24	22
FR 2216	.1722	.5991	-.1896	.4133	.6165	22	20
FR 2217	.0000	.0000	-.4625	.4625	.6755	9	8
FR 2084	.7100	.8950	.3392	.7795	.4537	29	23
FR 2085	.7519	.8649	.0533	.8534	.6649	29	27
FR 2086	.1609	.0161	-.3616	.5056	.6250	26	24
FR 2088	.2929	.4662	-.1638	.4424	.6768	25	24

Table 11. Correlation coefficient values for five parameter combinations in the samples from the detailed section below the Champ de Foire, Aubeterre. Significance levels $\alpha < 0.01$ bold, $\alpha < 0.05$ italics. ne is the number of embryonic measurements, nn the number of nepionic counts.

Sample	E – (L _i + l _i)	E–P	E/P – (L _i + l _i)	P – (L _i + l _i)	L _i /l _i – (L _i + l _i)	t – (L _i + l _i)	ne	nn
FR 2160	.6933	.7869	.1829	.7788	.3377	.6581	22	16
FR 2159	.7661	.8527	<i>.4453</i>	.7930	.2356	.6493	29	22
FR 2158	.6570	.7321	<i>.5277</i>	<i>.5142</i>	–.3720	.7652	26	19
FR 2157	.6509	.6660	<i>.4469</i>	.5758	.3789	.5729	25	22
FR 2156	.6276	.7209	.3382	.6881	<i>–.3954</i>	.4907	33	27
FR 2155	<i>.5994</i>	<i>.6146</i>	.3750	.4582	–.0562	.6826	21	14
FR 2154	.7922	.7907	.3290	.7846	.1806	.5650	28	22
FR 2152	.8032	.7358	.3460	.8467	–.2293	.8359	26	22
FR 2151	.7976	.8273	.3955	.7481	–.3042	<i>.5165</i>	26	24
FR 2150	.7340	.7176	.2041	.8225	–.1068	.8274	30	20
FR 2148	.7826	.8298	.5723	.7166	–.0043	.7560	27	22
FR 2145	.5474	.5777	.0235	.7890	–.3207	.6404	10	6
FR 2144	.7166	.8255	.2653	.7574	–.1042	.6397	25	24
FR 2143	<i>.5861</i>	.6410	.2245	.7782	–.4077	.5454	19	17
FR 2141	<i>.6086</i>	.6937	–.0737	.6374	.1332	.6543	23	16
FR 2140	.5569	<i>.5121</i>	–.2321	.6557	.3314	.8016	24	23
FR 2138	.7050	.6190	.0500	.7794	.0167	.7069	29	26
FR 2137	.6512	.7314	–.0139	.7284	–.0586	.6869	29	27
FR 2136	.6527	.7510	–.2346	.6835	.0721	.7093	26	21

Table 12. Correlation coefficient values for six parameter combinations in the samples from the main section at the southern end of the Plage de Cadet, Meschers. Significance levels $\alpha < 0.01$ bold, $\alpha < 0.05$ italics, ne is the number of embryonic measurements, nn the number of nepionic counts.

Plate 1

Thin-sections of calcarenites from the outcrops below the Champ de Foire, Aubeterre, showing a ground-mass of micrite, indeterminate skeletal fragments, and:

fig. 1. *Tremastegina roestae*

fig. 2. *Rotalia trochidiformis*, miliolid

figs. 3, 4. *Nummofallotia cretacea*.

Approximately $\times 75$.

