

**UTRECHT
MICROPALAEONTOLOGICAL
BULLETINS**

J. T. VAN GORSEL

**EVOLUTIONARY TRENDS AND STRATIGRAPHIC SIGNIFICANCE
OF THE LATE CRETACEOUS
HELICORBITOIDES-LEPIDORBITOIDES LINEAGE**

12

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J. T. VAN GORSEL

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ABSTRACT

Several thousands of specimens of *Lepidorbitoides* and its ancestor *Helicorbitoides* have been studied. All populations are considered to belong to one phylogenetic lineage. A subdivision is proposed of this lineage into seven species. The most important evolutionary trend is nepionic acceleration. Other trends have been observed as well, but these are less consistent and refer to features which may also be influenced by environmental factors. These trends are: increase in size of test, increase in flatness of test, increase in size of the initial chambers, increase in relative size of deuterocoenoch (i.e. ratio diameter deuterocoenoch/protoconch), crowding of the equatorial chambers and increasing complexity of equatorial chamber connections. All trends may be brought under the general aspect of increased rate of growth.

The lineage originates from *Pseudosiderolites vidali* in the lower Upper Campanian and continues up to the uppermost Maastrichtian. Contrarily to the opinion of earlier investigators, the Campanian-Maastrichtian boundary should be drawn between the *Lepidorbitoides campaniensis* and *L. bisambergensis* Zones or in the upper part of the *L. campaniensis* Zone.

Several types of wall structure of equatorial chambers are discussed and it is concluded that that of *Lepidorbitoides* agrees best with the rotaliid type. The Lepidorbitoididae are completely unrelated to *Orbitoides* and are to be classified in the superfamily Rotaliacea.

Chapter I

INTRODUCTION

I.1. SCOPE OF INVESTIGATION

In this paper a number of variable characters of the Upper Cretaceous genus *Lepidorbitoides* and its ancestor *Helicorbitoides* will be discussed, with the aim to determine which of these are evolving characters and which are influenced by environmental circumstances. The most conspicuous evolutionary trend, nepionic reduction, is by now well known. It is investigated how the zonation on the basis of this trend can be refined. Problems concerning the behaviour of other varying characters are amongst others the significance of the size of the initial chambers, the taxonomic value of ornamentation, the type of wall-structure of the equatorial chambers, and the nature of the connections of these chambers. The results may provide information about the validity of the species described and on the question whether there is one or more than one lineage within the Lepidorbitoididae, the relationship between these forms and other orbitoidal foraminifera, and their taxonomic position. An attempt will be made to determine to which geologic stages the successive species should be assigned.

Material from European localities only will be discussed in this paper. The American forms described as *Lepidorbitoides* should be assigned to *Orbitocyclina* (see a.o. van Gorsel, 1972, 1973b). The relation of the European *Lepidorbitoides* to Asiatic lepidorbitoids described as *Lepidorbitoides*, *Orbitocyclina* and *Orbitocyclinoides* is as yet unknown.

Dimorphism is present in *Lepidorbitoides*, but the microspheric generation is extremely rare, so all descriptions in this study refer to the megalospheric generation, unless otherwise indicated.

The material described is stored in the collections of the Geological Institute of the University of Amsterdam.

I.2. ACKNOWLEDGEMENTS

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1.3. TERMINOLOGY

The test of orbitoidal foraminifera is rather complicated, large specimens may consist of thousands of chambers. The test comprises an equatorial or median layer, consisting of equatorial chambers, and flanking the equatorial layer on either side the lateral layers, consisting of lateral chambers.

Most diagnostic features are found in the equatorial layer and can only be studied in horizontal (median, equatorial) thin sections. In the centre of the equatorial layer, the (sub-)circular first chamber or protoconch and the kidney-shaped, usually slightly larger second chamber or deuteroconch can be observed in cross-section. These two first chambers, usually surrounded by a relatively thick wall, are generally called the initial chambers or the embryo.

The third chamber (first post-embryonic chamber) originates from an aperture at the base of the wall of the deuteroconch and is called the primary auxiliary chamber. When the deuteroconch has two such basal apertures, two primary auxiliary chambers are formed in one chamber-forming period (also called budding stage, budding step or instar). In more advanced specimens, chambers of another type are formed, which originate from apertures (or stolons) in the deuteroconchal wall: adauxiliary chambers. These chambers are formed in the same budding stage as the primary auxiliary chambers. In a horizontal section the adauxiliary chambers are distinguished from other peri-embryonic (or nepionic) chambers by

having both upright parts of the wall standing directly upon the wall of the deuterocoel.

If there is one primary auxiliary chamber, the series of chambers beginning from this chamber and encircling the protoconch is called the protoconchal or the primary spiral, the series of chambers encircling the deuterocoel is called the deuterocoelal or retrovert spiral (see Fig. 1). If there are two auxiliary chambers, there may be two protoconchal and two deuterocoelal spirals around the embryo (quadriserial arrangement).

A spiral usually ends where it meets a spiral from the opposite direction. These spirals are then linked by a symmetric chamber or closing chamber (s in Fig. 1). The chambers of the primary spiral may be called the primary

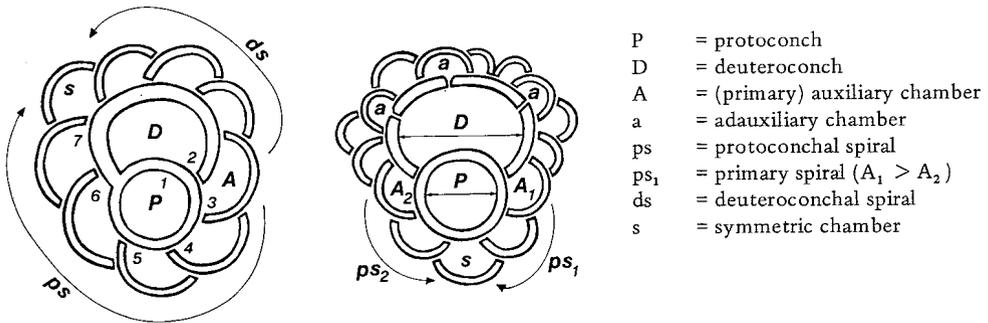


Fig. 1 Schematic drawings showing morphologic elements. Left: biserial nepion with seven chambers in primary spiral, six in deuterocoelal spiral (proto- and deuterocoel included in counting). Right: quadriserial nepion with 3 adauxiliary chambers. It is shown in which way the internal diameters of proto- and deuterocoel have been measured.

chambers, the other equatorial chambers the secondary chambers.

The chambers adjoining the initial chambers are mostly called the nepionic or peri-embryonic chambers. Several types of nepionic arrangement can be distinguished, depending on the number of chambers without a retrovert aperture (this number will be designated by the parameter Y):

uniserial: all stages with 3 or more primary chambers without a retrovert aperture ($Y > 2$, see Figs. 2a-d). When the primary spiral is reduced and $Y = 3$ or 4, this stage may be called reduced uniserial;

biserial: the third chamber (primary auxiliary chamber) is the first to have two apertures, so from here two spirals embrace the embryo ($Y = 2$, Figs. 2e-g);

quadriserial: a retrovert aperture appears already in the second chamber (deuterocoel), so two primary auxiliary chambers are formed, from each of which two spirals originate ($Y = 1$, Figs. 2i-j). When from the second auxiliary chamber only one spiral originates, this arrangement is called triserial;

multiserial: i.e. quadriserial with adauxiliary chambers: adauxiliary chambers are formed on the deuterocoel wall ($Y = 1$, see Figs. 2k-o; the parameter A is used to designate the number of adauxiliary chambers).

I.4. PREVIOUS RESEARCH

In this chapter only the more significant contributions to the knowledge of the Lepidorbitoididae will be dealt with. The type species of the genus *Lepidorbitoides* is *Lepidorbitoides socialis*, originally described as *Orbitolites socialis* by Leymerie (1851) from the surroundings of Gensac near St. Marcet (Haute Garonne, S France).

Schlumberger (1901) described the species *Orbitoides minor* from Maastricht without mentioning its differences with the species *socialis*.

In 1907, Silvestri introduced the name *Lepidorbitoides* for the Upper Cretaceous orbitoids with a *Lepidocyclina*-like type of embryo (two-chambered).

Douvillé (1920) mentioned that *Lepidorbitoides minor* from Maastricht is smaller than the type species, *L. socialis*, but exactly the same in all other characteristics; so he proposed to name the former *Lepidorbitoides socialis* race *minor*.

Thiadens (1937) disagreed with Douvillé and mentioned a number of differences which justified a specific separation. Tan Sin Hok (1939) found in the *L. minor* specimens from Maastricht a smaller number of adauxiliary chambers than in the French *L. socialis* specimens, so the latter were supposed to represent a more advanced stage of nepionic evolution.

In a statistical study of the embryonic and nepionic features of *Lepidorbitoides minor* from the Netherlands and *Lepidorbitoides socialis* from S France, MacGillavry (1955, 1959) found a progressive increase in the size of the initial chambers and in the number of adauxiliary chambers. The range of the protoconch diameter is about the same in both species, but there is a difference in deuterocoel size, and the number of adauxiliary chambers is distinctly larger in *L. socialis* (although there is some overlap between the two species). It was concluded that the *Lepidorbitoides* populations from Limburg and S France do not form successive stages of one lineage, but that they constitute different lineages. In the same paper more primitive forms without adauxiliary chambers were described from several localities.

Even more primitive stages of *Lepidorbitoides* have been found in Austria by Papp and Küpper (Papp and Küpper 1953ab, Papp 1954). From their

data it becomes apparent that the evolution of *Lepidorbitoides* is analogous in many respects to that of the Tertiary Lepidocyclinidae, investigated earlier by Barker and Grimsdale (1936) and Tan Sin Hok (1936a). In the early representatives the primary chambers are spirally arranged; during evolution the spiral stage is gradually reduced in favour of a more cyclical pattern of growth. Starting with the most primitive form the following early representatives of *Lepidorbitoides* were described by Papp and Küpper: (a) *Pseudorbitoides longispiralis* Papp and Küpper with a long spiral of primary chambers; (b) *Pseudorbitoides* cf. *trechmanni* Douvillé with a reduced uniserial nepionic arrangement; (c) *Lepidorbitoides minima pembergeri* Papp, nepionic biserial, but with a relatively long and unrolling primary spiral, extending beyond the contact with the embryonic wall; (d) *Lepidorbitoides minima minima* Douvillé with a normal biserial arrangement; (e) *Lepidorbitoides bisambergensis* Jaeger with a quadriserial nepionic arrangement, but devoid of adauxiliary chambers. The latter form had been described earlier by Jaeger (1914) as *Lepidorbitoides socialis* var. *bisambergensis* from the western slope of the Bisamberg, N of Vienna. *Pseudorbitoides longispiralis*, which shows similarities with the associated *Siderolites vidali*, may be derived from the latter form according to Papp and Küpper (1953b).

MacGillavry (1963) created a new genus, *Helicorbitoides*, for *Pseudorbitoides longispiralis*. Because of differences with the representatives of the American genus, it cannot be placed in *Pseudorbitoides*; it differs from *Lepidorbitoides* by the prolonged spiral of primary chambers.

In a description of primitive *Lepidorbitoides* specimens with a predominantly biserial nepionic arrangement from what is supposed to be the type section of the Campanian (Aubeterre, SW France), van Gorsel (1973b) proposed the new name *Lepidorbitoides campaniensis* for populations of *Lepidorbitoides* in which this stage predominates. The name *Lepidorbitoides minima* Douvillé cannot be used for these forms, as it designates the type species of the American orbitoidal genus *Orbitocyclina*, considered to be unrelated to *Lepidorbitoides*.

A new species of *Helicorbitoides*, *H. voighti*, has been described by van Gorsel (1973c) from southern Sweden. It shows characters intermediate between *Pseudosiderolites vidali* Douvillé and *Helicorbitoides longispiralis*, up to then the most primitive member known of the *Helicorbitoides-Lepidorbitoides* lineage. Accordingly, the Lepidorbitoididae may be considered to be derived rather definitely from this rotaliid foraminifer.

Species name and type locality	Nepionic arrangement at type locality	Suggested range of variation
<i>Helicorbitoides voighti</i> van Gorsel 1973 Bastad, S Sweden	long uniserial, an average of 13 uni-apertural chambers	long uniserial arrangement with an average of more than 7.5 uni-apertural chambers ($\bar{Y} > 7.5$)
<i>Helicorbitoides longispiralis</i> (Papp and Küpper) 1953 Silberegg, Austria	long uniserial, an average of 5.4 uni-apertural chambers	long uniserial arrangement with an average of 3.5 to 7.5 uni-apertural chambers ($3.5 \leq \bar{Y} \leq 7.5$)
<i>Lepidorbitoides pembergeri</i> Papp 1954 Pembergerriegel, Austria	ca. 25% reduced uniserial, ca 75% biserial with short helicorbitoid primary spiral	reduced uniserial and/or biserial arrangement with reduced helicorbitoid primary spiral ($2 < \bar{Y} < 3.5$)
<i>Lepidorbitoides campaniensis</i> van Gorsel 1973 Aubeterre, SW France	ca. 80% biserial, ca. 20% quadriserial	biserial arrangement predominates, primary spiral usually not unrolling in the helicolepidine manner
<i>Lepidorbitoides bisambergensis</i> (Jaeger) 1914 Bisamberg, Austria	ca. 20% biserial, ca. 80% quadriserial	quadriseiral arrangement without adauxiliary chambers predominates.
<i>Lepidorbitoides minor</i> (Schlumberger) 1902 Maastricht, Netherlands	quadriseiral with an average of 0.8 to 3 adauxiliary chambers	quadriseiral with an average of 0.5 to 4.5 adauxiliary chambers ($0.5 \geq \bar{A} > 4.5$)
<i>Lepidorbitoides socialis</i> (Leymerie) 1851 Gensac, St. Marcet, S France	quadriseiral with an average of 6 to 11 adauxiliary chambers	quadriseiral with an average of 4.5 or more adauxiliary chambers.

1.5. SPECIES CONCEPT

The evolutionary series of *Helicorbitoides* and *Lepidorbitoides* has been subdivided into a number of species. Papp and Küpper have done this by giving species names to each evolutionary nepionic stage. Variants within a single population were thus designated by different names, so that from one sample more than one species was mentioned (e.g. *Pseudorbitoides* cf. *trechmanni* and *Lepidorbitoides minima pembergeri* from the Pembergerriegel in Papp 1954a, *Lepidorbitoides minima minima* and *Lepidorbitoides bisambergensis* from the Bisamberg in Papp and Küpper 1953a, Papp 1956b). As discussed in an earlier paper (van Gorsel 1973b), this typological species concept is rather artificial; it is here preferred to consider each assemblage characterized by the joint presence of different stages as belonging to one species only. For this reason it has been proposed to name a specimen not after its nepionic state of development, but after the state of nepionic development of the majority of specimens present in the population to which the specimen belongs. The form described by Papp as *Pseudorbitoides* cf. *trechmanni* is thus included in the species *pembergeri*, *Lepidorbitoides minima minima* from the Bisamberg in the species *L. bisambergensis*.

Because of the above considerations and taking into account the state of development of the different species at their type localities, the following subdivision of the group into seven species is proposed from primitive to advanced: *Helicorbitoides voigti* van Gorsel, *Helicorbitoides longispiralis* (Papp and Küpper), *Lepidorbitoides pembergeri* Papp, *Lepidorbitoides campaniensis* van Gorsel, *Lepidorbitoides bisambergensis* Jaeger, *Lepidorbitoides minor* (Schlumberger) and *Lepidorbitoides socialis* (Leymerie). The suggested ranges of variation of the species are summarized in Table I.

The author is aware that this subdivision of a probably continuous evolutionary series is also artificial and that the proposed statistically defined boundaries are purely arbitrary. The lineage might also be subdivided into an other number of successive stages. Transitional populations between species may be found. Furthermore, within one species thus defined, more primitive and more advanced populations can be distinguished. For purposes of correlation and for an accurate description of the state of development of an assemblage, it is therefore best to determine which stages of nepionic development are present and in which proportions. In this method we have a useful tool for determining relative ages with a high discriminative power.

Apart from the species names mentioned above, a number of other names have been published. They are either younger synonyms of existing names or

they refer to unidentifiable specimens: *Lepidorbitoides paronai* (Silvestri) 1907, its varieties *asymmetrica* and *inermis* Marchesini 1941, all from Italy, *Lepidorbitoides eggeri* Silvestri 1908 and *Lepidorbitoides douvillei* Silvestri 1927 (both from S France) are probably all younger synonyms of *Lepidorbitoides socialis* (Leymerie), the *Lepidorbitoides* species which probably has the greatest distribution.

Lepidorbitoides vidali (Prever) 1904 (Aptian?, Spain) and *Lepidorbitoides? minuscula* Silvestri (Paleocene, Italy) have been described insufficiently; it is doubtful whether they belong to *Lepidorbitoides*.

From the Upper Cretaceous of the Caribbean and adjacent regions a number of species of *Lepidorbitoides* have been described, which should be assigned to the genus *Orbitocyclina* Vaughan (see also van Gorsel 1972, 1973b). The species names are *minima* (Douvillé 1927, Mexico), *planasi* (M. G. Rutten 1935, Cuba), *macgillavryi*, *palmeri*, *rutteni* (Thiadens 1937, Cuba), *floridensis* (Cole 1942, Florida), *estrellae* and *tschoppi* (van Wessem 1943, Cuba).

From strata assigned to the Danian from Tibet, the species *Lepidorbitoides polygonalis* and *L. tibetica* have been described (Douvillé, 1916), from the Maastrichtian of India *Lepidorbitoides blanfordi* and *L. inornata* (Rao, 1942). The relationship of these Asian forms (including forms described as *Orbitocyclina* and *Orbitocyclinoides*, see Rao 1942, Brönnimann 1944, Premoli-Silva 1970, Rama Rao 1970) to the European *Lepidorbitoides* is uncertain. The same can be said of the *Lepidorbitoides socialis* specimens from Madagascar (Maastrichtian, Bésairie 1972). In view of the supposed paleogeographic position of the island, these specimens may be related to the Indian species.

Chapter II

MATERIAL AND LOCALITIES

II.1. S SWEDEN

Båstad (type locality of *Helicorbitoides voighti* van Gorsel 1973)

Several hundreds of specimens (of which 120 horizontal and 25 vertical sections) are available from a sample collected by Prof. E. Voigt in the Malen quarry E of Båstad, province of Halland.

Nepionic arrangement: long uniserial; the total number of primary chambers may exceed 80 in large specimens (2.2 mm.), the number of chambers without a retrovert aperture varies between 6 and 22, average about 13. For a more detailed description, see van Gorsel (1973c) and Chapt. VIII of this paper.

Age: The presence of *Belemnitella mucronata mucronata* and *Belemnitella mucronata senior* points to an early Late Campanian age (in the Boreal zonation).

Stafversvad

From a small abandoned quarry near Stafversvad, 20 km NE of Kristianstad, province of Scania, four horizontally and three vertically sectioned specimens are available, collected by Prof. E. Voigt.

Nepionic arrangement: long uniserial; the number of primary chambers varies between 20 and 35, the number of chambers without retrovert aperture between 3 and 6. The slackening primary spiral may dissolve before the periphery is reached (see also van Gorsel 1973c).

Determination: *Helicorbitoides longispiralis* (Papp and Küpper).

Age: Late Campanian.

II.2. AUSTRIA

Most samples from this country have been collected in flysch type deposits, so this material may have been redeposited.

Silberegg (type locality of *Helicorbitoides longispiralis* (Papp and Küpper))

The type locality is a small abandoned quarry behind a house at the W side of the road Silberegg-Guttaring, several hundreds of meters NNW of the village of Silberegg, Carinthia. Rather ill-preserved specimens are available from samples Oostenrijk 4a and 6 (4 horizontal sections), collected by Prof. H. J. MacGillavry, and Gr842, collected by the author about two meters above the floor of the quarry (15 horizontal sections).

Nepionic arrangement: long uniserial, the number of chambers in the primary spiral varies between 20 and 55, the number of chambers without retrovert aperture between 3 and 8, average almost 6. The primary spiral usually continues up to the periphery.

Associated larger foraminifera: *Pseudosiderolites vidali*, *Orbitoides tissoti*.

Age: Campanian after Papp (1955), Late Campanian ("Untere Pemberger Folge") after van Hinte (1963).

Pembergerriegel (type locality of *Lepidorbitoides pembergeri* Papp)

23 horizontal sections are available from sample Gr851a, which was collected at the northern side of a large quarry on the hill called Pembergerriegel, above the Wietersdorfer cement works, about 2 km NW of the village of Klein St. Paul. In 1954 (Papp 1954) this quarry had been abandoned, but it is in exploitation again; it is not certain whether our sample is from exactly the same level as the type specimens of *Lepidorbitoides minima pembergeri*. The nepionic development of our specimens agrees very well with the description of Papp, so it is assumed that this sample can be used for describing the variability of *Lepidorbitoides pembergeri* at the type locality.

Nepionic arrangement: one specimen uniserial with $Y = 4$, four uniserial with $Y = 3$ and 14 specimens biserial ($Y = 2$). In the last group, the primary spiral is much longer than the retrovert one (average number of chambers 10 and 4.3 respectively) and the protoconchal spiral is usually continued in a few relatively large equatorial chambers (reduced helicorbitoid arrangement).

Associated larger foraminifera: *Orbitoides tissoti*, *Pseudosiderolites vidali*.

Age: Late Campanian.

North of Pemberger

This locality is situated on the same hill, south of the former locality, north of the farms of Pemberger and is indicated with P88 on the map of van Hinte (1963, Beilage 2) and with 6–7 on Fig. 2 of Papp (1955). Three samples are available from this locality: Oostenrijk 17 (17 horizontal sections, material collected by Prof. H. J. MacGillavry), P88 (4 horizontal sections, collected by Dr. J. E. van Hinte) and Gr849 (40 horizontal sections, collected by the author).

Nepionic arrangement: in samples Oost. 17 and P88, only biserial specimens ($Y = 2$, without helicorbitoid unrolling) were found; in sample Gr849, 19 nepionts have a biserial arrangement (one of which already possesses a second auxiliary chamber, but without subsequent chambers) and 5 have a quadriserial arrangement. One microspheric specimen has been sectioned (Gr849–52); it has a spirally arranged initial stage with presumably 6 chambers without a retrovert aperture.

Determination: *Lepidorbitoides campaniensis*.

Associated larger foraminifera: *Orbitoides* cf. *media*.

Age: Late Campanian or Early Maastrichtian (see Chapter VII).

South and east of Pemberger

South of the former locality younger strata are exposed, from which three samples have been collected by Dr. J. E. van Hinte, from old to young $\times 1961V2$, $\times 1961AG$ and $\times 1961AW$.

Nepionic arrangement: in sample V2 six quadriserial specimens, in AG ten quadriserial and one quadriserial with one adauxiliary chamber, and in sample AW twelve quadriserial and two quadriserial with one adauxiliary chamber. Most quadriserial specimens are of the “asymmetric quadriserial” type (see Fig. 2i), which is more primitive than “symmetric quadriserial”.

Determination: *Lepidorbitoides bisambergensis*

Associated larger foraminifera: *Orbitoides* (type locality of *Orbitoides media megaliformis* Papp and Küpper 1953a).

Age: Early Maastrichtian (above *Globotruncana calcarata* Zone).

Bisamberg (type locality of *Lepidorbitoides bisambergensis* Jaeger)

The Bisamberg is a hill on the left bank of the Danube river, about 8 km north of Vienna. Orbitoidal foraminifera are rather rare in the flysch at this locality. From sample Gr854, taken about halfway the western slope of the hill, one specimen with biserial and three with quadriserial arrangement have been sectioned. Papp (1956b) found 6 specimens with quadriserial and 1 with biserial arrangement at this locality.

Associated larger foraminifera: rare *Orbitoides* cf. *media* and *Siderolites* cf. *calcitrapoides*.

Age: presumably Early Maastrichtian.

II.3. GERMANY

Ilten

Some 30 horizontal sections are available, from a sample collected by Prof. E. Voigt. For a description of this locality in the neighbourhood of

Hannover and its fauna, see Voigt (1951).

Nepionic arrangement: quadriserial, number of adauxiliary chambers varying between 0 and 2, average 0.8.

Determination: (primitive) *Lepidorbitoides minor*.

Associated larger foraminifera: *Siderolites calcitrapoides*, *Omphalocyclus macropora*, *Daviesina fleuriauxi*.

Age: Late Maastrichtian.

II.4. LIMBURG, NETHERLANDS

All material from this area is from the collections in the Geological Institute of the University of Amsterdam. Part of it has already been described by MacGillavry (1955, 1959, 1965, 1971). From some of these samples, additional sections have been prepared. Several other samples have not been described yet.

Vlodrop

46 horizontal sections are available from well nr. LXX, drilled near Vlodrop, N. Limburg, in order to study the Carboniferous for the Beatrix coal mine (for exact locality, see Kimpe 1973). *Lepidorbitoides* is found in the interval between -444.00 and -444.80 meters.

Nepionic arrangement: all horizontal sections show a symmetric quadriserially arranged nepiont without adauxiliary chambers; in one specimen there may be two of these chambers.

Determination: *Lepidorbitoides bisambergensis*.

Associated larger foraminifera: one specimen of *Siderolites calcitrapoides* (with six spines).

Age: Maastrichtian.

Kunrade

From the Kunrade Chalk in quarry Schunck (south of Kunrade, outcrop 78 on the map of Francken, 1947), some 30 horizontal sections are available. An enumeration of the foraminifera present in this quarry was given by Hofker (1959).

Nepionic arrangement: 9 specimens quadriserial without adauxiliary chambers, 8 with one such chamber.

Determination: transitional population between *Lepidorbitoides bisambergensis* and *Lepidorbitoides minor*.

Age: Late Maastrichtian.

ENCI quarry (type Maastrichtian, type locality of *Lepidorbitoides minor*?)

This large quarry is situated about 3 km south of Maastricht in the famous Pietersberg. The fossil fauna of this and adjacent localities has been studied rather extensively since the 18th century. For the foraminifera, reference is made to Visser (1951) and to many papers by Hofker.

The subcommission on the Upper Cretaceous Stratigraphy of the International Commission of Stratigraphy has proposed to restrict the Maastrichtian stratotype to the Maastricht Tuff Chalk, and a type section has been proposed in the ENCI quarry below the Lichtenberg farm. The Maastricht Tuff Chalk in this quarry overlies the Gulpen Chalk with a slight hiatus, which disappears farther southward. Our samples are from a complete section, sampled by Mr. B. J. Romein. For a description of this section, see Romein (1962) and Francken (1947). *Lepidorbitoides* is only present in the upper Mc and the Md members of the Maastricht Tuff Chalk. Some 350 horizontal sections from different levels are available.

