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C.V. DRUKKERIJ v.h. CL. GOFFIN, NIEUWSTRAAT 9, MAASTRICHT

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PUBLICATIES

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NATUURHISTORISCH GENOOTSCHAP IN LIMBURG

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STUDIES OF FORAMINIFERA

by

J. HOFKER sen.

PART I

GENERAL PROBLEMS

(with 15 textfigures and 24 plates)

C.V. DRUKKERIJ v.h. CL. GOFFIN, NIEUWSTRAAT 9, MAASTRICHT

CONTENTS

INTRODUCTION

In this book the author has tried to give his ideas on Foraminifera in general and in later chapters on many genera of Foraminifera especially. It is not a mere compilation of papers published previously by the author; many of these papers were issued many years ago and some of the ideas given in them have proved to be erroneous as shown by modern investigators. Several of these topics have been analysed once again with modern methods and with the results of modern investigations in mind; other of these ideas have proved to be right, e.g. by the investigations by Reiss (1963); these topics need only to be mentioned without much alteration. Special attention was given to thin sections of the tests to try to solve questions which add to a better understanding of groups of genera or to special genera and species. In these sections, especially of smaller Foraminifera the structure of the test had special attention, since after the brilliant investigations by Wood (1949), Smout (1954) and Reiss (1957, 1958, 1963) many basal problems remained unsolved. I tried to get at the bottom of some of these problems, since the large modern work on the systematics of Foraminifera, the„Treatise" by Loeblich and Tappan (1964), which authors, obviously basing their system especially on these finer structures of the test wall, came to some conclusions as to the systematic place of groups of genera which seem to be rather artificial. In order to get a possibly better base for systematic arrangement, many groups of genera have been investigated once again, and in some cases errors on structure of walls could be detected, so that a better system in the future may be constructed.

This book does not aim at completeness; in many instances it will give a modern view of the subjects published earlier by the author in so many different journals and serials nowadays difficult to consult. At the end an index is given of all the papers published by the author on Foraminifera during a lifetime (1918-1968). It forms the end of a period in which investigators on Foraminifera pursued this topic as an hobby, of which group of scholars Franke, Rhumbler, Heron-Allen and Earland have set examples. Many of these „dilettantes" were attracted to Foraminifera by the beautifullness of their tests, as was the author; why were they? To solve this question the author studied many tests of Foraminifera in respect to the „sectio divina", which ratio puzzled already Leonardo da Vinci, who found it in so many living organisms, man included, and which has played such an important part in architecture, painting and sculpture; Leonardo believed it to be a divine ratio; we may also say that it forms one of the main rules in nature.

Foraminifera are a group which is often found in large quantities in the sea. So they can be studied in respect to evolutionary trends in an ideal way, since fossil samples with a large population are common and can be studied statistically. Doing so, we ought not to be hampered by already acquired ideas about the species concept which mostly forms a more or less subjective view of nature. Nor should our view be barred by ideas about finer test structure; it is true, that several groups of Foraminifera, showing a special microstructure of their tests, often form a natural group, but in phylogeny that structure may have changed considerably. It is more than probable, that in the genus *Bolivina* microstructure changed in course of time from aragonitic over microgranular to calcareous radial; in the Epistomariidae the change was from aragonitic to microgranular, and in some genera even to fibrous radial; in the Cibicidae the change was from monolamellar granular over „bilamellar" granular + calcareous radial to „trilamellar" granular+radial; etc. It often occurred that the original stock in a group remained aragonitical up into the Recent, but that side stocks got another structure; with these changes in microstructure of the test walls, changes in the development of toothplates also may be found within evolutionary trends. So it was necessary to study also the toothplates of many forms, which the author already did in former papers and which study is continued here. These studies showed that it is inconsequent to speak of toothplates in groups with a high speed spiral (*Bolivina*, *Bulimina*, etc.) but to speak of „columella", „partition", „column", etc. in those cases in which the speed of the trochoidal spiral is less or the test becomes nearly planospiral, as Loeblich and Tappan did in their „Treatise" (1964); Reiss (1963) as well as the author (many papers) showed that in reality all these structures, simple as well as highly developed ones, are nothing but toothplates, as will be shown here once again. In consequence, „double septa" formed by real walls and „double septa" formed by a wall and a flaring part of a toothplate are definitely different structures. It is obvious, that canals between real walls and canals between wall and flaring part of a toothplate (septal flap) are not homologous and thus can be used as characteristics for quite different groups. Canals in Calcarinidae are morphologically different from canals found in Streblidae.

I always believed that the toothplates of Foraminifera form a very reliable feature to define species; they could be used not only for clarifying many inner structures, but in some cases could also give indications as to the taxonomic position of many genera. Yet the structure of the toothplate within a genus can evolve during geologic time; an example is given here with the genus *Reussella*. The material for this study on *Reussella* came from many sources: from expeditions, but also, insofar it concerns fossil material, from my friends Hay, Van Voorthuysen and Bermudez.

I am especially thankful to my son Dr. J. Hofker jun. for the help given to me. He made the many photographs the reader will find in this book.

It is not possible to thank all the colleagues who sent their types of species to the author; they may be thanked through the concientiousness with which I studied their gifts and by the results which were obtained. But an exception should be made for Dr. Bermudez, who sent nearly all the types of his new genera as well as many species of which the systematic place was more or less doubtfull. His generous gift of many species of type-localities of *Streblus* has led to an exhaustive study of this group, which was the more necessary since during many years authors have described many different species as „*Rotalia beccarii*". (See part 2 of this book).

This book will appear in two parts, the first part dealing with generalities, the second one with systematic problems.

CHAPTER I

TRIMORPHISM

Life-cycles of Foraminifera have been published lately by several authors. Those given by Meyers and Grell deal with groups of Foraminifera which either are plastogamic or are dimorphic. The life-cycle that was given by Winter of *Peneroplis* was not complete, since the present author shows in this paper that megalospheric specimens of *Peneroplis* can give rise to plasmodiospores with a proloculus larger than that of the mother individual. In *Streblus flevensis* and in *Quinqueloculina* the present author showed that more than one megalospheric generations interchanged with one microspheric generation. He developed the idea that at least two megalospheric generations may occur with different size of the proloculus. This can be stated statistically, and several other authors have given instances for the occurence of these generations B, A_1 and A_2. Here more instances are given of this trimorphism. It is found that in geologic time a change may occur within a species or genus in the life-cycle, of which several examples are given.

The present author has given many examples in which the megalospheric forms of Foraminifera asexually form schizonts in which the proloculus is larger than that of the mother-individual. In this way three different generations occur, one the B-form, giving rise by schizogamy to a diploid generation (A_1) with smaller megalospheric proloculus; the latter giving rise by schizogamy to a haploid generation, (A_2), which, by forming gametes of which two fuse together, form the proloculus of the B-generation.

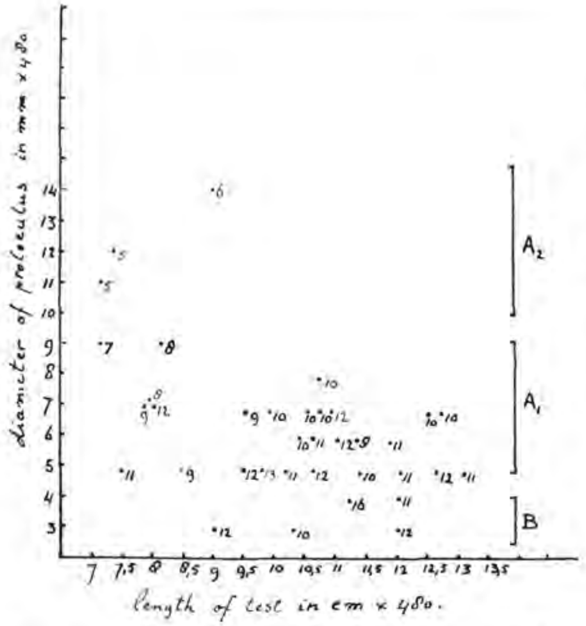
In the Treatise (1964, p. 64) Loeblich and Tappan believed that this kind of reproduction has never been demonstrated in cultures; this is not true. In Hofker 25, pp. 79-104, in a culture of *Quinqueloculina* the present author showed the forming of schizonts in a megalospheric individual and, more over, the same could be found in individuals of *Streblus flevensis* in the natural milieu, the Zuiderzee. Here the B-generation proved to survive during winter, the A_1-generation living in spring and early summer, the A_2-generation living in the late summer and autumn (Hofker, 57, p. 74-89). In Hofker 49 and in Hofker 93 the present author gave many examples in which statistically trimorphism could be proved.

Several other authors showed that trimorphism can be statistically detected in many species. Sigal stated it in *Choffatella decipiens* Schlumberger (Sigal, 1959, pp. 662-668); Maync (1959) found „clearcut trimorphism, in the sense of Hofker" in *Iberina lusitanica* (Egger); Cicha and Zapletalova described trimorphism in *Bolivina dilatata* Reuss (1961) and in *Textularia laevigata* d'Orbigny and *Spiroplectammina acuta* (Reuss) (1965, Sbornik Geol. Ved, vol. 6); Reyment observed true trimorphism in *Afrobolivina afra* Reyment (Acta Univ. Stockholm. Contr. Vol. 3, pt. 2, 1959, p. 25, fig. 4); Nogan described trimorphism in *Anomalinoides umboniferus* (Schwager) (Cushman Found. For. Res., spec. publ. no. 7, 1964, p. 44).

The present author showed that in many instances during geologic time the modus of reproduction of foraminiferal species changes (1962, N. Jahrb. Geol. Pal., Mitt., vol. 6, pp. 316- 329); the same could be observed by Cicha and Zapletalova in *Spiroplectammina carinata* (d'Orbigny) (1. c., 1965, p. 105). It is obvious that in phylogenetic studies the change from dimorphism into trimorphism has to be considered.

Papers on trimorphism are the numbers 8, 15, 20, 23, 25, 30, 31, 49, 57, 93, 105, 165 of the list of papers, published by the present author.

Here some new examples of statistically detected trimorphism are given from material from the Cocoa Sands, Alabama, Upper Eocene. If the discoveries by the present author about *Streblus flevensis* Hofker are correct, the B-generation has the largest longevity, whereas the A_2-generation has the shortest one. This can be verified by the number of chambers the generations show. The graph distinctly shows that in *Angulogerina danvillensis* Howe and Wallace, the B-individuals with proloculus diameter from 6-10 μ have 10-16 chambers; the individuals of the A_1-generation show 8-13 chambers, with a proloculus diameter of 10-16 μ; the A_2-generation, uncommon in the material, shows only 5-7 chambers, and has a proloculus dia-



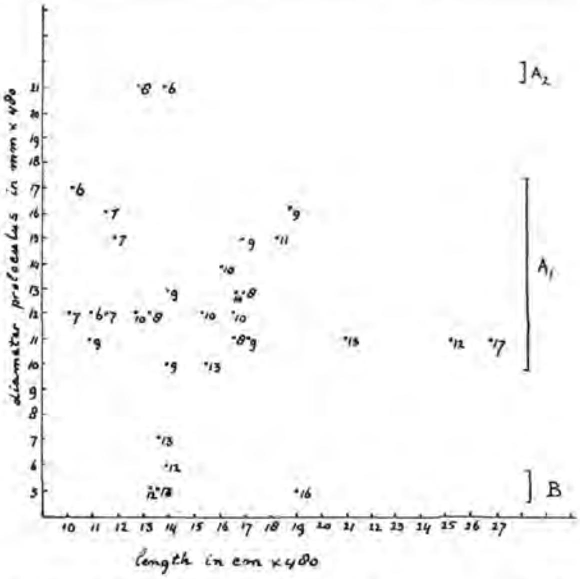
Textfig. 1. *Angulogerina danvillensis* Howe and Wallace, from Cocoa Sands; diagram, showing correlation diameter of proloculus and length of test. Numbers indicate number of chambers. There are three distinct generations.

meter of 18-28 μ (Pl. 1, Figs. 1-8; Textfig. 1).

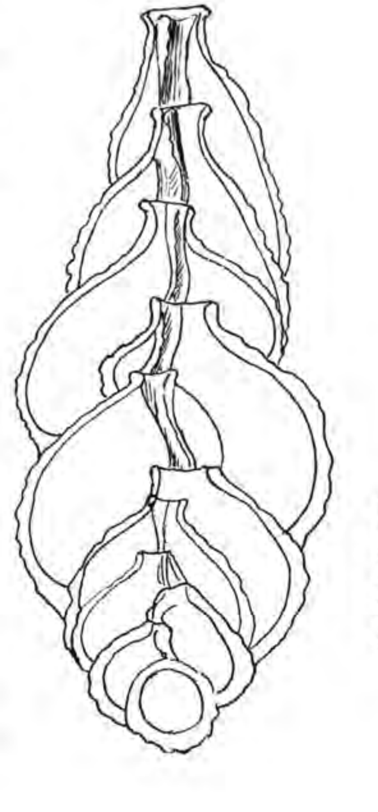
Euuvigerina gardnerae (Cushman) shows the same phenomena as discussed for *A. danvillensis:* the B-generation, with proloculus diameter of 10-14 μ shows 12-16 chambers; the A_1-generation, with proloculus diameter of 20-34 μ, shows in full grown specimens about 8-13 chambers; one specimen has 17 chambers but, though it has 20 μ proloculus diameter, may belong to the B-generation; the A_2-generation which is uncommon, has 6-8 chambers and a proloculus diameter of 42μ (Pl. 1, Figs. 9-11; Textfig. 2, 3).

In *Hanzawaya danvillensis* (Howe and Wallace) the microspheric generation with proloculus diameter of 10 μ, shows 23-25 chambers; the A_1-genertion with proloculus diameter of 12-14 μ shows 13-22 chambers; the A_2-generation, here the commoner one, shows a proloculus diameter of 18-28 μ and a chamber number of 15- 20 (Pl. 1, Figs. 12-16).

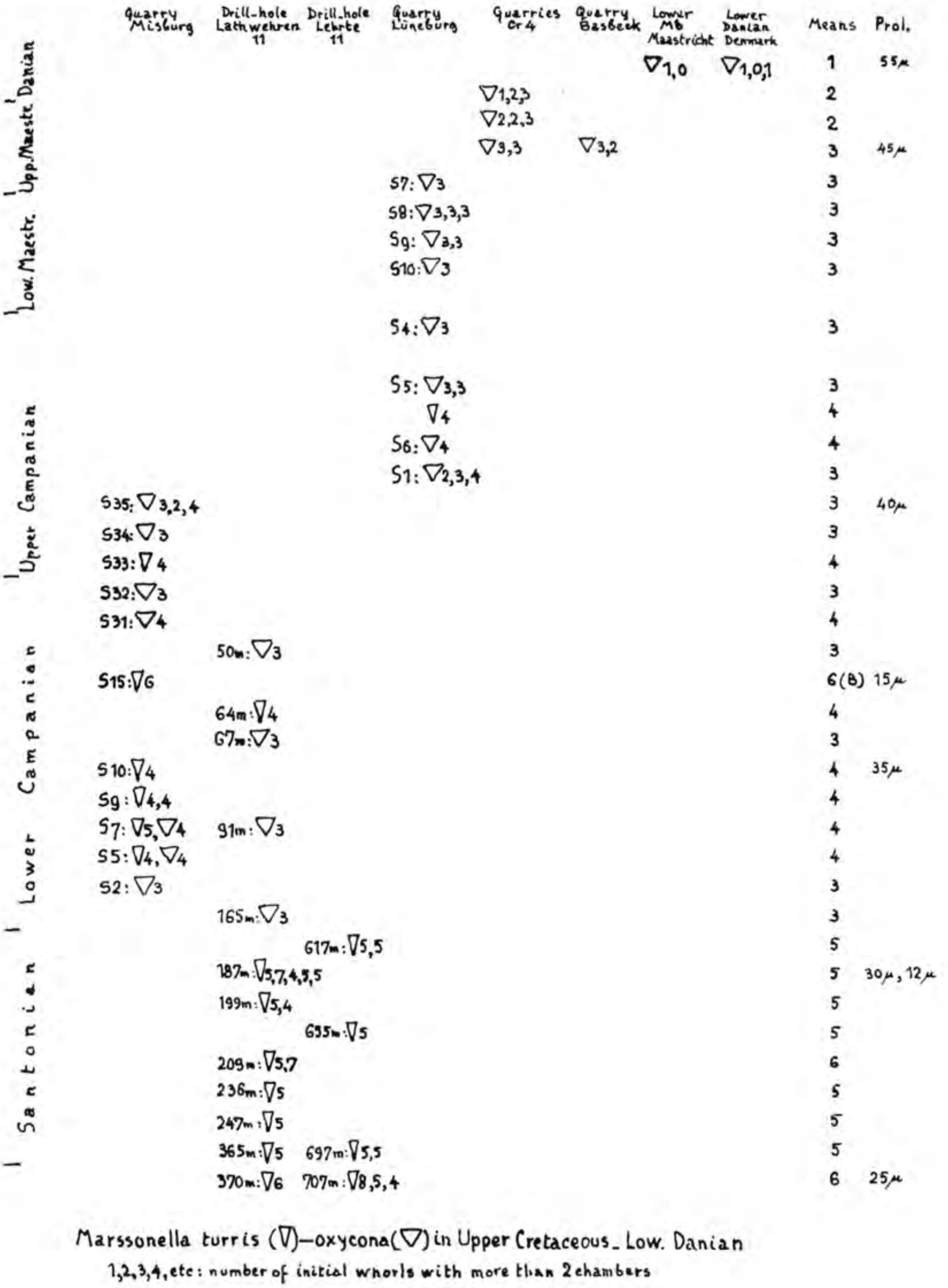
Parrelloides cocoaensis (Cushman) has a B-generation with proloculus diameter of 8 μ and a number of 22-28 chambers; the A_1generation, the more common one, has a proloculus diameter of 12-22 μ and a number of chambers of



Textfig. 2. Diagram about *Euuvigerina gardnerae* Cushman from the Cocoa Sands, showing correlation between diameter of proloculus and length of tests. Numbers indicate number of chambers. There are three generations.



Textfig. 3. *Euuvigerina gardnerae* Cushman, from the Cocoa Sands, showing the toothplates in section; x 300.