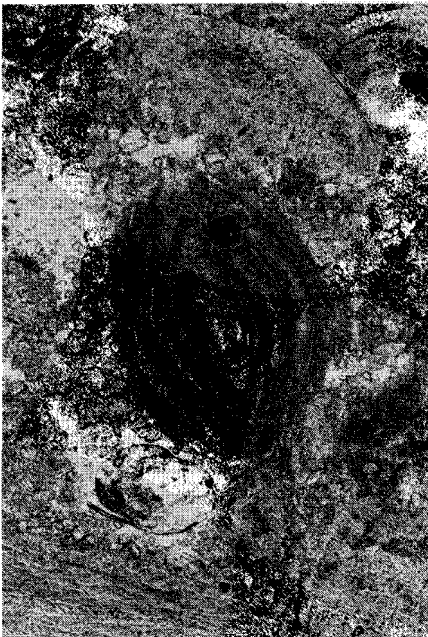
Plate 1



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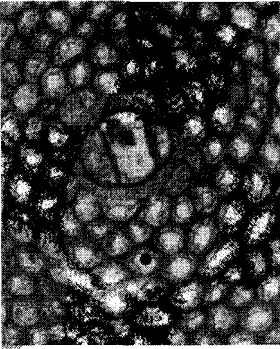


4

Plate 2

Variants of *Orbitoides media* (d'Archiac) from various assemblages from Aubeterre and Meschers.
Approximately $\times 45$.

Plate 2



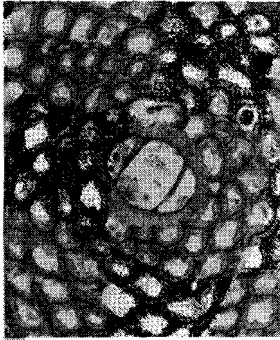
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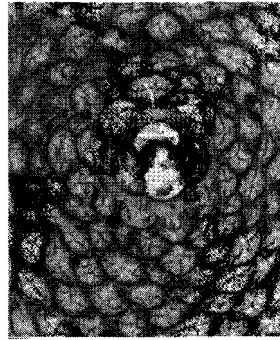
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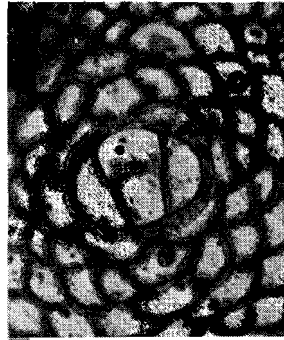
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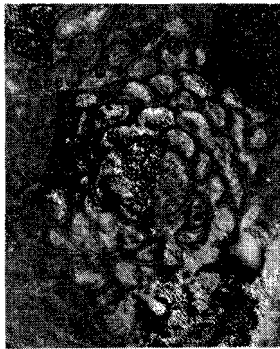
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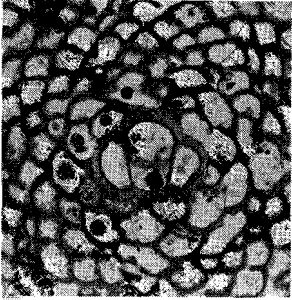


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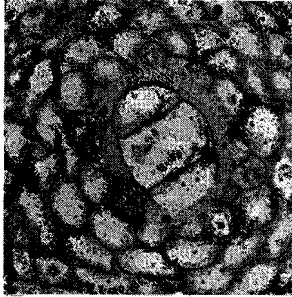
Plate 3

Variants of *Orbitoides megaliformis* Papp and Küpper from various assemblages from Aubeterre and Meschers. This plate shows mainly low-E-value morphotypes, such as are found regularly in the assemblages of *O. media* as well. Approximately $\times 45$.