Nepionic arrangement: The specimens from the type Maastrichtian show a quadriserial nepionic arrangement, without or with a small number of adauxiliary chambers. In Table II the distribution of the various stages in the section is indicated. This table contains all counts of the numbers of adauxiliary chambers and thus includes counts of specimens in which the diameter of one or both initial chambers could not be measured (these are excluded in the Appendix). The number of adauxiliary chambers in specimens from the Mc member varies between 0 and 2, average 1; in the Md member the number varies between 0 and 7, averages between 2 and 3. The sample means only roughly reflect the expected trend of increasing numbers of adauxiliary chambers in upward direction in the section, whereas the modal values (*italics* in Table II) indeed show this increase without relapses: in the lowest samples a quadriserial nepiont with one adauxiliary chamber is the most frequent stage, in the highest samples three of such chambers.

Associated larger foraminifera: Maastricht is also the type locality of *Orbitoides apiculata* Schlumberger, *Omphalocyclus macroporus* Lamarck, *Siderolites calcitrapoides* Lamarck and *Hellenocyclina visserae* (Hofker).

Age: Late Maastrichtian.

ENCI sportpark

12 horizontal sections from sample CK122, collected by Dr. C. Kruit in the Mc member of the Maastricht Tuff Chalk at the Pietersberg, north of the ENCI quarry (outcrop 8 in quadrangle 38 on the map of Francken 1947).

Nepionic arrangement: quadriserial, number of adauxiliary chambers between 0 and 2, average 0.9 (see also Table I). This agrees with the data on

the Mc specimens from the ENCI quarry.

Determination: (primitive) *Lepidorbitoides minor*.

Keerderberg

Some 250 horizontal sections from a suite of samples collected at different levels in the Keerderberg quarry (4 km E of the Pietersberg, W of Cadier en Keer, outcrop 21 in quadrangle 39 on the map of Francken 1947). K33 is the uppermost sample, K45 the lowest; stratigraphic distance between these samples about 6 meters.

Nepionic arrangement: quadriserial, the number of adauxiliary chambers varying between 1 and 4, averages between 1.8 and 2.3. In Table I the distribution of these chambers is given in the successive samples, showing a slight upward increase. The populations can be correlated with the Md samples from the ENCI quarry. This is in disagreement with earlier cor-

members	samples	number of adauxiliary chambers							average \bar{A}	
		0	1	2	3	4	5	6		7
	31.00–33.00		2	9	15	1				2.6
	30.50		1	12	15	3				2.6
	28.00		6	13	14	1				2.3
Md	24.00		2	8	3	4	2		1	3.0
	23.50	1	5	14	6	6		1	1	2.6
	22.00–22.50	3	5	10	4	4		1		2.2
	17.50–19.75	2	18	2						1.0
Mc	13.50–16.25	2	2	2						1.0

Distribution at other localities (Limburg and Ilten):

Keerderberg 33		15	27	28	6					2.3
Keerderberg 36		9	24	24	3					2.3
Keerderberg 38, 39, 40		3	6	6	1					2.3
Keerderberg 41, 42, 45		2	11	1						1.9
Schooverberg 168		1	4	1						2.0
Schooverberg 173, 174	1	7	17	7	2	1				2.1
Curfs		2	9	5	2					2.4
Jekerdal		3	5	5						2.2
CK 122, ENCI-Sportpark	3	6	2							0.9
Ilten	6	13	2							0.8
Kunrade	9	8								0.5

Table II. Distribution of the number of adauxiliary chambers in samples of *Lepidorbitoides minor* from the Maastrichtian type section (ENCI quarry).

relations based on lithology, on the basis of which all samples except K33 are Mc (see also MacGillavry 1955, p. 31).

Determination: Lepidorbitoides minor.

Jekerdal, Schooverberg, Curfs

All samples mentioned below are from the Md member of the Maastricht Tuff Chalk and the *Lepidorbitoides* specimens can be ascribed to *L. minor*. The frequency distribution of the number of adauxiliary chambers is given in Table I.

Jekerdal: quarry W of ENCI quarry, 20 horizontal sections.

Schooverberg: quarry Hamming, 2 km NE of Keerderberg (outcrop 17 in quadrangle 39 on the map of Francken 1947). Two samples: H168, 8 horizontal sections and H174 (2.3 m below H168), 50 horizontal sections.

Curfs: quarry W of Geulhem, 28 horizontal sections.

II.5. SOUTHERN FRANCE

Aubeterre (upper Campanian type section, type locality of *Lepidorbitoides campaniensis*)

Lepidorbitoides has been found at three levels in the classical section of Aubeterre, department of Charente; for a description, see van Gorsel (1973b). Because of the few data from the base and the top of the section, additional samples have been collected, with poor results, however: after searching the wash residues of several kilograms of sediment only two specimens could be added to those from the base of the section and only one to the specimen from the top sample.

Nepionic arrangement: Gr22 and Gr803 (base of section): 1 biserial with short helicorbitoid spiral, 3 biserial and two quadriserial specimens; Gr40 (middle part): 1 biserial with short helicorbitoid spiral, 10 biserial and 3 quadriserial specimens; Gr43 (top of section): 2 biserial specimens. As mentioned in the previous paper, these data are insufficient to differentiate nepionic development in the samples.

Determination: Lepidorbitoides campaniensis.

Associated larger foraminifera: abundant *Orbitoides media* and *Pseudosiderolites vidali*, *Pseudorbitolina marthae*, *Nummofallotia cretacea*, *Gouplaudina daguini*, *Abrardia mosae*, *Hellenocyclina charentensis*.

Age: Late Campanian.

Charente- Dordogne

From several other localities in this area, small numbers of specimens of *Lepidorbitoides* are available. For descriptions of localities and results of

measurements, the reader is referred to van Gorsel (1973b) and the Appendix. Specimens from one sample (Gr364 from Neuvic, Isle valley) show transitional characters between *Lepidorbitoides pembergeri* and *Lepidorbitoides campaniensis*, all other specimens can be assigned to the latter species.

Roquefort (Landes, NE of Mont de Marsan)

In the central part of the Aquitaine basin, Upper Cretaceous sediments are outcropping along a number of WNW-ESE running ridges. One of these outcrops is the "Ride de Roquefort-Créon". Sediments of Maastrichtian age, found west of Roquefort along the right bank of the Estampon (see Cuvillier, Dupouy-Camet and Sacal, 1951), are hard yellowish limestones. Near the last houses of Roquefort along road N626, a smaller road leads to the west (St. Jean), where, after about 1 km, it crosses a brook. Here, at the base of the steep bank, a less indurated level was found, containing large numbers of isolated specimens (sample Gr811, about 70 horizontal sections, preservation mediocre). Noteworthy in most of the *Lepidorbitoides* specimens is the presence of a distinct central thickening of the test, covered with pustules (variety *pustulata* of Douvillé 1920) and the relatively small size of the initial chambers.

Nepionic arrangement: quadriserial with 4 to 8 adauxiliary chambers, average 5.3.

Determination: *Lepidorbitoides socialis*.

Associated larger foraminifera: abundant *Orbitoides apiculata*, less frequent *Siderolites calcitrapoides*, *Omphalocyclus macroporus*, *Fallotia jacquoti* and *Abrardia mosae*.

Age: Late Maastrichtian.

Dumes (Landes, South of St. Sever)

Further south, the next outcrops of Upper Cretaceous sediments are found in the "Ride d'Audignon". A sample with many large specimens of *Lepidorbitoides* (test diameter up to 2 cm) was collected in the yellowish chalk of an abandoned, partly overgrown quarry W of the village of Dumes. This quarry is situated above a farm house at the W side of the hill with the castle of Dumes. Some 70 horizontal sections have been prepared from this sample (Gr813).

Nepionic arrangement: quadriserial with 4 to 10 adauxiliary chambers, average 6.4.

Determination: *Lepidorbitoides socialis*.

Associated larger foraminifera: abundant *Clypeorbis mamillata*, less frequent *Hellenocyclina visserae*.

Age: Late Maastrichtian.

St. Marcet and vicinity (type locality of *Lepidorbitoides socialis*)

The type locality of *Lepidorbitoides socialis* has been described rather vaguely by Leymerie (1851) as "Gensac, près de St. Marcet" (department of Haute Garonne). Accordingly, all specimens from this area might be considered as topotypes of the species. This does not cause much difficulty as only the more advanced stages of development of the *Helicorbitoides-Lepidorbitoides* lineage are found here: quadriserial with many adauxiliary chambers, the sample means of which are varying between 6 and 11.

Our material from the area has been collected by Mr. J. J. Rozeboom, and part of it has already been described by MacGillavry (1955). The most complete section was sampled W and SW of the village of St. Marcet (see MacGillavry 1955, fig. 3), from two lithologic units, a lower "Calcaire Nankin" and a higher "Marnes d'Auzas". Samples 144, 147 and R8851 are from the Calcaire Nankin in a quarry north of the cemetery of St. Marcet. Sample St. Marcet 121 was taken in a small quarry south of the road Prat Bédiaou-St. Marcet (also in the Calcaire Nankin); St. Marcet 122 is from the top of a larger quarry, connected with the former quarry (transitional strata Calcaire Nankin and Marnes d'Auzas). Samples St. Marcet 32 and 125 were taken in the Marnes d'Auzas along a small road leading from the road Prat Bédiaou-St. Marcet to the south along the brook "Ruisseau de la Louge". The uppermost sample, St. Marcet 153, was collected along the same road further south, close to the contact with the Danian.

The number of measurements and the frequency distributions of the number of adauxiliary chambers in the samples are given in Table III, which shows that there is a distinct increase in the number of these chambers going upward in the suite. The table contains all counts of the number of adauxiliary chambers, also those of specimens in which the diameter of one or both initial chambers could not be measured and which are therefore excluded from Table IV and the Appendix.

All other samples from the area are from the Marnes d'Auzas. After Rozeboom (1955), samples Larcan 133, Gensac 17 and Terme 154 are from the top of the unit; Biscanos 6, Larcan 5 and 135 are from the lower part of the Marnes d'Auzas. The stratigraphic position of the other samples is uncertain. The frequency distributions and sample means of the number of adauxiliary chambers are also given in Table III, with the samples placed in supposed stratigraphic succession. The results agree fairly well with the data from the St. Marcet section.

Associated larger foraminifera: Orbitoides apiculata, Orbitoides gensacicus, Omphalocyclus macroporus, Siderolites calcitrapoides, Hellenocyclina visserae.

Age: Late Maastrichtian.

Sample number	Number of adauxiliary chambers														\bar{A}
	3	4	5	6	7	8	9	10	11	12	13	14	15		
St. Marcet 153					2		1	1	2	3	1				10.4
St. Marcet 32+125					2	2	4	8	8	5	3				10.4
St. Marcet 122			1	3	4	5	1	1							7.3
St. Marcet 121	1	2	3	3	7	2									6.1
St. Marcet 144+147		1	5	10	1	2		1							6.1
St. Marcet R8851		1	5	6	5	2									6.1
Distribution in other localities in the area:															
Gensac 17								2	1	1	2	2		1	11.5
Terme 154				1				2	2	3	1	2			10.3
Larcen 133					1	1	1	1	2					1	10.1
Gensac 25								4	2	2	1	1			10.9
Naouarret 48			1	3			2	5	1	1	1				8.9
Terme 155				1			2	2	1						8.3
Larcen 4				1	1	2	4								8.1
Biscanos 6				2	2	1	3		1						8.0
Larcen 135			2	2			4	1							7.0
Larcen 5		2	3	1			2	1							7.0
Distribution in <i>L. socialis</i> from other areas:															
Olazagutia 22			3	6	2	3	4	8	1						8.0
Olazagutia B9694	2	1	5	10	6	2									5.9
Dumes	1	4	7	6	8	3	3	2							6.4
Salas		6	7	12	3										5.4
Roquefort		9	16	11	3	2									5.3

Table III. Distribution of the number of adauxiliary chambers in *Lepidorbitoides socialis* from the vicinity of St. Marcet (Hte Garonne, S France).

II.6 NORTHERN SPAIN

Orcau – Montesquiú (Province of Lerida)

About 6 km east of Tremp, at the highest point of the pass between Orcau and the abandoned village of Montesquiú, *Lepidorbitoides* was found at the base of a turbidite layer. From sample Gr832, 28 horizontal sections of rather recrystallized specimens have been prepared.

Nepionic arrangement: all interpretable specimens quadriserial; 9 specimens are without adauxiliary chambers, 2 specimens have only one such chamber.

Determination: Lepidorbitoides bisambergensis.

Associated larger foraminifera: rare Orbitoides.

Age: Early Maastrichtian.

Salas (Province of Lerida)

Numerous well-preserved, relatively large and flat specimens of *Lepidorbitoides* have been obtained by courtesy of Mrs. E. Caus (Barcelona) from an olisthostrome level in the "Serra dels Homes Mort", just below the "Arenisca de Aren" Formation (4 km NNE of Tremp). The protoconch is exceptionally large in specimens from this sample.

Nepionic arrangement: quadriserial with 4 to 7 adauxiliary chambers, average 5.4.

Determination: Lepidorbitoides socialis.

Associated larger foraminifera: Clypeorbis mamillata.

Age: Late Maastrichtian.

Olazagutia (Province of Navarra)

Some 250 horizontal sections from two samples collected by Dr. G. J. Bijvank in the vicinity of Olazagutia (40 km east of Vitoria). Preservation of the specimens is rather bad.

Nepionic arrangement: in sample B9694 quadriserial with 3 to 8 adauxiliary chambers, average 5.9; sample 22 with 5 to 11 of these chambers, average 8.0.

Age. Late Maastrichtian.

Chapter III

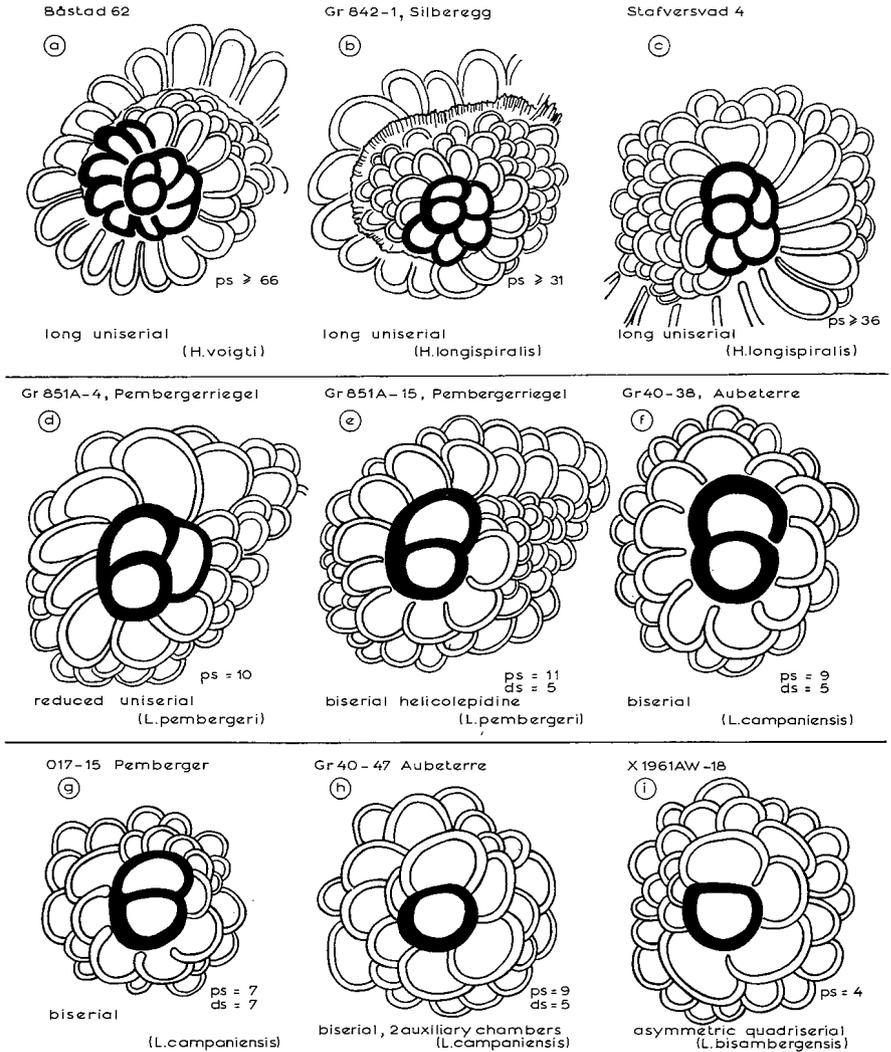
EVOLUTIONARY TRENDS

III.1 NEPIONIC ACCELERATION

The most conspicuous evolutionary trend in the *Helicorbitoides-Lepidorbitoides* lineage is the reduction of the ancestral spiral of primary chambers and the attainment of cyclical growth at progressively earlier ontogenetic stages. This development has been called nepionic acceleration or nepionic reduction and is known in many other groups of larger foraminifera as well, e.g. the Lepidocyclinidae (Barker and Grimsdale 1936, Tan Sin Hok 1936a, Grimsdale 1959, van der Vlerk op. div.), Miogypsinidae (Tan Sin Hok 1936b, Barker and Grimsdale 1937, Drooger op. div.), Pseudorbitoididae (Brönnimann op. div., Krijnen 1972), *Planorbulinella* and *Hellenocyclina* (Freudenthal 1969), etc.. For the *Lepidorbitoides* lineage, most pioneering work has been done by Papp, in his earlier papers in co-operation with K. Küpper (1953–1956). General discussions on this trend were presented by Drooger (1955, 1974) and MacGillavry (1963).

In the spirally arranged ancestor, each chamber has one basal (or proximal) aperture, from which the next chamber is formed. Then, in part of the population and usually at a late ontogenetic stage, in addition to the normal aperture a second (retrovert or distal) aperture is formed, from which secondary or retrovert chambers are formed. Once a retrovert aperture has appeared in a specimen, all subsequent chambers usually have two apertures, so from each chamber two new chambers are formed. This increases the number of chambers formed at one budding step, and in most cases leads to a radial or cyclical pattern of growth. In the primitive stages retrovert apertures and chambers appear only at a late stage in the ontogeny of the animal, but phylogenetically they appear earlier and earlier in the ontogeny.

In most groups of larger foraminifera the primary spiral ends when it meets a series of retrovert chambers; subsequently, cyclical growth starts. In *Helicorbitoides* and primitive *Lepidorbitoides*, however, the rate of growth in retrovert direction is much less than in the direction of the primary spiral: the number of budding stages represented in the retrovert chambers is lower



than in the primary chambers, and the retrovert chambers are smaller. As a result of the relatively large size of the chambers formed in the continuation of the primary spiral, we see an unrolling spiral of large chambers, between the whorls of which smaller secondary equatorial chambers are formed. A similar type of growth is found in the Tertiary *Helicolepidina*, and this unrolling arrangement has been called the helicolepidine arrangement (type IIB of MacGillavry, 1963). The presence of a structure of radial elements (in *Helicolepidina* a thickened spiral wall) between the secondary chambers and

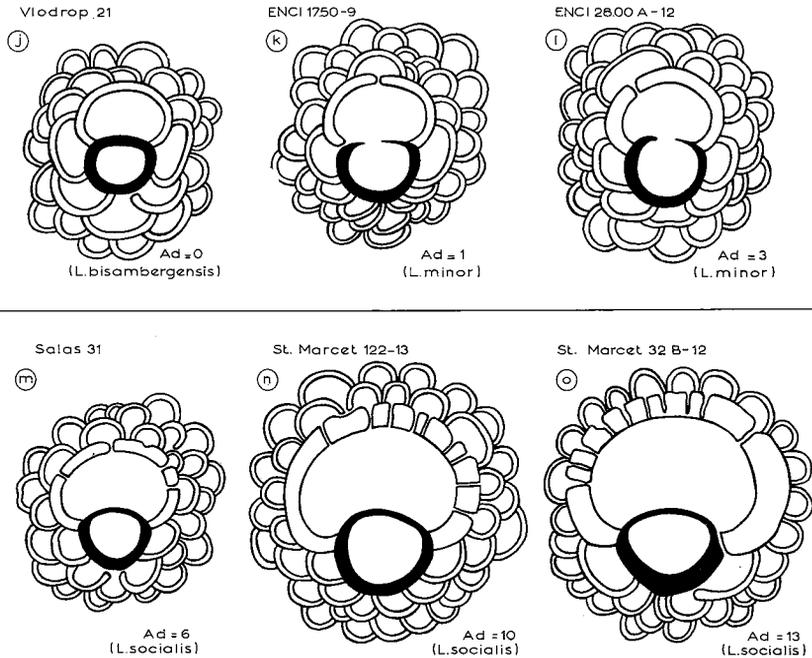


Fig. 2 Successive stages of nepionic arrangement in *Helicorbitoides* and *Lepidorbitoides*. The walls of the uni-apertural chambers (Y) are drawn in black. ps = the number of chambers in the protoconchal spiral, ds = the number of chambers in the deuterococonchal spiral, Ad = the number of adauxiliary chambers. Figs. a-c 45 X, all others 75 X.

the primary chambers of the next whorl suggests that these places formed the exterior of the test for some time, without subsequent chambers being added here. Drooger (1974, p. 27) compared the helicolepidine growth to the sectorial growth of *Miogypsina*, in which secondary equatorial chambers are formed along a certain sector of the test periphery only. In *Miogypsina* this sector of active growth remains more or less stable, but in the helicolepidine type it constantly shifts along the circumference of the test (see also Smout 1954, fig. 39).

In *Helicorbitoides*, the sector of active growth apparently increases during ontogeny, as in larger specimens of *Helicorbitoides longispinalis* and in the more primitive stages of *Lepidorbitoides* the primary spiral dissolves towards the periphery and a cyclical pattern of growth is reached. In this respect *Helicorbitoides* differs from *Helicolepidina* (sensu Tan 1936a), which never attains cyclical growth, but is similar to *Helicocyclina* (sensu Tan). In the phylogeny of the lineage, cyclical growth is reached earlier and earlier in the ontogeny and the last evidence of a helicolepidine type of growth is found in

the early biserial stage (*Lepidorbitoides pembergeri*).

For illustrations of the subsequent changes of the nepionic chamber arrangement, the reader is referred to Fig. 2. From primitive to advanced the following stages can be recognized:

uniserial ($Y \geq 3$, figs. 2a-d). Within this stage, more primitive and more advanced stages can be recognized by counting the number of chambers without a retrovert aperture (Y);

biserial ($Y = 2$, figs. 2e-g). In the primitive representatives, a short unrolling helicorbitoid (= helicolepidine) primary spiral can be seen (2d-e, *Lepidorbitoides pembergeri* stage). The biserial stage can be subdivided by counting the number of chambers in the protoconchal and deutoconchal spirals (ps and ds). In primitive populations, the average ps:ds ratio is about 9:5, in the more advanced ones this tends towards 7:7;

Intermediate stages between biserial and quadriserial are rare: *biserial with two auxiliary chambers* ($Y = 1$, fig. 2h, no subsequent chambers formed from the second auxiliary chamber) and *triserial* (subsequent chambers formed from the second auxiliary chamber in one direction only);

quadriseiral ($Y = 1$, figs. 2i-j). Early quadriseiral specimens are strongly asymmetric (fig. 2i, second auxiliary chamber and chambers originating there from are relatively small), advanced specimens have a tendency to be bilaterally symmetric (fig. 2j);

quadriseiral with adauxiliary chambers (figs. 2k-o). After the quadriseiral stage has been reached, the adauxiliary chambers are formed, originating from apertures in the deutoconchal wall. The number of these chambers is indicative for the stage of development of the populations. The maximum number of these chambers counted in our material is 15. The number may show considerable variation in one sample with the result that sample averages may fluctuate because of the presence or absence of specimens with an exceptionally large number of these chambers. As a consequence, it is found that modal values have more consistency than sample means. The size of the adauxiliary chambers is usually inversely proportional to the number of these chambers.

Starting from the supposition that nepionic acceleration is an irreversible evolutionary trend, which is not influenced by environmental circumstances, the samples can be arranged in hypothetical chronological order according to the stages of nepionic acceleration. The validity of this supposition had been shown in many other groups of larger foraminifera, and also in *Lepidorbitoides* it proved to be correct wherever the relative stratigraphic position was known. It is of course possible that a population that becomes isolated may evolve at a different speed, so that contemporaneous populations may

show different types of nepionic arrangement. In that case nepionic arrangement cannot automatically be correlated with time. The presence of two lineages within the European *Lepidorbitoides* has been suggested earlier (MacGillavry, 1955, 1959) because two population groups show different combinations of parameter values. On the basis of new evidence, this difference may be explained by ecologic factors. This will be discussed more extensively in a later chapter. The area from which our samples have been obtained is not excessively large, and it is preferred to start from the simpler model of one evolving lineage. Whenever conflicting evidence is found, this hypothesis will be reconsidered.

A number of other variable characters of *Helicorbitoides* and *Lepidorbitoides* have been studied in order to determine whether they show a distinct trend in time or that they are influenced by other factors. Nepionic arrangement will be the tool to determine the relative ages of the populations.

III.2 EVALUATION OF OTHER VARIABLE CHARACTERS

Size of test

Measurements of the size of the test are restricted in number (but not selective) because, it can be argued, there are too many factors which may influence the final result of the measurements. Firstly, the size is determined by the ontogenetic growth stage; when different samples are compared, different mature/juvenile ratios may be found. Secondly, posthumous transport may separate smaller specimens from the larger ones. Thirdly, it can be imagined that the maximum size of the test may also be influenced by ecologic factors. Large tests, for instance, may be indicative of a favourable environment. In many animal taxa, large tests point to favourable circumstances. Laboratory studies showed that in foraminifera the reverse may be the case, due to the fact that the parental test is abandoned after reproduction. In the study of Bradshaw (1957), specimens of *Streblus beccarii* were seen to grow until some mature stage was reached (usually 13 chambers), after which they started to reproduce. Under unfavourable circumstances, the specimens continued to grow beyond this stage and reproduced only when circumstances returned to normal again. So, larger tests are then formed under unfavourable circumstances. A similar result was obtained by Föyn (1936) in *Discorbina vilardeboana*: specimens reproduced and abandoned their tests at an earlier stage when kept in running water.

Although not too much value should be attributed to the size of the test,

our observations suggest that there probably is an overall increase during the phylogeny of the *Helicorbitoides-Lepidorbitoides* lineage. Specimens of *Helicorbitoides* hardly ever exceed 3 mm, in our *L. campaniensis* specimens 5 mm is the maximum, whereas in *L. socialis* most specimens have a diameter between 5 and 10 mm, with some rare giants up to 25 mm.

Diameter / thickness ratio

The diameter and thickness of the test of a number of specimens from different samples have been measured and the results suggest that there is a distinct flattening of the test in the course of the phylogeny. The average ratios are: *H. voighti* from Bastad 2.0, *H. longispiralis* from Stafversvad 2.3, from Silberegg 2.6; *Lepidorbitoides campaniensis* from the Pembergerriegel 3.0, from Aubeterre 3.8, *L. bisambergensis* from Orcau 3.6, from Vlodrop 3.9, *L. minor* from the ENCI quarry 4.5 and *L. socialis* from Dumes 5.4, from Salas 8.3. This selected sequence suggests an increasing tendency towards flattening.