	Quarry Misburg	Drill-hole Lathwehren 11	Drill-hole Lehrte 11	Quarry Lüneburg	Quarries Cr 4	Quarry Basbeck	Lower Mb Maastricht	Lower Danian Denmark	Means	Prol.
Danian							▽1,0	▽1,0,1	1	55μ
Upp. Maestr.					▽1,2,3				2	
					▽2,2,3				2	
					▽3,3	▽3,2			3	45μ
Low. Maestr.				S7: ▽3					3	
				S8: ▽3,3,3					3	
				S9: ▽3,3					3	
				S10: ▽3					3	
				S4: ▽3					3	
Upper Campanian				S5: ▽3,3					3	
				∇4					4	
				S6: ▽4					4	
				S1: ▽2,3,4					3	
	S35: ▽3,2,4								3	40μ
	S34: ▽3								3	
	S33: ∇4								4	
	S32: ▽3								3	
	S31: ▽4								4	
Lower Campanian		50m: ▽3							3	
	S15: ∇6								6(8)	15μ
		64m: ∇4							4	
		67m: ▽3							3	
	S10: ∇4								4	35μ
	S9: ∇4,4								4	
	S7: ∇5, ▽4	91m: ▽3							4	
	S5: ∇4, ▽4								4	
	S2: ▽3								3	
		165m: ▽3							3	
Santonian			617m: ∇5,5						5	
		187m: ∇5,7,4,5,5							5	30μ, 12μ
		199m: ∇5,4							5	
			635m: ∇5						5	
		209m: ∇5,7							6	
		236m: ∇5							5	
		247m: ∇5							5	
		365m: ∇5	697m: ∇5,5						5	
		370m: ∇6	707m: ∇8,5,4						6	25μ

Marssonella turris (∇)—oxycona(▽) in Upper Cretaceous_ Low. Danian

1,2,3,4, etc: number of initial whorls with more than 2 chambers

Textfig. 4. The evolution of *Marssonella turris-oxycona*.

20-26; the A_2-generation with proloculus diameter of 22-26 μ has 17-18 chambers (Pl. 1, Figs. 17-20, Pl. 2, Figs. 1-4).

Of *Globigerina yeguaensis* Applin and Weinzerl only few specimens could be analysed; it is remarkable that the specimens with large tests were coiling to the left, whereas specimens with small tests mostly were coiling to the right. Moreover, it seems that especially specimens with large proloculus coil to the right; this is different from what has been found in *Parelloides wuellerstorfi* (Schwager), where the microspheric specimens were coiled to the right (Pl. 2, Figs. 5-11).

The present writer (32, 1933) and Buchner (1940, p. 405, pl. 1) stated that there exists true trimorphism in *Nodosaria scalaris* (Batsch); the B-generation is an *Amphicoryna*, the A_1-generation is a *Nodosaria*, the A_2-generation a *Lagena*. Cushman found that *Marginulina hirsuta* d'Orbigny is the B-generation of *Nodosaria aculeata* d'Orbigny, whereas the A_2-form is *Lagena hispida* Reuss. So a knowledge of dimorphism and trimorphism may, in some cases, lead to simplification of the system.

Especially the Foraminifera around „*Discorbis*" have yielded material for experimental study of the life cycles of Foraminifera; however, most of these species *(Rotaliella heterocaryotica, Rubratella intermedia, Patellina corrugata, Spirillina vivipara, Glabratella patelliformis)*, belong to a group of Foraminifera which show plastogamy and so do not show a microspheric generation or two megalospheric generations. We know now for certain that the life-cycle, as given by Winter (1907) of *Peneroplis pertusus* does not conform reality, since in many species of Peneroplidae megalospheric plasmodiospores have been found to derive from megalospheric agamonts, which plasmodiospores show larger proloculi than found in the mother individual; the author could also state the phenomenon in *Quinqueloculina seminulum* (also stated in *Spiroloculina* by Arnold, 1964). So there must be species or groups of species which never form microspheric individuals. It is very remarkable that, though thousands of specimens were studied by the author of many species of *Neoflabellina*, not even one microspheric specimen could be detected. Was this genus plastogamic? Or the microspheric generation repressed? Lister (1895) described the life-cycle of *Elphidium crispum* (Linné) as a continuous succession of gamonts and agamonts; the gamonts (schizonts) are the B-generation, distinctly much larger than the agamonts, the A-generation. However, the present writer, studying many sections of A-individuals, could show two distinct peaks in the diagram of diameters of the proloculi, so only at the end of two or several A-generations, gamogony may take place, just as the author could prove in *Streblus flevensis* Hofker.

Well known is the trimorphism of *Idalina antiqua* d'Orbigny as described by Schlumberger and Munier Chalmas (1885, pp. 299-308). The B-generation with very small proloculus begins with a quinqueloculine test, and changes through a triloculine stage into the biloculine end stage; the A_1-generation has a larger proloculus, followed by a triloculine stage, ending with the biloculine stage; the A_2-generation with very large proloculus only shows the biloculine stage. This instance shows that with enlargement of the proloculus an accelleration towards the end-stage takes place. Moreover, as the author already found in *Streblus flevensis* Hofker the total number of chambers decreases with the increase of the proloculus diameter, and, obviously, the life-time in the same way. Quite the same phenomenon has been stated by the author in many other Foraminifera, e.g. *Rectobolivina dimorpha* (Parker and Jones), *Rectobolivina virgula (Brady)*, *Rectobolivina columellaris* (Brady), (Hofker 49); here the original biserial arrangement of the chambers more rapidly changes into the uniserial one with increase of the proloculus diameter. The author showed that e.g. in *Sorites orbitolitoides* Hofker the chambers with partitions are reached earlier with the increase of the proloculus diameter. (Hofker, 48, p. 105, fig. 53).

It is obvious that this accelleration in attaining the end-stage of structure of the test can also be followed during geologic time. In *Marssonella oxycona* (Reuss) during the Santonian-Upper Maestrichtian the size of the megalospheric proloculus gradually increases; with this increase the number of series of chambers with more than two chambers gradually decreases from 6 to 2, so that gradually the tests reach the two-chambered series. This decrease of polyserial chambers may obviously lead in the end to tests which have the biserial stage directly after the proloculus and thus may be named *Textularia*. In the Danian of Denmark several megalospheric specimens of *Marssonella oxy-*

cona were traced which had reached the *Textularia*-stage. The microspheric specimens of the same level, however, showed 6 series of polyserial chambers, followed by only few biseral rows. (Text fig. 4).

Grabert (1959) showed that the triserial stage in *Gaudryina-Spiroplectinata* diminishes and the biserial stage increases. This author, however, did not connect this change with the size of the proloculus, though the present author showed (Hofker 41) the connection between size of proloculus and number of triserial chambers; an investigation of the material used by Grabert in this respect might change our view of the supposed evolution of *Spiroplectinata*.

Zedler (Pal, Zeitschr., 1961, vol. 35, pp. 28-61) described a *Spiroplectammina dorni* in the Hauterive which, according to this author changed into *Marssonella kumi;* in the light of what has been described here about the genotype, *Marssonella oxycona*, it is not very likely that this species is a *Marssonella*. It is more likely to suppose that *M. kumi* is a *Textularia*, possibly deriving from *Spiroplectammina*. Specimens of this *Textularia kumi* are common in some beds of the type-locality of the Hauterivian, but do not show the typical test-structure of *Marssonella*.

The change by accelleration due to the increase of diameter of the proloculus during time, complicated by the change of life-cycle as found by the present author in several instances implies that phylogenetic studies have to include all these factors; such was done by Hofker Jr. in his study on *Orbitolina* (1963).

Accelleration together with increase of the size of the megalospheric proloculus was also observed by Papp in *Heterostegina;* here the accelleration consists in the forming of secondary septa in chambers placed more and more initially (1963, Mitt. Geol. Gesellschaft Wien, vol. 56, pt. 1, p. 291, pl. 1).

CHAPTER II

PHYLOGENETIC STUDIES IN FORAMINIFERA

There is a general tendency in Foraminifera to increase the size of the test during existence of the species (or gens). With this increase of size also an increase of the size of the megalospheric proloculus is found. The species or gens may try to escape the inconvenients of these increases by different measures. This may be done by an increase of pore-diameter, or by strengthening the tests with heavy ornamentation. *Orbitolina* forms chamberlets around the increasing proloculus to escape collaps of the large globule formed. Or, it may be that the development of an A_1-generation with its smaller proloculus makes it possible to sail around the ever increasing proloculus. But measures taken by the gens also may lead to extinction.

The tendency to enlarge the tests during time is found in many Foraminifera. In planktonic groups this is a well-known fact (Hillebrandt, 1964, Pal. Zeitschr., vol. 38, p. 193, fig. 1-3). At the end of the period of existence many *Globotruncanae* reached a diameter never reached before (Upper-Cretaceous). *Globigerina pseudobulloides* Plummer begins its evolution in the uppermost Maestrichtian with very small specimens; it ends its evolution in the Lower-Paleocene with the largest tests known for the species. In the forms of the Upper-Cretaceous and basal Danian the tests are very thin-walled, and gradually the thickness of their tests increases during time. Together with the enlargement of the tests the ornamentation changes gradually; in the first stages of the evolution small pustules are seen between the pores; afterwards, in the Danian, the pores open into small pits; then the borders of the pits fuse into a honeycomb structure. Moreover, the whole test gets a more compact appearance, changing after Danian into forms known as *Globigerina varianta*. The changes in ornamentation can be explained as an answer of the living species to the gradual enlargement of the test. It is obvious that the increase of volume during time necessitates the increase of thickness of the test; however, planktonic life is possible only with relatively thin test walls; here the honeycomb structure gives the solution (See Hofker, 143, pp. 120-121, pl. 2; 164, pp. 1070-1071, textfig. 23). Pl. 2, Figs. 12-17.

A second example of gradual enlargement of tests of planktonic Foraminifera is found in *Globigerina daubjergensis* Brönnimann, changing in the lower Paleocene-Montian into a form, described as *Globigerina kozlowskii* Brotzen and Pozaryska (see Hofker, 198, pp. 66-68, figs. 1-6; 164, pp. 1068-1070, textfig. 22; 166, pp. 122-124, textfig. 61, 62, 63; 143, pp. 119-120, pl. 1; 164, p. 117, textfig. 48; 136, pp. 74-76, textfig. 31-34, table 1). Here also, the species begins in the uppermost Cretaceous with very tiny individuals and gradually increases the volume of the specimens during time. Together with the increase of volume some remarkable characteristics have been developed. In this species the pores are very small and the aperture in the umbilical hollow is very narrow. The geologically oldest individuals have only narrow apertures; in the Middle Danian more and more specimens are found which have secondary apertures at the dorsal sutures, just where two chambers meet at the spiral suture. Later, in the end of the Danian specimens appear with a 'bulla' over the umbilicus. The test gets a more conical appearance during this period, which characteristic remains in the Montian specimens. Together with this change more openings on the dorsal side are formed till in the end rows of these tiny openings are found at the dorsal side along the spiral sutures. Such specimens are known as *Globigerina askanona* Loeblich and Tappan and *Globigerina kozlowskii;* pl. 2, Figs. 18-25.

In the *Globigerina daubjergensis-kozlowskii* gens the increase of the volume during time seems the primary, inevitable evolutionary change. The other changes which appear more suddenly at distinct times, can be explained as the answer of the species to the enlargement of the volume of the individuals. It is not impossible that the forming of bullae is a means to increase the floating capacity, though it may also be interpreted as an apparatus serving a change in propagating, since just at that time this change also begins, two different kinds of proloculi appear (Hofker 164 p. 122, textfig. 61); Pl. 3; Pl. 5, Fig. 12. The appearance of extra apertures must be due to the necessity to produce more feeding pseudopodia, since the larger animals need more nutrition, whereas the main aperture remains narrow.

Other instances of enlargement of tests during time are *Globigerina cretacea* d'Orbigny (Hofker, 159, pp. 95-100, diagram 1 and pl. 1); *Gavelinella danica* Brotzen (Hofker, 67, pp. 49-53), in which also the pores increase during time; *Coleites reticulosus* (Plummer) (Hofker, Natuurhist. Maandblad, 1956, vol. 45, p. 77-78, fig. 1-8; 1962, Journ. Pal., vol. 36, pp. 1065-1066, textfig. 17), in which the ornamentation on the wall also increases; *Bolivinoides decoratus* gens (Hofker, 133, pp. 248-249, fig. 1-5; 119, pp. 145-159, textfig. 1-11), in which the ornamentation of the test wall increases with the increase of volume; species of *Nummulites* (Staub, 1963; see also Pl. 3, Fig. 2; Pl. 3. Fig. 3-9).

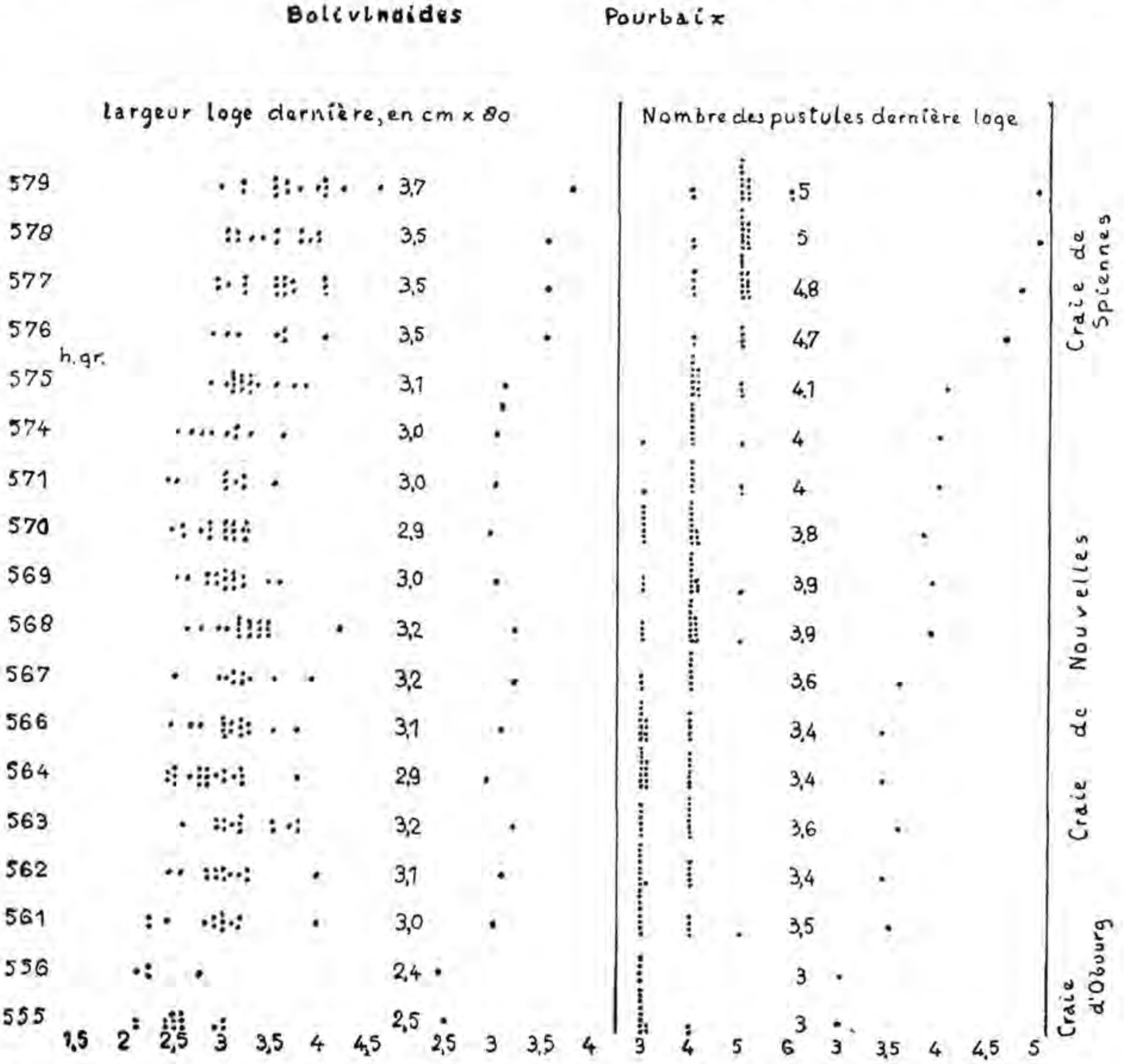
In the *Globigerina-cretacea*-gens the author observed a thickening of the test walls during the increase of volume which can easily be explained; in the end of the evolution series the tests get ridges on the surface, strengthening the wall. The same can be said about *Gavelinella danica* Brotzen in which, moreover, a gliding increase of the diameter of pores could be observed, which will be explained later. In *Coleites reticulosus* Plummer the ornamentation on the test wall increases with the increase of volume during time; it was necessary for the organism to strengthen the wall when the tests became larger; moreover there is a change in the position of the aperture, due to an uncoiling of the test in the later forms. The enlarging test of the *Bolivinoides strigillata - decorata - australis - gigantea* - lineage show more and more retral processes on the sutures, whereas in the largest forms these processes form elongate ridges over the test wall, strengthening in this way the test. It is possible that these animals crept over weeds to seek their food and that the large tests found in the end of the period of evolution became too heavy to do so; suddenly, in the end of the Maestrichtian, the whole gens disappeared; Pl. 3, Fig. 10; Pl. 4; Pl. 5, Figs. 1, 2; Textfig. 5.

Staub (l. c. 1963) proved that in the *Assilina-exponens*-lineage and in the *Assilina-spira*-lineage the outer walls and the spiral walls increase in thickness when the tests, especially in the microspheric form (l. c., fig. 4 and 5), increase in volume.

In the gens *Neoflabellina leptodisca-praereticulata-reticulata-postreticulata* the tests decrease in thickness during time; the species develop ridges as a strengthening of the test wall; these ridges develop into a reticulate pattern in the end; in the end of the Western European lineage specimens become small and show indications of degeneration; what the causes of the extinction of the lineage were, could not be traced till now (Hofker, 119, p. 150, fig. 2; 133, fig. 1). See also Pl. 5, Figs. 3-11.

In *Globigerina daubjergensis* the first forms show only relatively small megalospheric proloculi; during the evolution of this species, two kinds of megalospheric proloculi develop; one of them getting larger and larger during time. Together with the building of high trochoid tests in the Upper Danian, it was stated that these forms had always a small megalospheric proloculus, whereas the flat forms have a large proloculus (Hofker, 166, p. 122, fig. 61); see also Pl. 5, Fig. 12. Obviously this is an instance of change of the modus of reproduction during time. Such changes could also be detected in *Bolivina incrassata* Reuss (Hofker, 105, pp. 235-247, textfig. 295-302), *Daviesina fleuriausi* (d'Orbigny) (Hofker, 170, pp. 79-82). *Siderolites calcitrapoides* Lamarck (Hofker, 165, pp. 316-329). In some cases the present author could state that in the beginning of the appearance of a species the generations B and A occur; later in geologic time an A_2-generation differentiates, so that we then have the generations B, A_1 and A_2. In the end of an evolution lineage it may occur that only one of the generations remains, in some species the A_1-generation, so that in these cases the average diameter of the proloculus of the megalospheric generation first increases, later decreases; this phenomenon also was observed by Cosijn (1942, Leidsche Geol. Mededeelingen, vol. 13, pp. 140-171). When a species migrates to a new habitat, this migration seems to take place by means of the flagellospores (which by fusing give rise to the microspheric proloculus). In this respect several species where found suddenly to appear in the Maastricht Tuff Chalk; so, the first specimens detected of *Daviesina fleuriausi* are all microspheric.