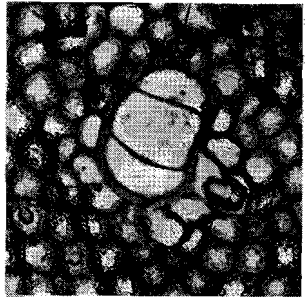
Plate 3



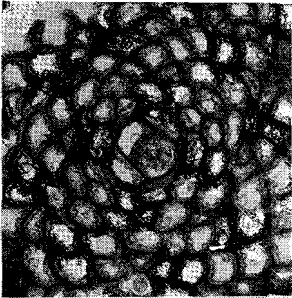
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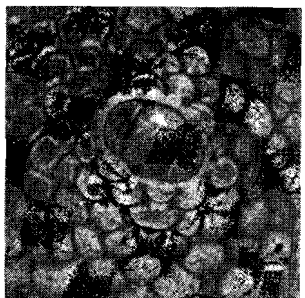
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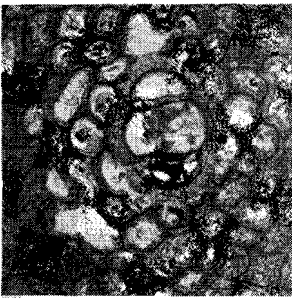
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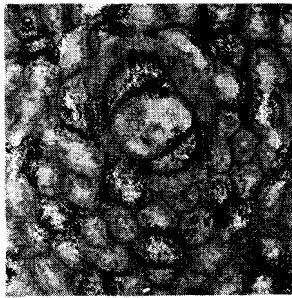
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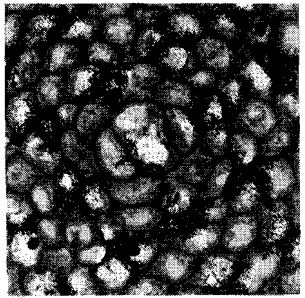
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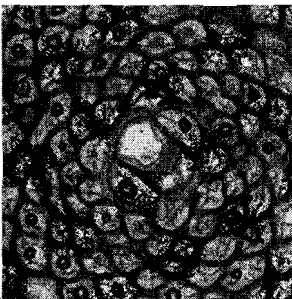
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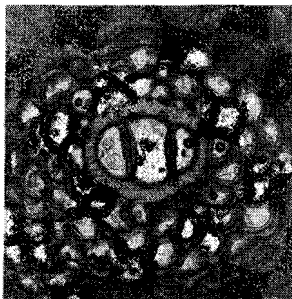
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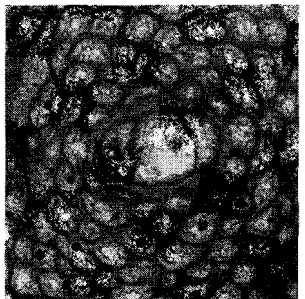
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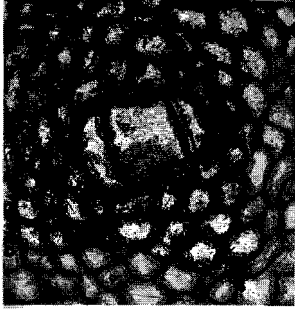


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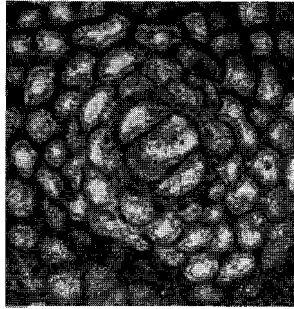
Plate 4

Variants of *Orbitoides megaliformis* Papp and Küpper from various assemblages. This plate shows mainly high-E-value morphotypes, which are common especially in *O. megaliformis*. All figures from Aubeterre. Approximately $\times 45$.