The flattening of the test may be the result of nepionic acceleration: cyclical growth is reached earlier and earlier in the ontogeny, which means that a faster growth of the equatorial layer sets in sooner. If lateral chambers should always appear after the same number of budding stages, the result will be flatter tests.

If the diameter/thickness ratio is an accurate reflection of the internal nepionic arrangement, the laborious sectioning would no longer be required for species determination. Unfortunately, certain factors disturb the reliability of this ratio. Firstly, it seems to depend partly on the ontogenetic stage, smaller specimens being relatively thick. Secondly, from populations with the same nepionic arrangement, different results were obtained (Pembergerriegel – Aubeterre, Dumes-Salas), suggesting that there may be also some kind of environmental control. In the Miogypsinidae, the relative thickness of the test seems to be influenced by the turbulence of the water; specimens from turbulent waters have thicker tests (Drooger 1963, p. 338). Nevertheless, the exterior of the test can give a useful first indication of the phylogenetic state of development: small, rotund specimens are primitive, whereas large, flat specimens are highly advanced.

Ornamentation

Randomly distributed rounded pustules, which are the external continuations of the pillars, are usually found on the exterior of *Lepidorbitoides* tests. The degree of pustulation may vary considerably. Thick pustules may be present all over the test, or pustules may be absent or present only in the central or marginal parts of the test. Douvillé (1920) distinguished a number

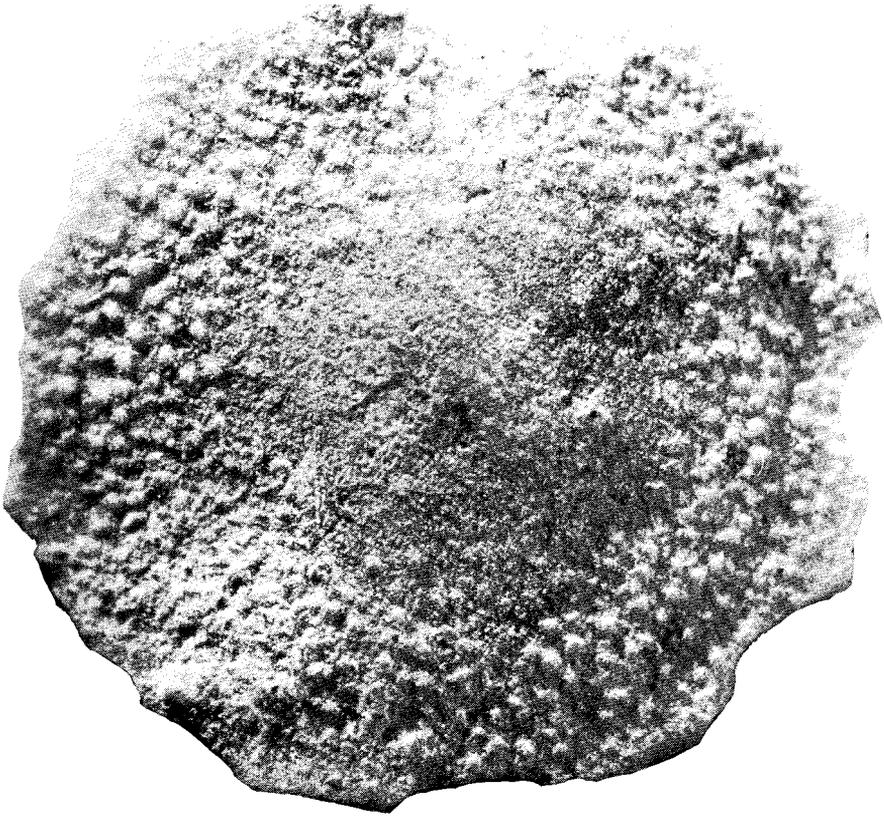


Fig. 3a Specimen of *Lepidorbitoides socialis* from sample St. Marcet 122, 13 X. No pustules are present in the central part of the test (variety *calva*).

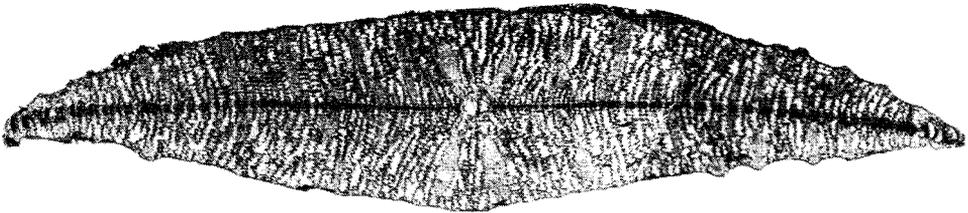


Fig. 3b Vertical section of specimen with a *calva* type of ornamentation from the same sample, showing that thick pillars are present in the central part, but do not continue up to the surface of the test (13 X).

of varieties of *Lepidorbitoides socialis*, based on the type of ornamentation (all varieties from the surroundings of St. Marcet, S France):
variety *regularis*: pustules regularly distributed all over the test;
variety *calva*: pustules only in the marginal zone of the test;
variety *intermedia*: intermediate type between the two former ones; large pustules in the marginal zone, smaller ones in the centre;
variety *pustulata*: in the central part of the test a small number of large pustules, which are larger than those on the rest of the test.

Ruiz de Gaona (1948) distinguished a fifth variety of *Lepidorbitoides socialis*, variety *levis*, for specimens without or with hardly any pustules.

These varieties are frequently found associated in one sample and transitional forms are not uncommon. It should be noted that specimens of the variety *calva*, with pustules only in the marginal zone, are usually large (about 10 mm). Vertical sections show a number of pillars in the central part of the test, which do not continue to the surface. In an earlier ontogenetic stage, these specimens probably had large pillars mainly in the centre, and thus to be assigned to the variety *pustulata* (see Fig. 3). Towards the exterior the pillars become thicker, apparently until a maximum thickness or length is attained, after which further growth ceases; then they are covered with subsequent layers of lateral chambers. The varieties *pustulata*, *intermedia* and *calva* may therefore represent successive ontogenetic stages.

The different types of ornamentation are considered to have little or no taxonomic significance, as they may reflect the influence of environmental conditions in addition to ontogenetic changes. In other groups of foraminifera, variations in the degree of ornamentation have been found as well. According to Bettenstaedt (1962, p. 399), this depends on the CaCO₃-content of the sea-water; when this content is high, pillars, spines and other ornaments are formed more easily. Drooger (1963) stated that pillars in the Miogypsinidae are more developed in specimens from turbulent waters. Lutze (1964) found a decreasing ornamentation with increasing water depth in recent *Bolivina*.

In *Lepidorbitoides*, ornamentation may also be mainly determined by water depth: well-pillared specimens will then be expected in shallower waters; firstly, because turbulence there is usually higher and a solid test with pillars will be more protective; secondly, because the temperature of the water is generally higher, which facilitates taking up CaCO₃ from the sea-water.

Size of Protoconch

In many groups of foraminifera, an increase in size of the first chamber(s) is found to be an evolutionary trend, although in several recent papers it has

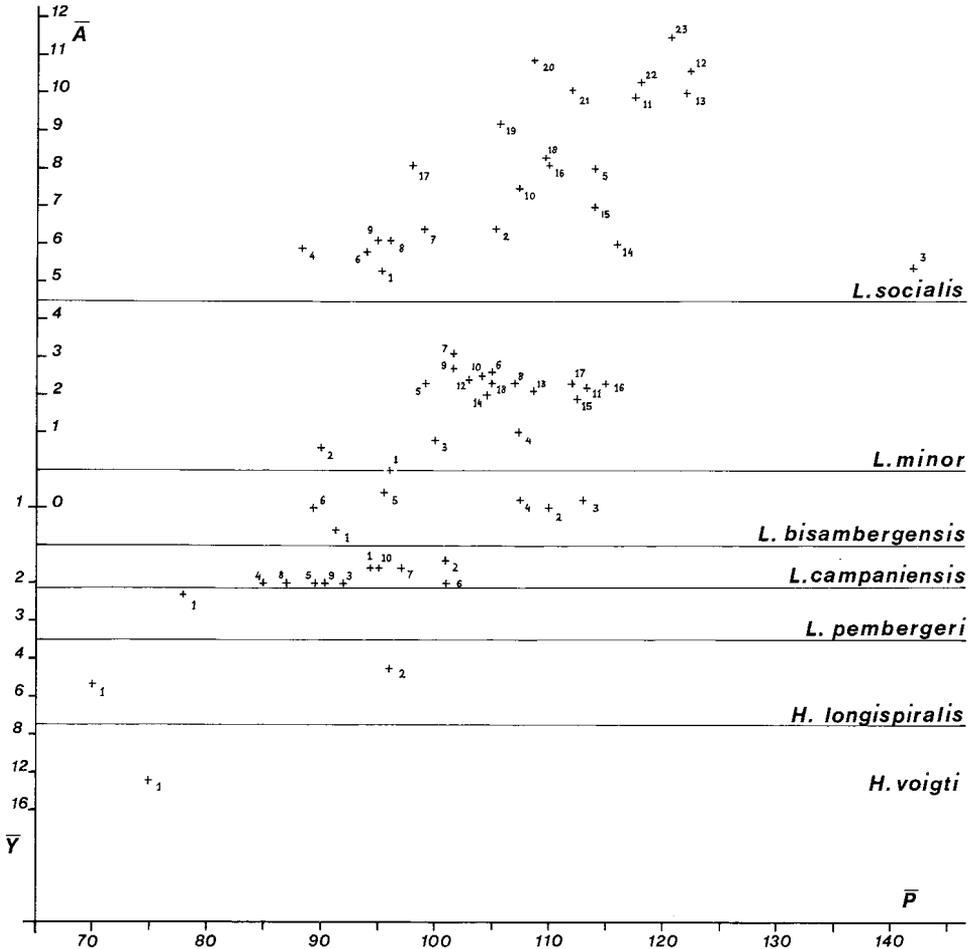


Fig. 4 Relation between nepionic arrangement (expressed in \bar{Y} and \bar{A} values) and mean diameter of protoconch. The numbers refer to the code numbers of the samples in Table IV.

been suggested that this size may also be influenced by environmental conditions. As has been pointed out by MacGillavry (1965, 1971), the variability in size in one sample may be very large, the standard deviation being as much as one-fifth of the mean. As a result differences between samples will only be statistically significant when these differences are large and/or when many measurements are available.

In Fig. 4 the sample means of the protoconchal diameter have been plotted against the corresponding nepionic arrangement, as expressed in \bar{Y} (average number of uni-apertural chambers) and \bar{A} (average number of

adauxiliary chambers) values. It is seen that there is an overall increase in protoconchal size during the phylogeny of *Lepidorbitoides*, but the variability in \bar{P} at each taxonomic level is considerable. The data from samples with the same nepionic arrangement (e.g. *L.socialis* from Olazagutia B9694 and Salas) may be significantly different, whereas populations of the primitive species *L.campaniensis* may have the same mean protoconch diameter as populations of the advanced *L.socialis*. Consequently, it is not possible to use this character to determine the relative age of a population with any degree of accuracy. The data suggest that there is some genetically controlled increase in the diameter of the protoconch from about 70 to 120 microns, but this diameter may be considerably affected by environmental conditions.

A similar situation has been found in the Tertiary Miogypsinidae; Drooger and Raju (1973) discussed which circumstances may have been responsible for these variations. They suggested that populations from higher geographic latitudes generally have larger protoconches than those near the equator and that the protoconchal size might depend on the amount of light in the habitat, because orbitoidal foraminifera probably depended for their food supply on the photosynthetic activity of commensal algae. If this is true, the size of the protoconch must also depend on the depth of living (more illumination in shallower habitats). This leads to the assumption that relatively large protoconches may be expected at higher geographic latitudes and/or at larger depths.

The results of our measurements on *Lepidorbitoides* may be explained rather satisfactorily with this phylogenetic increase – latitude – depth model (although the differences in latitude of our samples are not very large and relative depths are hard to determine from the sediment, as the depth interval of the orbitoidal foraminifera is already restricted to the interval in which sufficient light can penetrate):

– the size of the protoconch of *Helicorbitoides longispiralis* from Austria is considerably smaller than that of the same species from Sweden (higher latitude).

– the range of sample means of the protoconchal diameter of *Lepidorbitoides minor* from the Netherlands is about the same as that of *Lepidorbitoides socialis* from southern France, although the latter species, which has a more advanced number of adauxiliary-chambers, should have a larger protoconch. This again may be explained by the difference in latitude.

Unfortunately, the sample with the largest initial chambers is also from the lowest geographic latitude (Salas, N Spain). This might be explained, however, by assuming a large depth; this is supported by the association with *Clypeorbis* (see Chapter V on ecology).

graphing symbol	sample	N	\bar{P}	\bar{D}	\bar{D}/\bar{P}	reduced major axis
<i>Lepidorbitoides socialis</i>						
23	Gensac 17	9	120.7	268.3	2.22	D= 1.85 P + 44.7
22	Terme 154	14	117.8	258.5	2.19	D= 1.29 P + 106.3
21	Larcen 133	9	112.0	230.7	2.06	D= 1.60 P + 51.2
20	Gensac 25	11	108.5	236.3	2.18	D= 1.93 P + 54.2
19	Naouarret 48	14	105.7	221.4	2.10	D= 2.46 P - 38.5
18	Terme 155	8	109.6	221.5	2.02	D= 2.38 P - 39.2
17	Larcen 4	10	98.1	200.5	2.04	D= 1.42 P + 61.0
16	Biscanos 6	9	110.0	222.6	2.02	D= 2.48 P - 50.2
15	Larcen 135	13	113.9	233.9	2.05	D= 1.52 P + 61.1
14	Larcen 5	10	116.1	225.2	1.94	D= 1.37 P + 65.9
13	St. Marcet 153	14	121.8	248.4	2.04	D= 2.17 P - 15.9
12	St. Marcet 32	22	122.2	272.0	2.23	D= 1.74 P + 58.9
11	St. Marcet 125	10	117.3	260.9	2.22	D= 1.55 P + 78.6
10	St. Marcet 122	18	107.2	232.4	2.17	D= 1.65 P + 55.7
9	St. Marcet 121	28	95.2	175.6	1.84	D= 1.55 P + 27.8
8	St. Marcet R 8851	26	95.9	182.4	1.90	D= 1.71 P + 18.6
7	St. Marcet 147	12	99.1	181.1	1.83	D= 1.24 P + 57.7
6	St. Marcet 144	13	94.2	173.2	1.84	D= 2.36 P - 49.4
5	Olazagutia 22	38	113.9	232.1	2.04	D= 1.92 P + 13.5
4	Olazagutia B 9646	27	88.4	185.6	2.10	D= 2.18 P - 7.5
3	Salas	29	142.1	262.5	1.85	D= 1.30 P + 78.5
2	Gr 813, Dumes	39	105.3	207.8	1.97	D= 2.57 P - 62.7
1	Gr 811, Roquefort	51	95.3	165.7	1.74	D= 1.62 P + 11.1
<i>Lepidorbitoides minor</i>						
18	Keerderberg 33	96	105.1	174.5	1.66	D= 1.51 P + 15.8
17	Keerderberg 36	64	112.0	182.4	1.63	D= 1.48 P + 16.6
16	Keerderberg 38, 39, 40	23	115.0	185.5	1.61	D= 1.38 P + 26.6
15	Keerderberg 41, 42, 45	16	112.6	180.9	1.61	D= 1.28 P + 37.0
14	Schooverberg 168	8	104.5	167.6	1.60	D= 1.23 P + 39.5
13	Schooverberg 173, 174	44	108.6	180.2	1.66	D= 1.43 P + 24.8
12	Curfs	19	102.9	172.0	1.67	D= 2.16 P - 50.0
11	Jekerdal	16	113.3	181.3	1.60	D= 1.18 P + 47.4
10	ENCI 31.00 - 33.00	34	104.2	171.2	1.64	D= 1.26 P + 40.4
9	ENCI 30.50	36	101.6	167.1	1.64	D= 1.43 P + 21.3
8	ENCI 28.00	39	107.0	177.3	1.66	D= 1.45 P + 21.7
7	ENCI 24.00	26	101.6	176.6	1.74	D= 1.74 P - .4
6	ENCI 23.50	55	104.9	176.6	1.68	D= 1.26 P + 44.3
5	ENCI 22.00 - 22.50	35	99.2	171.1	1.73	D= 1.70 P + 2.4
4	ENCI 13.50 - 19.75	28	107.3	165.0	1.54	D= 1.15 P + 41.1
3	ENCI-Sportpark	11	100.1	161.8	1.62	D= 1.20 P + 41.4
2	Ilten	24	90.0	153.4	1.70	D= 1.44 P + 24.0
1	Kunrade	16	96.2	151.5	1.57	D= 1.67 P - 9.3
<i>Lepidorbitoides bisambergensis</i>						
6	Vlodrop	29	89.3	145.6	1.63	D= 1.35 P + 25.2
5	Gr 832, Orcau	19	95.5	130.3	1.36	D= 1.05 P + 30.4
4	X 1961AW, PEMBERGER	14	107.4	145.6	1.36	D= 1.38 P - 2.5
3	X 1961AG, PEMBERGER	11	113.2	162.2	1.43	D= 1.36 P + 8.8
2	X 1961V2, PEMBERGER	6	110.2	159.0	1.45	D= 1.68 P - 25.8
1	Gr 854, Bisamberg	4	91.4	139.2	1.52	D= 1.42 P + 9.8
<i>Lepidorbitoides campaniensis</i>						
10	Gr 849, PEMBERGER	26	94.7	127.0	1.34	D= 1.31 P + 1.2
9	O 17, PEMBERGER	10	90.3	116.4	1.29	D= 1.47 P - 16.6
8	Gr 369, St. Louis	7	87.0	114.5	1.32	D= 1.54 P - 19.4
7	Gr 105-112, Chalais	28	97.3	122.1	1.25	D= 1.18 P + 7.2
6	Gr 139, Festalemps	6	100.9	134.4	1.33	D= 1.28 P + 5.3
5	Gr 365, Neuviac	12	89.5	118.3	1.32	D= 1.20 P + 11.1
4	Gr 359, Issac	7	85.0	113.1	1.33	D= 1.02 P + 26.2
3	Gr 364, Neuviac	8	91.9	118.0	1.28	D= 1.21 P + 6.8
2	Gr 40, Aubeterre	22	100.9	124.0	1.23	D= 1.18 P + 4.4
1	Gr 22, Aubeterre	6	94.5	116.0	1.23	D= 1.29 P - 5.6
<i>Lepidorbitoides pembergeri</i>						
1	Gr 851, PEMBERGERRIEGEL	20	77.9	89.9	1.15	D= 1.24 P - 6.5
<i>Helicorbitoides longispinalis</i>						
2	Stafversvad	4	96.2	113.1	1.18	D= 1.03 P + 14.0
1	Gr 842, Silberegg	12	69.8	77.8	1.11	D= 1.12 P - .2
<i>Helicorbitoides voighti</i>						
1	Bastad	45	75.1	80.2	1.07	D= 1.19 P - 8.9

Table IV. Results of measurements of internal diameter of proto- and deutoconch (in microns). N = number of observations, \bar{P} and \bar{D} are average diameters of proto- and deutoconch respectively.

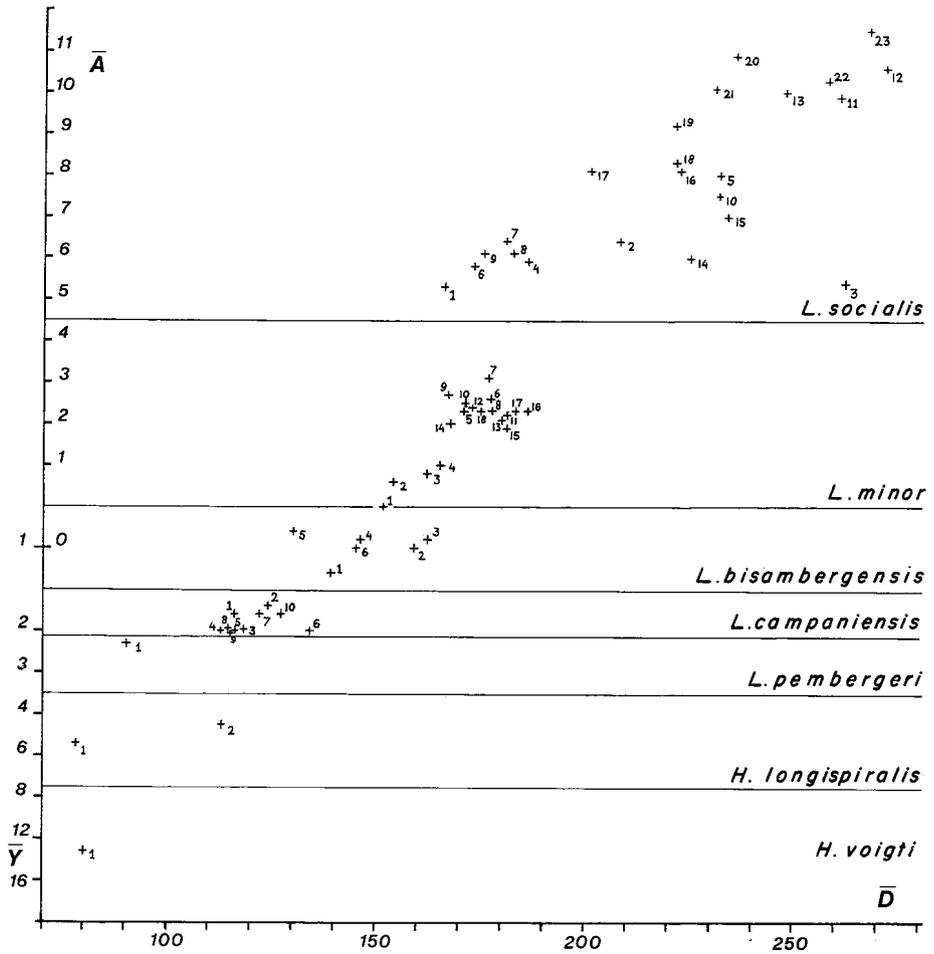


Fig. 5 Relation between nepionic arrangement ($\bar{Y}-\bar{A}$) and mean diameter of deuterocoenoch (\bar{D} , in microns).

Noteworthy is furthermore the relatively small size of the initial chambers of *Lepidorbitoides socialis* specimens from limestones (Roquefort, St. Marcet Calcaire Nankin) in comparison with specimens from sediments with a larger amount of non-calcareous terrigenous detritus (Dumes, St. Marcet Marnes d'Auzas). This may be explained with the illumination hypothesis by assuming a deposition of the limestones in shallower water, but we may also think of a third factor which influences the amount of illumination at the surface of the sediment: the transparency of the water. Less light will reach the bottom when the water contains much sediment

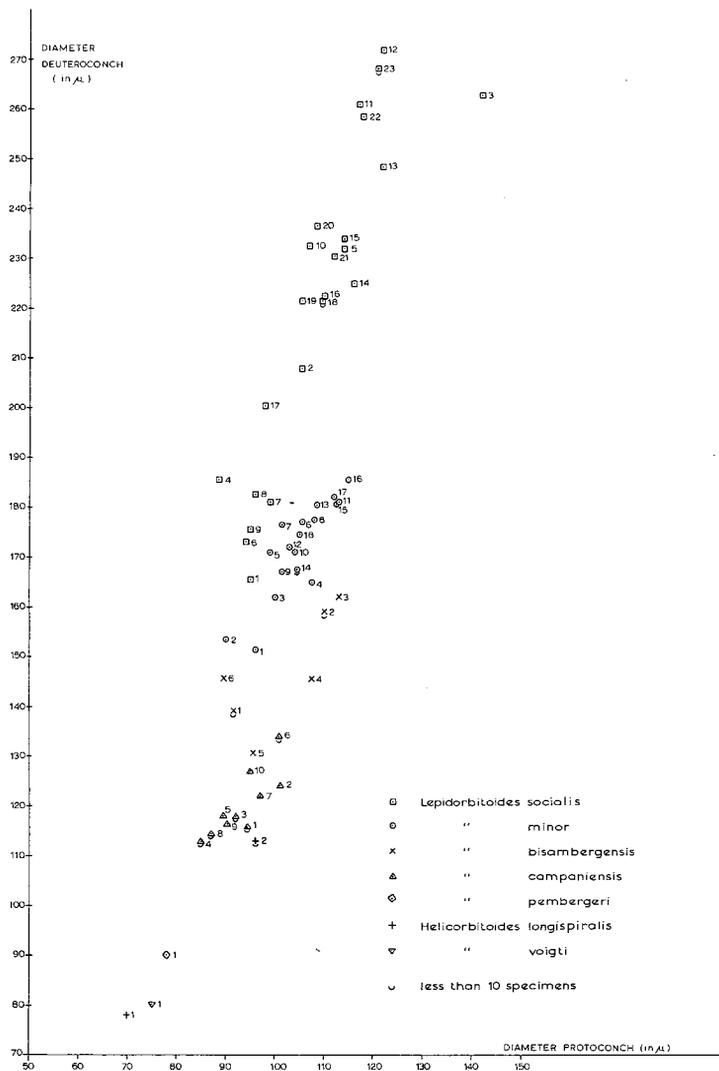


Fig. 6 Scatter diagram showing the relation between the average diameters of proto- and deuterococh. Phylogeny is from bottom left to top right.

(which would result in larger initial chambers).

Summarizing, it may be concluded that our data are not incompatible with the illumination hypothesis of Drooger and Raju.