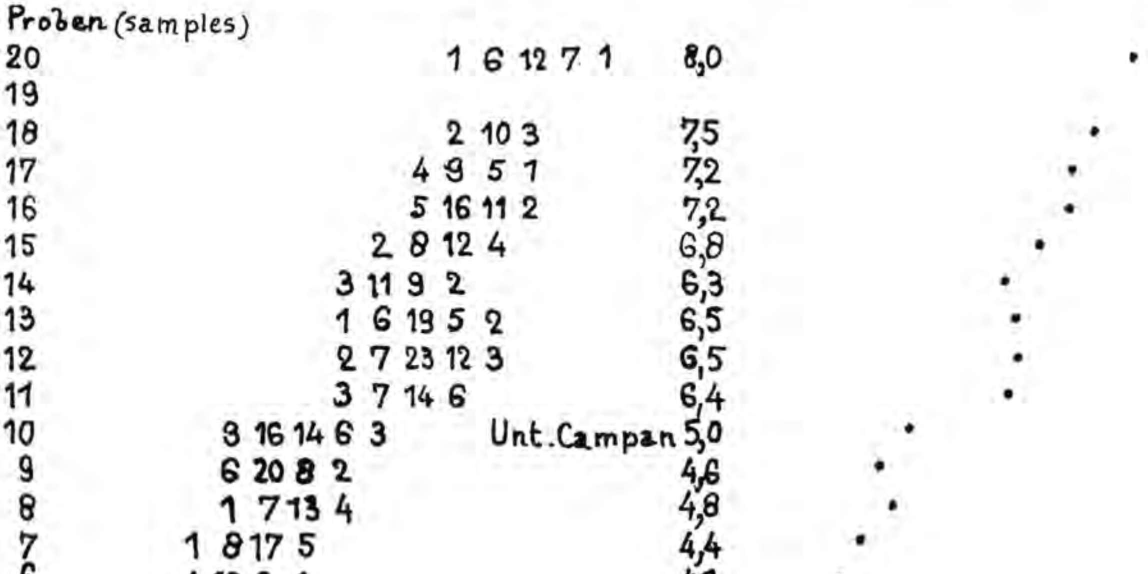
Beautiful examples of the two described tendencies, enlargement of the volume of tests and increase of diameter of the megalospheric proloculus, have been analysed by Schaub in *Nummulites*. This increase of the volume of the average megalospheric proloculus was also found by the author in *Siderolites calcitrapoides* Lamarck, *Siderolites vidali* Douvillé, *Rota-*



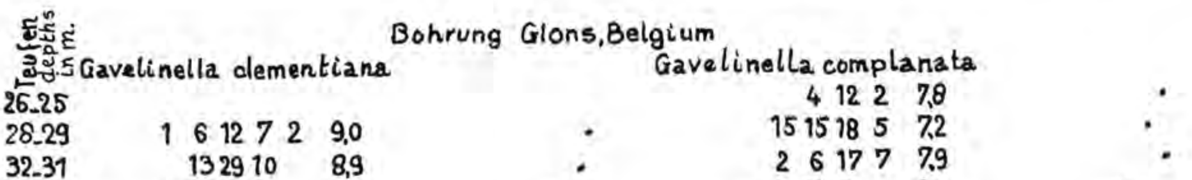
Textfig. 5. Increase of the number of pustules in the last formed chamber of the *Bolivinoides decorata-australis* gens, in the quarry at Pourbaix, near Mons, Southern Belgium. Here the lowest samples are lowest upper Campanian, so that the mean of pustule number here is lower than in the quarries and drill-hole of Boirs, Hallembaye and Glons. The hard ground is much less conspicuous and is found between the samples 575 and 576; the hiatus was smaller, so that the leap also is less typical (from 4,1 to 4,7); moreover, in the quarries in North East Belgium the hiatus embraces Lower Maestrichtian; near Mons a part of the Lower Maestrichtian (Craie de Spiennes) is present, hence the less conspicuous leap in the number of pustules. The author already pointed to *Bolivinoides* as an important tool for stratigraphy (111, pp. 329-333).

lia trochidiformis Lamarck (Hofker, 132, pp. 298- 301, p. 289). *Bolivinoides decorata-gigantea* (Hofker, 105, p. 265), *Globorotalites* (ibid., 1957, p. 411). The phenomenon is also known to occur in *Orbitoides, Lepidocyclina, Miogypsina* (McGillavry, Van der Vlerk, Drooger). It is obvious that the enlargement involves a change in the shape and arrangement of the following initial chambers too. The forming of the spiral in the case of a small megalospheric proloculus, following the pattern found in the microspheric generation, is thus gradually changed by the forming of auxilliary chambers, the number of which obviously increases with the increase of the diameter of the proloculus. In addition the forming of more than one system of spirally arranged chambers is a natural consequence, and the gradual change in these initial chambers is due to the strengthening of this part, which gets weaker with the increase of the volume of the megalospheric proloculus. The relation between the diameter of the proloculus and the arrangement of the following chambers in tests of Foraminifera could be traced in many instances by the present author; it will be obvious that in this way the whole test can change due to the changing volume of the proloculus; in species in which the test is first biserial but ends uniserially, the number of biserial chambers decreases with the increase of the size of the megalospheric proloculus (Hofker, 49, pt. III, *Rectobolivina dimorpha*, p. 117, fig. 68); in *Marginulina decorata* (Reuss) from the Miocene of Malta the author found three generations, B, A_1 and A_2; the B-generation has an initial part which is distinctly coiled, the coil being formed by 8 chambers; in the A_1-generation the proloculus is larger and the coil is formed by 4 chambers; in the A_2-generation the coil is formed by only 2 chambers; it is obvious that the three forms differ considerably, and that, when in the course of evolution of such a species the A_2-proloculus increases in size, there may be a time in which this species will have an entirely straight test in this generation; then it will belong to a different genus as well. (See Pl. 6, Figs. 1-7). When, moreover, one or more of the generations is suppressed in the end of the evolution series, *Vaginulinopsis decorata* gradually may have changed into a *Nodosaria*. (See Pl. 6, Figs. 1-7). See also Hofker, 34, *Nodosaria vertebralis* (Batsch), pp. 108-114, pl. IV, fig. 1-13, textfigs. 23 a-d).

An important analysis has been made by J. Hofker Jr. on *Orbitolina* (1963). He concluded that the whole range of „species" in reality forms a single gens, *Orbitolina lenticularis* (Blumenbach). This gens during its long existence of about 35 millions of years gradually enlarges its test from about 5 mm up to 60 mm and, moreover, is subject to a gradual increase of the diameter of the megalospheric proloculus. In consequence the whole embryonic apparatus, consisting of the proloculus, the deuteroconch and several epi-embryonic chambers, changes during time. In the development of these secondary embryonic chambers we are able to read the answer of the organism (here the whole gens) to the tendency of enlargement of the proloculus. In the Barremian and Lower Aptian only chitinous walls divide the globular proloculus from the deuteroconch and peri-embryonic chambers. Gradually the diameter of the embryonic apparatus increases and the pseudochitinous wall becomes calcareous, so as to divide the proloculus and the peri-embryonic chambers. Only in animals with the smallest megalospheric apparatus this change from chitinous to calcareous took place and obviously only these specimens could do so (Upper Aptian). The epi-embryonic chambers strengthen their walls gradually by means of a honeycomb structure of secondary walls which structure is also present at the outer walls of the deuteroconch. The enlarging proloculus, however, at one moment cannot maintain its globular form any longer and flattens at the upper side. In the Albian this tendency of flattening gave even rise to a concave upper wall; then the organism reconstructs the epi- embryonic chambers, dividing them by the honeycomb walls into numerous chamberlets with more or less globular appearance, thus strengthening the whole embryonic apparatus, and the upper wall of the proloculus once again becomes convex. In the Upper Cenomanian a second megalospheric generation could be distinguished, with a smaller proloculus and a more conical test in which the proloculus once again is more or less globular (A_1-generation). The specimens with the largest proloculus (A_2-generation) enlarge the embroyonic apparatus in the later Cenomanian ad absurdum, and in the end most specimens of that generation mainly consist of this enormous apparatus only. In the Upper Cenomanian only the conical A_1-generation remains and the B-generation, always present among the older populations, is probably suppressed (J. Hofker Jr. 1964, Revue Micropal., vol. 7, pp. 72-76, textfigs. 1-3, pl. 1, 2). The organism became apogamous. This latest measure of the gens to escape the difficulties originating from the increase of the volume of the A_2-proloculus, however, ends in a total failure for the whole gens. *Orbitolina* lived in clastic environments only, in shallow tropical seas. When the environment became unfavourable for the species, it had to



Textfig. 6. Increase of diameter of pores in *Stensiöina exsculpta* (Reuss) during time; a distinct hyatus in sedimentation has come to light in the quarry at Misburg, Germany between the samples 10 and 11.



Textfig. 7. The increase of diameter of pores in *Gavelinella clementiana* (d'Orbigny) and *Gavelinopsis complanata* (Reuss), in the drill-hole Glons.

migrate to a similar peculiar environment; we saw already that the migration of Foraminifera is mainly possible by means of the microsphric generation (it is very remarkable that Hofker Jr. found one sample, 115130, Le Puch, 1, core 9. 1399.50 m. Lower Albain, in which only small microspheric specimens occurred; (l. c. 1963. p. 188). The apogamic conical form of latest *Orbitolina lenticularis*, however, lacked the microspheric generation. This lack thus gave rise to a sudden disappearance of the gens over the whole world in the end of the Cenomanian, when orogenetic changes occurred over wide areas in a large scale; see Pl. 6. Fig. 8.

This instance clearly shows that we deal with three tendencies:

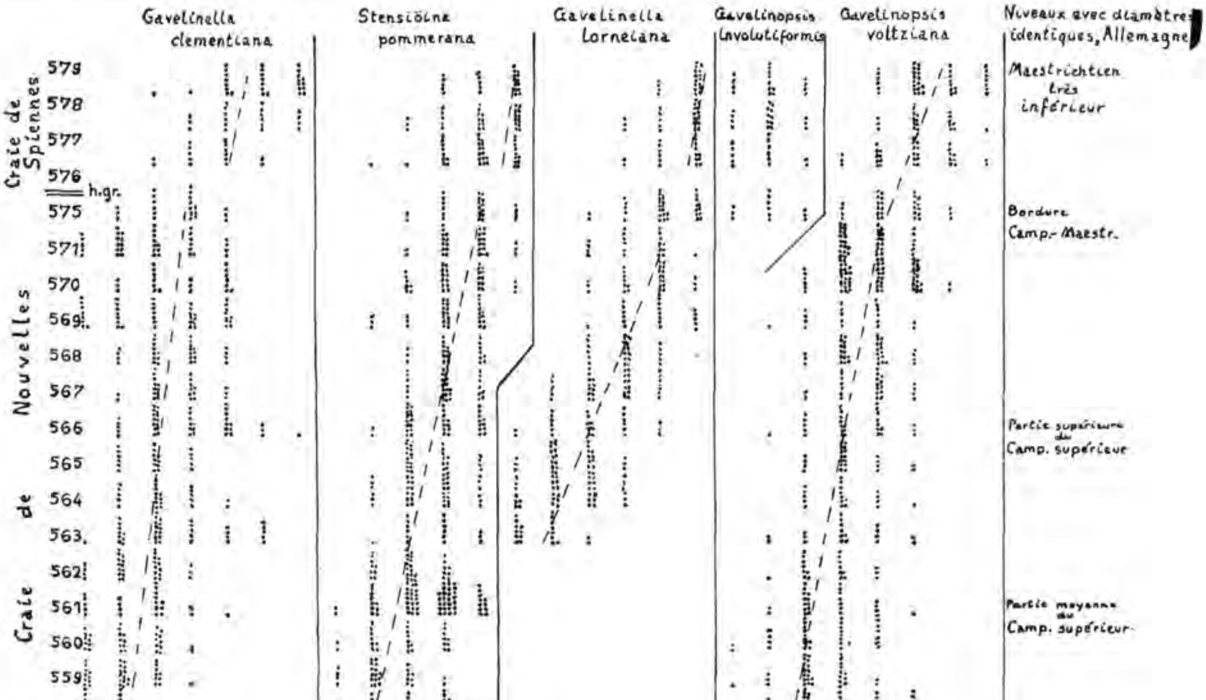
1) gradual increase of the whole test till absurd forms are reached;
2) increase of the diameter of the megalospheric proloculus;
3) measures taken by the gens (as a biologic entity) to escape the disastrous results of these orthogenetic changes.

In the case of *Orbitolina* the enormous platelike tests (especially in the microspheric form) might give rise to suppression of the B-generation; the forming of an enormous embryonic apparatus in the A_2-generation eliminated this generation in the end of the evolution lineage; the only remaining form, the A_1-generation, had not the disadvantage of the large flat test. But the apogamy in the end made a flight from unfavourable environments impossible and consequently the whole gens extinguished. The consequences of the increase in volume of the megalospheric proloculus were met with by the forming of calcareous walls in the embryonic apparatus and later once again by the forming of numerous epi-embryonic chambers, dividing the tension on the upper wall of the proloculus.

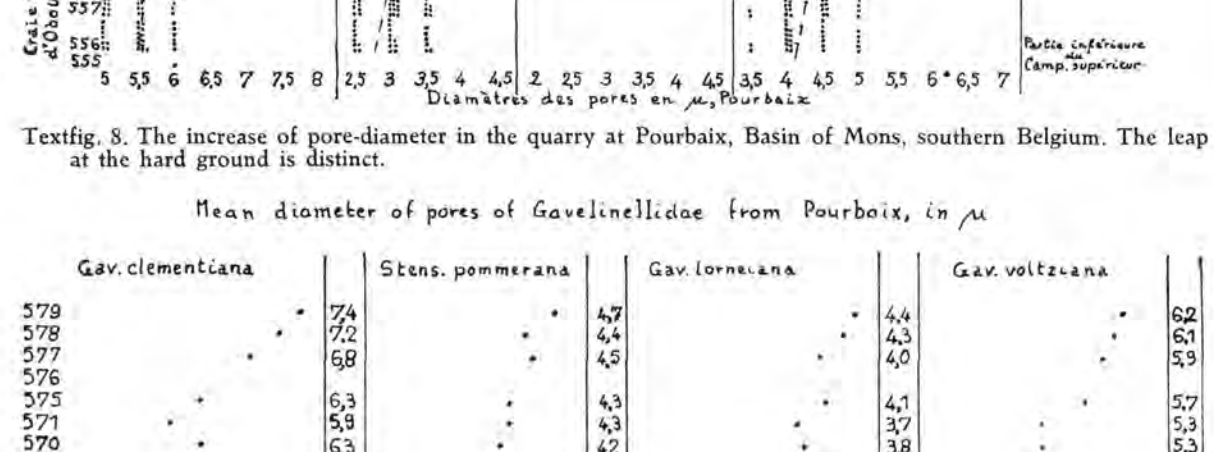
Both orthogenetic tendencies (1 and 2) are independent of the environment so that at one geologic time-level the stage of evolution in the gens is the same over the world, as could be proved by Hofker Jr., comparing specimens from Asia and America with those found in Europe. Thus such a gens can be used as a stratigraphic tool (see also Hofker, 111, pp. 329-333, pl. 1, 2). Geologic chronology can thus be founded on these orthogenetic changes (*Miogypsina, Orbitolina, Lepidocyclina, Bolivinoides;* see also: Hofker, 165, pp. 338-342).

Another instance of the increase of the diameter of the megalospheric proloculus during time, together with change in the nepionic chambers (which change may be due to an intervention by the organism on the orthogenetic increase of the proloculus) can be found in McGillavry, 1962; Hofker, 212, p. 28.

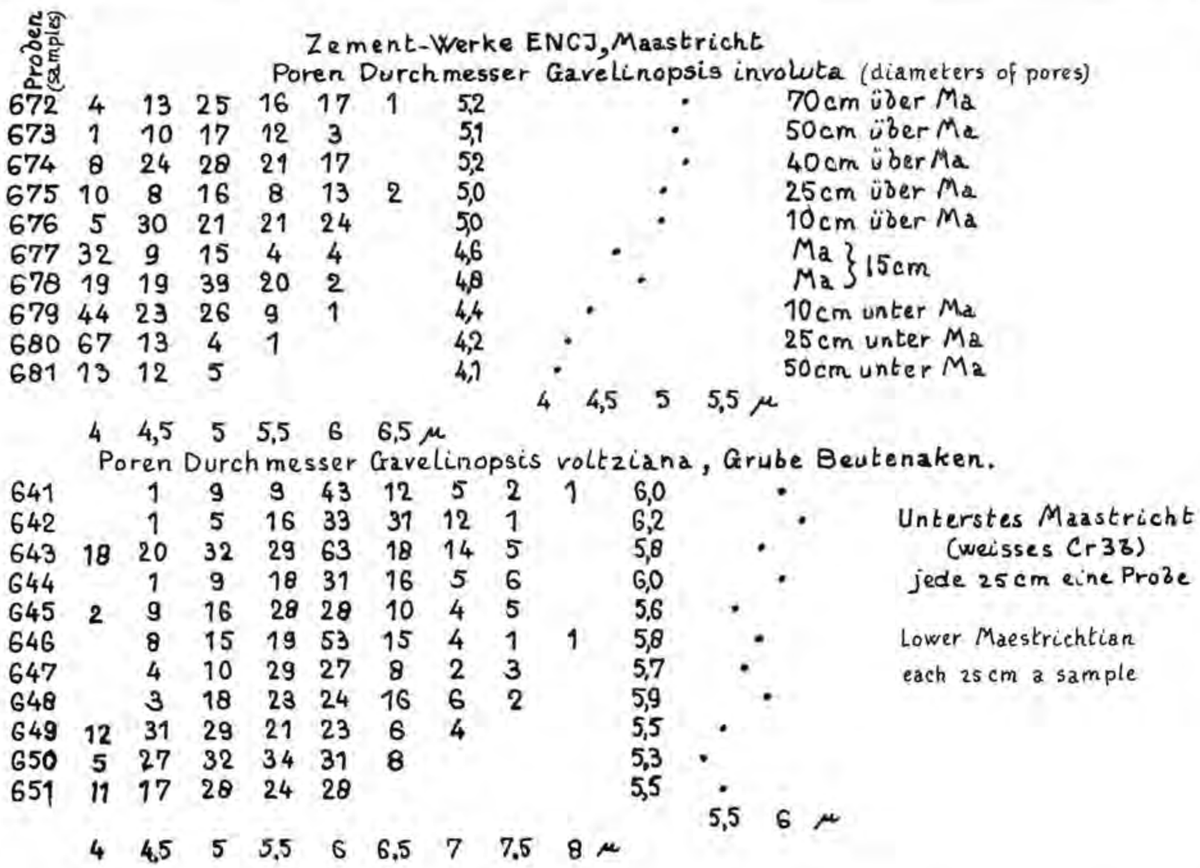
Remarkable are the Gavelinellidae which gradually increase the diameter of the pores of their tests during time. Many species of *Stensiöina, Gavelinella* and *Gavelinopsis* have been analysed in this respect by the present author (Hofker, 105, pp. 356-365; 370-374; 85, pp. 99-110, table; 133, pp. 249-254, textfig. 8-11; 164, p. 1075, text fig. 21a). In the group of *Stensiöina* several species succeed each other in north western Germany and in Holland from the Coniacian up into the Maestrichtian. Each species begins its evolution with small pores (diameter 1-2 μ) and ends its specific life with pores of about 7-8 μ. When a species attains a pore diameter of 4 μ, a new species starts and it is very propable that each new species is a kind of mutant of a former one (Hofker, 105, p. 355, text fig. 411). The same phenomenon was traced in species of *Gavelinella* and *Gavelinopsis;* here also the diameters of pores gradually increase during time from 1 to 8 μ, and in several instances a new, closely allied species abruptly appears when in the ancestral form the pores reach a diameter of 4 μ. This could be established for *Gavelinella costata* and *G. costata tumida* Brotzen, *G. pertusa* (Marsson) and its descendant *G. pertusa maestrichtiensis* Hofker. Moreover, it was found that in *Gavelinella*, when the pore-diameter of 4 μ is reached, the animals with larger pores succeeding this stage secrete an inner pseudochitinous membrane (see Hofker, 190, p. 114, fig. 203) It is suggested by the present writer, that the increase of pore-diameter is an answer of the animals to the increase of volume which is an orthogenetic phenomenon. The diameter of pores of 4 μ is here a critical point. Pores larger than 4 μ may easily give access to parasites and, moreover, make the animal more vulnerable; at a diameter of about 7-8 μ each species extinguishes, due to these unfavourable conditions. Some species in the stage of evolution of 4 μ diameter of the pores produced a new species which once again began with small pores; other species produced the pseudochitinous layer, obviously to eliminate the access by parasites. Most species did not even reach the pore-diameter of 8 μ. We have here another instance of an orthogenetic change which, when becoming unfavourable



Textfig. 8. The increase of pore-diameter in the quarry at Pourbaix, Basin of Mons, southern Belgium. The leap at the hard ground is distinct.