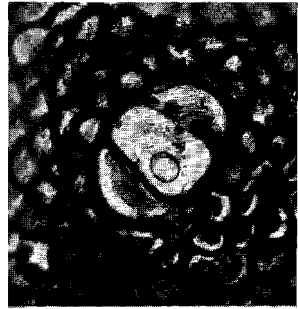
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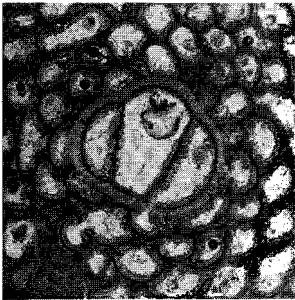
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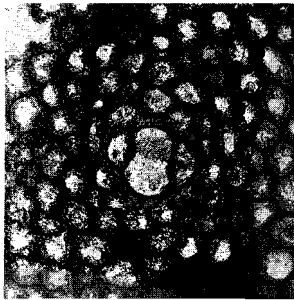
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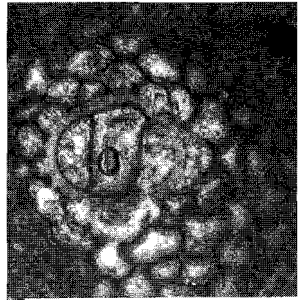
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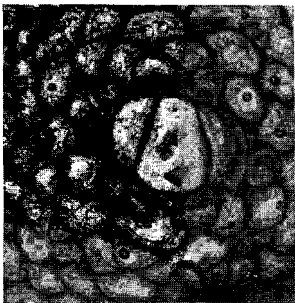
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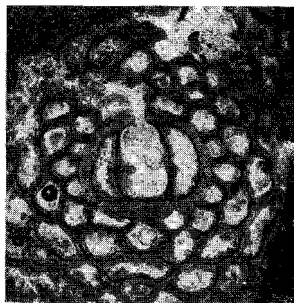
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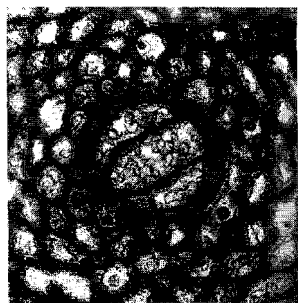
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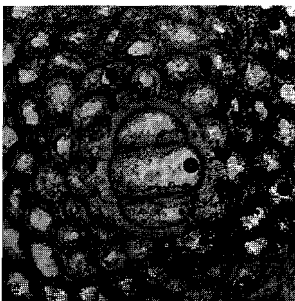
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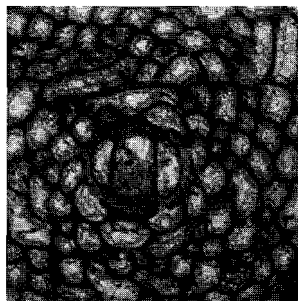
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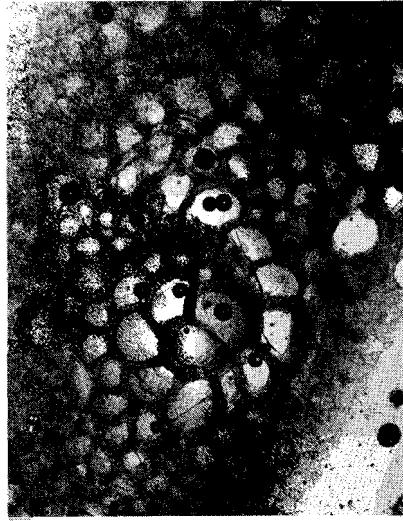
Plate 5

The embryonic-nepionic stage in median sections of four individuals of *Lepidorbitoides campaniensis* Van Gorsel from the section below the Champ de Foire, Aubeterre. Approximately X 75.

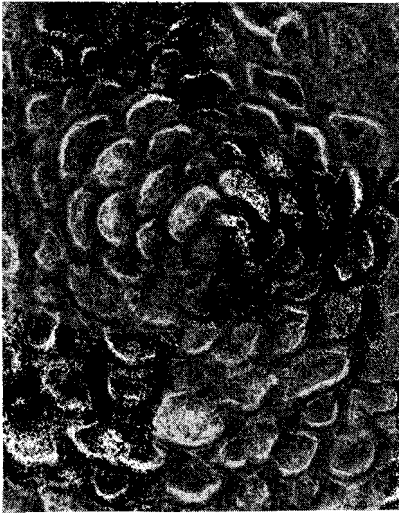
Plate 5



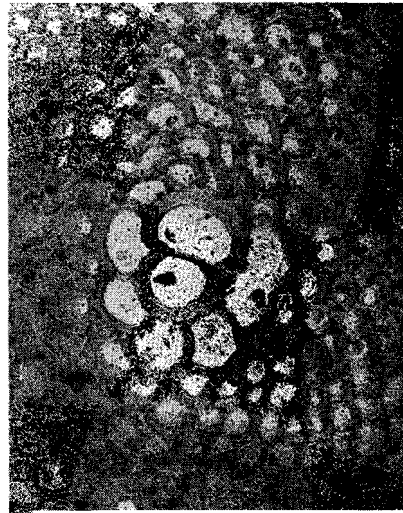
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4

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- Bull. 20. J. HAGEMAN – Benthic foraminiferal assemblages from the Plio-Pleistocene open bay to lagoonal sediments of the Western Peloponnese (Greece). 171 p., 10 pl., 28 figs. (1979) f 54,–
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