Size of Deuteroconch

The behaviour of the size of the deuteroconch is comparable with that of the protoconch (see Fig. 5 and Table IV). There is an increase during the phylogeny (from about 80 to 270 microns) and the influence of environmental circumstances is similar to that in the protoconch. The diameter of the deuteroconch increases much faster, however, than that of the first chamber, so the trend towards an increasing diameter is more distinct. The

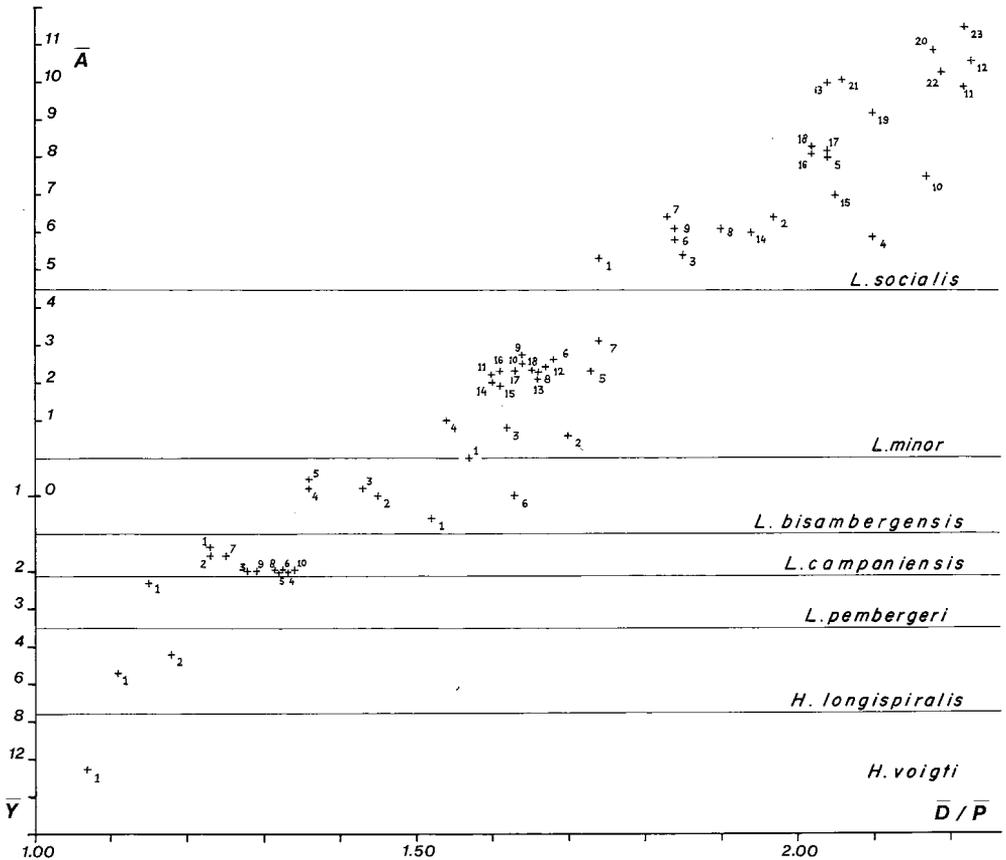


Fig. 7 Relation between nepionic arrangement ($\bar{Y}-\bar{A}$) and ratio between mean diameters of deutero- and protoconch.

great variability renders also the deuteroconch size a rather unreliable criterion for relative age determinations.

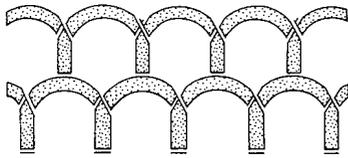
D / P ratio

Owing to the rapid increase of the diameter of the deuteroconch as compared to the diameter of the protoconch, the ratio between these diameters will also increase in the phylogeny. This trend is called embryonic acceleration (Drooger, 1956). If proto- and deuteroconch are affected by environment in the same way, this ratio may be independent of ecology.

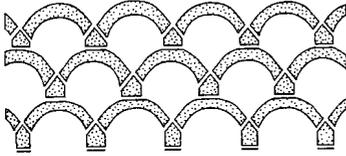
For comparisons between samples, the relation between the two initial chambers may be expressed by the slope of the regression lines or reduced major axes, which can be computed from the individual P-D pairs. However, these often show aberrant values (see Table IV). If the ratio between the sample means of the diameters is used a fairly good correlation is obtained with the nepionic acceleration (Fig. 7). The alignment is much closer than it is for either \bar{P} or \bar{D} values. The ratio between sample means of the internal diameter deuteroconch/protoconch increases from about 1.1 in the primitive *Helicorbitoides*, via 1.2–1.3 in the biserial *Lepidorbitoides campaniensis* to about 1.7 in *L. minor* and 1.7–2.2 in *L. socialis*. If for some reason, for instance in extremely badly preserved samples, the nepionic arrangement cannot be determined, the average D/P ratio seems to give a rather reliable indication of the level of development.

Shape of equatorial chambers

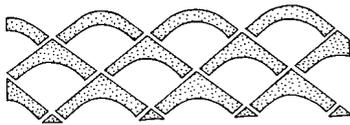
In the evolution of the *Helicorbitoides-Lepidorbitoides* lineage, a distinct change in the shape of the secondary equatorial chambers can be observed. In the early representatives, only open arcuate chambers are found. The bases of the chambers of the same budding step, as seen in a horizontal section, are not touching each other. During phylogeny more chambers appear to be formed simultaneously, as the chambers become more closely spaced. The bases of the coeval chambers will be touching. When this crowding trend continues, the adjacent chambers will even compress each other, as it were, and via the transitional stages pointed arcuate and ogival, the shape of the equatorial chambers eventually becomes spatulate (see Fig. 8). This trend towards crowding of the equatorial chambers can also be observed in the successive ontogenetic stages of one specimen. In the earliest parts only primitive, arcuate chambers are found. It depends on the phylogenetic stage of development of the population, if and when in the ontogeny more closely spaced chamber types are developed. Ogival and spatulate chambers appear to be introduced for the first time in the marginal zone of larger specimens of *Lepidorbitoides bisambergensis*. In the



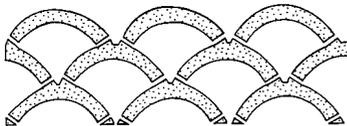
- e spatulate chambers with diagonal and annular stolons. The diagonal stolons cross each other at different levels.



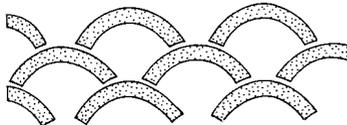
- d ogival chambers with diagonal and annular stolons.



- c pointed arcuate chambers. These are normal arcuate chambers with the bases of adjacent chambers in contact. In sections, in which the raised basal stolons are cut, the fused chamber bases appear as isolated points on top of the previously built chambers.



- b arcuate chambers with slightly raised basal stolons.



- a open arcuate chambers with basal stolons.

Fig. 8 Schematic drawings showing chamber shape and chamber connections at successive stages of crowding. Fig. a is the most primitive stage, e the most advanced.

more advanced species *Lepidorbitoides minor*, the outer half of the equatorial section usually consists of such chambers and in *Lepidorbitoides socialis* all except the first few cycles have spatulate equatorial chambers.

Intercameral connections

Simultaneously with the crowding of the equatorial chambers, the connections between these chambers become increasingly complex. These connections, usually called stolons, are rather thin (up to 5 microns in diameter)

and have been observed in scarce well-preserved specimens only. Most of our observations were made in *Lepidorbitoides socialis* specimens from Salas, N Spain. The system of chamber connections changes as follows from centre to periphery (see also Fig. 8):

a. in the primitive, open arcuate chambers only two basal foramina or apertures are present in each chamber. This is called a “four stolon system”, as each chamber lumen has four connections with adjacent chambers. According to MacGillavry (1963, p. 153), this is an incorrect term as only two apertures are present in each chamber wall.

b. when the basal parts of two adjacent chambers are close to each other, these foramina can be seen to bend upward towards the exterior (Fig. 8b).

c. in a further stage of crowding, the bases of the arcuate chambers are in contact. In order to maintain the connections with the exterior, the formerly basal foramina must shift outward and/or become more oblique. In sections in which the stolons are cut, the basal parts of the chambers appear as

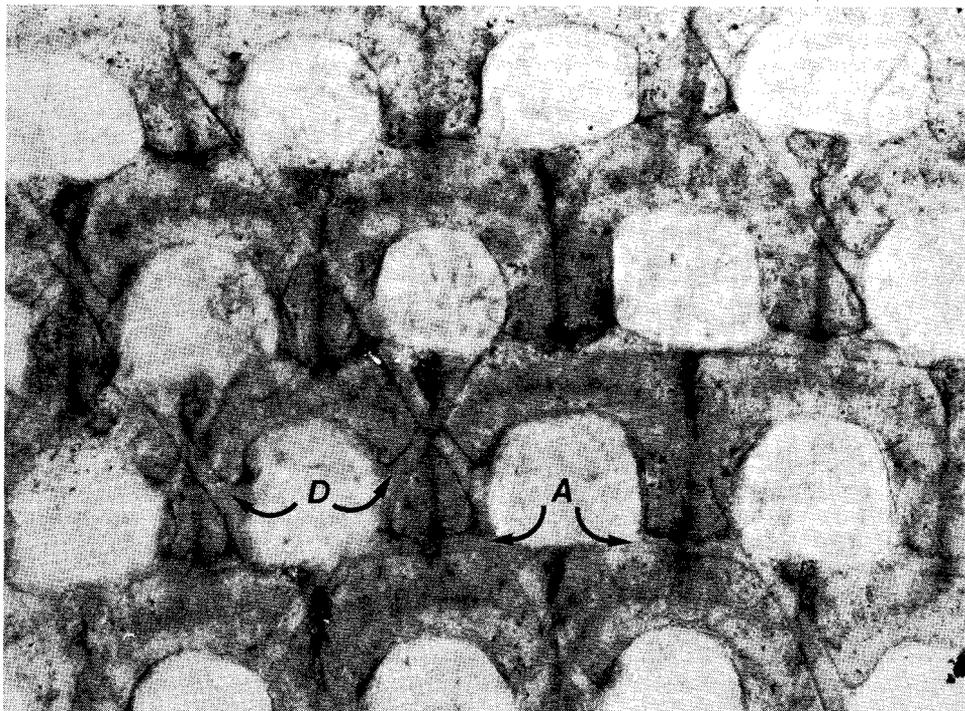


Fig. 9 Salas 36, *Lepidorbitoides socialis*, 350 X. Part of equatorial section showing spatulate equatorial chambers with diagonal (D) and annular (A) stolons.

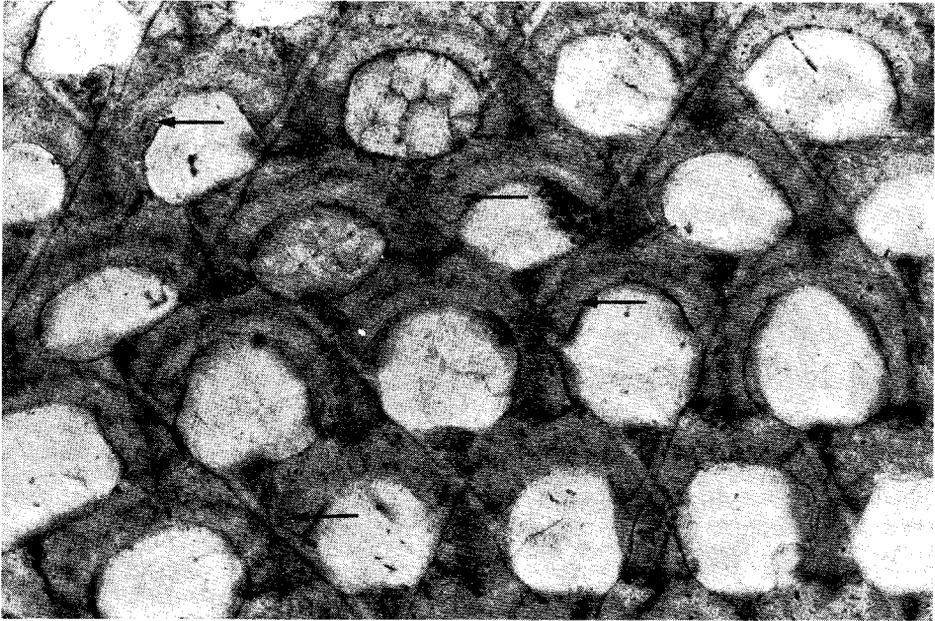
isolated points on top of the previously formed arcuate chambers, thus suggesting that the exterior side of the chamber wall is pointed (Fig. 8c).

d. at the next stage of crowding, the adjacent equatorial chambers start compressing each other (ogival chambers). To keep contact with the exterior, the foramina must shift further outward and instead of basal foramina they are now called diagonal foramina or stolons. In order to improve the communication between the adjacent chambers, another type of foramen is introduced at the base of the common wall of two adjacent chambers of the same cycle (annular foramen or stolon). This leads to a so-called "six stolon system", each chamber having six connections with adjacent chambers (see Figs. 8d and 9).

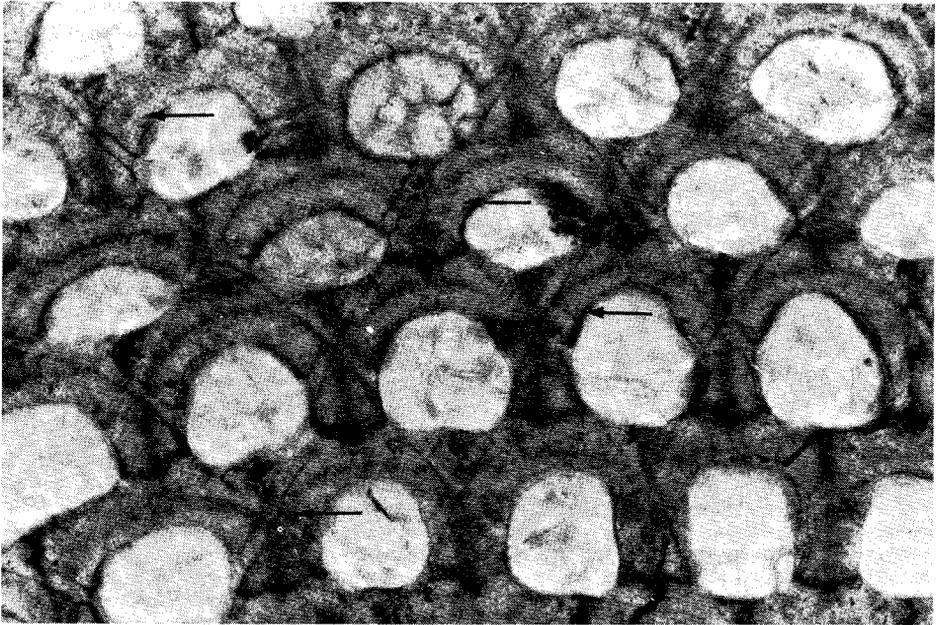
e. in spatulate chambers (which are the more crowded equivalent of ogival chambers), the same type of intercameral connections is present. The diagonal stolons have continued their outward shift and increased their inclination (see Fig. 8e). The diagonal stolons are usually in direct line with diagonal stolons in earlier and subsequent cycles of equatorial chambers. It should be noted that the diagonal stolons cross each other at different levels, and always at the junction of two adjacent chambers (Fig. 8e, Fig. 10). This is not quite in agreement with the drawing of Neumann (1972b, fig. 4c), which shows the imaginary lines connecting the diagonal stolons of successive chambers to be crossing each other somewhere within the chamber lumen. The position of these stolons at the "sutures" of the spatulate chambers is not surprising, as they are considered to be the equivalent of the basal apertures of the open arcuate chambers, which, due to the crowding of the equatorial chambers, were forced to shift outward in order to maintain the communication with the exterior. The diagonal stolons may therefore be considered to be homologous with the basal apertures of the primitive chambers, whereas the annular stolons, which are now situated at the chamber bases, are a new feature. Some vertical sections reveal several diagonal stolons to be probably present above each other (up to 3 or 4) in each spatulate chamber. It is not known at which stage these stolons are being formed at different levels and when the multiplication of the stolon system starts.

The morphogenesis of the equatorial chamber shape and chamber connections in *Lepidorbitoides* seems to be entirely analogous to that of the Tertiary *Lepidocyclinidae*, as described amongst others by Grimsdale (1959), Eames et al. (1962) and Fortuin (1970). For excellent spatial drawings of the intercameral connections at the successive stages of crowding, the reader is referred to figs. 4 and 5 in the paper of Eames et al. . .

Communication between equatorial and lateral chambers and between



a



b

Fig. 10 a, b Salas 14, *Lepidorbitoides socialis*, 300 X. Two photographs of the same equatorial chambers, focused at different levels to show the crossing of the diagonal stolons at different levels (especially well visible at spots indicated with arrows).

lateral chambers is maintained by numerous coarse pores (diameter 3 to 4 microns, compare also with fig. 5 of Eames et al.).

III.3 SYNTHESIS OF EVOLUTIONARY TRENDS

It has been argued that the following changes may be considered as evolutionary trends in *Lepidorbitoides*, although most of them may also be influenced by environmental factors:

- a. nepionic acceleration;
- b. increase in absolute size of the initial chambers;
- c. increase in relative size of deuteroconch, i.e., of the ratio diameter deuteroconch/diameter protoconch;
- d. crowding of equatorial chambers with subsequent increase in complexity of intercameral connections;
- e. increase in size of test;
- f. increase in flatness of test.

It may be asked whether all these trends are independent of each other or the expression of one governing principle.

Recently, Drooger (1974) advanced a model in which nepionic acceleration and increase in size of the embryo in larger foraminifera are explained as co-operating factors in attaining a certain critical volume Q in a small number of budding steps. A further increase in the size of the test beyond this volume would no longer be advantageous. According to Drooger it would be an ideal situation in orbitoidal foraminifera when the hypothetical volume Q is reached at the same ontogenetic stage as the beginning of radial growth. When the stage of radial growth has not been reached yet at this volume, nepionic acceleration is supposed to be the strongest evolutionary trend. In more advanced stages, when radial growth starts before reaching this critical size, an increase in dimensions of the embryo will be more important.

For *Lepidorbitoides*, we have modified this hypothesis, explaining all these evolutionary trends as serving one goal: trying to reach a certain, large volume in a small number of budding steps. It is a somewhat altered version of the model of Drooger, from which it differs mainly in suggesting a phylogenetic increase in the rate of exponential growth, which was supposed to be constant in Drooger's model, and in the disregarding of the importance of Drooger's volume P .

Like in many other animal taxa, the volume of the test of foraminifera increases at an exponential rate under ideal circumstances. This means that

with each growth step, the protoplasm volume increases with a certain, fixed percentage of its previous volume. This may be expressed by the equations:

$$V_{n+1} = V_n + b/100.V_n = (1+b/100)^n.V_1$$

V_n is the volume after n budding steps, b represents the rate of growth and is the percentage with which the volume increases at each budding step. The formulae are basically the same as those of Drooger (1974, p. 18). In simple spirally arranged foraminifera, this type of growth is realized by the steady increase in volume of ontogenetically later chambers.

Supposing a large size to be favourable in certain environments, it can be imagined that it might be advantageous to reach a certain volume as soon as possible. The same volume in a lesser number of budding steps can then be attained in two ways:

- a. phylogenetic increase of the initial volume V_1 . With the same growth rate, all subsequent chambers will be also larger, and a certain volume will be reached earlier;
- b. phylogenetic increase of the growth rate b . All subsequent chambers will be relatively larger, and the volume after n budding steps will be larger.

If rapidly attaining a larger volume is useful, specimens with a relatively large embryo and/or a larger rate of growth may be in a selective position. A slight increase of the growth factor b will eventually be more effective than a slight increase of the initial volume, and a higher rate of growth may have the higher selective value.

Increase of the rate of growth in spirally arranged foraminifera will eventually lead to the formation of extremely large chambers late in the ontogeny. According to Smout (1954, p. 16), there is a limiting size beyond which the normal shape of a spiral chamber cannot be maintained and modification of the shape or fragmentation of the chamber must follow. In our case the answer to the supposed augmented rate of growth (which may have been made possible by the larger quantities of food becoming available after the colonization of the foraminifera by algae, Grimsdale 1959, p. 23) is the formation of more chambers in one budding step, by the acquisition of a second, retrovert aperture, leading to the formation of secondary chambers. In our group of species this is the transition from *Pseudosiderolites* to *Helicorbitoides*. Instead of one chamber being formed at each budding stage, several chambers are formed simultaneously along a small part of the periphery. The increase in rate of growth is continued by the following morphologic changes:

- secondary chambers are formed earlier and earlier in the ontogeny;

- in later ontogenetic stages the sector of active growth extends further and further over the periphery, until radial growth is finally reached;
- radial growth will be attained earlier and earlier in the ontogeny, until this is already attained after the fourth budding stage in the most advanced stages of *Lepidorbitoides*;
- in ontogenetically later stages of radial growth, more and more chambers must be formed in order to accommodate the increasing amounts of protoplasm produced per budding step. This results in a gradual replacement of the open arcuate chambers by a larger number of relatively high, spatulate chambers;
- the crowded, spatulate chambers will appear earlier and earlier in the ontogeny.

The increase in the relative size of the deuteroconch (embryonic acceleration) in itself may be seen as an augmented growth rate.

The increase in the size of the test may also be the result of the increased rate of growth.

The increasing flatness of the test may be explained as a consequence of the neponic acceleration (see Chapt. III.2, Diameter/thickness ratio).

Summarizing, it may be concluded that all evolutionary trends in the *Helicorbitoides-Lepidorbitoides* lineage may be the result of such specimens having selective advantage, which are able to reach a certain size in the smallest possible number of budding steps. Specimens with a larger embryo and a larger rate of growth are in an advantageous position and the change from a spiral towards an orbital pattern of growth may be seen as a means to reach a higher rate of growth.

It may be noted that further increase of the rate of growth would lead to *Discocyclus*-like forms (protoconch more enveloped by deuteroconch, extreme crowding already in the earliest post-embryonal chambers). The ancestor and primitive stages of *Discocyclus* are unknown, but the *Cycloclipeus*-like initial stage of the microspheric Discocyclinidae s.s. (see Brönnimann 1945, Neumann 1958, Caudri 1972) seems to be prohibitive for *Discocyclus* to be derived from *Lepidorbitoides*. The microspheric centre of the Orbitoclypeidae (Brönnimann, 1945) is similar to that of the Lepidorbitoididae; it has been suggested that the Orbitoclypeidae may have originated from the Lepidorbitoididae (MacGillavry, 1963). Further investigations are required.

III.4. TWO LINEAGES IN EUROPEAN LEPIDORBITOIDES?

In a biometrical study of *Lepidorbitoides minor* from Limburg and *Lepidorbitoides socialis* from southern France, MacGillavry (1955, 1959) concluded to two evolutionary trends, operative in both species: increase in size of proto- and deutoconch and increase in the number of adauxiliary chambers. Because of the larger number of adauxiliary chambers, *Lepidorbitoides socialis* must be more advanced than *L. minor*, though the diameter of the protoconch has the same range in the two species. It was suggested that the two species evolved independently at different speeds in different areas. As stated in a previous chapter, however, there is indeed an overall increase in the size of the protoconch, but the size appears to be considerably affected by environmental circumstances. Several samples of *Lepidorbitoides campaniensis* and *L. bisambergensis* have the same mean protoconch diameters as some samples of the species *L. minor* and *L. socialis*. This author therefore prefers the alternative hypothesis that the species *minor* and *socialis* represent successive stages of one lineage. It will be hard to prove or disprove this, as the difference in age, if any, is very small geologically, and hardly any other methods are available to determine such small differences.

Some arguments for a difference in age may be:

– The Upper Maastrichtian larger foraminifera *Clypeorbis* and *Orbitoides gensacicus*, the latter of which is considered to be the final stage of the *Orbitoides* lineage, are found associated with the French *Lepidorbitoides socialis*, but are absent in Limburg. However, this may also be due to other, e.g. climatic, circumstances.

– The greater part of the Maastricht Tuff Chalk can be assigned to the *Belemnitella junior* Zone, which represents the lower Upper Maastrichtian of the Boreal classification. Only the upper meters of the Md member can be assigned to the youngest belemnite zone, the *Belemnella casimirovensis* Zone (Schmid 1959). This suggests that the uppermost part of the Maastrichtian Stage is not represented in the type section (see also Deroo, 1966). It is therefore quite possible that younger representatives of *Lepidorbitoides* can be found in other areas.

When populations evolve at different speeds, they must be geographically separated from each other. The following may be an argument against the supposed separation of the *Lepidorbitoides minor* and *L. socialis* stocks. Larger foraminifera are supposed to have lived in warm (sub-)tropical waters, and therefore they are very rare in the Boreal Upper Cretaceous. The appearance of *Lepidorbitoides*, *Orbitoides*, *Omphalocyclus*, *Siderolites* and

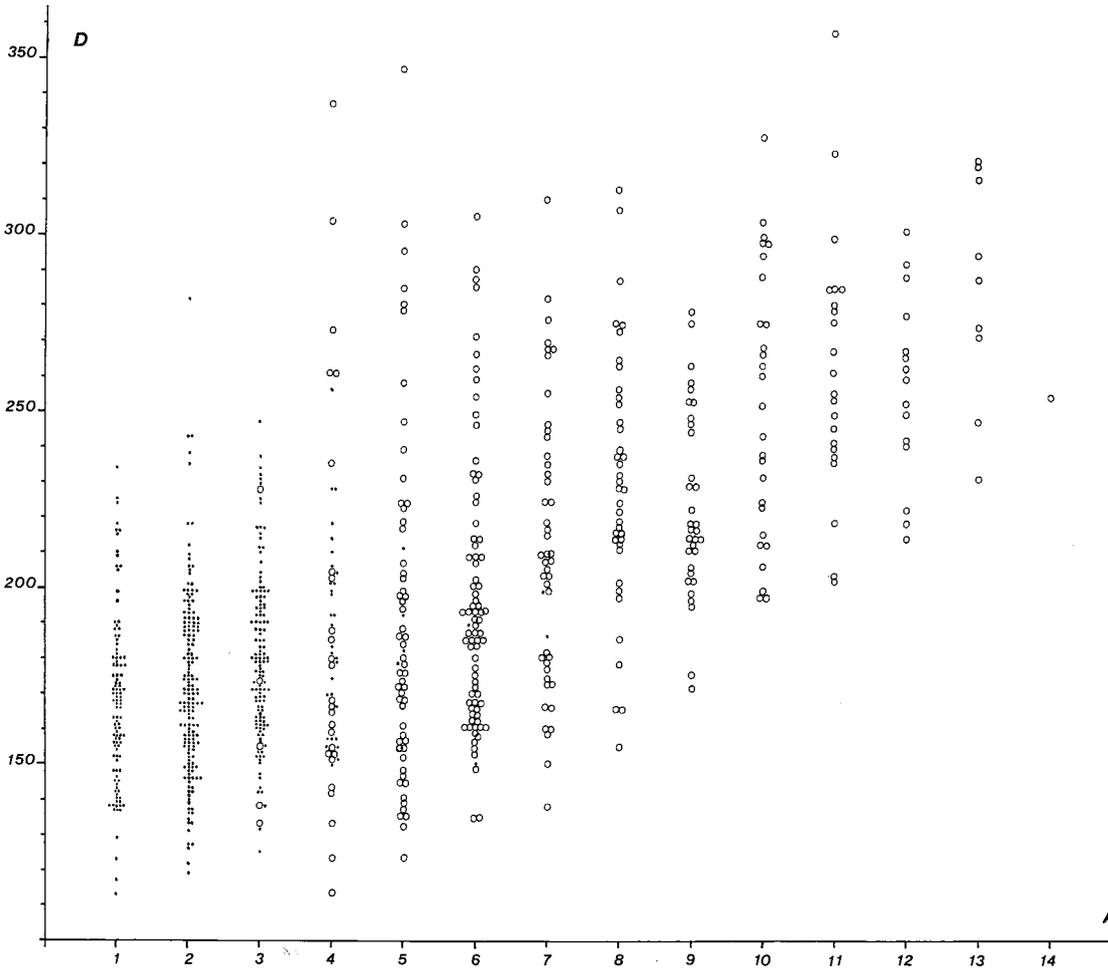


Fig. 11 Relation between diameter of deuterocoenoch (D, in microns) and the number of adauxiliary chambers (A) in *Lepidorbitoides minor* (•) and *Lepidorbitoides socialis* (○).

other tropical taxa such as corals, rudists, giant reptiles, etc., in the Boreal Upper Cretaceous is usually interpreted as a migration of a meridional fauna to the north as a result of an improving climate in the Late Maastrichtian (see a.o. Voigt, 1965). This fauna must have come from the south, which is the realm of the *Lepidorbitoides socialis* stock. If so, the required geographic separation cannot have lasted very long.