Textfig. 9. The same, in mean diameters.



Zement-Werke ENCI, Maastricht
Poren Durchmesser Gavelinopsis involuta (diameters of pores)

Proben (samples)	4	4,5	5	5,5	6	6,5 µ		
672	4	13	25	16	17	1	5,2	70 cm über Ma
673	1	10	17	12	3		5,1	50 cm über Ma
674	8	24	28	21	17		5,2	40 cm über Ma
675	10	8	16	8	13	2	5,0	25 cm über Ma
676	5	30	21	21	24		5,0	10 cm über Ma
677	32	9	15	4	4		4,6	Ma } 15 cm
678	19	19	39	20	2		4,8	Ma
679	44	23	26	9	1		4,4	10 cm unter Ma
680	67	13	4	1			4,2	25 cm unter Ma
681	13	12	5				4,1	50 cm unter Ma

Poren Durchmesser Gavelinopsis voltziana, Grube Beutenaken.

	4	4,5	5	5,5	6	6,5	7	7,5	8 µ	
641		1	9	9	43	12	5	2	1	6,0
642		1	5	16	33	31	12	1		6,2
643	18	20	32	29	63	18	14	5		5,8
644		1	9	18	31	16	5	6		6,0
645	2	9	16	28	28	10	4	5		5,6
646		8	15	19	53	15	4	1	1	5,8
647		4	10	29	27	8	2	3		5,7
648		3	18	23	24	16	6	2		5,9
649	12	31	29	21	23	6	4			5,5
650	5	27	32	34	31	8				5,3
651	11	17	28	24	28					5,5

Unterstes Maastricht
(weisses Cr3b)
jede 25 cm eine Probe

Lower Maestrichtian
each 25 cm a sample

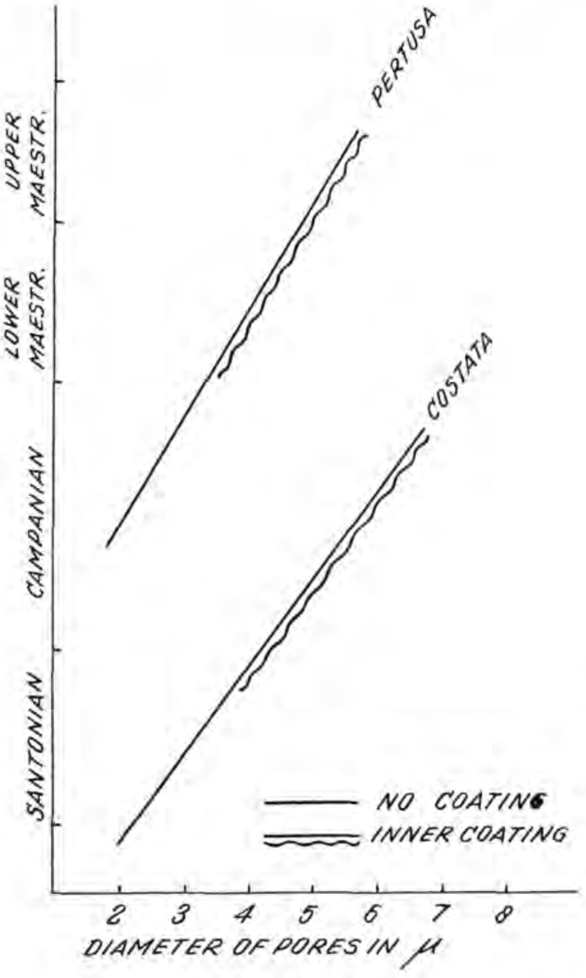
Textfig. 10. The increase of pore diameter of *Gavelinopsis involuta* (Reuss) in the Uppermost Maestrichtian and in the Maastricht Tuff Chalk and that of *Gavelinopsis voltziana* (d'Orbigny) in the Lower Maestrichtian of the quarry at Beutenaken, both in South Limburg, Netherlands. In both samplings the distance between two successive samples was about 25 cm. These instances prove that the increase of diameter of pores is a gliding one (orthogenesis).

for the species, lead to measures to prevent extinction; Textfig. 11.

It is obvious that these increases of diameters of pores in the Gavelinellidae can be used stratigraphically. Gaps in the sedimentation can be detected and even the relative duration of that gap can be found. Moreover it was found that this orthogenesis is independant of the environment.

All Gavelinellidae show the increase of size of tests during time. The first species of *Stensiöina* in the Coniacian and Santonian were small, those of the Maestrichtian had the largest tests known. Gradual increase of the diameter of the animals results in an increase of the surface to the second and the volume to the third power. Obviously conditions for respiration, to which pores mainly serve, gradually deteriorated, and thus the increase of the pores is plausible. Here once again the organism takes a measure to meet this deterioration by means of a gradual increase of the pores. This measure, however, leads in the end to extinction of the species; see Pl. 6, Fig. 9, 10; Textfigs. 6, 7, 8, 9 and 10.

The mentioned „mutations" in Gavelinellidae, leading to a new form or species beginning with small pores are not mutations in the sense of De Vries; the change, though sudden, has a special target and has obviously been caused



Textfig. 11. Two species have been studied, *Gavelinella costata* Brotzen and *G. pertusa* (Marsson). When the pores reach the diameter of about 4μ, in both instances an inner coating of pseudochitine appears, closing the pores from the inside, so that the pores can function as respiration openings but cannot be penetrated by parasites. This is an instance of active interference of the gens in the steady change caused by the orthogenesis.

purposefully by the organism itself, whereas De Vries' mutations are always at random. Obviously all these changes to divert the unfavourable results of the orthogenetic changes lead to the conclusion given by Teilhard de Chardin that a living entity (species, gens or even genus) has the inclination to reach a certain goal, though measures taken can also lead to extinction.

CHAPTER III

THE FORAMINIFERA AND THE SECTIO DIVINA

Why are the tests of Foraminifera so beautiful? This chapter gives the answer, proving that Foraminifera grow in such a way that the aesthetic ratio called the Sectio divina by Leonardo da Vinci is used. Also the spiral made by many tests is that, called by Goethe the „spiral of life". This spiral too has to do with the Sectio. Many examples are given here.

Most tests of Foraminifera are, to our eyes, beautiful. It was shown by Leonardo da Vinci that in nature, in the body of man, and in art, beautiful proportions often show the ratio which has been known since olden times as the Golden Section, or Golden Ratio. He called it Sectio divina, thinking that it was a token designed by God. This proportion seems first to have been used by Imhotep in 2500 B. C. when building his grandiose temple complex now known as the pyramid of Saccara; since this proportion had been prescribed to all artisans who made the art of Old Egypt; later the proportion was largely used in art by the Greeks and in the middle-ages, especially in pictures and in the building of cathedrals.

Many modern investigations in biology show that the Sectio Divina is found in plants (Schüep, 1959; Van Iterson, 1907; etc); Da Vinci showed that especially in molluscs the Sectio Divina ruled the proportions of shells.

Imhotep contructed the sectio in an easy and peculiar way which can be seen in the construction of the whole floor-plan of the temple-complex. He erected a large rectangular wall of stone around an area in the form of a double square, ABCG; constructing the diagonal AC, he found on it a point D so that DC = CB, the small side of the rectangle. Taking the length of AD, he found on AB a point E, so that AE = AD. The line AB is cut by E into two parts, AE and EB, and is thus divided according to the Sectio Divina. The proportion in this figure is AB:AE = AE:EB. This aquation can be easily demonstrated. Pl. 7, Fig. 1.

$$AC = \sqrt{(a^2 + 4a^2)} = a\sqrt{5} \text{ (Theorem of Pythagoras in triangle ABC)}$$

$$AD = a\sqrt{5} - a = a(\sqrt{5} - 1) = AE$$

$$EB = 2a - a\sqrt{5} + a = a(3 - \sqrt{5})$$

$$\frac{AE}{EB} = \frac{a(\sqrt{5} - 1)}{a(3 - \sqrt{5})} = \frac{\sqrt{5} - 1}{3 - \sqrt{5}} = \frac{2{,}236 - 1}{3 - 2{,}236} = 1{,}618$$

$$\frac{AB}{AE} = \frac{2a}{a(\sqrt{5} - 1)} = \frac{2}{\sqrt{5} - 1} = \frac{2}{2{,}236 - 1} = 1{,}618$$

This number 1,618 is called Phi (for Phidias) and has remarkable characteristics:

$$(\text{Phi})^2 = 2{,}618 = 1{,}618 + 1 = \text{Phi} + 1 \qquad (a)$$

$$\frac{1}{\text{Phi} - 1} = \frac{1}{0{,}618} = 1{,}272 = \sqrt{\text{Phi}} \qquad (b)$$

Equation (a) may be written as:

$$(\text{Phi})^2 = (\sqrt{\text{Phi}})^2 + 1^2$$

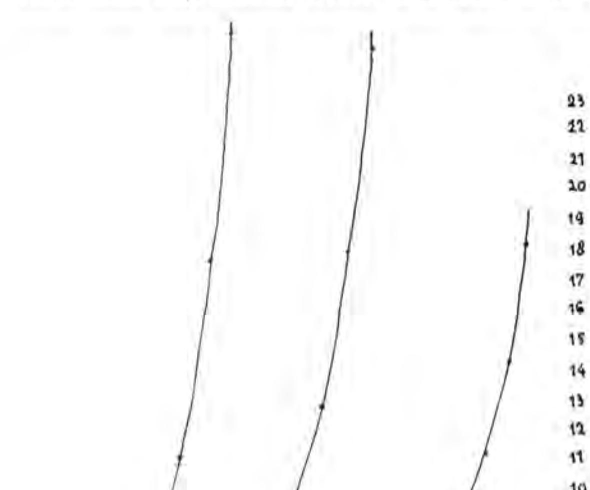
and corresponds with a rectangular triangle with sides Phi, $\sqrt{\text{Phi}}$ and 1.

This remarkable triangle is found in the rib, the height and half of a diagonal of the ground plan of the Pyramid of Cheops. In our design we can construct that triangle by constructing the angles found in that pyramid at A and B respectively 38° 10′ and 51° 50′. The right angle on top, F, is situated just above the point E, and thus the line FE divides AB according to the Sectio divina.

It will be obvious that in a gnomon, constructed with this triangle, the sides forming the right angles wil have the proportion $\sqrt{\text{Phi}}$:1, whereas all lines in the gnomon deviding the hypotenuse of the triangles will do so in the proportion

$(\sqrt{5}-1) : (3-\sqrt{5}) = \text{Phi} : 1.$ Such a gnomon is given in Pl. 7, fig. 2; to our delight we see that the tops of the triangles with right angles form together a beautiful spiral which has been called by Goethe the „spiral of life", since in many living organism, plants and animals, it can be detected; we only have to think of the beautifull section of a *Nautilus* to find that spiral.

When, in fig. 1, we take side $BF=1$, side $AF=\sqrt{\text{Phi}}$ and side $AB=\text{Phi}$, it will be obvious that any animal which will show a test with that spiral, will form such a test by a growing ratio which will equal more or less the equation $x=1:\sqrt{\text{Phi}}$, or $x=1{,}274$. It also may be possible that the volume increases proportionally to Phi, or $x=1.618$. In the case that horizontal sections are studied, this proportion will be $(\sqrt[3]{\text{Phi}})^2$ in the last mentioned case. $(\sqrt[3]{\text{Phi}})^2 = 1{,}378$.



Textfig. 12. Ideal curves of gnomons derived from resp.:

$$\text{Phi} = 1{,}618 \qquad (\sqrt[3]{\text{Phi}})^2 = 1{,}378 \qquad \text{and} \qquad \frac{1}{\sqrt{\text{Phi}}} = 1{,}274$$

In Foraminifera which are coiled in a planospiral, we will find that in many cases, in which the spiral is flat and the chambers are not overlapping at their sides, these numbers will come true. Obviously Foraminifera grow by means of the Sectio divina. We will even find in case of other modes of growth, such as a rectilinear growth, the proportion of growth is also that of the Sectio. I gave special attention to such forms, as *Neoflabellina*, *Plectofrondicularia*, *Rectobolivina*. etc., which during the growth of their tests change the pattern of chamber arrangement; it was found that the ratio of growth does not alter in such forms: the rule of the Sectio divina is maintained very carefully.

It will be obvious that in species in which the chambers overlap on one or both sides, the rule of the Sectio divina will be maintained in the proportion of growth of the whole chamber volume; consequently the spiral they will show on horizontal section will be narrower than Goethe's spiral. This can be demonstrated in the family of the Polystomellidae and the Nummulitidae. In some forms in which the chambers do not overlap, the spiral is that of Goethe; when the chambers are overlapping, the spiral becomes narrower than the typical spiral. So, in *Operculina* there is a typical spiral, whereas in *Assilina* with slightly overlapping chambers, the spiral is already narrower; in the strongly overlapping forms of *Nummulites*, the spiral belongs to the narrowest forms known. (One may compare in Staub, Evolutionary trends in Foraminifera, 1963, the Figs. 2 and 3 on pp. 288-289 dealing with *Nummulites*, with the Figs. 4 and 5 on pp. 292-293, dealing with *Assilina)*. Schaub, Lehman and Hottinger (Extrait Colloque sur le Paléogène, 1962, p. 633 and 635) gave two series of the group of „*Nummulites laevigata*", one (p. 633) with serrate spirals, the other (p. 635) with much looser spirals; it might be interesting to know, whether the transverse sections of the two groups also differ in overlapping of the chambers or the volumes of the alar prolongations. That might lead to a revision of the definition of the two groups.

We will now prove these statements.

Stilostomella sp., Tegel of Baden, quarry Sooss, Austria, Tortonian (Pl. 7, Fig. 3):

Chamber	Optical section	Approxim. volume	Ratio sections	Ratio volumes
1	21	84	1,1	1,1
2	23	92	1,3	1,6
3	29	145	1,4	1,5
4	42	210	1,1	1,3
5	48	272	1,7	2,0
6	78	546	1,2	1,4
7	96	768	1,4	2,0
8	137	1520	1,4	1,4
9	193	2130	1,4	1,6
10	270	3240		
	averages		1,34	1,6
			$(\sqrt[3]{\text{Phi}})^2$	Phi

A *Dentalina* from Ingolf St. 90, South off Greenland. gave the means 1,36 and 1.6 (Pl. 7. Fig. 4). *Vaginulina lata* Hofker from drill-hole Lathwehren 11, 67 m deep, Lower Campanian, gave following data (Pl. 7, Fig. 20):

Chamber	Optical section	Approxim. volume	Ratio sections	Ratio volumes
1	125	1000	0,4	0,2
2	50	200	1,7	2,1
3	85	425	3	5
4	245	2425	1,1	0,9
5	270	2140	1,7	2,9
6	475	6175	1,1	1,2
7	515	7210	1,6	1,8
8	850	13050	0,9	1,1
9	800	14400	1,4	1,6
10	1100	23200	0,8	0,9
11	1040	20800	1,2	1,4
12	1290	28380		
	averages		1,35	1,7
			$(\sqrt[3]{\text{Phi}})^2$	Phi

Chamber No 4 is an abnormal one, hence the too large mean in volume. We will now discuss the result of some coiled specimens.

Globorotalia canariensis (d'Orbigny). Challenger St. 300, Juan Fernandez (Pl. 7, Fig. 5):

In planktonic forms some of the later formed chambers are often more voluminous than the ratio of the section would suggest; but in many of these forms the last-formed chambers are much smaller and so the total increase is once more established, as will be given in the next instance:

Chamber	Optical section	Approxim. volume	Ratio sections	Ratio volumes
1	8	24	1,1	1,1
2	9	27	2	2,7
3	18	72	1,5	1,9
4	27	135	1,2	1,2
5	32	160	1,7	2,5
6	58	400	2,0	2,2
7	110	880	1,1	1,1
8	124	980	1,5	2,1
9	195	2125	2,1	3,0
10	430	6450	1,5	1,8
11	660	11220	1,3	1,4
12	800	15200	1,2	1,6
13	1000	25000		
	averages		1,5	1,6
			?	Phi

Globigerina spec., same locality (Pl. 7, Fig. 6)

Chamber	Optical section	Approxim. volume	Ratio sections	Ratio volumes
1	27	81	2,3	2
2	39	193	1,9	3
3	75	600	1,2	1,5
4	86	940	1,9	2,1
5	160	1900	2,1	2,5
6	325	4800	1,4	1,2
7	475	7000	1,5	2,1
8	725	15500	1,7	1,8
9	1250	28000	0,9	0,9
10	1125	27000	0,6	0,5
11	650	14000	0,8	0,6
12	590	9000		
	averages		1,4	1,65
			$(\sqrt[3]{\text{Phi}})^2$	Phi

Hyalinea baltica (Schwager), Bay of Napels, B-individual. Pl. 7, Figs. 7-9.