For Drooger (1974), the data of Freudenthal (1969) on *Hellenocyclina* were strongly supporting the contemporaneity of the Dutch *Lepidorbitoides minor* and the French *L. socialis* populations. No definite conclusion can be

drawn from these data, however, as *Hellenocyclina* seems to have reached its final stage of nepionic acceleration in Maastricht and St. Marcet and does not change much any more. When differences in nepionic development cannot be detected, this does not necessarily imply equal age. In *Hellenocyclina* from the Mc and Md members of the Maastricht Tuff Chalk, no differences have been found either (Freudenthal op. cit.), whereas in *Lepidorbitoides* from these strata a distinct progressive change was observed.

In the same paper by Drooger (p. 25) it is suggested that the number of adauxiliary chambers depends on the size of the embryonal chambers; as the latter show wide local variations, the number of adauxiliary chambers would have only a limited value for interregional correlations. It is true that in our samples usually there is some positive correlation between the number of adauxiliary chambers and the size of the deuterocoenoch, but it is questionable whether the former depends on the latter. To visualize this, the values of all specimens of *Lepidorbitoides minor* (Limburg and Ilten) and *L. socialis* (France, N Spain) have been plotted in a D-A scatter diagram (Fig. 11). Considering the extremely wide ranges of the deuterocoenochal diameter in each class of adauxiliary chambers and the large areas of overlap, some sort of "mechanical" relation between these two characters seems to be hardly probable. The deuterocoenochal diameter of many *Lepidorbitoides minor* specimens is equal to that of several *Lepidorbitoides socialis* specimens with 8 or 10 adauxiliary chambers. Since *L. minor* specimens never have so many chambers, the number of adauxiliary chambers is apparently mainly genetically controlled. Some restrictive influence of the size of the deuterocoenoch on the number of adauxiliary chambers may be expected in highly advanced populations: the number of these chambers is primarily determined by the number of stolons in the deuterocoenochal wall, thus when the deuterocoenoch is small and has a large number of adauxiliary stolons, lack of space may limit the number of adauxiliary chambers formed out of these stolons.

Chapter IV

MICROSPHERIC GENERATION

In contrast with most other genera of larger foraminifera, dimorphism in *Lepidorbitoides* is not reflected by differences in size of the tests. The microspheric generation can only be recognized by the different arrangement and the smaller size of the initial chambers.

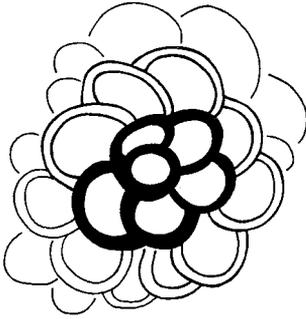
In our material only 18 thin sections can be assigned to the microspheric generation; this suggests that the ratio microspheric/megalospheric is about 1:100. However, because of the small dimensions of the initial chambers, many microspheric specimens may not have been recognized as such when preparing the thin sections. Relatively many specimens of this generation may therefore have been wasted in the grinding process. Even if the actual number of microspheric specimens is two or three times larger, the ratio between the two generations still will be extremely low.

In Table V the measurements on the interpretable specimens are presented. The diameter of the protoconch varies between 14 and 24 microns, the average is 19.3. This is followed by a number of spirally arranged chambers (probably slightly trochoid, see van Gorsel 1973b, Pl. IV, fig. 3). The number of chambers without a retrovert aperture varies between 4 and 11, and great differences in the length of the initial spiral of the microspheric specimens of different species have not been established. In other orbitoidal groups the microspheric generation also shows nepionic acceleration (Drooger 1963 in the Miogypsinidae, Krijnen 1972 in the Pseudorbitoididae). This may also be the case in *Lepidorbitoides*, but the available data are insufficient to prove this supposition.

As has been noted by MacGillavry (1963), the primary spiral does not continue in the helicolepidine manner, after the primary and retrovert chambers have joined into a symmetrical chamber. Apparently, the microspheric generation shows primitive characters, but the initial stage is not necessarily a reduced copy of an ancestral nepionic stage of the megalospheric generation.

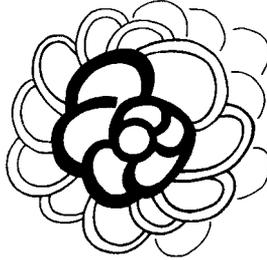
No microspheric specimens have been observed in species more primitive than *L. campaniensis*. This is in agreement with MacGillavry (1963), who

Gr 849-52, Pemberger
(*L. campaniensis*)



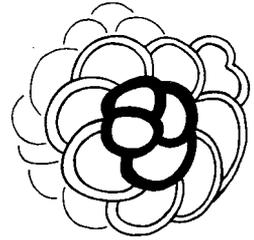
Y = 6
ps = 13

ENCI 3150 B-5
(*L. minor*)



Y = 7
ps = 12

Olazagutia S 22-63
(*L. socialis*)



Y = 4
ps = 8

Fig. 12 Initial stages of microspheric specimens. The uni-apertural chambers (Y) have been drawn with black walls, ps is the number of chambers in the primary spiral.

Specimen number	Species	Diameter protoconch in microns	Number of uni-apertural chambers	Number of chambers in primary spiral
Aubeterre, Gr22A-7	<i>campaniensis</i>	14	11?	≥ 19
Pemberger, Gr849-52	<i>campaniensis</i>	24	6	13
ENCI 31.50B-3	<i>minor</i>	16	7	12
ENCI 31.50B-5	<i>minor</i>	20	7	12
Keerderberg 33-76	<i>minor</i>	17	6	10
Keerderberg 36-53	<i>minor</i>	21	6	11
Schooverberg 174-15	<i>minor</i>	23	5	11
Curfs 17	<i>minor</i>	19	5	12
Salas 21	<i>socialis</i>	20	6	11
Olazagutia S22-63	<i>socialis</i>	19	4	8

Table V. Measurements and counts on the initial stage of microspheric *Lepidorbitoides*.

concluded that dimorphism seems to be absent in the earliest members of each group of Cretaceous larger foraminifera. In our case, this might as well be due to the scarce specimens available. In the Pseudorbitoididae, moreover, Krijnen (1972) has since described dimorphism in the most primitive species of that family known so far.

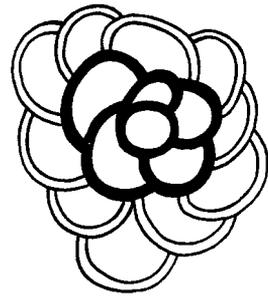
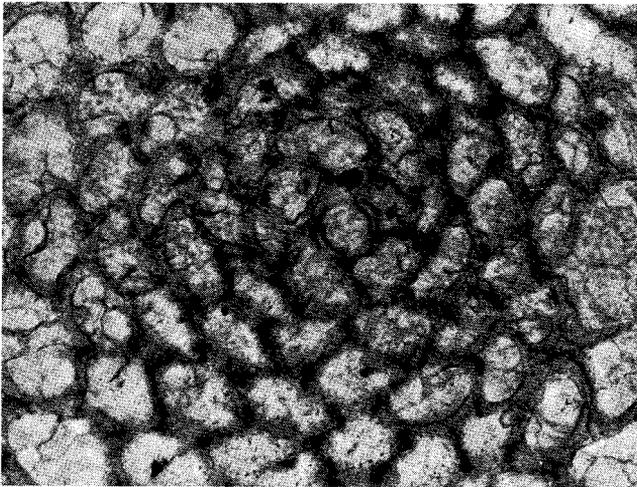
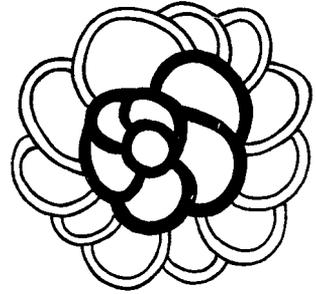
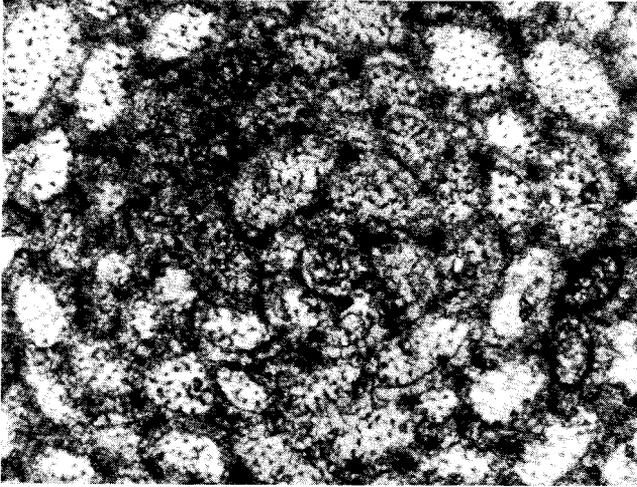


Fig. 13 Initial stages of microspheric specimens. Top: ENCI 31.50-5, *L. minor*, 270 X; Bottom: Salas 21, *L. socialis*, 340 X.

Chapter V

REMARKS ON ECOLOGY

V.1. HABITAT

Orbitoidal foraminifera are benthonic organisms, (hemi-)sessile or moving freely. In analogy with comparable recent forms, they are probably restricted to the zone in which sufficient light can penetrate (down to about 100 m) in order to satisfy the needs of the supposedly symbiotic zooxanthellid algae. In any case they may be used as indicators for a warm, shallow marine environment.

V.2. ASSOCIATIONS OF LARGER FORAMINIFERA

In our samples, wide variations in the relative numbers of different orbitoidal genera can be observed; this suggests that these genera have slightly different ecological requirements. In the Campanian and Maastrichtian, the most frequent genera are *Orbitoides* and *Lepidorbitoides*. The proportions in which they are present vary considerably and at many localities only one of these genera is found. In the Upper Maastrichtian, the samples with only or mainly *Orbitoides* usually also contain *Omphalocyclus* and less frequently also meandropsinids (Roquefort, St. Marcet), whereas in samples in which *Lepidorbitoides* predominates the orbitoidal genus *Clypeorbis* is usually present as well (Dumes, Salas, Olazagutia).

The variation in proportions of *Orbitoides* and *Lepidorbitoides* has been noticed before by several authors. Neumann (1958, p. 22) reported that at the southern border of the Aquitaine basin mainly *Orbitoides* and *Omphalocyclus* are found, whereas towards the center of the basin *Lepidorbitoides* and *Clypeorbis* are more frequent. In northern Spain, in the limestones near Villarcayo (Province of Burgos), Radig (1963) found mainly *Orbitoides* and *Omphalocyclus*, whereas in the vicinity of Olazagutia (Province of Navarre), in sediments deposited farther away from the ancient coast, *Lepidorbitoides* is predominant. In the Maastrichtian Tozal Formation in the Spanish

Pyrenees, *Lepidorbitoides* was found more frequently in a finer matrix, whereas relatively more *Orbitoides* were found in a coarser matrix (van de Velde, 1967, p. 177).

Only a few data are available on the relative depths at which our specimens have been living. According to Bouroullec and Deloffre (1972), the "Couches de Dumes" (with *Lepidorbitoides* and *Clypeorbis*) must have been deposited in deeper water than the "Marnes d'Auzas" (with *Orbitoides*, *Lepidorbitoides* and *Omphalocyclus*). From the figures of Schnitker (1972), it can be inferred that the strata of Dumes must have been formed at a depth between 50 and 100 meters, while deposits farther to the north (Roquefort, with *Orbitoides*, *Lepidorbitoides*, *Omphalocyclus* and *Fallotia*) have been formed in shallower water.

The observations mentioned above suggest that the distribution of the larger foraminifera may be mainly determined by water depth. *Orbitoides* and *Omphalocyclus* may have lived in shallower water than *Lepidorbitoides* and *Clypeorbis*, with overlapping depth ranges. This seems to be corroborated by the morphological differences between *Orbitoides* and *Lepidorbitoides*. One of the most prominent differences is the thickness of the chamber walls. The relative thickness of the chamber walls in *Orbitoides* may point to a shallower habitat than that of *Lepidorbitoides* because (a) it offers a better protection against the higher turbulence, (b) thicker tests are formed more easily in shallower waters (higher temperature, lower CaCO₃ saturation level) and (c) when chamber walls are thin more light can penetrate into the interior parts of the test, so *Lepidorbitoides* may require a smaller amount of illumination than *Orbitoides* and could survive in deeper water. This may also be reflected by the geographic distribution of *Orbitoides* and *Lepidorbitoides*. At the Boreal localities, *Orbitoides* is absent (Ilten, Vlodrop, Sweden) or relatively rare (Limburg). However, the available data are not conclusive.

In the Spanish Pyrenees, van de Velde (1967) found tests of *Orbitoides* and *Lepidorbitoides* arranged in vertical tubes. He suggested that these foraminifera must have been attached to some type of seaweed. However, the tubes were probably formed by some animal living in the sediment and using the orbitoidal tests only as building stones to fortify the part of its dwelling tube protruding above the sediment. A more detailed description and discussion will be given in a separate paper.

Chapter VI

ON THE TAXONOMIC POSITION

VI.1. ORIGIN

Since the most primitive representatives of the *Helicorbitoides-Lepidorbitoides* lineage, *Helicorbitoides voighti*, are known, a complete transitional sequence from the rotaliid *Pseudosiderolites vidali* to the most advanced *Lepidorbitoides* species has been established; a derivation of the lineage from *P. vidali* can hardly be doubted any more (van Gorsel 1973c). In a natural classification, the Lepidorbitoididae should therefore be placed close to *Pseudosiderolites*, in the superfamily Rotaliacea.

VI.2. WALL-STRUCTURE

Although Drooger (1960) tentatively considered *Lepidorbitoides* to be a rotaliid foraminifer, even in the most recent classifications it is not classified in the Rotaliacea, but always close to *Orbitoides*, either in the same family (Cole in Loeblich and Tappan, 1964, Neumann 1972b) or in the same superfamily (Reiss 1963). In the mentioned papers *Lepidorbitoides* is supposed to have a bilamellid wall structure; this is prohibitive in considering this genus being derived from a rotaliid foraminifer. In order to solve this apparent discrepancy, it has been investigated whether the different types of wall structure as recognized in spirally arranged lamellar foraminifera (monolamellid, bilamellid, rotaliid) can be distinguished in the equatorial chambers of the orbitoidal foraminifera as well.

Hyaline calcareous foraminifera are known to have lamellar tests. With the formation of each new chamber the whole test is covered by a lamella and the chamber lumen is a space between two consecutive lamellae. As a result of this layering, the ontogenetically latest chambers have the thinnest walls. Three fundamentally different types of layering were distinguished in spirally arranged lamellar foraminifera (see Smout 1954, Reiss 1958, 1963), which types differ in the nature of the chamber septa (see also Fig. 14):

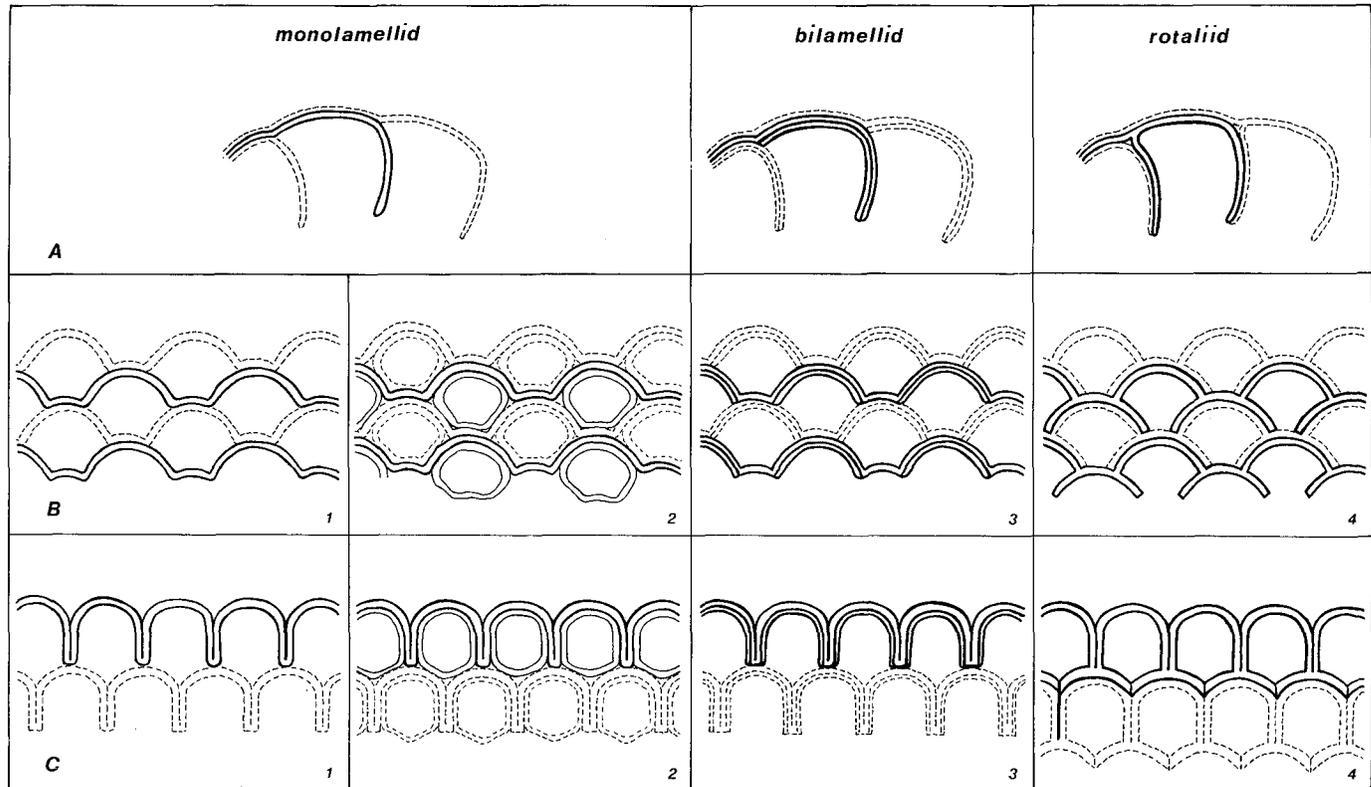


Fig. 14 A: different types of layering as distinguished in spirally arranged lamellar foraminifera;

B: same types of layering, transformed to the equatorial chambers of orbitoidal foraminifera.

Fig. B-2 is monolamellid with secondary inner lining (corresponds with figs. 41–43 of Smout, 1954);

C: same types of layering at advanced stage of crowding of the equatorial chambers.

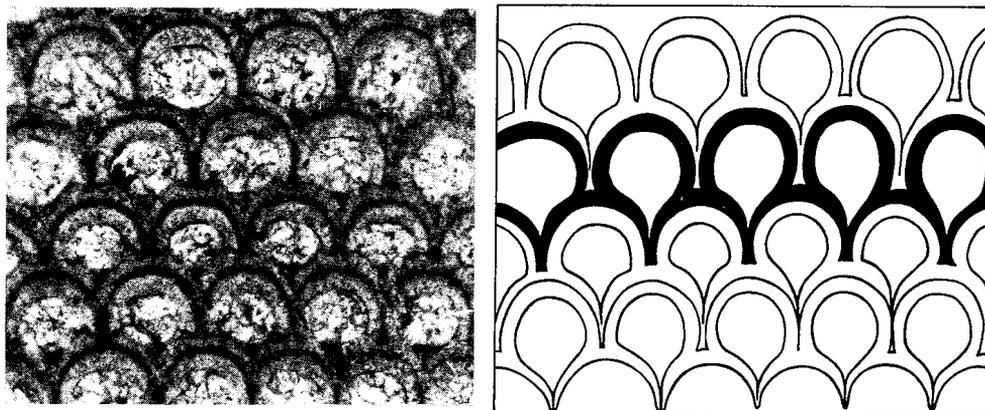


Fig. 15 Spatulate equatorial chambers of *Lepidorbitoides socialis* (St. Marcet 122–3) and interpretation of the layering of these chambers; the blackened part is supposed to be one lamella with its septal flaps.

monolamellid (fig. 14A1): the chamber septa consist of a single lamina;

bilamellid (fig. 14A2): chamber walls are primarily double;

rotaliid (fig. 14A3): septa are primarily single, but simultaneously with the formation of a new chamber the face of the previous chamber is covered with a septal flap, thus giving rise to secondarily doubled septa.

As has been explained by Smout (1954), the cyclical growth of the equatorial chambers of the orbitoidal foraminifera is not fundamentally different from the spiral growth of lamellar foraminifera. Instead of one chamber being formed between two consecutive lamellae, periodic arching, as it were, of these lamellae leads to the formation of many spaces between two successive lamellae. Elaborating this idea, the different spiral types of layering can be transformed into corresponding cyclical types. The result will be as in Figures 14B-C.

Comparing these models with our specimens, it may be concluded that the layering of *Lepidorbitoides* agrees well with the pattern of the rotaliid type (walls secondarily doubled, see Fig. 15) and not with the bilamellid type (walls primarily double), because:

- the inner layer of a chamber is often in direct line with the outer layer of the previous chambers;
- in advanced stages of crowding of equatorial chambers, the common wall between two adjacent chambers is always double. If the chamber walls would be primarily double (bilamellid), four laminae could be expected in this situation.

It may be concluded that the wall structure of *Lepidorbitoides* supports a

rotaliid derivation of the *Helicorbitoides-Lepidorbitoides* lineage. Examination of the layering of the equatorial chambers in other orbitoidal taxa of unknown origin may give valuable information on the taxonomic position of the ancestor.

It should be noted that the layering can only be studied in well-preserved, non-recrystallized specimens, preferably in sections in which the stolons are missed as these are interrupting the continuity of the individual lamellae.

VI.3. RELATION TO ORBITOIDES

In most classifications *Orbitoides* and *Lepidorbitoides* are supposed to be closely related genera, but it has been doubted whether they are derived from the same group. There seems to be little disagreement that they differ in the following features (see also MacGillavry 1955, p. 31):

– embryo: two-chambered in *Lepidorbitoides*, two-, three-, four- or multi-chambered in *Orbitoides*;

– equatorial chambers: in *Orbitoides* arcuate with basal apertures, in *Lepidorbitoides* varying from arcuate (with basal apertures) to spatulate (with diagonal and annular stolons);

– lateral chambers: as seen in vertical section, the lateral chambers of *Lepidorbitoides* are regular chambers with relatively thin walls, in *Orbitoides* these chambers resemble low, irregular cavities between thick calcareous lamellae (see also Hofker, 1963), on one side often different from those on the other side of the equatorial layer;

– ornamentation: in *Lepidorbitoides* isolated rounded pillars, in *Orbitoides* joint pillars, forming radially arranged ridges.

Differences of more fundamental nature such as ancestry and wall structure are still disputed and will therefore be discussed more extensively below:

– microspheric generation and ancestry: contrarily to that of *Lepidorbitoides*, which is derived from *Pseudosiderolites vidali*, there is no agreement yet on the origin of *Orbitoides*. Valuable information may be obtained from the initial stage of the microspheric generation, which in larger foraminifera shows primitive characters. Several authors have argued in favour of a stage of alternate growth (also called biserial; not to be confused with the term biserial nepiont used above), which may be preceded by or alternate irregularly with spiral growth, and a derivation from the Heterohelicidae has been suggested (Küpper 1954, MacGillavry 1955, 1963, Reiss 1963, van Hinte 1965, 1968). Others deny the presence of an alternate stage in microspheric

Orbitoides (Hofker 1963) or consider this as an aberrant development of a spiral arrangement, due to environmental circumstances (Neumann 1972a). Hofker Jr. (1967) figured a section of a microspheric specimen with a biserial stage, preceded by a number of spirally arranged chambers. He doubts it being derived from the Heterohelicidae; the wall structure of *Orbitoides* would be more similar to that of the Cibicididae.

It seems rather difficult to maintain the assumption that alternate growth in microspheric *Orbitoides* is an abnormality, as it is undoubtedly present in the greater part of the microspheric specimens. Whether the ancestor of *Orbitoides* is a heterohelid (Küpper, MacGillavry, Reiss, van Hinte) or some aberrant *Cibicides* (Hofker, Hofker Jr., Neumann), there is hardly any doubt that it has to be looked for among forms with a mixed spiral and alternate pattern of growth. The ancestor of *Lepidorbitoides* shows a simple spiral arrangement and in microspheric *Lepidorbitoides* a sign of alternate growth has never been observed. It may be concluded that *Orbitoides* and *Lepidorbitoides* have derived from different ancestors, and that they are not closely related.

– wall structure: the equatorial chambers of *Lepidorbitoides* show double walls, and *Lepidorbitoides* was supposed to have a bilamellid wall structure (Reiss, 1963). In a previous chapter it was explained that these walls are not primarily double, but secondarily doubled by the subsequent lamella and its septal flaps; therefore the wall structure should be described as rotaliid. This is in agreement with the derivation of the genus from *Pseudosiderolites*.

An analysis of the layering of *Orbitoides* has been given by van Hinte (1968). We agree with Reiss (1963) and van Hinte that the wall structure of *Orbitoides* is bilamellid (primarily double). The chamber walls consist of a hyaline outer layer and a thinner, dark inner lining. Generally a supplementary hyaline layer is formed at the inner side of the chamber, but this is not consistently present. Thus, if our analysis of the wall structures is correct, this is another argument against the supposed relationship between *Orbitoides* and *Lepidorbitoides*.

– “black line”: one of the main arguments of Neumann (1972b) for classifying *Orbitoides*, *Lepidorbitoides*, *Lepidocyclina* and *Discocyclina* in one family is the presence of a “black line” in the chamber walls of these genera. We disagree with her statement that this black line is basically the same in all these genera. In *Orbitoides*, the dark line is a thin calcareous layer (microgranular after Hofker Jr., 1967). The walls subdividing the embryo usually consist of this layer only, and in the other equatorial chambers (and also in the lateral chambers) it forms the inner lining of the bilamellid wall. It may be considered as the calcified primary chitinous membrane. Neumann (op.

cit.) stated rightly that in *Lepidorbitoides* the black line is mostly hard to see and is invariably covered at both sides by a calcareous lamella. This agrees with our interpretation of the wall structure: the dark line in the equatorial chambers of *Lepidorbitoides* is not a section through a substantial layer, but is the parting line between the successive hyaline lamellae. So this dark line is not similar in *Orbitoides* and *Lepidorbitoides*, but fundamentally different.