Chamber	Optical section	Approxim. volume	Ratio sections	Ratio volumes
3	4	8	1,2	1,25
4	5	10	1,2	1,8
5	6	18	1,1	1,17
6	7	21	1,1	1,6
7	11	33	0,9	1,1
8	10	30	1,0	1,0
9	10	30	1,0	1,0
10	10	30	1,1	1,1
11	11	33	0,9	0,9
12	10	30	1,5	2,0
13	15	60	1,1	1,1
14	16	64	1,1	1,28
15	18	90	1,15	1,16
16	21	105	1,25	1,0
17	26	104	1,0	1,2
18	26	125	1,2	1,5
19	32	192	1,15	1,15
20	37	222	1,8	1,65
21	61	366	1,1	1,13
22	69	414	1.08	1,1
23	74	444	0,9	0,9
24	68	414	0,8	0,7
25	56	336	1,9	2,4
26	104	832	0,9	0,8
27	99	693	1,3	1,85
28	130	1300	1,1	1,12
29	146	1460	1,4	1,59
30	209	2299	1,2	1,4
31	250	3250	0,9	0,75
32	240	2640	1,4	1,9
33	343	5145	0,8	0,7
34	305	3965		
	averages		1,18	1,268
			$\sqrt[3]{\text{Phi}}$	$\sqrt{\text{Phi}}$

The spiral of this B-specimen of *Hyalinea baltica* (Schwager) shows that the specimen, in which the chambers do not overlap has really Goethe's spiral; this can be verified in Pl. 7, Fig. 7;

Ratios of sides enclosing angles of 90°:	Ratios of parts in which hypotenuses have been divided by verticals:
68:55 = 1,23	52:32 = 1,62
55:42 = 1,3	32:20 = 1,6
42:34 = 1,23	20:12 = 1,65
34:26 = 1,3	12:7 = 1,7
26:21 = 1,24	7:5 = 1,4
21:16 = 1,31	43:22 = 1,9
16:13 = 1,23	22:11 = 2,0
13:10 = 1,3	11:10 = 1,1
10: 8 = 1,25	10: 6 = 1,6
average 1,26 √Phi	average 1,618 Phi

These two values indicate Goethe's spiral. In that spiral all lines through the centre of the spiral are divided by that centre into two parts which show the ratio Phi. These lines, more numerous than those forming the triangles with the sides Phi, 1, √Phi may show, from small to great, the result of the series of fractions known as the series of Fibonacci:

1+: 1/2, 2/3, 3/5, 5/8, 8/13, 13/21, 21/34, 34/55, 55/89, etc. This series is also the issue of the continuing fraction

$$1+\cfrac{1}{1+\cfrac{1}{1+\cfrac{1}{1+\cfrac{1}{1+1}}}}$$

etc.

The decimal fractions of these issues more and more approximate 1,618 (Phi). In the megalospheric generation of *Hyalinea baltica*, though the proloculus is much larger than the microspheric proloculus (in our method of measuring 4:58), the chamber following the proloculus is smaller and the following chambers again show in their ratio of growth 1,18, ($\sqrt[3]{\text{Phi}}$), in the ratio of approximate volumes 1,27 (√Phi) and in the ratio of divisions of lines through the centre of the spiral 1,29 (√Phi) and 1.6 (Phi). It will be obvious that, comparing the two generations, in the B-generation the number of chambers per evolution of the spiral is larger than in the A-generation (in our instance 13 and 11 in the last formed whorl):

Hyalinea baltica, Bay of Naples, A-individual (Pl. 7, Fig. 9).

Chamber	Optical section	Approxim. volume	Ratio sections	Ratio volumes
2	30	210	1,43	1,17
3	43	258	0,95	0,95
4	38	234	1,1	1,2
5	40	280	1,15	1,18
6	46	322	1,4	1,8
7	74	592	1,1	1,1
8	82	656	0,9	0,9
9	77	539	1,3	1,53
10	103	824	1,2	1,39
11	125	1125	1,2	1,35
12	150	1500	1,1	1,2
13	165	1815	1,13	1,34
14	184	2428	1,6	1,8
15	295	4425	0,8	0,7
16	254	3301	1,1	1,4
17	274	4658		
	averages		1,18	1,27

Ratios of sides enclosing angles of 90°:	Ratios of parts in which hypotenuses have been divided by verticals:
59:48 = 1,23	46:31 = 1,5
48:40 = 1,20	31:20 = 1,55
40:31 = 1,3	20:11 = 1,81
31:25 = 1,24	11: 7 = 1,71
25:19 = 1,31	39:24 = 1,62
19:15 = 1,27	24:15 = 1,6
15:11 = 1,27	15: 9 = 1,66
11: 9 = 1,22	9: 6 = 1,33
average 1,26 √Phi	average 1,61 Phi

These numbers show that *Hyalinea baltica* is an ideally built species, showing the law of the Sectio divina in Foraminifera.

In many species of the Polystomellidae the spirals are nearly ideal when the chambers, as in *Hyalinea baltica*, are not overlapping on the sides of the test. This could be proved in the following cases.

Elphidiononion poeyianum (d'Orbigny) (Pl. 7, Fig. 9-10).

sides of angle 90°	parts of hypotenuses
60:46 = 1,3	47:27 = 1,74
40:33 = 1,4	27:16 = 1,68
33:26 = 1,26	16:10 = 1,6
26:20 = 1,3	36:19 = 1,89
20:16 = 1,25	19:12 = 1,59
16:12 = 1,33	12: 6 = 2,0
means: 1,29 √Phi	means: 1,69 Phi

Elphidiononion oregonense (Cushman) (Pl. 7, Figs. 14-15).

ratio sides of angle 90°	ratio parts of hypotenuses
66:57 = 1,16	51:36 = 1,41
57:46 = 1,24	36:22 = 1,63
46:37 = 1,38	22:13 = 1,7
37:29 = 1,27	44:29 = 1,5
29:22 = 1,3	29:16 = 1,8
22:18 = 1,2	16:11 = 1,45
means: 1,26	means: 1,59
√Phi	Phi

Elphidium macellum (Fichtel and Moll) (Pl. 7, Figs. 12, 13).

ratio sides of angle 90°	ratio parts of hypotenuses
57:45 = 1,26	45:29 = 1,8
45:36 = 1,25	29:16 = 1,8
36:29 = 1,24	16:11 = 1,5
29:22 = 1,32	35:22 = 1,6
22:16 = 1,36	22:13 = 1,68
16:13 = 1,23	13: 8 = 1,6
means: 1,27	means: 1,65
√Phi	Phi

The spirals of species with overlapping chambers at both sides (chambers with alar prolongations) also have chamber volumes which grow with the ratio 1,27, but it is impossible to prove this, since the transverse sections of these chambers cannot be given in exact figures. It will be obvious that such species must have a spiral which is narrower than Goethe's spiral; this will be expressed by the ratios which must give smaller numbers and an average smaller than Phi and √Phi.

Elphidiononion schenki (Cushman and Dusenbury) (Pl. 7, Figs. 16, 17).

ratio sides of angle 90°	ratio parts of hypotenuses
56:48 = 1,27	42:29 = 1,4
48:38 = 1,27	29:21 = 1,4
38:33 = 1,15	21:14 = 1,5
33:28 = 1,2	14: 9 = 1,55
28:24 = 1,15	9: 6 = 1,33
24:19 = 1,25	38:25 = 1,5
19:16 = 1,2	25:18 = 1,4
16:13 = 1,2	18:12 = 1,5
13:10 = 1,3	12: 8 = 1,5
average: 1,21	average: 1,45
smaller than √Phi	smaller than Phi

Elphidiononion striatopunctatum (Fichtel and Moll) (Pl. 7, Figs. 18, 19).

ratio sides of angle 90°	ratio parts of hypotenuses
55:44 = 1,25	43:28 = 1,5
44:40 = 1,1	28:18 = 1,55
40:36 = 1,1	18:12 = 1,5
36:28 = 1,3	12: 8 = 1,33
28:23 = 1,22	35:28 = 1,27
23:19 = 1,2	28:18 = 1,55
19:17 = 1,1	
17:13 = 1,3	
average: 1,19	average: 1,44
smaller than √Phi	smaller than Phi

It will be obvious that the wide spiral of „*Operculina*" is Goethe's spiral (spiral of life), whereas „*Assilina*" with broad triangular chambers has already narrower spirals and that the narrowest spirals will be found in „*Nummulites*" with their strongly overlapping chambers at the sides of the tests (alar prolongations).

In forms in which during the animal life the pattern of chamber building changes, the rule of the sectio divina prevails. *Peneroplis planatus* Cushman from the West Indies has an entirely flat test with hardly any embracing chambers; in the end the chambers become flaring; yet the result of the averages of optical sections is 1,3, which is close to the value of √Phi, 1,272.

The same may be said of flat *Neoflabellina* sp. from drill-hole Lathwehren 11, 187 m, Lower Campanian (Pl. 7, Fig. 21).

Chamber	Optical section	Ratio sections
1	25	1,3
2	34	1,9
3	67	3,0
4	205	0,8
5	169	1,7
6	274	0,9
7	260	1,6
8	425	1,4
9	595	1,5
10	910	1,2
11	1145	1,4
12	1600	1,4
13	2225	1,4
	average:	1,34
		$(\sqrt[3]{\text{Phi}})^2$

Neoflabellina sp., drill-hole Lathwehren 11, 67 m, Campanian.

Chamber	Optical section	Ratio sections
1	47	0,8
2	37	1,3
3	54	2,0
4	102	1,1

5	115	1,5
6	195	1,6
7	300	1,5
8	475	1,4
9	700	1,5
10	1100	1,2
11	1300	1,4
12	1800	1,5
13	2750	
	average:	1,4 $(\sqrt[3]{\text{Phi}})^2$

In the specimen of *Neoflabellina* from 187 m, the change in the building of chambers from spirally into overlapping at both sides and rectilinear occurs between the chambers 8 and 9; in the specimen from 67 m, the change occurs between the chambers 5 and 6; yet no accountable change occurs in the ratios.

Another type of change of chamber-pattern is found in *Plectofrondicularia;* here the pattern changes from biserial into uniserial. Several specimens from the Eocene of Ecuador, *P. dentifera* Cushman and Stainforth, showed the following ratios of the succeeding chambers in optical section:

Individual A	Ratio
A	1,36
B	1,30
C	1,26
D	1,32
E	1,37
F	1,37
G	1,34
average:	$1{,}33=(\sqrt[3]{\text{Phi}})^2$

Here also the change of pattern does not result in a change of the ratio. This can be seen in individual D (Pl. 8, Fig. 2):

Chamber	Optical section	Ratio sections
1	26	1,7
2	45	1,0
3	45	1,5
4	68	1,7
5	120	1,3
6	156	0,9
7	152	1,3
8	203	1,7
9	360	0,8
10	324	1,2
11	400	1,1
12	441	1,4
13	608	1,4
14	854	1,2
15	930	
	average:	1,32

In this individual the change in building pattern is found between the chambers 10 and 11, but the ratio does not change notably.

Quite a similar result was obtained when analysing *Rectobolivina;* here the average of the ratio of optical sections of the chambers was also 1,32-1,37, and no change in the ratio occurred when the pattern changed.

It will be obvious that flat forms which change the pattern from coiled into circular will show the rule of the Sectio divina and here it was also found that in forms like *Heterostegina* and *Cycloclypeus* the ratio does not change at the change of pattern. The change of pattern seems to be the way in which the animal can continue the rule of the Sectio without altering the entire form of the test. Specimens beginning with a small proloculus will be able to maintain the first primitive pattern much longer than individuals beginning with a larger proloculus. This phenomenon which has been stated by the author in many Foraminifera *(Spiroplectinata, Gaudryina, Plectofrondicularia, Rectobolivina, Bolivinopsis, Heterostegina, Cycloclypeus)* is widely known. When, during the evolution of a species or a group of species the megalospheric proloculus has the tendency to become larger and larger *(Orbitoides, Orbitolina, Orbitolites,* etc.) the necessity of changing the pattern will come sooner and sooner in the ontogeny of the individuals. Such changes which have caused authors to create many sub-groups and species in such an evolution series. They are only due to the rigorous rule of the Sectio divina. Within one species this difference in the chamber number in which the change of pattern takes place can consequently be stated in the difference between the microspheric and the megalosperic forms. An example is *Frondicularia sagittula* van den Broek (Pl. 7, Figs 22, 23).

In the B-form of *F.sagittula* the characters are those of the genus *Palmula*, with an abrupt change from coiled chambers into uniserial chambers between the chambers 6 and 7. We find only a small increase of the ratio here:

Chamber	Optical section	Ratio
1	15	1,2
2	18	1,7
3	31	1,7
4	52	1,5
5	76	1,8
6	135	2
7	275	1,7
8	430	1,8

9	800	1,5
10	1275	
		average: 1,6

Since the test is extremely thin, the thinckness of the volume of each chamber is to be neglected; hence the ratio is not $(\sqrt[3]{\text{Phi}})^2$ but nearly 1, 618, Phi itself.

The megalospheric test has no change of the pattern since the proloculus is so large: directly the proloculus is followed by embracing chambers.

Chamber	Optical section	Ratio sections
1	1600	0,8
2	1225	2,0
3	2400	1,23
4	2950	1,51
5	4450	
	average:	1,56, thus

pointing to Phi, when we do not incalculate the very large proloculus.

A specimen of *Puteolina discoidea* (Flint) showed the following ratios: (it begins with a spiral and ends with circular chambers) (Pl. 7, Fig. 24):

Chamber	Horizontal section	Ratio chambers
1	50	1,0
2	50	1,2
3	60	1,66
4	100	1,15
5	115	1,3
6	140	1,0
7	140	1,61
8	225	1,64
9	360	1,42
10	510	1,18
11	600	1,5
12	920	1,14
13	1040	1,32
14	1375	1,3
15	1675	
	average:	1,317
		$(\sqrt[3]{\text{Phi}})^2$

There is a change in the pattern from coiled to flaring at chambers 6-7 and flaring into circular at chambers 13-14.

A specimen of *Sorites orbitolitoides* Hofker with small proloculus gave data (Pl. 8, Fig. 1, 3) which, compared with those of *Plectofrondicularia* and *Neoflabellina* are quite similar though the architecture of these three genera is quite different.

CHAPTER IV

THE SEPTA OF THE FORAMINIFERA

After the investigations by Smout and Reiss, the septa of the Foraminifera seen in horizontal sections (transverse to the septa) were thought to have special importance as to their structure. Loeblich and Tappan and Reiss based their systems of Foraminifera on the monolamellar or bilamellar structures of these septa.

A study of a large number of species showed, however, that the structures of the septa and of the septal borders of the foramina are so variable that they cannot be used for suprageneric division. Moreover, septal flaps hamper the judgement considerably.

Planktonic species have simple septa as a rule; these septa invariably are hyaline, mostly crystalline radial; this structure seems to be caused by the planktonic life.

Benthonic species in most cases show agglutinated or granular primary walls, which may be simple, or may be thickened by fibrous radial or crystalline material at one of the sides of the septa (inner or outer sides) or on both sides. The primary wall remains visible. When the thickening occurs on both sides, with small magnification a double septum may appear, with two layers (lamella) separated by a dark line. With large magnification this dark line shows to be the primary wall. In rare instances the walls are really double (bilamellar). Many genera suggested to be bilamellar, are monolamellar but with a primary wall which is the sole wall in the more initial chambers.

The part of a chamber wall between the aperture of a chamber and the outer wall of the whole test is the septum. The structure of such a septum may be of value for the taxonomic position of a species, the more since Reiss has laid much stress on that structure.

In the Protoforaminata the septa are always simple, at least in the groups which have no Rotaliid arrangement of the chambers. Buliminidae, Bolivinidae, Lagenidae, etc, have simple septa, formed by the former apertural parts of a chamber wall.

In the trochoid Foraminifera which have, moreover, calcareous walls, many groups have also simple chamber walls. But in case these forms with simple chamber walls have toothplates, such a plate may also add a lamellum to that wall; the whole septal wall may be covered by this toothplate, as is the case in *Schubertia tessellata* (Schubert) and in *Alfrobolivina*, or it may partly cover the septal wall, as is the case in many Rotaliidae, such as *Streblus* and *Elphidium;* that part of the toothplate is known as the „septal flap". Even the attached parts of toothplates in Protoforaminifera, such as *Bulimina, Praebulimina, Buliminella, Bolivina, Cassidulina*, etc., are nothing but the very scantily formed „septal flaps". Since each toothplate begins at the border of a protoforamen, it is obvious that only in forms which have such a protoforamen, or a foramen in which the protoforamen is only part of the whole foramen (foramen compositum), real toothplates can be found, and, consequently," septal flaps".

The septa, as parts of the chamber walls, often have the inner structure of those walls. Forms with hyaline walls have also hyaline septa. As these septa are formed primarily by the protoplasm, and this always is found in the last formed chamber at the inner side of the outer wall, they have to be called primary septa. There is always the possibility that after having been formed, in a later period of the life of the animal secondary walls may be formed within the primary walls; in most observed cases such walls consist of tectin, or pseudochitin. There are, however, instances known in which these walls secondarily formed, are built of calcite; in any case, these inner secondary walls, later formed, do not possess the pores in species with porous walls.

Primitive palaeozoic Foraminifera often show double walls, and consequently double septa. In most cases the outer wall is finely agglutinated, whereas the inner wall is more hyaline and calcareous (e.g. *Tetrataxis)*. In the species studied these walls do not show two distinct layers, but the outer agglutinated layer more or less gradually becomes more hyaline. Similar walls are found in many of the Rotaliid Foraminifera. There is an inner layer which is granular (with high enlargement distinct granules of different forms are seen and in some instances small parts of coccolithes and other organic matter is also inclosed). When studying the building of a new chamber, one may see that the outer protoplasm, before the wall takes shape, is also filled with fine granules, deriving from food particles. Many calcareous Foraminifera with hyaline calcareous walls show these granulations in the inner part of the primary wall. I emphasize that two kinds of calcareous walls can be found. There are aragonitic walls, and in that case the septa are mostly simple; but calcitic walls occur in many more groups of the Foraminifera. These calcitic walls can be separated again into two kinds: there are walls which consist, when we do not consider basal granulation, of hyaline chalk, often showing in polarised light that the whole wall of one chamber is a single crystal (sphaerocrystal); there are other calcareous walls which consist of fine calcitic prisms which form together a sphaerocrystal such as amylum does. There also exist calcareous hyaline walls which do not show the phenomena in polarized light which are typical of crystallisation.