VI.4. CLASSIFICATION

Several arguments have been presented to show that *Orbitoides* and *Lepidorbitoides* have the orbitoidal morphology in common but differ in all other respects, and that they are phylogenetically unrelated. The classification of Neumann (1972b), in which *Orbitoides*, *Lepidorbitoides*, *Lepidocyclina* and *Discocyclina* are united in one family, must therefore be rejected. In a natural classification in which phylogenetic relations are taken into consideration, these orbitoidal homoeomorphs should be placed close to the ancestral forms. A classification of these unrelated groups into one taxon is just as artificial as a classification with all planispirally coiled forms placed in one taxonomic unit.

The *Helicorbitoides-Lepidorbitoides* lineage may be classified in a separate family Lepidorbitoididae, which should be placed in the superfamily Rotaliidea. The only genus which may be considered phylogenetically related is *Arnaudiella* (see van Gorsel 1974). It is questionable whether *Clypeorbis* and *Hellenocyclina* are to be placed in the Lepidorbitoididae also.

Chapter VII

AGE

For a long time the presence of *Lepidorbitoides* and *Orbitoides* has been used to assign a Maastrichtian age to the sediment in which they were found. Papp and Küpper (op. div.) proved that the early members of these genera already appeared in the Campanian.

The presence of *Belemnitella mucronata mucronata* (Link) and *Belemnitella mucronata senior* Nowak at the type locality of *Helicorbitoides voighti* suggests that the *Helicorbitoides-Lepidorbitoides* lineage arose in the early part of the Late Campanian of the Boreal stratigraphic subdivision.

Lepidorbitoides is found in parts of the stratotypes of the Campanian and the Maastrichtian. There is no agreement on the exact position of the type Campanian; for a discussion see van Gorsel (1973a). *Lepidorbitoides campaniensis* is present in the section of Aubeterre (SW France), which may be considered as the (upper) type Campanian. In the upper half of the Maastrichtian type section at the ENCI quarry, *Lepidorbitoides minor* is found.

Between the Campanian and Maastrichtian stratotypes, there is a time gap. *Lepidorbitoides bisambergensis* must have lived in this gap, and the boundary between the two must be drawn somewhere in this gap. The most frequently used boundary in the Boreal Cretaceous area has originally been defined (biostratigraphically) by the first appearance of *Belemnella lanceolata* and *Discoscaphites constrictus* (Seitz 1952). The top of the *Globotruncana calcarata* Zone (planktonic foraminifera) is thought to coincide with the boundary. It may then be asked where this boundary is to be drawn in the evolutionary series of *Helicorbitoides* and *Lepidorbitoides*. Papp (1955), after studying associated smaller foraminifera as *Bolivina*, *Bolivinoidea*, *Neoflabellina* and *Globotruncana* (not *calcarata*), concluded that the Campanian-Maastrichtian boundary should be drawn above the *Lepidorbitoides bisambergensis* Zone. However, this does not fit very well with the supposed position of the stratotypes. The section of Aubeterre (with *L. campaniensis*) is considered to represent the uppermost Campanian, the Maastrichtian type section (the middle part with very primitive *Lepidorbitoides minor*) part of

the Upper Maastrichtian. An Early Maastrichtian age for at least part of the *Lepidorbitoides bisambergensis* Zone will therefore be more compatible with these ideas, and several indications are in support of them. Our sample with *Lepidorbitoides bisambergensis* from the pass between Orcau and Montesquiu, N Spain, is from a level above the *Globotruncana calcarata* Zone (the latter occurs in marls near Montesquiu, see Garrido Megias and Rios Aragues, 1972). The samples with *L. bisambergensis* from Pemberger, Austria, are also from above the range of *G. calcarata*. According to Dr. van Hinte (pers. comm.), even his sample P88-5 with biserial *Lepidorbitoides campaniensis* would be from above the *calcarata* Zone, which suggests that the top of the

supposed span of stratotypes	stages	phylozones
Maastricht Tuff Chalk 	MAASTRICHTIAN	<i>L. socialis</i>
		<i>L. minor</i>
Aubeterre profile 	Lower	<i>L. bisambergensis</i>
	Upper	<i>L. campaniensis</i>
		<i>L. pembergeri</i>
		<i>H. longispiralis</i>
		<i>H. voighti</i>
		(<i>Pseudosiderolites vidali</i>)

Fig. 16 Tentative correlation of *Helicorbitoides-Lepidorbitoides* zones with geological time scale. The vertical scale is not considered proportional to the relative duration of the time intervals.

calcarata Zone (agreeing with the Campanian-Maastrichtian boundary) must be somewhere in the upper part of the *Lepidorbitoides campaniensis* Zone. Unfortunately, the *Lepidorbitoides* specimens from Orcau and Pemberger are from turbidites, and they may be different in age from the planktonic foraminifera. However, in view of the distinct evolution shown by *Lepidorbitoides* in the strata near Pemberger and the absence of any indications of mixing of populations of larger foraminifera, such a difference in age, if any, is probably not large in that area. Additional investigations, preferably also in other areas, are desired.

Summarizing, it is concluded that *Helicorbitoides*, *Lepidorbitoides pembergeri* and *L. campaniensis* may be indicative of a Late Campanian age, *L. bisambergensis* of an Early Maastrichtian and *L. minor* and *L. socialis* of a Late Maastrichtian age (see also Fig. 16).

Chapter VII

SYSTEMATICAL PART

FAMILY LEPIDORBITOIDIDAE

Genus *Helicorbitoides* MacGillavry 1963

(type species *Pseudorbitoides longispiralis* Papp and Küpper 1953)

Description: rotund lenticular test. The equatorial layer consists of spirally arranged chambers, between the whorls of which smaller secondary chambers are formed, an arrangement similar to that of the Eocene *Helicolepidina*. A structure of radial calcareous elements and spaces is formed at those places where, during growth of the animal, no chamber addition takes place for some time (at the periphery of the test and between the peripheral secondary chambers of one whorl and the primary chambers of the next). Lateral chambers are present, but in the early representatives these are only weakly developed. There is no distinct roof and floor between the equatorial and lateral layers. The thickness of the equatorial layer may fluctuate considerably, especially in the more primitive specimens, due to the difference in size between the primary and the secondary equatorial chambers. No microspheric specimens are known.

Remarks: *Helicorbitoides* is an intermediate form between *Pseudosiderolites* and *Lepidorbitoides* and might also be considered as a subgenus of the latter. It differs from primitive Pseudorbitoididae by its helicolepidine arrangement and by the absence of sulcoperculinoid features; from *Arnaudiella* by the presence of secondary equatorial chambers and from *Helicolepidina* by its radial canal structure and the different stratigraphic distribution (Campanian vs. Eocene).

Helicorbitoides voighti van Gorsel 1973

(Text fig. 2a, Plate I)

Helicorbitoides voighti van Gorsel, 1973, p. 276–280, Pl. I, figs. 2–4, Pl. II, Pl. III, figs. 2–6.

Type locality: Malen quarry near Båstad, S Sweden.

Age: early Late Campanian.

Plate I *Helicorbitoides voighti* van Gorsel, Båstad, Sweden (type locality).

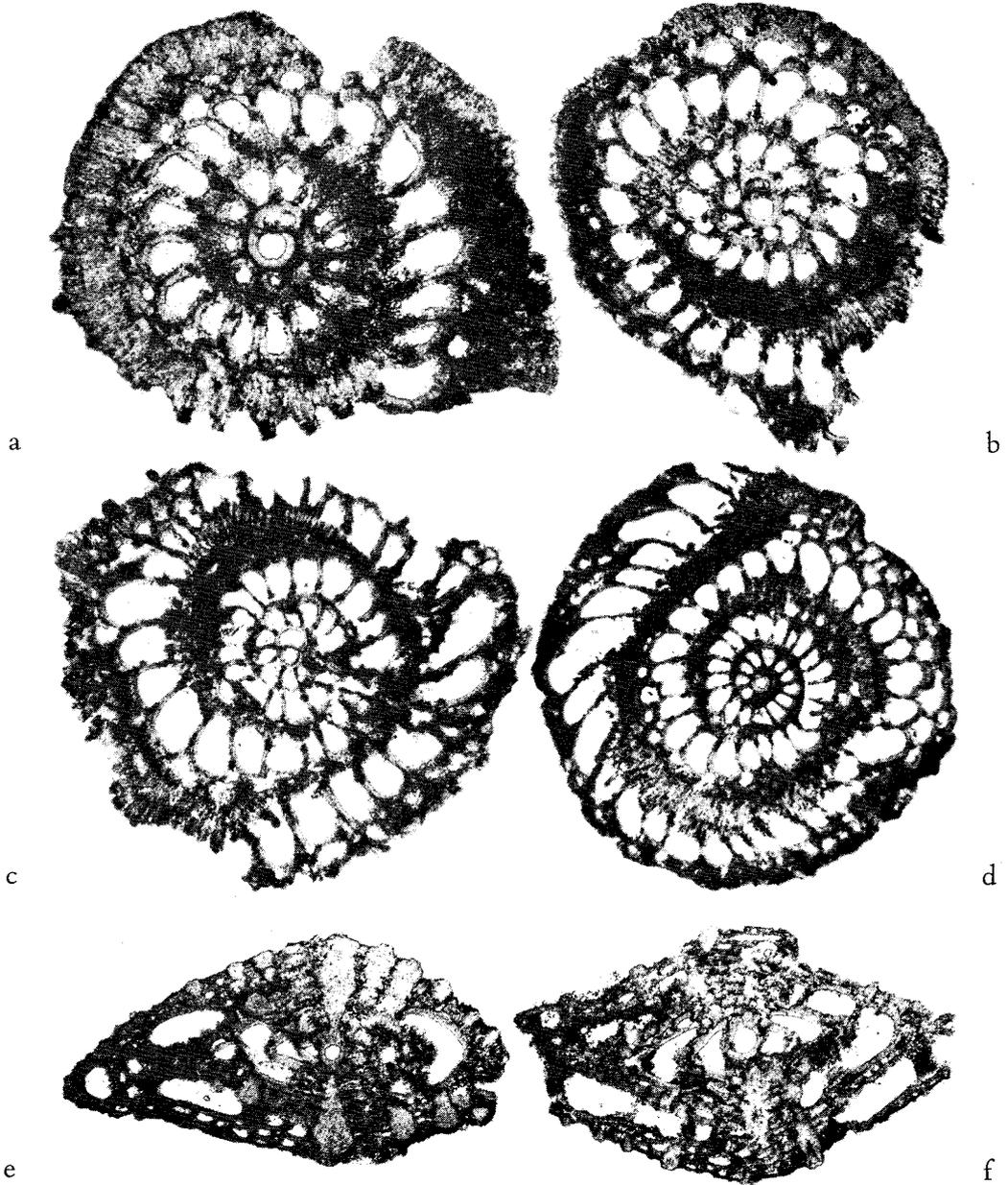


Plate 1 a Båstad 99, 60 X; b Båstad 108, 40 X; c Båstad 111, 40 X and d Båstad 85, 25 X: Horizontal sections. Note small secondary chambers and structure of radial elements between the whorls of the primary spiral. e Båstad-vert. 10, 30 X and f Båstad-vert. 11, 30 X: Vertical sections, showing semi-involute whorls of primary spiral, lateral chambers, pillars and in fig. f slightly trochoid initial stage.

pustules, diminishing in size towards the periphery.

The diameter of the protoconch varies between 55 and 110 microns, with an average of about 75 microns. The second chamber is usually slightly larger, with an average of about 80 microns. Only a few arcuate secondary equatorial chambers are formed between the 3 to 4 whorls of primary chambers, the first ones only after the 7th to 23d primary chamber has been formed (average 14). In vertical sections the large primary chambers are seen to be semi-involute. Lateral chambers are only weakly developed.

Geographic distribution: only known from Båstad, southern Sweden.

Helicorbitoides longispiralis (Papp and Küpper) 1953
(Text fig. 2b-c, Plate II-III)

Pseudorbitoides longispiralis Papp and Küpper, 1953c, p. 352–354, Pl. 2, fig. 3; Hottinger, 1967, p. 70–71.

Helicorbitoides longispiralis (Papp and Küpper), MacGillavry, 1963, p. 160–161, Pl. V, figs. 1–2, Pl. VI, fig. 1; van Gorsel, 1973c, p. 280–283, Text fig. 2, Pl. 1, figs. 5–6, Pl. 4, figs. 1–4.

Type locality: abandoned quarry NNW of Silbereg, Carinthia, Austria.

Age: Late Campanian.

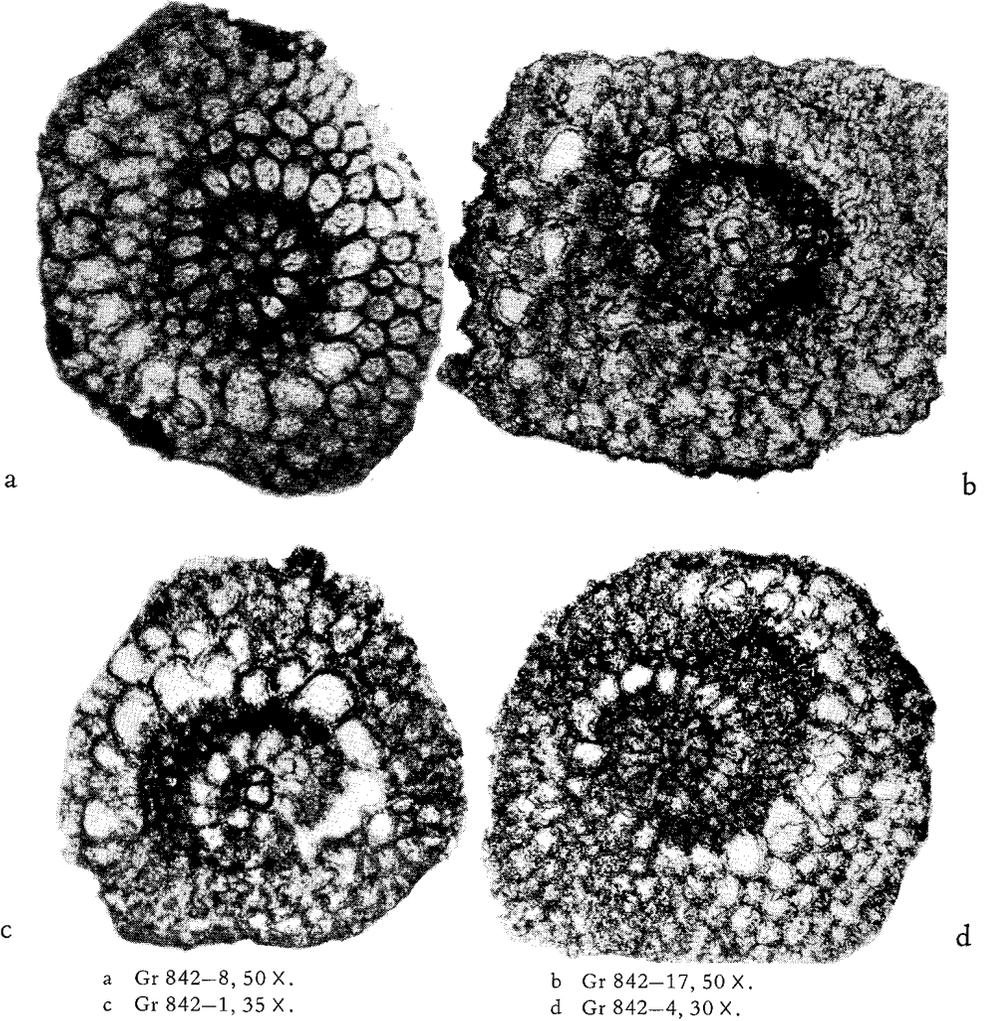
Description: rather thick lenticular test, diameter usually less than 3 mm, average diameter/thickness ratio about 2.5. The internal spiral arrangement is not visible externally.

At the type locality, the average diameter of the protoconch is 80 microns, the deuteroconch is slightly larger. These two chambers are followed by 2 to 3½ whorls of spirally arranged primary chambers, between the whorls of which open arcuate secondary chambers are formed. The first secondary chamber originates from the 4th to the 9th chamber. A radial structure is often present but usually weakly developed. The primary spiral usually continues up to the periphery, but in some advanced specimens the chambers in the continuation of the primary spiral cannot be distinguished from the adjacent open arcuate equatorial chambers. The equatorial layer is more regular in thickness than in *Helicorbitoides voighti*, but still one or more abnormally large chambers can often be seen in a vertical section of the equatorial layer; these chambers belong to the primary spiral.

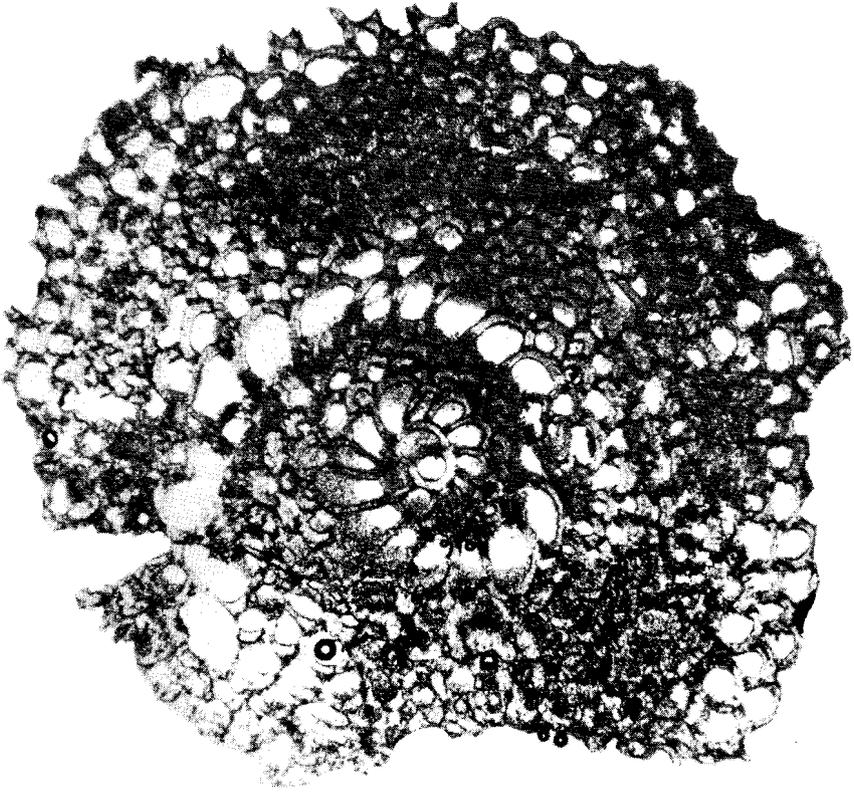
Remarks: *Helicorbitoides longispiralis* is a more advanced form than *H. voighti*, from which it differs by the earlier appearance and the larger number of retrovert chambers between the consecutive whorls of the primary spiral. All populations with an average of 4 to 7 chambers without a retrovert aperture may be assigned to this species.

Geographic distribution: Austria, Switzerland, southern Sweden.

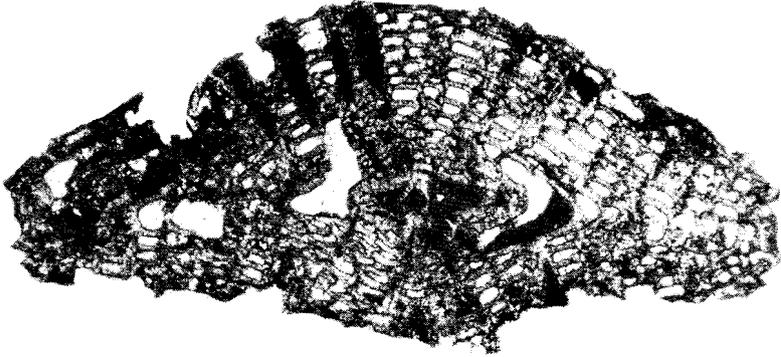
Plate II *Helicorbitoides longispiralis* (Papp and Küpper), Silbereg, Austria
(type locality).



Description: small rotund lenticular test, usually with flattened border. At the type locality the maximum diameter is 2.2 mm, thickness up to 1.1 mm, average diameter/thickness ratio is 2.0. Radial elements may be protruding at the periphery and may consist of simple radially arranged (pseudorbitoid) vertical plates or of a more complex and irregular, historbitoid radial structure. The ontogenetically latest, semi-involute primary spiral chambers can be observed at the exterior of the test. The test is ornamented with rounded



a



b

- a Stafversvad 5, 50 X. Horizontal section, primary spiral not up to periphery.
b Stafversvad 6, 35 X. Vertical section. Note large, semi-involute primary chambers.

Genus *Lepidorbitoides* Silvestri 1907
(type species *Orbitolites socialis* Leymerie 1851)

Description: flat, often slightly asymmetric lenticular orbitoidal test with well-differentiated equatorial and lateral layers, diameter usually below 10 mm; rarely some giants up to 25 mm may be found. The test is ornamented with rounded pustules, which are the continuations of textural-inflational pillars, traversing the lateral chambers. The number and dimensions of these pustules are variable and different types of distribution of the pustules over the test have been observed.

The embryo invariably consists of two chambers, a (sub)spherical protoconch and a larger reniform deutoconch. The other equatorial chambers vary from open arcuate to spatulate in shape. In the open arcuate chambers only basal stolons occur, whereas the spatulate chambers communicate with each other by diagonal and annular stolons.

In vertical sections the lateral chambers form a regular pattern of low, flattened arcuate chambers; in off-centre horizontal sections these chambers are very irregular in shape. The walls of the lateral chambers and the walls between the equatorial and lateral chambers are traversed by numerous coarse pores (diameter about 3 microns), except for the upright parts (in vertical section) of the lateral chamber walls, which are imperforate and mostly thickened.

The microspheric generation is very rare and can only be distinguished by the different arrangement and smaller size of the initial chambers.

Lepidorbitoides pembergeri Papp 1954
(Text fig. 2d-e, Plate IV)

Lepidorbitoides minima pembergeri Papp, 1954a, p. 163–164, Pl. I, figs. 3–4.

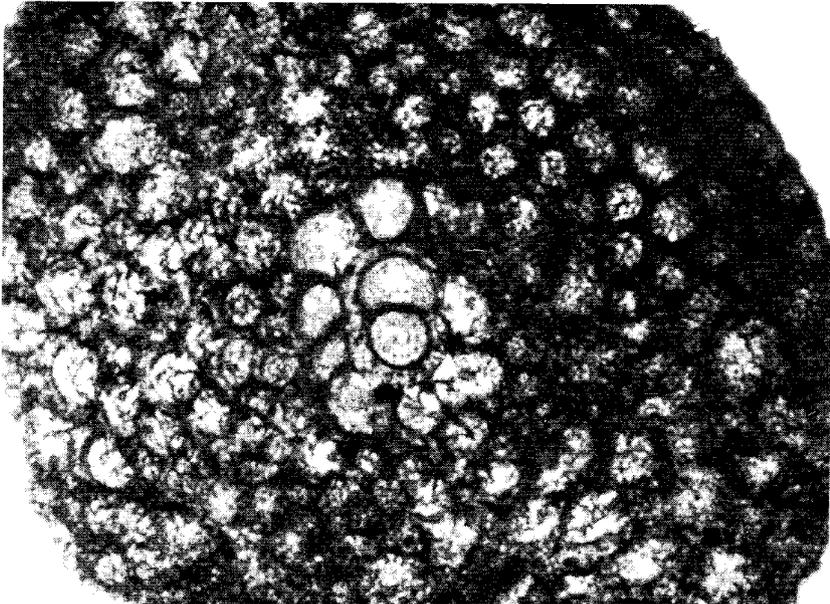
Pseudorbitoides cf. *trechmanni* Papp, 1954a, p. 163, Pl. I, fig. 2. (not *Pseudorbitoides trechmanni* Douvillé 1922)

Type locality: quarry at Pembergerriegel, Carinthia, Austria.

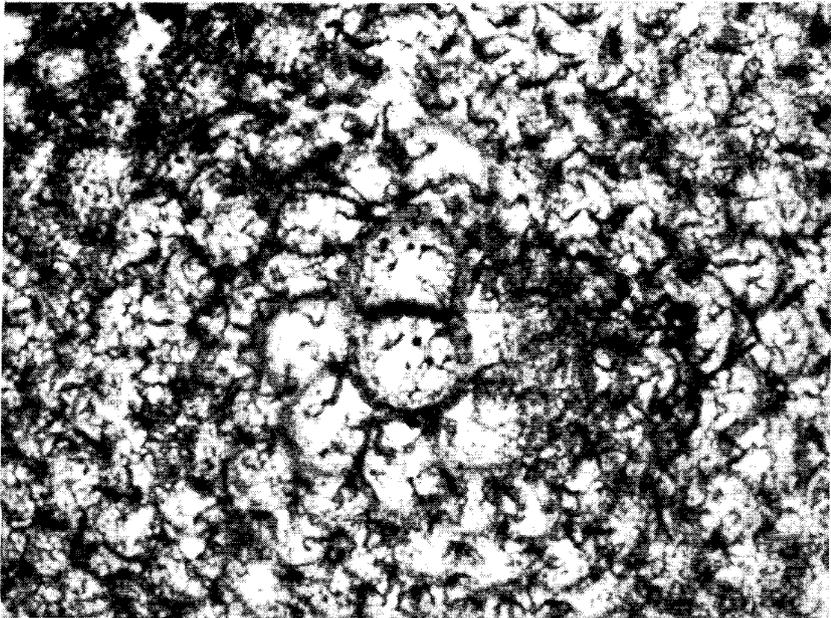
Age: Late Campanian.

Description: this *Lepidorbitoides* species is characterized by a rather primitive reduced uniserial or biserial arrangement. The primary spiral is considerably longer than the retrovert one and usually continues as an unrolled primary spiral for a few chambers beyond the last point of contact with the deutoconch, in the helicolepidine manner. The diameter of the protoconch varies between 55 and 100 microns, average 78, the deutoconch is usually slightly larger with an average diameter of 90 microns. The equatorial chambers are almost invariably open arcuate.

Plate IV *Lepidorbitoides pembergeri* Papp, Pembergerriegel, Austria (type locality).



a



b

- a Gr851-23, 110 X. Reduced uniserial arrangement with short unrolling primary spiral.
- b Gr851-22, 140 X. Biserial arrangement with short unrolling primary spiral.

Remarks: in the sample from the supposed type locality (see Chapt. II), the ratio between reduced uniserial ($Y = 3$) and biserial ($Y = 2$) specimens is 5:14. It is proposed to assign to this species all populations in which specimens are predominant with a reduced uniserial and/or biserial arrangement with a short helicolepidine primary spiral.

Geographic distribution: up to now this species has only been found in Austria. Populations transitional to *Lepidorbitoides campaniensis* have been found in the department of Dordogne, SW France (van Gorsel 1973b).

Lepidorbitoides campaniensis van Gorsel 1973

(Text fig. 2f-h, Plate V-VI)

Lepidorbitoides minima minima Douvillé, Papp, 1954a, p. 164–166, Pl. I, figs. 5–6. (not *Lepidorbitoides minima* Douvillé 1927)

Lepidorbitoides socialis Hofker, 1959, p. 138, figs. 196–197. (not *Orbitolites socialis* Leymerie 1851)
Lepidorbitoides minima minima Douvillé, Goharian, 1971, Pl. 2, figs. 7–11; Neumann 1972b, p. 168, Pl. 2, figs. 3, 6, 7.

Lepidorbitoides campaniensis van Gorsel, 1973b, p. 263–267, Pl. I-IV.

Type locality: Aubeterre, department of Charente, SW France.

Age: latest Campanian, possibly also earliest Maastrichtian.

Description: this species is distinguished by its biserial peri-embryonic arrangement, usually without a helicolepidine unrolling of the primary spiral. In the early representatives the number of chambers in the primary spiral is larger than in the retrovert one, in more advanced specimens these numbers tend to be equal. The diameter of the protoconch varies between 60 and 150 microns in our specimens, the average is almost 100 microns. The deuteroconch is somewhat larger, average diameter about 125 microns. The diameter of the test may reach 5 mm, the thickness 1.5 mm, diameter/thickness ratio between 3 and 4.5. Equatorial chambers are open arcuate.

Geographic distribution: Austria, SW France, N Spain (Neumann 1972b).

Lepidorbitoides bisambergensis (Jaeger) 1914

(Text fig. 2i-j, Plate VII-IX)

Orbitoides (Lepidorbitoides) socialis Leymerie var. *bisambergensis* Jaeger, 1914, p. 160, Pl. IV, figs. 3–3a.

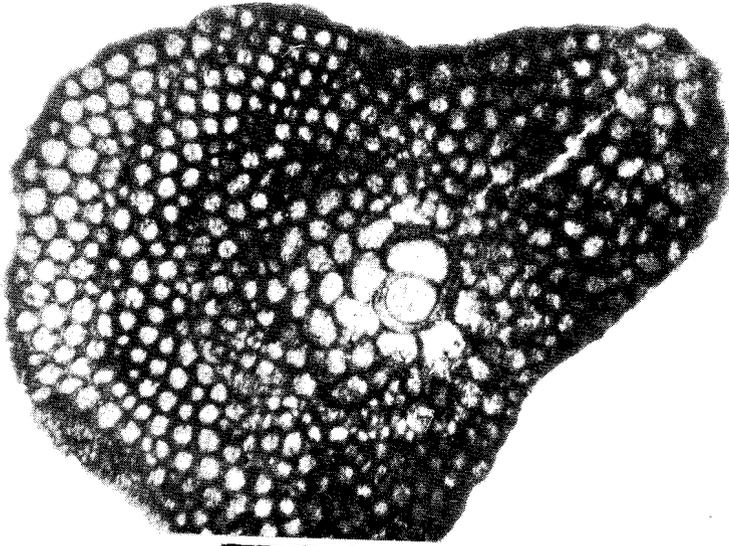
Lepidorbitoides bisambergensis (Jaeger) Papp and Küpper, 1953a, p. 77–78, Pl. 1, figs. 10–12, Pl. 3, figs. 3–4; Papp, 1956b, p. 135, Figs. 2–3, Trümper, 1970, Pl. II, fig. 3.

Type locality: north-western slope of the Bisamberg, north of Vienna, Austria.

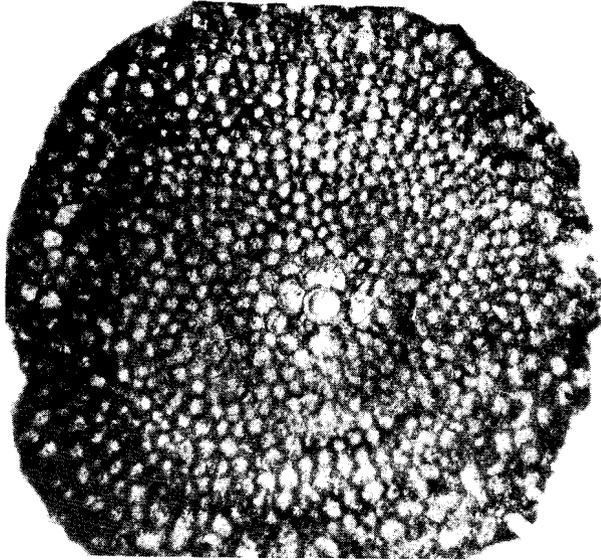
Age: Early Maastrichtian, possibly also early part of the Late Maastrichtian.

Description: this species is characterized by a quadriserial nepionic arrangement, without adauxiliary chambers. The nepiont of primitive specimens is

Plate V *Lepidorbitoides campaniensis* van Gorsel, Austria.



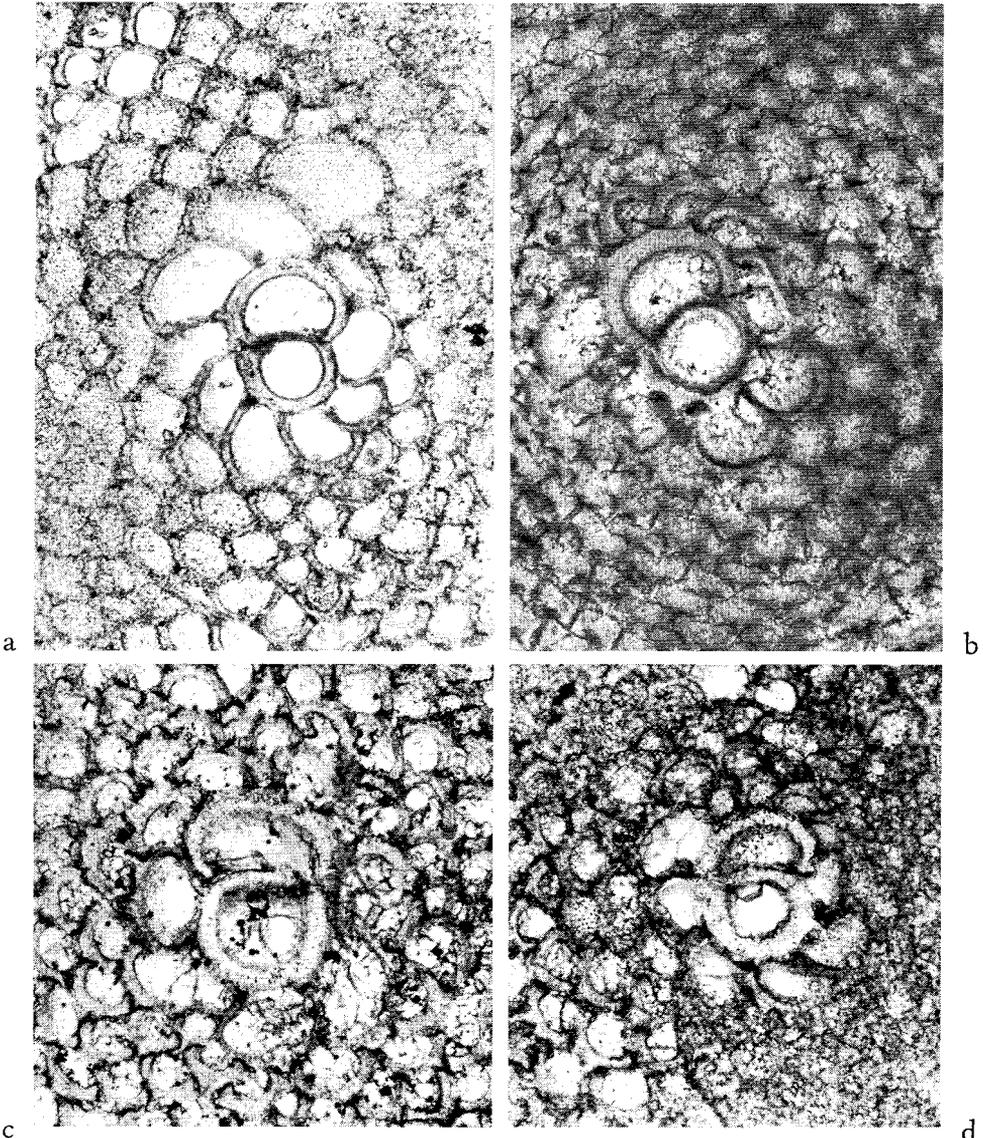
a



b

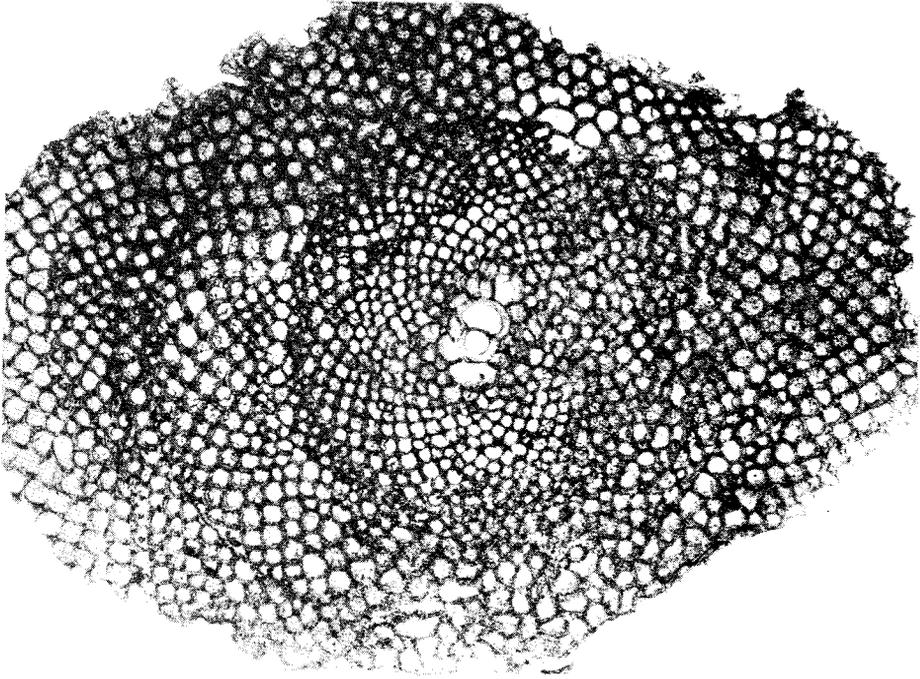
a Gr849-30, Pemberger, 50 X. Horizontal section.
b Gr849-42, Pemberger, 45 X. Horizontal section.

Plate VI *Lepidorbitoides campaniensis* van Gorsel.

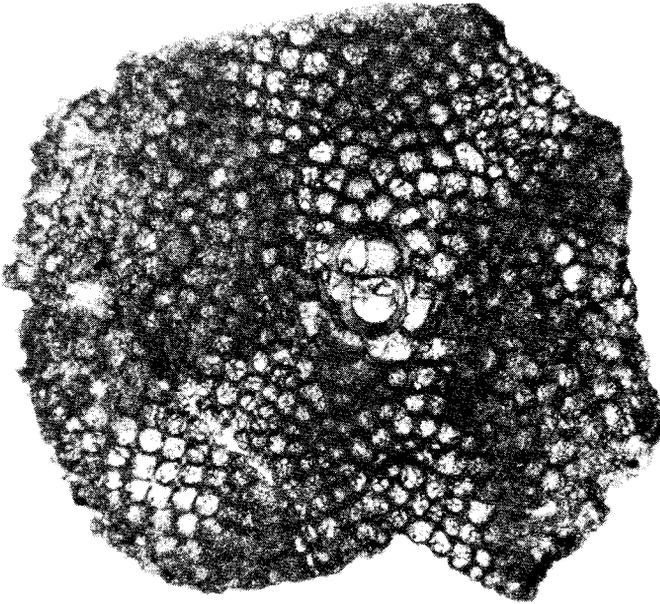


a Gr359-1, Issac, SW France, 105 X. Biserial with short helicorbitoid unrolling primary spiral. ps = 10, ds = 4.
b Gr139-12, Festalemps, SW France, 105 X. Biserial, ps = 9, ds = 7.
c Gr849-58, Pemberger, Austria, 110 X. Biserial, ps = 8, ds = 6.
d 017-15, Pemberger, Austria, 110 X. Biserial, ps = 7, ds = 7.

Plate VII *Lepidorbitoides bisambergensis* Jaeger, Austria.



a

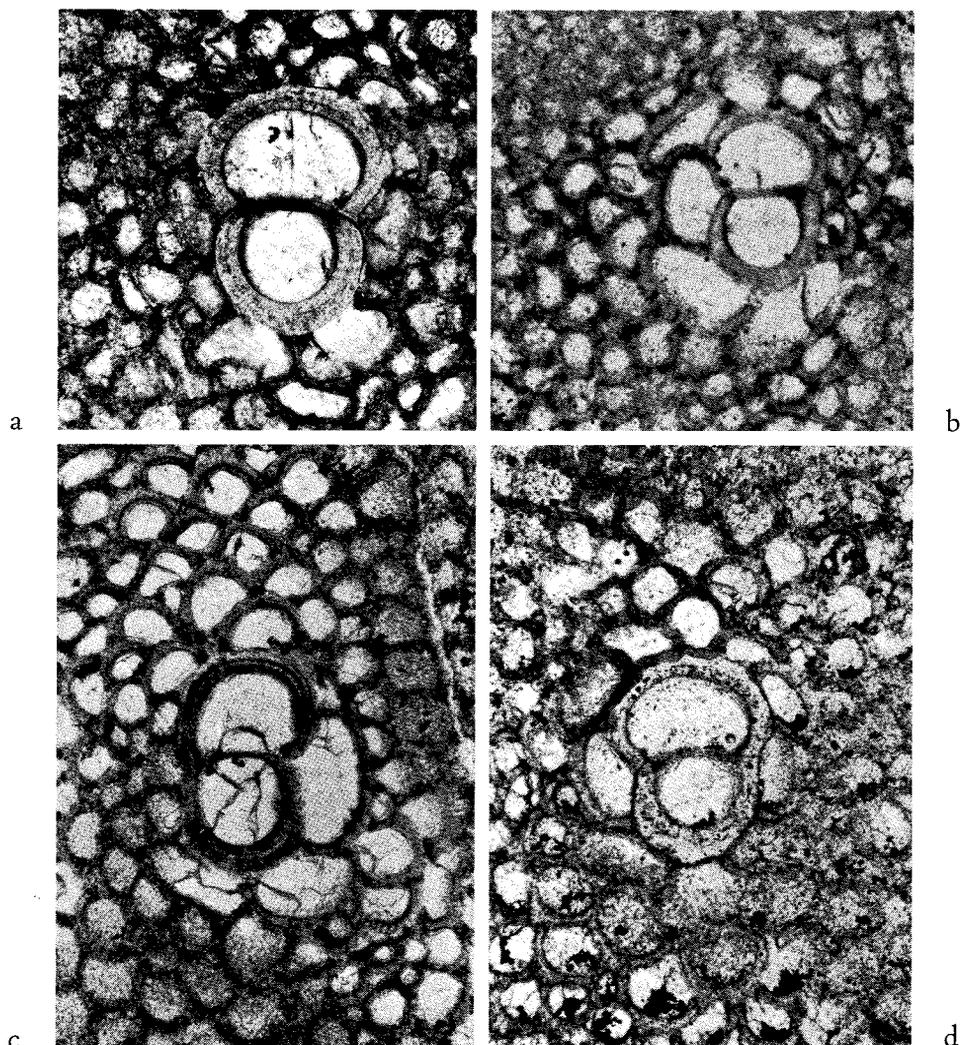


b

a Gr854-6, Bisamberg (type locality), 40 X. Horizontal section.

b X1961AG-9, Pemberger, 55 X. Horizontal section.

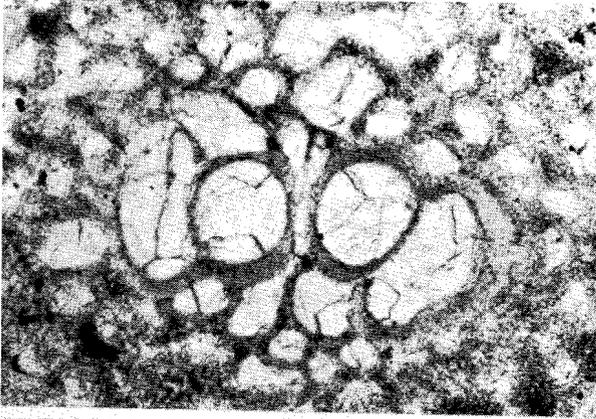
Plate VIII *Lepidorbitoides bisambergensis* Jaeger, Austria.



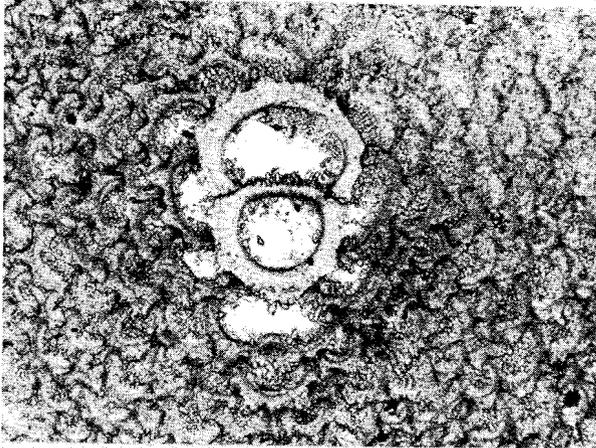
- a Gr 854--1, Bisamberg (type locality), 110 X. Nepionic arrangement \pm symmetric quadriserial.
b X 1961 AW-18, Pemberger, 90 X. Asymmetric quadriserial.
c X 1961 AW-12, Pemberger, 105 X. Asymmetric quadriserial.
d X 1961 AW-13, Pemberger, 105 X. Symmetric quadriserial.

asymmetric (asymmetric deutoconch and relatively small second principal auxiliary chamber, from which only few and small subsequent chambers are formed), in more advanced forms the nepionic is bilaterally symmetric. The internal diameter of the protoconch varies between 60 and 135 microns,

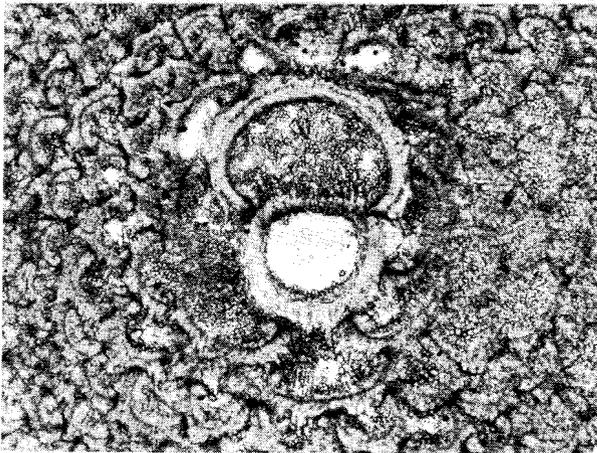
Plate IX *Lepidorbitoides bisambergensis* Jaeger.



a X1961AG-6, Pemberger,
Austria, 115 X.
Specimen with double
embryon.



b Vlodrop 42, Netherlands,
115 X.
Symmetric quadriserial.



c Vlodrop 44, 100 X.
Symmetric quadriserial.

sample averages between 90 and 110, that of the deuteroconch between 95 and 200 microns, sample averages between 130 and 155. Most equatorial chambers are arcuate, with ogival chambers appearing at the periphery of larger specimens.

Geographic distribution: Austria, Netherlands, E Germany, N Spain.

Lepidorbitoides minor (Schlumberger) 1901
(Text fig. 2k-l, Plate X-XII)

Orbitoides minor Schlumberger, 1901, p. 466, Pl. VIII, figs. 2, 3, 5, Pl. IX, figs. 2-3.

Lepidorbitoides socialis race *minor* Schlumberger, Douvillé, 1920, p. 224, fig. 27.

Lepidorbitoides minor (Schlumberger), Rutten, 1935, p. 186-187, figs. 1-4, 8, 9; Thiadens, 1937, p. 99-100, Pl. 16, fig. 4; Tan Sin Hok, 1939, p. 74, Pl. 1, figs. 4-5; Rutten, 1940, p. 263-267, figs. 2-5; Rutten, 1941, p. 48-49, Pl. 2, fig. 3; Schijfsma, 1946, p. 119-121, Pl. 9, figs. 7-12; Visser, 1951, p. 297, Pl. 9, fig. 3, Pl. 11, figs. 4, 6; Voigt, 1951, p. 29-33, Pl. 1, figs. 1-4, Pl. 2, fig. 1; Papp and Küpper, 1953b, p. 276, figs. 2a-b; MacGillavry, 1955, p. 11-43; Papp, 1956b, p. 137, Pl. 1, fig. 4; Neumann, 1958, p. 70-72, Text fig. 18, Pl. 8, figs. 1-7; Hofker, 1959a, figs. 198, 202, 212A; Hanzawa, 1962, p. 134, Pl. 1, figs. 3-7; Hiltermann and Koch, 1962, p. 338, Pl. 50, fig. 18; Hofker, 1963, p. 40-42, figs. 7-11; MacGillavry, 1963, Pl. VI, fig. 2; Voigt, 1963, p. 498-500, Pl. 37, figs. 1-2; Trümper, 1970, Pl. I, fig. 1, Pl. II, figs. 4-6, Pl. III-V; Neumann, 1972b, p. 169, Text fig. 3, Pl. 2, figs. 8-11, Pl. 3, fig. 4.

Orbitoides faujasi DeFrance, Hofker, 1949, p. 43-60, fig. 20 (pars).

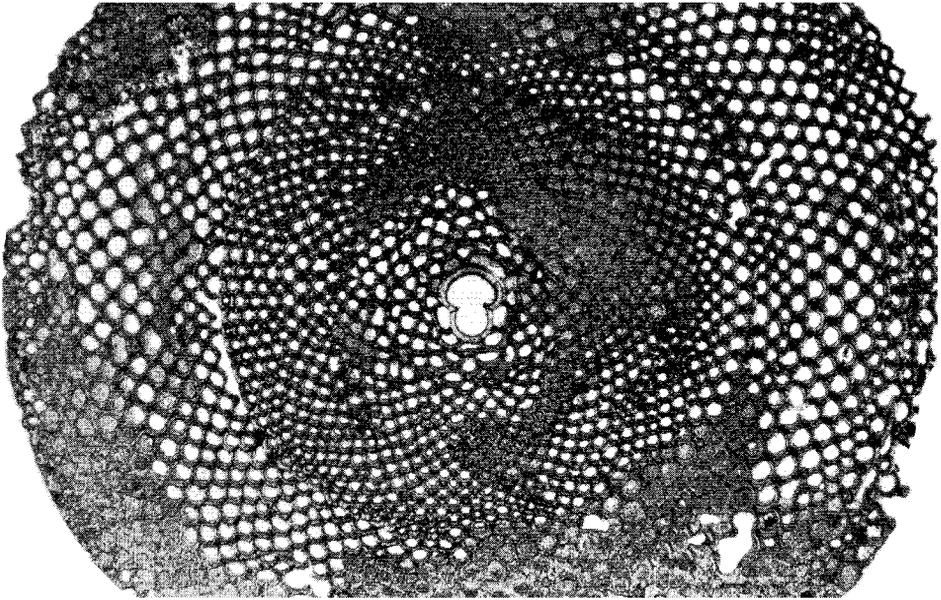
Lepidorbitoides socialis (Leymerie), Reiss, 1963, Pl. III, fig. 19. Not: *Lepidorbitoides minor* (Schlumberger), van Wessem, 1943, p. 53-54, Pl. 3, fig. 15.

Type locality: Maastricht, Netherlands (no exact locality mentioned in the type description).

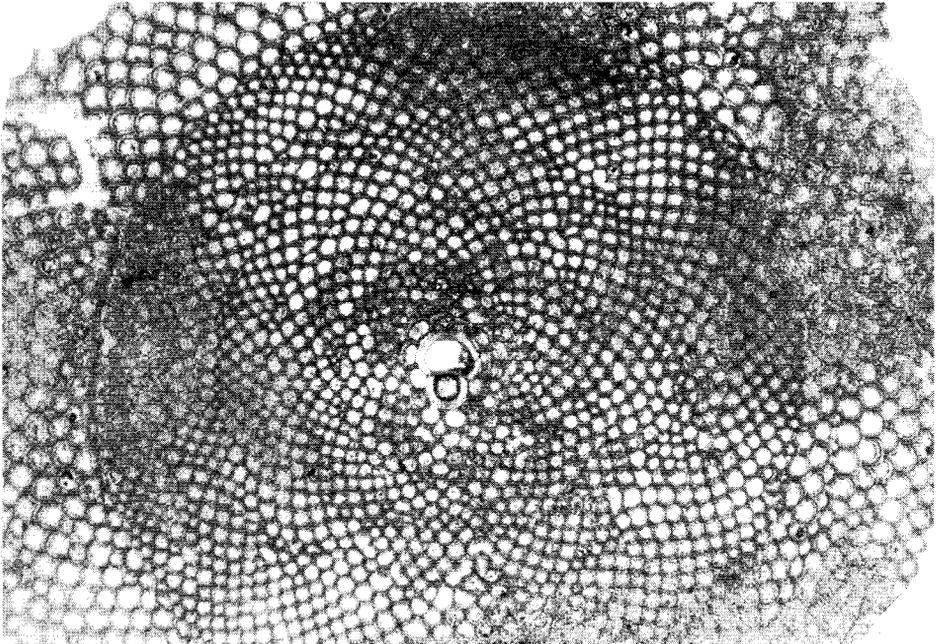
Age: Late Maastrichtian (Maastrichtian stratotype).

Description: this species can be distinguished by its quadriserial arrangement, and a small number of adauxiliary chambers. In samples from the vicinity of Maastricht, the average number of these chambers varies between 1 and 3. In the type region the diameter of the flat lenticular test is rarely more than 4 mm, the diameter/thickness ratio is usually between 4 and 5. Sample averages of the diameter of the protoconch vary between 90 and 115 microns, those of the deuteroconch between 150 and 185. The average D/P ratio varies between 1.5 and 1.8. The ontogenetically early equatorial chambers are arcuate in horizontal section, the outer half of the horizontal section is usually occupied by ogival and spatulate equatorial chambers.

Geographic distribution: Netherlands, Germany, Austria, Scandinavia? (see Voigt, 1963).