I will here distinguish calcareous walls, hyaline walls and crystalline walls. It is remarkable that aragonitic walls, which occur especially in primitive species (e.g. *Bolivina rumbleri* Franke from the Jurassic in contrast to the *Bolivinae* of the Cretaceous to Recent), always show crystalline structure in polarised light.

Hyaline as well as crystalline walls may show granulations in the inner parts; of them these granulations form a more or less distinct layer in the wall of a septum; such a layer might be considered as a distinct wall; but in most cases high magnification reveals that as in the Palaeozoic forms, the granulated wall gradually becomes hyaline more to the outside. I do not consider such septa as double. In the genus *Mississippina* there is an inner granulated wall covering the whole chamber, and this wall is partly covered by a crystalline wall at the margins of the chambers and nearer to the sutures. Here the inner granulated (or even agglutinaed) wall is the primary wall, and the crystalline wall parts are formed secondarily at the outer surface. But in this instance too, there is often no sharp border between the two kinds of walls.

On the other hand, there are walls which are granulated throughout. I believe that in reality they are agglutinated, though the agglutination is rather a fine one.

In some Foraminifera (species of *Cibicides, Planulina, Mississippina)* it seems that at first a thick layer of agglutinated material is formed. It may be added that this layer was thickened at the outside by a hyaline or crystalline layer, and afterwards a hyaline or crystalline inner calcareous layer may be added. Such forms thus have septa which consist of three layers.

Simple hyaline septa.

They have been found in:
- *Cancris auriculus* (Fichel and Moll)
- *Neoconorbina neapolitana* Hofker
- *Pileolina parisiensis* (d'Orbigny)
- *Discopulvinulina globularis* (d'Orbigny)
- *Palmerinella palmerae* Bermudez
- *Höglundina hyalina* Hofker
- *Höglundina elegans* (d'Orbigny)
- *Lamarckina atlantica* Cushman
- *Sorites orbitolinoides* (Hofker)
- *Orbitolites complanata* Lamarck
- *Orbitolites hemprichii* (Ehrenberg)
- *Buccella frigida* (Cushman)
- *Halkyardia* sp.
- *Linderina visserae* Hofker
- *Pararotalia tuberculifera* (Reuss)
- *Pararotalia mexicana* (Nuttal)
- *Pararotalia inermis* (Terquem)
- *Baculogypsina sphaerulata* (Parker and Jones)
- *Daviesina fleuriausi* (d'Orbigny)
- *Elphidiononion semistriatum* (d'Orbigny)
- *Globigerina triloculinoides* Plummer
- *Globigerina pseudobulloides* Plummer
- *Globigerina cretacea* d'Orbigny
- *Globigerina bulloides* d'Orbigny (toothplate may make a sling)
- *Globigerina triloba* Reuss (toothplate may make a sling)
- *Globigerina eggeri* Rhumbler
- *Globotruncana linneiformis* Hofker
- *Globotruncana paraventricosa* Hofker
- *Globotruncana globigerinoides* Brotzen
- *Globorotalia tumida* (Brady) (toothplate may make a sling)
- *Globorotalia menardii* (d'Orbigny) (toothplate may make a sling)
- *Globorotalia truncatulinoides* (d'Orbigny) (toothplate may make a sling)
- *Hantkenina alabamensis* Cushman
- *Myogypsina ecuadorensis* Tan Sin Hok

In these species, especially in the planktonic forms, the toothplate, which also forms an outer umbilical plate, may form at the foramen a sling bending backward over the rim of the foramen and may follow the septum for a short distance, thus giving it partly a double structure.

Septum simple, hyaline, with septal flap.

The septal flap, formed by the toothplate, is already formed in a way in the planktonic forms mentioned above (the sling); here it is more prominent and mostly doubles the septum from the outer wall on, but seldom reaches the foramen.

Daviesina fleurausi (?) (d'Orbigny)
Parrellina imperatrix (Brady)
Notorotalia clathrata (Brady)
Elphidium crispum (Linné)
Elphidium advenum (Cushman)
Asterorotalia papillosa (Brady)
Asterorotalia pulchella (d'Orbigny)

Septum simple, crystalline.

Candeina nitida d'Orbigny
Globigerinatella insueta Cushman and Stainforth

Septum simple, with septal flap, crystalline.

Calcarina defrancei d'Orbigny

Septum simple, granular.

Osangularia lens Brotzen
Alabamina midwayensis Brotzen
Globorotalites, young
Parrelloides succedens Brotzen
Cibicides ribbingii Brotzen, young
Anomalina alazanensis Nuttal
Planulina renzi Cushman and Stainforth
Eponides umbonatus (Reuss)
Eponides crebbsi Hedberg
Eponides antillarum (d'Orbigny)
Nonionella communis (d'Orbigny)
Nonionella troostae (Visser)
Planorbulinella cretae (Marsson), young
Mississippina binkhorsti (Reuss) (partly)
Mississippina concentrica (Parker and Jones) (partly)

Some of these species show simple septa only in the initial parts of the tests; in older chambers double septa, or septa with only a granulation in the inner parts may develop.

Septum simple, basal (inner) part granular, becoming more and more hyaline towards the outer part of the septum.

Parrelloides alleni (Plummer)
Parelloides midwayensis (Plummer)
Eponides parantillarum Galloway and Heminway
Eponides repandus (Fichtel and Moll)
Eponides jacksonensis Cushman
Eponides toulmini Brotzen
Eponides byramensis (Cushman)
Eponides procera (Brady)
Streblus beccarii (Linné) (with septal flap)
Pseudorotalia schroeteriana (Parker and Jones) (with septal flap)
Planorbulina mediterranensis d'Orbigny
Gypsina discus (Carter)
Acervulina spec.
Ferrayina coralliformis Frizzel
Siphonina pulchra Cushman
Planulina wuellerstorfi Schwager
Asterigerina carinata d'Orbigny
Lepidocyclina yurnagunensis Cushman
Operculina complanata (Defrance) (with septal flap)

Septum simple, crystalline, inner part granular, then becoming crystalline in the outer parts.

Gypsina globulus (Reuss)
Lepidorbitoides minor Schlumberger
Siderolites (Calcarina) spengleri (Gmelin)
Siderolites calcitrapoides Lamarck
Siderolites vidali Douvillé
Rotalia trochidiformis Lamarck (with septal flap)

Septum double, two hyaline layers without granulation between.

Miniacina miniacea (Pallas)
Nummulites hyalina Hofker
Biarritzina proteiformis (Goës)

No other instances could be found up to now.

Septum double, inner layer granular, outer layer crystalline, with sharp border between the two layers.

Gavelinella danica Brotzen (from Maestrichtian)
Stensiöina exsculpta (Reuss)
Stensiöina pommerana Brotzen
Gyroidinoides planulata Cushman and Renz
Gyroidinoides girardana (Reuss)
Gavelinonion pompilioides (Fichtel and Moll)

Planorbulinella cretae (Marsson), adult
Mississippina binkhorsti (Reuss) (partly)
Mississippina concentrica (Parker and Jones) (partly)
Parrelloides foveolata (Brady)
Cibicides ribbingii Brotzen, adult

Septum double, inner layer granular, outer layer hyaline.

Gyroidinoides subangulata (Plummer)
Gyroidina orbicularis d'Orbigny

Septum double, outer layer granular, inner layer crystalline.

Gyroidinoides nitida (Reuss)
Gyroidinoides cochleata Cushman
Cibicides lobatulus (d'Orbigny)

Septum double, both layers granular.

Eponides beisseli Schijfsma
Gyroidinoides depressa (Alth)

Septum double, or better trifold; middle layer granular, inner and outer layers hyaline.

Gavelinopsis involuta (Reuss)
Gavelinopsis perlucida (Nuttal)
Cymbaloporetta squammosa (d'Orbigny)
Cibicides refulgens Montfort
Homotrema rubrum (Lamarck)

Septum double, or better trifold; middle layer granular, both inner and outer layers crystalline.

Gavelinella tumida Brotzen
Parrelloides dutemplei d'Orbigny
Mississippina binkhorsti (Reuss) (partly)
Planulina ariminensis d'Orbigny

These lists do not give us much hope for a supra-generic characteristic formed by the structure of the septa in the sense used by Reiss. Nearly all sections studied were taken from air-filled material, and all sections were very thin horizontal sections. It was found, that most of the structures of the septa can be used as specific characteristics, and only in some cases (planktonic Foraminifera, *Pararotalia* and its allies, *Baculogypsina* and *Miogypsina*, the two groups of *Eponides*, *Elphidium* and allies, *Asterorotalia*, possibly *Pseudorotalia*, *Stensiöina*, *Mississippina* (all kinds of structures together), *Parrelloides)* the structure of the septa is of generic importance. But there is no supra-generic characteristic which can be used constantly.

There are some remarkable contradictions between the observations by Reiss and others and my statements. Reiss believes the *Globotruncanae* to be bilamellar (1957); sections of air-filled specimens of three different species, however, showed simple septa; but at the border of the septal foramina the toothplate adheres, often forming a string with a short flap running a short way along the septum, thus giving the idea of a double septum; this toothplate at the umbilical part of the foramen compositum changes into the umbilical plate covering a large part of the umbilical hollow.

The outgrowths of the toothplates of *Afrobolivina* and *Schubertia tessellata* (Brady) also cause double septa; double septa are not restricted to the Rotaliiformes; but in these two cases the doubling of the septa is entirely due to the toothplate and is thus comparable with the structures in *Rotalia*, *Streblus*, *Elphidium*, *Asterorotalia;* they are „septal flaps". It is not entirely impossible, that some double walls, as they have been found in *Gavelinella*, as they result in a prolongation of the bending foraminal border, may originally have been formed by the toothplate; in that case, the curling toothplate of the planktonic forms and the toohplates originating from the border of the septal foramina (former apertures) may be homologous. In reality, toothplates are always formed at the outer side of a former chamber, beginning at the border of a protoforamen; in that case the foramina of such forms might be protoforamina, or, as I stated in the case of *Globotruncana*, foramina composita (Hofker, 1956). It might be, that this explains, why in some species of Foraminifera with double septa the inner layer, and in other species the outer layer is hyaline. Toothplates, spreading within the chamber to which they belong, over the inner, mostly basal, septum *(Afrobolivina. Schubertia)* may form a somewhat more granular outer septal layer; toothplates forming a septal flap often show, that the septal flap is more granular than the hyaline septum underneath. In *Rotalia trochidiformis*, large parts of the toothplate follow the basal septal parts of a chamber; this toothplate in this species is largely granular, whereas the chamberwall is crystalline. In the case that such a toothplate would be restricted to a layer, beginning at the upturned border of the foramen and only forming a tectum over the primary septum, a double septum would be formed. It may be that here is the cause of some confusion, in the case of *Globorotalia*, where septa of more initial chambers are simple, and some septa of adult chambers may be taken as double; for in *Globorotalia* I also stated the occurrence of foramina composita (1962).

Structure of the apertural border of the septa

When sectioning forms such as *Bolivina*, *Bulimina*, *Uvigerina* in the longitudinal direction, the foramina are mostly cut transversely. In this way we get an idea of the lips at the border of the foramina as well as of the attachment of the toothplates. All these forms show simple septa and, when lips are present, these lips are in section totally hyaline or crystalline, without traces of granulations.

In case we wish to know apertural conditions in rotaliform species, we have to section horizontally, since here the foramina open in planes in which also the axis of the test is situated.

When a lip at the border of the foramina is present, it has mostly the form of an S in the sections; this is also the case in forms like *Uvigerina*. I will mention these bordering lips as „sigmoid". The majority of rotaliform Foraminifera has such lips.

Just as in the Foraminifera of the groups mentioned above, when toothplates are present, these plates are attached at the outer side of these lips. Since I found that toothplates are always attached proximally to protoforamina, it is obvious that when structures are found attached to sigmoid foraminal borders, these foramina must also be protoforamina. When foramina composita are found, then the toothplates are attached to the protoforaminal part of the foramen compositum. In thin sections, the place where the toothplate is attached to the lip can clearly be seen as a dictinct bordering line. This shows that the toothplate is formed later, when the next chamber is built up, and it belongs to the next chamber.

In the case that granulation is found in the septa, it also continues in the sigmoid lip. This means that the lip is built at the same time as the septum itself. In some instances the latest formed chamber had a very thin wall; in that case only the granulated part of the wall was found here in those cases in which the granulation in the older septa was found in the inner part of the septum. Obviously the granulated part of the wall is the primary one, and the hyaline outer part is secondarily thickened.

We may distinguish the following kinds of apertural borders:

Sigmoid lip, hyaline wall, mostly with toothplate attached to the lip

1. *Globigerina triloba* (Reuss)
2. *Globorotalia truncatulinoides* (d'Orbigny)
3. *Globorotalia menardii* (d'Orbigny)
4. *Globigerina bulloides* d'Orbigny
5. *Hantkenina alabamensis* Cushman
6. *Globorotalia tumida* (Brady)
7. *Globigerina cretacea* d'Orbigny
8. *Afrobolivina afra* Reyment
9. *Streblus beccarii* (Linné)
10. *Elphidium crispum* (Linné)
11. *Parrellina imperatrix* (Brady)
12. *Asterorotalia papillosa* (Brady)
13. *Asterorotalia pulchella* (d'Orbigny)
14. *Globotruncana linneiformis* Hofker
15. *Globotruncana globigerinoides* Brotzen
16. *Globotruncana paraventricosa* Hofker
17. *Notorotalia clathrata* (Brady)
18. *Globigerina triloculinoides* Plummer
19. *Globigerina pseudobulloides* Plummer
20. *Daviesina fleuriausi* (?) (d'Orbigny)

Some of these species, especially the planktonic ones, develop the toothplate into a plate covering the umbilical cavity; in other forms, the plate is developed into flanges bordering the aperture *(Hantkenina)*; in *Globorotalia* part of the plate runs down the septa and may give rise to the idea that part of the septum is double, whereas another part of the toothplate here forms a distinct lip over the larger part of the aperture; in many of the species the toothplate is complex and runs down the septum forming the „septal flap" with its canals and sutural openings *(Elphidium, Notorotalia); in Asterorotalia* this flap forms canals ventrally between two adjacent chambers, which canals are partly closed by secondary plates, in which pores are found. In many species of the *Asterigerinidae* covering plates are found too, also pierced by pores, which plates close the protoforamen or that part of the foramen compositum which is formed by the protoforamen. This may also be so in Epistomariidae, *Reinholdella, Robertinoi-*

des. Pseudobulimina. The hollows within these plates have often been described as secondary chamberlets. These covering plates with pores are formed by toothplates in many cases *(Asterorotalia)*.

Sigmoidal lips, with granular part, mostly otherwise hyaline, and the granular layer continuing in the middle of the septum (trifold structure).

21 *Planularia ariminensis* d'Orbigny (crystalline)
22 *Gavelinopsis perlucida* (Nuttal)
23 *Cymbaloporetta squammosa* (d'Orbigny)
24 *Parrelloides dutemplei* (d'Orbigny) (crystalline)
25 *Cibicides temperata* Cushman and Renz
26 *Gyroidinoides girardana* (d'Orbigny) (crystalline)
27 *Gavelinella tumida* Brotzen
28 *Cibicides refulgens* Montfort
29 *Gavelinopsis involuta* (Reuss)
30 *Melonis affinis* (Reuss)

Sigmodal lips, with granulation, but this granulation continues in the inner part of the septum.

31 *Eponides byramensis* Cushman
32 *Asterigerina carinata* d'Orbigny
33 *Pseudorotalia schroeteriana* (Carpenter, Parker and Jones) with toothplate attached to lip)
34 *Operculina complanata* (Defrance) (with septal flap)
35 *Eponides parantillarum* Galloway and Heminway
36 *Planorbulina mediterranensis* d'Orbigny
37 *Hyalinea baltica* (Schwager)
38 *Parrelloides foveolata* (Brady)
39 *Parrelloides alleni* (Plummer)
40 *Gyroidinoides planulata* (Cushman and Renz)
41 *Gyroidinoides cochleata* (Cushman)
42 *Parrelloides midwayensis* (Plummer)
43 *Acervularia* spec.
44 *Eponides repandus* Fichtel and Moll
45 *Eponides jacksonensis* Cushman
46 *Eponides procera* (Brady)
47 *Eponides toulmini* Brotzen
48 *Siphonina pulchra* Cushman
49 *Pararotalia inermis* (Terquem)
50 *Osangularia mexicana* (Cole)
51 *Planulina wuellerstorfi* Schwager
52 *Valvulineria nuttalli* Palmer and Bermudez

It is probable, that the hyaline part of the septum in the *Eponides* species mentioned here, especially *E. repandus* Fichtel and Moll. is nothing but a toothplate running along the outer primary septal wall, since in these species the attachment of this hyaline layer with the foraminal border does not differ from that of real toothplates. In *Parrelloides succedens* (Brotzen) and *Cibicides refulgens* Montfort there are also indications of such a, highly reduced, toothplate.

Sigmoid lip, granulation continuing as an outer layer of the septum.

53 *Cibicides lobatulus* (Walker and Jacob)
54 *Gavelinella danica* Brotzen

No typical lip observed; wall mostly hyaline.

55 *Orbitolites hemprichii* (Ehrenberg)
56 *Orbitolites complanata* Lamarck
57 *Halkyardia* sp.
58 *Valvulineria nuttalli* Palmer und Bermudez
59 *Valvulineria venezuelana* Hedberg
60 *Pararotalia mexicana* (Nuttal)
61 *Pararotalia tuberculifera* (Reuss)
62 *Elphidiononion semistriatum* (d'Orbigny)
63 *Cancris auriculus* (Fichtel and Moll)
64 *Baculogypsina spaerulata* (Parker and Jones)
65 *Gypsina globulus* (Reuss)
66 *Calcarina spengleri* (Gmelin) (crystalline)
67 *Palmerinella palmerae* Bermudez
68 *Globigerina pseudobulloides* Plummer
69 *Discopulvinulina globularis* (d'Orbigny)
70 *Cibicorbis herricki* Hadley

In *Glob. pseudobulloides*, there is a toothplate-lip at the foraminal border but in horizontal section only the umbilical foramina are cut, and these do not have the sigmoid lip or toothplate.

No typical lip; granulations begin abruptly at the apertural border

71 *Rotalia trochidiformis* Lamarck (crystalline)
72 *Stensiöina pommerana* Brotzen

73 *Stensiöina exsculpta* (Reuss)
74 *Gyroidinoides subangulata* (Plummer)
75 *Eponides procera* Brady
76 *Eponides toulmini* Brotzen (partly)

No typical lip, but totally granular.

77 *Eponides umbonatus* (Reuss)
78 *Anomalina alazanensis* Nuttal
79 *Nonionella communis* (d'Orbigny)
80 *Mississippina binkhorsti* (Reuss)
81 *Mississippina concentrica* (Parker and Jones)
82 *Globorotalites micheliniana* (d'Orbigny)
83 *Gyroidinoides depressa* (Alth)
84 *Eponides antillarum* (d'Orbigny)
85 *Gavelinonion umbilicatulum* (Montagu)
86 *Osangularia lens* Brotzen
87 *Alabamina midwayensis* Brotzen

Though the study of the border of the aperture (or foramina) clears up many points regarding the structure of the septa and the existence of toothplates, it does not give us much data for the taxonomy. Obviously closely related forms show large differences in this characteristic, though there are groups of species which show similar conditions. See for figures: Pl. 8, Figs. 4 and 5. The numbers correspond with those found in the lists above.

CHAPTER V

CHANGES IN THE STRUCTURE OF TEST IN GENERA OF FORAMINIFERA IN THE COURSE OF GEOLOGIC TIME

In many genera the finer structures of the test walls and septa change during geologic time. This change may be from aragonitic to calcareous fibrous radial, or to granular, even to crystalline radial. Moreover, a change may be found from „monolamellar" to „bilamellar" (apparently). Dividing genera and groups on the basis of these changing structures is meaningless. The change in test wall structure has been demonstrated in several groups of Foraminifera (*Gyroidina, Planulina, Marssonella, Cibicides, Cymbalopora, Bolivina, Siphonina*).

In recent literature the structure of the test of Foraminifera has been discussed; since Rhumbler (1911, 1913) showed the radial crystalline structure of many tests when seen in polarized light, especially Wood (1949) contributed to the knowledge of this structure; some tests are aragonitic, other tests are calcareous; the aragonitic tests of trochoidally built tests mostly are also radially crystalline; calcareous tests may be microgranular, fibrous crystalline and wholly radially crystalline.

When we consider the group of species which have a biserial, trochoidal, porous test and a loop-shaped aperture which may be sutural, or in end-series even areal, always provided with a simple or slightly more complicated toothplate running from the border of one foramen towards the next (or the aperture), we deal with the group known as *Bolivina*.

The oldest species known is *Bolivina rhumbleri* Franke from the Liassic. The species shows all the characteristics mentioned above, and its test is aragonitic; the author gave an analysis of this species in 49, p. 50, fig. 19 and 105, fig. 290.

In the Upper Cretaceous another group appears with well-known species as *Bolivina incrassata* Reuss, *Bolivina plaita* Carsey, *Bolivina decurrens* (Ehrenberg) and *Bolivina basbeckensis* Hofker; all these species show simple toothplates, fine densely placed pores over the whole chamber wall and a granular microstructure. They have been gathered in the genus *Coryphostoma* Loeblich and Tappan (1962), but they do not differ in all characteristics from *Bolivina* in the usual sense.

In the early Tertiary for the first time species appear with all the characteristics mentioned, but now with hyaline walls; the primitive forms have pores all over the chamber wall, but more specialized forms may have pores in part of each chamber wall only. They have been gathered in the genus *Brizalina* Costa by Loeblich and Tappan in 1964 (p. 552). It is obvious that where in the primitive forms of the latter group the toothplates are also primitive and do not differ from those found in the Cretaceous and Liassic forms, it is not very opportune to create a different genus for them. In reality, we have here a very good example of a group, *Bolivina*, which in the course of time changes its wall structure from aragonitic through granular into crystalline radial. (Pl. 9).

Very interesting is the evolution of the test wall of *Gyroidinoides*. The characteristics of this genus are: wall calcareous, finely porous; test trochoid, all chambers visible at the dorsal flat side, only those of the last formed whorl at the much inflated ventral one; aperture always at the ventral suture, slit-like, not extending to the umbilicus and neither to the margin. A second opening of each chamber may be seen above the umbilical part of the chamber wall which bends upward into the umbilicus in most instances, though in some cases in the last formed chambers this wall-part may bend over the hollow of the umbilicus. Typical for the genus is that at the dorsal side the chamber walls form a part which bends proximally, more ventrally from the aperture (foramen); but at the dorsal side itself this structure cannot be seen. The oldest form of the Lower Cretaceous (Albian), *Gyroidinoides gracillima* (Ten Dam) (Pl. 11, Fig. 5) has a totally granular test in polarized light, only the inner side of the lip over the foramina is hyaline, radial crystalline; the agglutination is typical and consists of fine calcitic grains which are often somewhat larger and show distinct angles; the granulation seems to be a distinct agglutination. In *Gyroidinoides nitida*

(Reuss) from the Upper Turonian (Pl. 11, Figs. 3, 4), the test is nearly identically built, but at the foraminal lips the hyaline part is somewhat larger. In *G. nitida* from the Santonian (Pl. 11, Fig. 6), this part is not only found at the inner side of the lip, but also at the inner side of the septa in the neighbourhood of the lip. In *G. nitida* from the Lower Campanian (Pl. 12, Fig. 3), nearly the whole septum has this inner hyaline lining, whereas the outer side of the septum remains granular. *Gyroidinoides nitida* forma *globulus* (from the lower part of the Upper Maestrichtian) shows the inner lining of hyaline substance also at the inner side of the outer wall of each chamber, so that now the whole chamber wall consists of an inner lining which is hyaline, radial crystalline, and an outer lining which is agglutinated, granular (Pl. 12, Fig. 4, 5). In *Gyroidinoides subangulata* (Plummer) from the Danian-Paleocene, the agglutinated lining is thinner and also an outer hyaline, radial crystalline lining is added, so that the whole chamber wall, also the septum, consists of three linings, an inner and an outer hyaline, radial crystalline lining, and a central lining which is agglutinated, granular. This structure is seen in all later forms, such as mid-Tertiary *Gyroidinoides girardana* (Reuss) (Pl. 12, Figs. 1, 2).

The author avoided here to speak of „lamella". For with low magnification one would be inclined to assume the Tertiary forms to be „bilamellar"; but the observation of very thin sections makes clear, that there are not two hyaline „lamella" separated by a dark line, but there is a middle agglutinated lining which gradually changes at the inner and the outer side into a hyaline, radial crystalline „lamellum". It is obvious that the granular lining is the primary wall (it developed as such during time) and that the inner lining in upper Cretaceous forms and also the outer lining in Tertiary forms are secondary structures, gradually developed during time.

Such hyaline linings originally covering agglutinated test walls are not restricted to socalled calcareous groups. Typical agglutinated forms, such as *Marssonella*, have an inner lining of fibrous radial material and an outer lining of agglutinated substance; in the type-species of *Valvulina*, *V. triangularis* d'Orbigny, there is an inner fibrous radial lining in the septum only; this is also the case in another species belonging to the Valvulinidae, *Vacuovalvulina keyzeri* (Van Bellen) from the type-Montian. It is remarkable that all these species also have pores in the outer chamber walls. (See Hofker, 191).

An example of an outer fibrous radial lining over an agglutinated, granular, primary wall is found in *Mississippina binkhorsti* (Reuss) from the Upper Cretaceous-Danian, and in recent *Mississippina concentrica* (Parker and Jones) (Pl. 13, Figs 1-5). Even in 1964, Loeblich and Tappan (P. 776) concluded that there are supplementary apertures along the periphery in this genus; many sections reveal that in reality there is an inner primary agglutinated, granular wall which lies open in some typical places, e.g. at the dorsal and ventral peripheral „openings", but continues over the whole chamberwall. At some other places, e.g. at the margin, over parts of the ventral side, at the sutures of the dorsal side, there are thick linings of fibrous radial substance. The whole test, moreover, is poreless; at some places even an inner hyaline lining can be observed. The agglutination of the granular primary wall is often relatively coarse; organic matter can be detected regularly. So, the study of the test of *Mississippina* reveals, that this genus cannot be placed in the Epistomininae, as Loeblich and Tappan do (1964, p. 776). Obviously it is a poreless, agglutinated group which tries to develop a calcareous test, but up to now in vain. (See: Hofker, 180).

Cymbalopora martini (Brotzen) from the Santonian shows a totally agglutinated, granular wall with a lining of larger grains in the centre of each chamber wall. At the dorsal side the wall is pierced by many pores, at the ventral side only scattered pores are found. In *Cymbalopora radiata* Hagenow from the Maestrichtian Tuff Chalk, the central lining consists of finer grains, whereas the outer and inner linings show fine lamellae of secondary calcite which show a fibrous radial structure. In Paleocene *Cymbalopora hemiglobosa* Ten Dam the dorsal wall has become thicker, the ventral pores are more distinct, the outer lining shows coarse agglunation, the inner lining is fibrous radial. In Recent *Cymbaloporetta poeyi* (d'Orbigny) the total form of the test much resembles that of *Cymbalopora hemiglobosa*, but for the distinct lateral apertures of the chambers. The wall, seen in sections with high magnification, shows a granular central lining, whereas outer and inner linings are typically hyaline; here, as in *Mis-*

sissippina, these different linings have no distinct boundaries but gradually one lining passes into the next one. So it is not at all impossible that *Cymbalopora* and *Cymbaloporetta* form a series of species which during time changed its wall-structure from totally agglutinated through granular-fibrous radial into crystalline radial. Hitherto the author denied a connection between these two genera (49, 93) but Reiss (1963, p. 67) also indicated this possibitity. If this is true, we have here also an instructive case of the change in wall structure during time (Pl. 14, Fig. 1-6).

These changes strongly emphasize that a taxonomy based on the structure of walls must lead to unsatisfactory results. *Ceratobulimina* was placed by Loeblich and Tappan in the Familiy Ceratobuliminidae, with aragonitic walls; but a genus with a structure of the toothplate very much reminding of that of *Ceratobulimina, Palmerinella* (see: Hofker, 110) with a calcareous though radial wall structure, was placed in the Epistomariidae, together with *Epistomaria* with its typical structures very much reminding of *Cushmanella* (Ceratobuliminidae) but with a calcareous wall, and, moreover, together with *Epistomaroides* (see: Hofker, 51) which possesses a quite different toothplate and areal apertures as found in *Epistomaria*. Obviously the tendency to stress the structure of the test wall has dominated all other characteristics, so that closely related groups have been separated from each other. Following this tendency, it would be obvious that in the very homogenous group of *Gyroidina* there would be at least two, or even three genera; this has already been done by Loeblich and Tappan in the case of *Bolivina;* it is to be hoped that they will not be imitated.

The oldest *Epistomaria* the author knows of is „*Ceratobulimina*" *bundensis* Van Bellen in the Belgian and Dutch Montian. The species is slightly more primitive than *Epistomaria rimosa* (Parker and Jones) from the Lutetian of France; it is more robust, with fewer chambers in a whorl and in general features more like *Ceratobulimina;* but the toothplateforamina are already present on both sides and the toothplate itself is much more complicated then that of *Ceratobulimina*. The test is much thinner than that of *E. rimosa* and in section shows smaller pores; the septa are simple and at least part of the chamber walls is aragonitic so that it is more soluble in a calcareous surrounding. This species, *Epistomaria bundensis* (Van Bellen) obviously forms the transition from aragonitic *Ceratobulimina* to calcareous *Epistomaria* and there are some indications that in reality the species derived from *Cerobertina* rather than from *Ceratobulimina*. So, in reality *Epistomaria* is related to *Ceratobulimina*, though its wall in the type-species *E. rimosa* is calcitic. *Cushmanella* and *Epistomaria* are both offsprings from the *Ceratobulimina*-stock.

Loeblich and Tappan place the genus *Pulsiphonina* in the Anomalininae, whereas the closely allied genus *Siphonina* is placed in the Family Siphoninidae. Their main objections to place these two genera together are found in the shape of the aperture and in the wall structure. In reality the aperture of *Pulsiphonina* seems to be a simplification of the aperture of *Siphonina*, and Eocene *Siphonina* often lacks a distinct neck; the place of the aperture, ventral but just at the margin, in both genera is the same. According to Loeblich and Tappan, the microstructure of the wall of *Siphonina* should be radial, whereas that of the wall of *Pulsiphonina* should be granular. The author found, that Eocene and Oligocene *Siphonina* have walls which are not quite hyaline and in polarised light only feebly show the radial fibrous structure; in Miocene and Recent specimens the walls become more hyaline and show more and more the radial fibrous structure. On the other hand, well-preserved specimens of *Pulsiphonina prima* (Plummer) from the Paleocene often distinctly show the granular structure, especially in air-filled specimens and on sections. The wall-structure is of no value for placing the two genera in different families. Both genera have in common: the strongly bent dorsal sutures; the slightly curved radial ventral sutures without umbilicus; the distribution of the large pores at the keeled margin; the distinct pores at the dorsal side only found near the sutures; the distinct pores at the ventral side only found near the centre; the occurrence of fine pores over the whole chamber wall. Obviously *Pulsiphonina* is a primitive *Siphonina*, not yet having developed the apertural necks. With the other groups of Anomalidae, as conceived by Loeblich and Tappan, *Pulsiphonina* has nothing in common; but an erroneous concept of the value of the wall structure seems to have been the main reason to place this genus in the Anomalinidae. In the group as a whole, the Siphoninidae seem to have developed first with a granular structure, and later a hyaline radial fibrous structure is added (See Pl. 14, Figs. 7, 8).

As a result of this study, it may be stated, that granular walls or linings in the walls are primary walls which are originally built from foreign material, so are agglutinated. Planktonic species cannot form walls from foreign material and thus must have developed hyaline, radial walls. This means that groups, originally having granular walls, suddenly developed radial hyaline walls in case they became planktonic. This can be demonstrated in the group with granular walls with a spiral biserial test (Cassidulinidae). The benthonic forms have granular tests; but some forms developed with hyaline tests, radial in microstructure, with more scattered pores *(Islandiella)*. Very probably this took place more than one time *(Stichocassidulina)* and more than once such groups with radial tests conquered the planktonic environment *(Candeina* from *Virgulinella; Cassigerinella* from *Stichocassidulina; Sphaeroidina* from *Globocassidulina)*. Similarly we must regard the origin of most of the radial planktonic Foraminifera. The author (Hofker, 91) gave such a conception for the Globotruncanidae. It seems that keeled *Globorotalia* developed from *Pararotalia* (Hofker, 152), or both from *Discorbis (Conorboides)*-like forefathers.

Another instance of the change of the wall structure during time is formed by the genus *Cibicides* s.s. (Pl. 10, Figs. 1-5; Pl. 11, Figs. 1, 2). The oldest known species is *Cibicides excavatus* Brotzen from the Santonian-Lower Campanian. In this species the walls are simple, also the septa; the whole wall consists of fine grains, cemented together by calcite; often the grains contain particles of organisms so that the wall may be described as micro-agglutinated or granular. A similar structure has the wall of *Cibicides subbosqueti* Hofker from the Upper Campanian-Lower Maestrichtian; here, however, the septa remain simple, whereas the outer wall may be thickened in older chambers by an outer layer which is more fibrous radial, but not typically so. In *Cibicides beaumontianus* d'Orbigny from the Upper Campanian and Maestrichtian, not only the outer wall shows this second calcareous lining, but also the septa, so that the septa now show two linings, an inner one which is distinctly agglutinated or granular, and an outer lining which is calcareous, fibrous radial. In the recent type-species of the genus, *Cibicides refulgens* Montfort, there are three linings, in the septa as well as in the outer wall. The inner lining consists of crystalline calcareous material, radial; the middle lining is the primary wall, likewise consisting of fine granular material; the outer, often secondary thickened layer consists of radial fibrous material. In Recent *Cibicides lobatulus* (Walker and Jacob) the thin-walled test also consists of these three layers, the inner hyaline one, the central granular one and the outer fibrous one.

Yet all these species of which the wall structure is decribed above have quite the same forms of test, with the typical more or less flattened dorsal (spiral) side, the marginally placed crescent-shaped aperture more or less continuing at the dorsal side along the suture (an evidence that the tests were attached in life to a substratum with the dorsal side) and the more or less overlapping chambers at the ventral side. They evidently belong all to the same genus, *Cibicides* s.s. Yet their wall structures change during time, with only the agglutinated primary wall (granular wall layer) as a feature found in all of them. During time a second layer is formed, at first only in the outer wall, later also in the septa; this layer has a fibrous radial structure. In the later Tertiary and Recent forms a third layer of calcareous radial material has been developed, covering the inner side of the whole wall. This last formed lining is often not pierced by the pores at the margin, but at the dorsal and ventral sides only. In many forms with large pores, an inner pseudochitinous lining is added, especially in the older chambers (Hofker, 210).

CHAPTER VI

THE TOOTHPLATES

Since the discovery of the toothplates in many species of protostomal Foraminifera by Höglund, the present author has given many descriptions of these structures in protoforaminal and deuteroforaminal Foraminifera. Reiss as well as the present author showed the homology of all these structures, Loeblich and Tappan denied them to be homologous in the genera with a speed of spiral of less than ¼. The author tries to ascertain the importance of these structures, not only in respect of the life of the individuals, but also as a tool for systematic division.

Toothplates are found already in the agglutinated group of the Valvulinidae and in triassic *Duostomina*. As they are built simultaneously with or even before the building of the primary walls, they show a granular structure, even in radial tests. In the higher organised calcareous genera they may build very complicated structures, as septal flaps and gutters to form toothplate foramina leading to the umbilical cavity or toward suteral openings. Of these complicated toothplates many are described here. Moreover, in one genus, *Reussella*, the evolutionary change of the toothplate could be followed from Upper Cretaceous to Recent. In this group the toothplate becomes so complicated in the end of the evolution, that it forms a large part of the inner side of the large aperture which forced Loeblich and Tappan to create a new genus, *Fijiella*. It can be proved that this genus has no meaning.