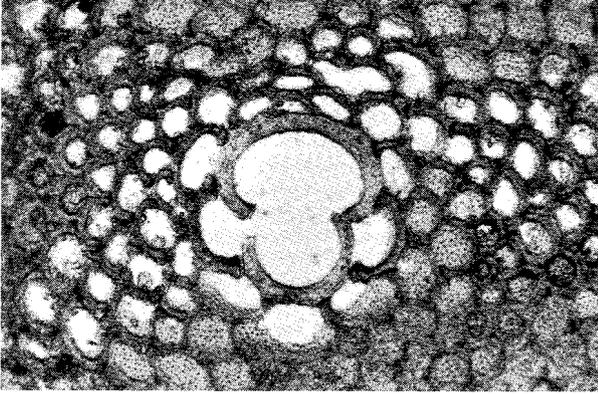
a



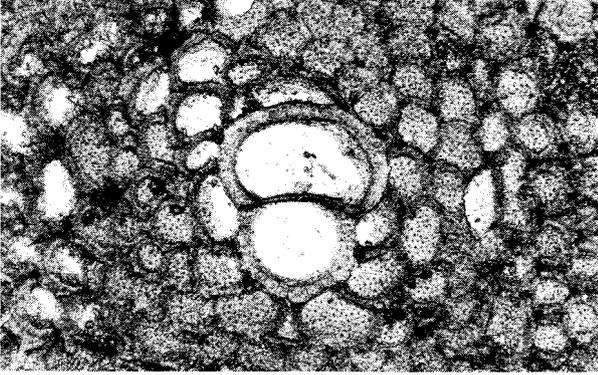
b

a ENCI 28.00-12, 40 X and
b Curfs 3, 40 X, horizontal sections.

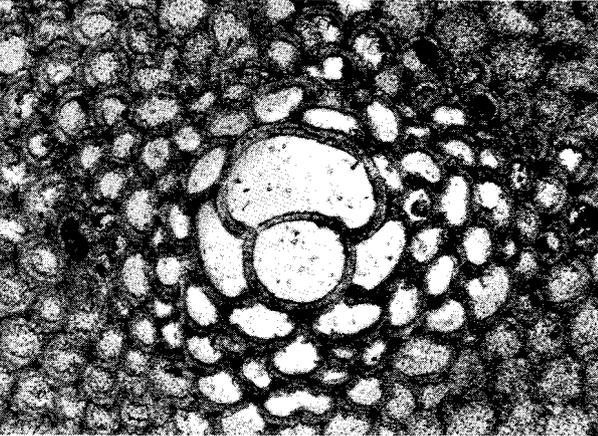
Plate XI *Lepidorbitoides minor* (Schlumberger), Limburg, Netherlands (type locality).



a ENCI 17.50B-2, 110 X.
1 adauxiliary chamber.

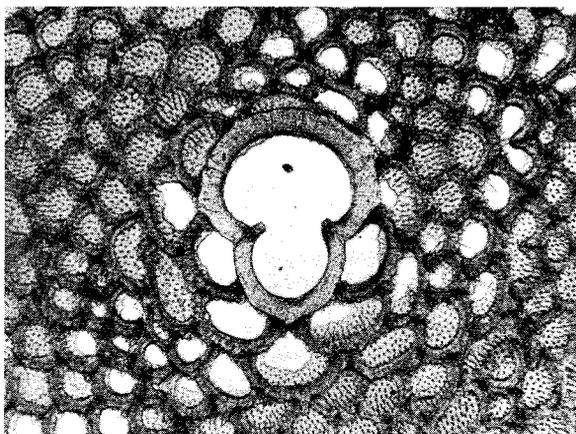


b ENCI 17.50B-6, 110 X.
1 adauxiliary chamber.

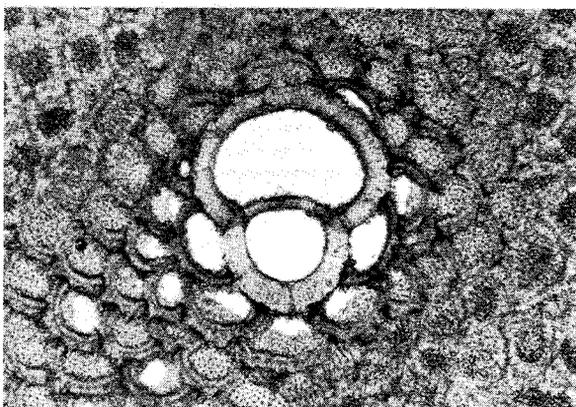


c ENCI 17.50B-4, 110 X.
2 adauxiliary chambers.

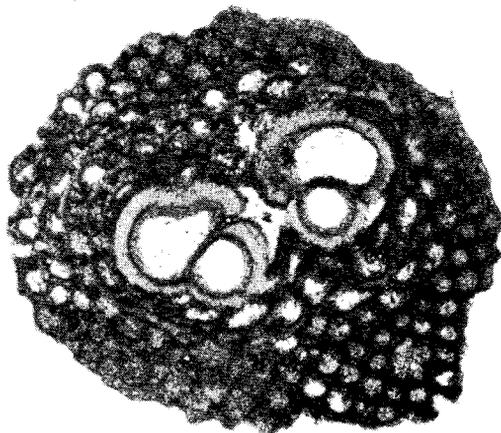
Plate XII *Lepidorbitoides minor* (Schlumberger), Limburg, Netherlands.



a Keerderberg 36-38, 110 X.
2 adauxiliary chambers (with
adauxiliary stolons).



b ENCI 28.00A-8, 115 X.
4 adauxiliary chambers.



c Keerderberg 40-13, 75 X.
Specimen with double embryo.

Lepidorbitoides socialis (Leymerie) 1851
(Text figs. 2m-o, Plate XII-XV)

Orbitolites socialis Leymerie, 1851, p. 191, Pl. IX, figs. 5a-c.

Orbitoides socialis Leymerie, Schlumberger, 1902, p. 258, fig. 2, Pl. VI, fig. 7, Pl. VIII, figs. 15-16.

Orbitoides paronai Silvestri, 1907b, p. 168.

Lepidorbitoides socialis (Leymerie), Silvestri, 1907d, p. 80; Douvillé, 1920, p. 221-224, Text figs. 22-25, Pl. VIII, figs. 1-4; Silvestri, 1927, p. 117-121; Renz, 1936, p. 559, Pl. XXIX, figs. 1-2, Pl. XXXI, figs. 1, 3; Rutten, 1937, p. 82-84, figs. 1-2; Thiadens, 1937, p. 99-100, Pl. 16, fig. 5, Pl. 19, fig. 9; Tan Sin Hok, 1939a, p. 74, Pl. 1, fig. 6; Rutten, 1940, p. 263-266, fig. 1; Ruiz de Gaona, 1943, p. 92, Pl. I, figs. 1-10; Ruiz de Gaona, 1948, p. 119-120, Pl. III, Pl. IV; MacGillavry, 1955, p. 11-43; Papp, 1956b, p. 137-138, Pl. 1, fig. 5; Neumann, 1958, p. 72-75, Textfig. 19, Pl. VII, fig. 7, Pl. VIII, fig. 8, Pl. IX, figs. 1-8; Köhler, 1962, p. 115-116, Pl. XII, fig. 4; Hanzawa, 1962, Pl. 1, figs. 1-2; Papp, 1970, p. 118-119, Pl. 14, fig. 3; Neumann, 1972b, p. 169, Textfig. 4, Pl. 2, figs. 12-15, Pl. 3, figs. 1-2, 5-6.

Lepidorbitoides paronai (Silvestri), Silvestri, 1908b, p. 150, Pl. XX (IV), figs. 5-6; Vettors, 1925, p. 6-7, Pl. IV, figs. 1-4; Silvestri, 1927, p. 112-114; Marchesini, 1941, p. 167-168, Pl. IV (II), figs. 25-26.

Lepidorbitoides eggeri Silvestri, Silvestri, 1927, p. 117.

Lepidorbitoides socialis pustulata Douvillé, Papp, 1954b, p. 89-90, Pl. 1, figs. 3a-b, Pl. II, fig. 3; Köhler, 1960, p. 81, Pl. IV, figs. 1-3; Papp, 1964, p. 121, Pl. 2, fig. 3.

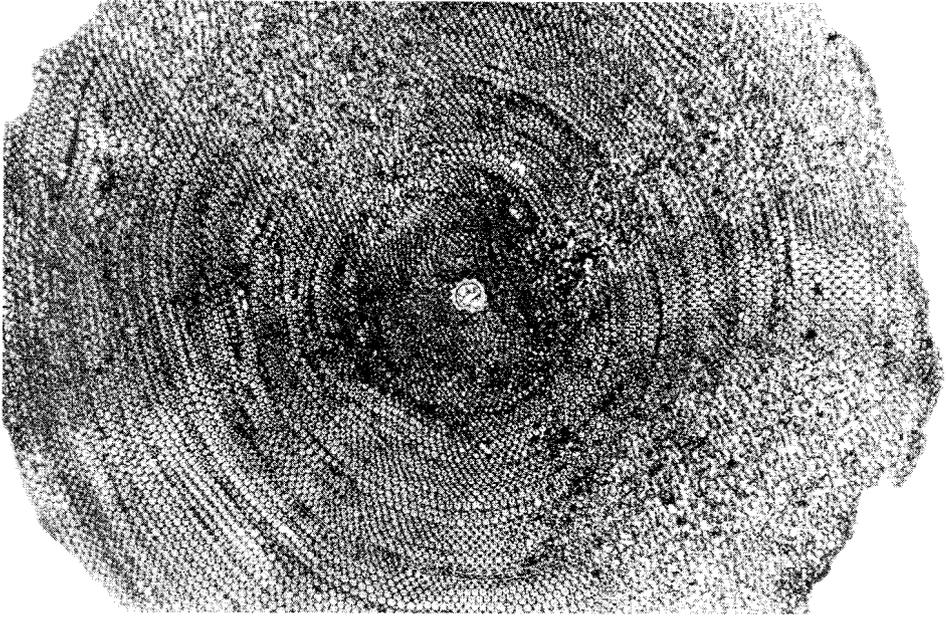
Type locality: Gensac, near St. Marcet (department of Haute Garonne, S France, no exact locality mentioned in the type description).

Age: Late Maastrichtian.

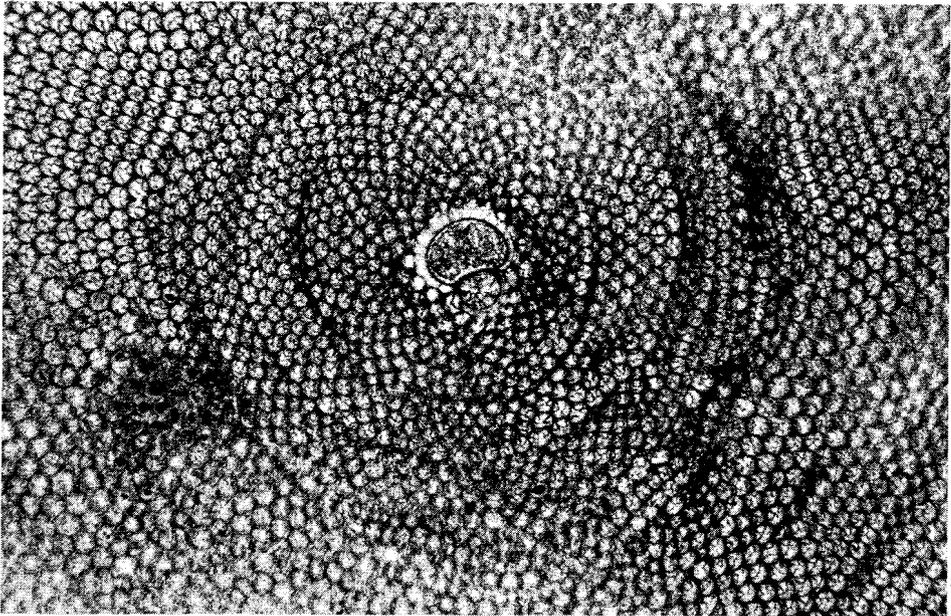
Description: rather thin lenticular test, diameter usually between 5 and 10 mm, frequently with central thickening at one side ("pustulata" type). The species is characterized by its advanced nepionic arrangement: quadriserial with many adauxiliary chambers (= multiserial). In samples from the type region the average number of adauxiliary chambers varies between 6 and 11. It is proposed to assign all populations with an average of 4.5 or more of these chambers to the species *socialis*. The average diameter of the protoconch varies between 85 and 125 microns, that of the deuterococonch between 165 and 270. The \bar{D}/\bar{P} ratio ranges from 1.7. to 2.2. All equatorial chambers, except a few ontogenetically early ones, are ogival, spatulate or hexagonal in shape.

Geographic distribution: Austria, Switzerland, all European countries bordering the Mediterranean, and several Eastern European localities.

Plate XIII *Lepidorbitoides socialis* (Leymerie), S France (type region).

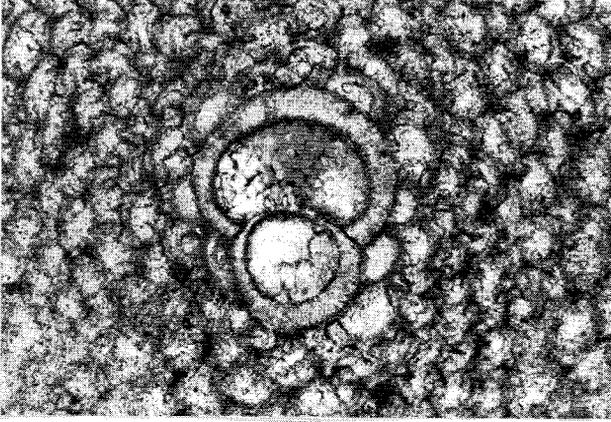


a

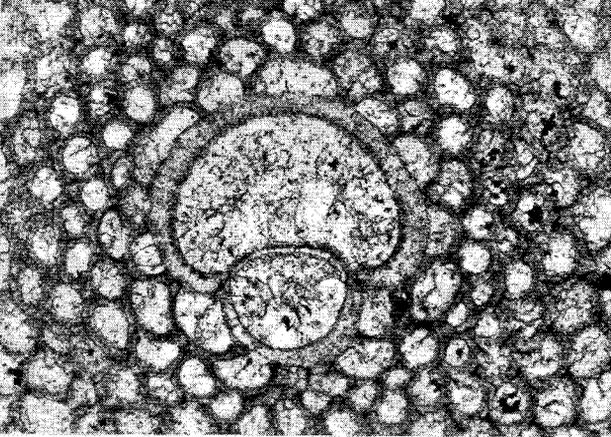


b

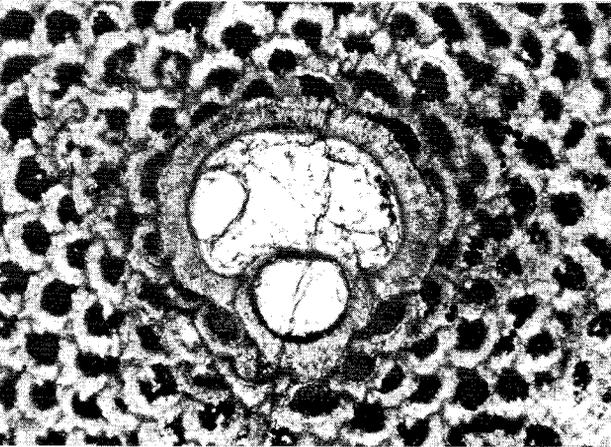
a PA388, Larcen 4, 15 X;
b \St. Marcet 125-4, 40 X.



a St Marcet R8851-38, 125 X.
4 adauxiliary chambers.

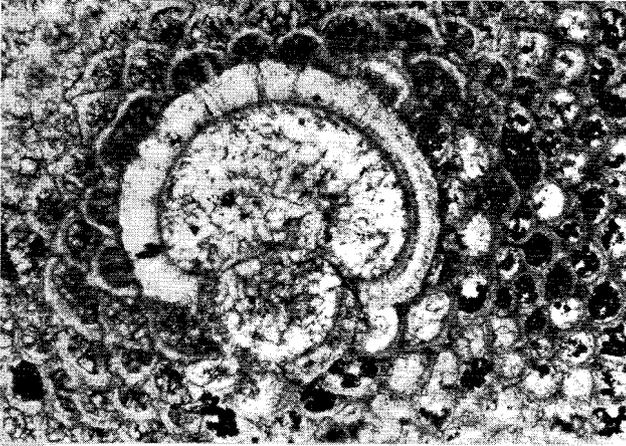


b St Marcet 122-3, 110 X.
8 adauxiliary chambers.

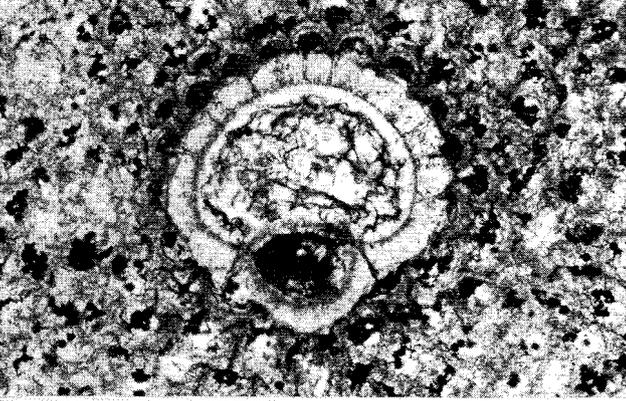


c Larcen 5-PA397, 125 X.
8 adauxiliary chambers.

Plate XV *Lepidorbitoides socialis* (Leymerie), S France.



a St Marcet 122-13, 115 X.
10 adauxiliary chambers.



b Gensac 25-PA483, 115 X.
12 adauxiliary chambers.
Note adauxiliary stolons.



c St Marcet 32B-12, 115 X.
13 adauxiliary chambers.
Note adauxiliary stolons.

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APPENDIX

Results of measurements and counts. P, D = internal diameter of protoconch, deuteroconch (in microns); Y = nr. of chambers without retrovert aperture; ps, ds = nr. of chambers in primary, deuteroconchal spiral; wh = nr. of whorls of primary spiral; A = nr. of adauxiliary chambers; N = nr. of observations; s.d. = standard deviation (computed with N in the denominator instead of N-1).

sample	N _{P,D}	P			D			Y				ps		wh	
		range	mean	s.d.	range	mean	s.d.	N _Y	range	mean	s.d.	range	mean	range	mean
<i>Helicorbitoides voighti</i>															
Bastad	45	53-114	75.1	12.7	62-111	80.2	15.0	40	6-22	12.8	3.7	+25-71	+45	2 $\frac{1}{2}$ -4 $\frac{1}{4}$	3.3
<i>Helicorbitoides longispiralis</i>															
Silberegg	12	52-87	69.8	11.7	60-102	77.8	13.0	12	3-8	5.4	1.3	28-55	38.3	2 $\frac{1}{2}$ -3 $\frac{1}{4}$	2.9
Stafversvad	4	76-114	96.2	13.5	99-133	113.1	12.9	4	3-6	4.5	1.1	18-36	27.0	1 $\frac{3}{4}$ -2 $\frac{1}{4}$	2.1
<i>Lepidorbitoides pembergeri</i>															
Gr 851, Pembergerriegel	20	56-101	77.9	11.0	55-112	89.9	13.6	19	2-4	2.3	0.6	9-11	10.1	ds	
<i>Lepidorbitoides campaniensis</i>															
Aub. Gr 22 + 803	6	76-135	94.5	20.9	97-166	116.0	26.8	5	1-2	1.8	0.4	8-11	9.3	5-6	5.5
Aub. Gr 40	22	61-153	100.9	20.2	81-176	124.0	23.9	13	1-2	1.7	0.5	5-10	8.2	4-7	5.2
Aub. Gr 43	2	74-98	86.0	-	80-133	106.5	-	2	2	2.0	-	8	8.0	4-6	5.0
Neuvic, Gr 364	8	66-108	87.3	13.3	90-146	112.1	16.1	8	2	2.0	-	8-11	9.5	4-6	4.6
Issac, Gr 359	7	68-106	85.0	12.3	95-131	113.1	12.6	7	2	2.0	-	7-10	8.6	4-7	5.4
Neuvic, Gr 365	12	78-116	89.5	10.6	102-142	118.3	12.7	8	2	2.0	-	7-10	8.1	4-7	5.6
Festalemps, Gr 139	6	83-134	100.9	17.0	95-168	134.4	21.7	2	2	2.0	-	9-10	9.5	4-7	5.5
NW of Chalais, Gr 105-112	28	63-120	97.3	16.3	87-162	122.1	19.3	21	1-2	1.9	0.3	7-11	8.9	4-7	5.5
St. Louis, Gr 369	7	66-95	87.0	9.4	91-139	114.5	14.6	3	2	2.0	-	7	7.0	5-6	5.3
Pemberger, Gr 849	26	76-125	94.7	14.9	85-162	127.0	17.8	23	1-2	1.8	0.4	4-8	7.1	5-7	6.2
Pemberger, Oostenrijk 17	10	69-119	90.3	16.5	76-148	116.4	24.3	8	2	2.0	-	7-8	7.3	6-7	6.7
Pemberger, P 88-5	3	83-110	98.3	11.3	97-148	120.7	21.0	3	2	2.0	-	8	8.0	5-6	5.7
<i>Lepidorbitoides bisambergensis</i>															
Bisamberg	4	66-117	91.4	18.3	99-171	139.2	25.9	4	1-2	1.3	0.9	4-9	5.5	6	-
A															
Pemberger, X 1961 V2	6	104-124	110.2	6.6	147-175	159.0	11.0	6	0	0.0	-				
Pemberger, X 1961 AG	11	91-129	113.2	10.0	136-179	162.2	13.5	11	0-1	0.1	0.3				
Pemberger, X 1961 AW	14	92-121	107.4	8.9	123-166	145.6	12.2	14	0-1	0.1	0.4				
Orcau, Gr 832	19	62-136	95.5	18.7	96-190	130.3	19.5	10	0-1	0.2	0.4				
Vlodrop	29	67-136	89.3	18.4	106-199	145.6	24.7	28	0	0.0	-				

sample	N _{P,D}	P			D			A			
		range	mean	s.d.	range	mean	s.d.	N _A	range	mean	s.d.
<i>Lepidorbitoides minor</i>											
Schunck, Kunrade	16	67-117	96.2	12.4	113-189	151.5	20.7	15	0-1	0.5	0.5
Ilten	24	66-112	90.0	9.8	129-180	153.4	14.1	21	0-2	0.8	0.5
CK 122, ENCI-Sportpark	11	72-130	100.1	17.2	120-195	161.8	20.6	11	0-2	0.9	0.7
ENCI 13.50 - 19.75	28	76-179	107.3	23.1	117-234	165.0	26.7	25	0-2	1.0	0.5
ENCI 22.00 - 22.50	35	71-150	99.2	16.7	122-255	171.1	28.4	23	0-6	2.3	1.4
ENCI 23.50	55	74-154	104.9	16.6	142-235	176.6	20.9	32	0-6	2.6	1.4
ENCI 24.00	26	68-141	101.6	18.1	103-274	176.6	31.5	19	1-7	3.1	1.5
ENCI 28.00	39	62-157	107.0	19.5	113-231	177.3	28.4	33	1-4	2.3	0.8
ENCI 30.50	36	75-150	101.6	19.0	125-228	167.1	27.2	29	1-4	2.7	0.7
ENCI 31.00 - 33.00	34	73-157	104.2	18.9	133-216	171.2	23.8	26	1-4	2.5	0.7
Jekerdal	16	76-147	113.3	26.1	143-282	181.3	30.9	13	1-3	2.2	0.8
Curfs	19	81-123	102.9	11.6	136-218	172.0	24.9	18	1-4	2.4	0.8
Schooverberg 168	8	74-162	104.5	25.5	131-238	167.6	31.2	6	1-3	2.0	0.6
Schooverberg 173, 174	44	76-148	108.6	20.9	136-245	180.2	30.0	35	0-5	2.1	1.0
Keerderberg 41, 42, 45	16	78-132	112.6	14.1	154-224	180.9	18.0	14	1-3	1.9	0.5
Keerderberg 38, 39, 40	23	77-165	115.0	21.4	152-256	185.5	29.6	16	1-4	2.3	0.9
Keerderberg 36	64	83-159	112.0	14.5	119-247	182.4	21.5	60	1-4	2.3	0.8
Keerderberg 33	96	72-147	105.1	14.7	119-238	174.5	22.2	76	1-4	2.3	0.9
<i>Lepidorbitoides socialis</i>											
Gr 811, Roquefort	51	66-153	95.3	16.2	122-235	165.7	26.3	41	4- 8	5.3	1.1
Gr 813, Dumes	39	79-139	105.3	15.9	133-347	207.8	40.9	34	3-10	6.4	1.8
Salas, N. Spain	29	103-218	142.1	25.5	185-337	262.5	33.1	28	4- 7	5.4	0.9
Olazagutia B 9646	27	59-123	88.4	16.7	113-247	185.6	36.5	26	3- 8	5.9	1.3
Olazagutia 22	38	70-157	113.9	23.4	152-328	232.1	44.9	27	5-11	8.0	1.9
St. Marcet 144	13	76-110	94.2	9.0	150-215	173.2	21.3	9	5- 8	5.8	0.9
St. Marcet R 8851	26	72-148	95.9	16.7	137-268	182.4	28.6	19	4- 8	6.1	1.1
St. Marcet 147	12	66-137	99.1	16.7	152-217	181.1	20.8	11	4-10	6.4	1.5
St. Marcet 121	28	73-123	95.2	14.5	132-224	175.6	22.5	18	3- 8	6.1	1.4
St. Marcet 122	18	78-153	107.2	19.4	166-299	232.4	32.0	14	6-10	7.5	1.1
St. Marcet 125	10	90-152	117.3	21.7	212-313	260.9	33.7	8	8-12	9.9	1.4
St. Marcet 32	22	90-158	122.2	19.3	213-357	272.0	33.6	19	7-13	10.6	1.7
St. Marcet 153	14	86-160	121.8	21.1	168-320	248.4	45.7	10	7-13	10.4	2.0
Larcan 5	10	91-156	116.1	18.0	188-263	225.2	24.7	9	4- 9	6.0	1.8
Larcan 135	13	87-140	113.9	14.9	198-278	233.9	22.6	9	5- 9	7.0	1.4
Biscanos	9	81-128	110.0	12.5	164-280	222.6	31.0	8	6-11	8.1	1.6
Larcan 4	10	78-114	98.1	11.6	171-218	200.5	16.5	8	6- 9	8.1	1.1
Terme 155	8	85-146	109.6	16.1	193-275	221.5	38.3	6	6-10	8.3	1.3
Naouarret 48	14	81-139	105.7	14.6	165-287	221.4	35.9	13	5-13	9.2	2.3
Gensac 25	11	79-151	108.5	23.4	175-323	263.3	45.1	10	9-14	10.9	1.8
Larcan 133	9	95-155	112.0	17.6	199-285	230.7	28.2	7	7-15	10.1	2.4
Terme 154	14	81-150	117.8	19.5	201-304	258.5	25.2	12	6-13	10.3	2.0
Gensac 17	9	93-149	120.7	17.0	211-316	268.3	31.5	9	9-15	11.6	1.9