In many papers the author has emphasized the homology of structures connected with a protoforamen; these structures were named „toothplates". In this he has been followed by Reiss (l.c., 1963); but Loeblich and Tappan (Treatise, 1964a; Journ. Geol. Soc. of India, vol. 5, p. 13, 1964b) followed only in respect of Buliminidae, Cassidulinidae and Robertinidae, but not with respect to the rotaliform Foraminifera, where they speak of „partitions", „septal flaps", etc. This misinterpretation is somewhat astounding. For it will be obvious, that rotaliform Foraminifera only differ from Buliminidae or Robertinidae (as treated by Loeblich and Tappan) in the number of chambers in a whorl. In *Bolivina* and allied genera the speed of the spiral is $^1/_2$, meaning that a whorl consists of only two chambers; in *Bulimina* s.s. the speed is $^1/_3$, meaning that here three chambers are forming a whorl; in *Praebulimina* the speed is $^1/_4$, meaning that four chambers form a whorl. In *Buliminella* the speed is $^1/_5$ to $^1/_8$, so that here 5 to 8 chambers form a whorl; in *Rotalia* the speed became $^1/_9$, 9 chambers forming a whorl, and in *Streblus* the speed reaches $^1/_{13}$, 13 chambers forming a whorl. In some of the more primitive forms, with a low speed, such as *Ceratobulimina* (speed about $^1/_6$), the „partition" in the chambers does not differ from that found in many other Robertinidae and is called „toothplate" by Loeblich and Tappan (1964b), but „partition" in 1964a (Pl. 9); yet here only one aperture exists from whose border the toothplate originates, just as in *Bulimina*. In primitive *Streblus* (or *Ammonia)* there are two foramina, one connected with the toothplate („septal flap"), the other obviously secondarily formed, not connected with the toothplate. Why deny the homology of both structures? In both cases these structures have the following characteristics in common: granular microstructure; a folded part and a free folded lip; running from one protoforamen to the next; all plates forming together a more or less complicated tube connecting the inner chambers, where the resting nucleus is situated, with the outer world by means of a direct funnel that is obviously built to get a straight passage for the enzymated protoplasm to the nutritive pseudopodia. Some of these toothplates obviously have also other functions, as in *Laticarinina* (Pl. 9), where all toothplates of the successive chambers form the broad carina of the test; but even here the original function may be the same, since we do not know how this animal feeds. The forming of complicated canals by toothplates, such as are found in *Pseudorotalia*, *Asterorotalia*, *Elphidium*, Nummulitidae wholly restricts their function to the original one: distribution of enzymatic substances from the source of these enzymes, the nutritive nucleus towards the feeding pseudopodia. Reduction of toothplates may indicate a change in the nutritive processes. Some toothplates in *Laticarinina*, *Lamarckina* (Pl. 9), *Globobulimina* (Pl. 15) show the tendency to form extracameral extensions, which may have special functions. Remarkable is, that Loeblich and Tappan do not recognise toothplates in the agglutinated Valvulinidae, though in many groups these plates do not differ from those found in protoforaminal groups of calcareous Foraminifera (Pl. 9. Figs. 1-4). The author believes, that toothplates are by no means restricted to calcareous groups and the agglutinated triassic forms, first discovered by Tollmann-Kristan, show toothplates connected with at least one of the apertural openings, (Tollmann-Kristan, 1966). The author thinks that most Foraminifera not allied to the Lagenidae had originally toothplates and that during the evolution toothplates may have disappeared in some groups. In species in which a straight row of chambers is found, toothplates seem less necessary than in species in which a spiral growth of the chambers is typical. In the spirally built Lagenidae (*Cristellaria* e.g.) the marginal place of the apertures does not necessitate a funnel to lead the streaming protoplasm from the nucleus towards the outer world in a short time. But especially in coiled forms in which the foramina are not situated in the direction of the flow of the protoplasm, such funnels are necessary. Once the toothplate was constructed in the course of the evolution. it has been reshaped in quite different ways to conform to the chamber structure and the placing of the apertures, but in main characteristics it remained a plate with a folded part (funnel-principle) and with a free folded part. running from one protoforamen to the next. in the shortest way. All these structures must be homologous, and consequently they form a characteristic which must be of high taxonomic value.

There is a large group of Foraminifera possessing toothplates as more or less important structures of the test. A simple toothplate is a plate of calcitic material (in some agglutinated Foraminifera (Valvulinidae) it may consist of pseudochitine and may also show some agglutination; Pl. 9 Fig. 1-4). It originates from the proximal border of a protoforamen (by proximal is meant here that border which is closest to the proximal chamber suture, or that suture and that wall which is closest to the initial part of the test, see Hofker, 39, p. 11); it is more or less shaped like a gutter. One border of the gutter is attached to the chamber wall in which the protoforamen of the former chamber lies, from which it originates. In the case in which only protoforamina are found, the toothplate creeps up to the next foramen, and attaches itself to one side of the border of that next foramen. In many cases one side or the gutter remains free (free folded part). If the chamber is twisted for about 180° with the former chamber, the toohtplate is also twisted into the same angle (*Bolivina*); if the chamber stands at an angle of 120° to the former one, the toothplates also show a twisting of 120°; etc. In case of a test in which the initial part is biseral, whereas becoming uniserially arranged in the later part, the toothplates of the uniserially placed chambers maintain the angle of 180°, thus demonstrating that the uniseriality is in reality an elongated biseriality. In *Spirobolivina* the toothplates of the plano-spirally coiled initial part show twisting of 180°; so the spiral part is a coiled *Bolivina* and the genus must have been derived directly from *Bolivina* (Pl. 9).

In many groups the toothplate remains simple (*Bolivina*, *Praebulimina*, *Cassidulina*; Pl. 9); in other groups the toothplate may become rather complicated in structure. The simplest complication is found in Tertiary and Recent species of *Bulimina*, where the plate forms a hollow tube at the attached part of it, forming a special small opening at the base of the protoforamen (aperture); this has been called by me a toothplate foramen. Especially in more complicated toothplates toothplate-foramina are more common. They are found at the dorsal sutures of the chambers of *Robertinoides*, a complication of the plate as found in *Robertina*; *Cushmanella*. *Operculina*, *Nummulites*, *Elphidium* (Pl. 9, Pl. 15) and allied genera possess two of them right and left from the sutural symmetric aperture; *Pseudoeponides* (Pl. 15) has toothplate-foramina at the angles between the spiral and radial dorsal sutures; *Rotalia* (Pl. 15) forms a toothplate-foramen leading into the cavity of the umbilicus, ventrally; this is also the case with many other genera allied to *Rotalia*; even the toothplate-foramina found in *Elphidium* (Pl. 15) open into the umbilical hollows. Such umbilical toothplate-foramina may lead to the building of spiral-canals in the umbilical part, when that part is closed by secondary calcite.

In some cases the toothplate which is nearly always formed simultaneously with the chamber, gives rise to very characteristic plate-formed structures. Such plates are already formed in a way in *Cushmanella* (Pl. 9) and become more common in the genera around *Rotalia*. In principle plates are built from the attached part at the suture with the chamber wall; in *Afrobolivina* (Pl. 9) they creep along the basal chamber wall till they reach the outer wall; here the plate forms fan-shaped divisions which give rise to the so-called retral processes of that genus;

in *Schubertia tessellata* this same phenomenon is repeated several times giving rise to complicated partitions in each chamber. It is obvious, that both genera are related in some way.

In the large group around *Rotalia*, the flange beginning at the attached part of the toothplate often runs along the basal septum (the former apertural wall) and forms there a „doubling" of the septum by means of a „septal flap"; this flap once again may leave hollows between the primary septum and the septal flap, which are known as septal canals. The typical characteristic of more complicated toothplates to form toothplate-foramina at the sutures, is once more demonstrated: rows of sutural openings may be formed by a folding of the „septal flap" to form the well-known sutural canal-openings in *Elphidium*, *Parrellina*, *Pseudorotalia* (Pl. 15). This septal flap in many instances ends at the septum, at the suture which the next chamber wall forms with that of the former chamber; here it attaches itself to that outer wall, simulating a doubling of the septum by means of the outer chamber wall bending inward; close observation, however, reveals that it is the flap which forms the second layer of the septum, not the chamber wall. This is often difficult to observe, the more so, since there are Foraminifera in which the outer walls of the chambers at the dorsal and ventral sutures bend inward to form partly „double" septa *(Pararotalia, Siderrolites, Baculogypsina)*; when one observes tangential sections, however, the difference between walls bending inward and real septal flaps can easily be cleared up. So, sutural openings of septal canals are always the openings of canals which are, at least partly, surrounded by the wall of the septal flap.

It is not necessary for toothplates to remain within the lumen of the chamber which was built simultaneously with them. Already in some *Bolivinae* the free folded parts of toothplates may protrude from the protoforamen (Pl. 9). In *Globobulimina* and allies the free folded part of the toothplate forms a protruding flange which is rather conspicuous. In *Lamarckina* (Pl. 9) a large part of the toothplate protrudes to form a plate covering the umbilical cavity. In many rotaliid Foraminifera such covering plates occur and they may continue to exist though the toothplates themselves, so far as the part within the chambers is concerned, are reduced nearly totally. In Foraminifera in which two kinds of foramina are formed, viz. the Biforaminata, the toothplate, always beginning at the border of a protoforamen, may form huge plates running to the deuteroforamen as well *(Höglundina*, Pl. 9). In *Asterigerina* (Pl. 15) and allies such plates are found, together with foramina composita, and are here forming the partition between the true chamber and the protoforaminal hollow covered by a porous plate (which may be part of the toothplate), forming the so-called secondary chamberlets at the ventral side (*Asterigerina, Amphistegina)*. Especially in rotaliform Foraminifera with such foramina composita, the covering plate, always poreless, is always attached to the border of the protoforaminal part of the foramen compositum *(Globorotalia, Globotruncana, Globigerina;* Pl. 18, Fig. 12). These covering plates cannot be other than modified toothplates. In *Globotruncana* they begin at the protoforaminal part with a hollow tube, just as in highly developed *Bulimina*, and between protoforamen and deuteroforamen they unfold to form the covering plate over the umbilical hollow. They are known under the name of „tenon". That these tena are parts of toothplates may be seen in species of the genera *Neoconorbina* and *Reinholdella*, where they occur in direct connection with true toothplates running through the lumen of the chambers. But also in *Rotalia trochidiformis* Lamarck and *Pseudorotalia schroeteriana* (Parker and Jones) (Pl. 15), tena are found partly covering the umbilical hollow; in sections it is easily seen, that these tena are not parts of the chamber walls, but emerge from the peculiarly folded toothplate, protruding when forming the ventral toothplate foramen and fanning out. This can especially be seen in *Rotalia trochidiformis*, where the real chamber wall is crystalline, whereas the toothplate is granular in structure. Such fanning toothplates are by no means restricted to the rotaliform Foraminifera: in many species of the Valvulinidae, agglutinated forms with pores in the outer walls, they are common; such fanning toothplates form plates covering the umbilical hollow or part of the large aperture. Especially in *Cushmanella*, *Pseudobulimina*, and *Robertinoides* very complicated toothplates are found, forming fans, toothplate foramina, hollow tubes and septal flaps.

We do not know much about the meaning of many toothplates. Yet it seems, that the original function may have been the shortest possible connection between the nucleus, as producer of the metabolic substances (DNA-RNA), and the outer world (aperture). In such forms as *Bolivina* and *Bulimina* this seems obvious. But the forming of teeth on the toothplate *(Reussella, Ceratobulimina, Höglundina)* reveals that later the toothplate may also have got other functions (attachment of protoplasm); the fact that in the later Epistomariidae toothplates are resolved in the former chambers strongly points to another function of the toothplate than to serve mainly as a way for nutritive protoplasm. On the other hand, the building of toothplate-foramina may once again be an indication for the primitive function, but here it serves to bring the protoplasm as soon as possible to the surface in several directions; it is characteristic that just in such forms the main aperture is narrow.

Very remarkable are the toothplate-conditions in the genera *Buliminella* (Pl. 9), *Buliminoides* and *Heronallenia*. In these closely allied genera the complicated toothplate also forms part of the apertural wall which, consequently, is poreless. The fan-shaped outer part of the toothplate here shows radiating folds; to the border of this part of the toothplate the real chamber wall adheres smoothly, just as in the case of many „septal flaps". Another example of an apertural wall which is obviously formed by the changed toothplate is found in *Pulvinulinella* where the toothplate is not only found within the chamber, but also forms a kind of „infundibulum" of the apertural wall. Such infundibula are also present in the genus *Alabamina* and in „*Eponides*" *antillarum* d'Orbigny; they are also found in several other groups, and always have poreless walls; though Reiss (1960) denies any connection of these structures with toothplates, I believe I am right in suggesting that they are reduced toothplates, the more, since they have always some close connection with protoforamina.

It is obvious, that the toothplate, in all its different forms, is one of the most valuable structures for taxonomic purposes. First, in the different species it is very constant in form and place; but secondly its structure is highly typical for genera and even for supergeneric groups. Moreover, it gives the only reliable answer to questions such as the taxonomic status of uniserial genera with toothplates. So it was found, that real *Stilostomella* has toothplates in reversed position in successive chambers; this indicates a spiral mode of growth with a rotation of 180° between the chambers, so that typical *Stilostomella* must be derived from a typically biserial genus.

Some genera show very much reduced toothplates; such reduced plates have been found in *Stichocassidulina, Cassigerinella, Candeina, Globigerinatella*. Normal Cassidulinidae always show toothplates of the reversed type, so that it is obvious that these groups must have derived from biserial straight forefathers. The oldest known biserial species with toothplates is *Bolivina rhumbleri* Franke from the Lias; here, as well as in the Cretaceous species of *Bolivina* the thoothplate is a very simple one; this is also the case in Cretaceous *Bolivinoides*, closely allied to this group (and to the Heterohelicidae?); but in the Tertiary, more complicated toothplates are found in many species of *Bolivina (Bolivina quadrilatera* Schwager — a true *Bolivina; Bolivina alata* Seguenza); in *Rectobolivina* the toothplate is typical in the biserial chambers, but becomes free from the chamberwall in the uniserial chambers when the aperture also looses the contact with the suture (areal position). *Bitubulogenerina* is an instance of a genus which in the initial part is triserially built, and in the adult becomes biserial; one might suggest that this genus were a group allied to *Bolivina*, or even that *Bolivina* might have arisen from triserial types; but the toothplates of all known species of *Bitubulogenerina* are much more complicated than in any known *Bolivina*, and in reality have features which point to triserial *Reussella*. In the latter genus, the Cretaceous and Lower Tertiary forms show very simple toothplates, together with fine pores in the outer walls of the chambers (Pl. 16); from Middle Tertiary to Recent, very different forms appear, also known as *Reussella* (the genotype belongs to them) with much coarser pores in the chamberwalls and much more complicated toothplates, whereas in apparently allied *Chrysalidina* the toothplates only occur in the initial chambers in a reduced state and totally vanish in the uniserial part of the test.

In Cretaceous and Lower Tertiary *Praebulimina* the toothplate is of a simple type in all species known (Pl. 9); but in *Bulimina*, especially in higher Tertiary and Recent, the toothplate becomes much more complicated. In Cretaceous *Eouvigerina* in the forms with an indentated chamberwall *(E. stormi* Brotzen, *E. aculeata* (Ehrenberg), *E. cretacea* (Heron-Allen and Earland), *E. cretae* (Ehrenberg) the toothplate in the later chambers with areal aperture is of a shape which is also found in *Euuvigerina;* but in *Eouvigerina gracilis* (Egger), which does not show the indentations of the chambers, the toothplate has quite a different form, such as is encountered in the genus *Aluvigerina* or in *Angulogerina.* This certainly points to two different genera, but also to the possibility that certain Tertiary Uvigerinidae have derived from (biserial!) *Eouvigerina.* The genus *Heterohelix,* type of the Heterohelicidae, does not show any traces whatever of a toothplate, not even in its oldest forms known. But many groups, such as *Chiloguembelina* (now known as *Stainforthia) Bolivinoides, Bolivinita, Tappanina* (a synonym for *Eouvigerina), Eouvigerina, Siphogenerinoides,* which genera are all placed in the Heterohelicidae by the most recent author, Montanaro Gallitelli, have distinct toothplates and thus cannot be placed in the same group in which forms are placed which, typically, have no toothplates at all.

Toothplates all are homologous structures, and in consequence all groups of Foraminifera having toothplates must be placed in one supergroup, which the author has called Foraminifera dentata or Ordo Dentata. The most typical feature apart from the toothplate in that group is the primarily coiled arrangement of the chambers; for even biserial arrangement shows to be a coiled arrangement with a speed of 180°; some uniserial groups show, by means of the toothplate, a coiling of the chambers with speeds of 180° or 120°. In *Praebulimina* the speed is 90°, in *Buliminella* 60° to 40°, and in many Rotaliform Foraminifera the speed is even less. *Bolivinopsis,* in reality an arenaceous genus without pores and also without toothplates, has obviously nothing to do with *Spirobolivina,* which shows the same outer arrangement of the chambers, but is calcareous, possesses pores and has toothplates in all the chambers, in the planispirally coiled as well as in the biserially arranged ones, which is characteristic of primitive *Bolivina.* So, *Bolivinopsis pulchella* (Cushman and Stainforth), the type of *Spirobolivina,* as well as Danian *Bolivinopsis scanica* Brotzen, belong to *Spirobolivina.* Here we have something of parallelism in arrangement of chambers between initially coiled *Heterohelix, Bolivinopsis* and *Spirobolivina.* The latter genus must have derived from *Bolivina,* since all older *Bolivinae* known have not got the spiral arrangement of the initial part of the test.

A similar instance forms *Lacosteina gauskovi* Marie. Here a trochoidally built initial part is followed by chambers in a triserial arrangement. The toothplate is rather simple, and could be compared with that of primitive *Bulimina.* This upper-Cretaceous form may thus be the first form of *Bulimina* (as Marie suggested), which also begins in the uppermost Cretaceous, but it is also possible that it is a peculiarly outgrown *Conorboides;* yet the toothplate as it is found in the coiled initial chambers has no features typical of *Conorboides.* The toothplate looks more like those of *Pseudoparrella* or *Pulvinulinella.* It may be that *Lacosteina* is closely allied to the *Caucasina*-group. In the latter group, which also belongs to the Foraminifera dentata, the later more or less triserially arranged chambers develop in such a way that the axis of the whole test remains the same, whereas in *Lacosteina* the axis of the later part of the test stands obliquely to that of the coiled part. The toothplate may solve the question more accurately. *Nuttallides* is a genus which has been separated from other groups; but the identity of the toothplate conditions, together with the structure of the whole test so strongly point to the genus *Asterigerina* that there cannot be much doubt as to the synonymy of the genera.

A. PSEUDOROTALIA SCHROETERIANIA (Parker and Jones)
(Pl. 15)

Each chamberwall consists of an outer thick porous wall and the distal simple septal wall; some tests show some granulation in the inner layer of this distal septum which may continue in the inner layer of the outer wall. The toothplate adheres around the axially situated relatively small and oval foramen and especially at its proximal border; near to the axis it forms a distinct lip attached to the wall of a chamber of the former whorl; at the distal border of the foramen, which forms an indistinct sigmoid lip, the toothplate continues as a straight plate, in a narrow strip running close to the primary septum of the former chamber, but in most places leaving a canal between itself and that septum. Close to the outer wall it attaches itself brusquely to the wall, now and again forming a passage just at the suture, which connects the lumen of the open space between septum and toothplate with the outer world. More axially from the foramen the toothplate at its axial end forms a funnel-shaped part which runs more radially out into the canal-space, so that an opening is formed from the lumen of the chamber to the „septal canal". More to the ventral side the toothplate, now placed axially with respect to the main chamber lumen, forms a gutter-shaped part of the axial wall, which gutter, however, more downward and axialward closes forming a regular funnel, the beginning of the canal, opening into the cavities in the central umbilical chalk mass which is formed by thickened tena of former whorls. This canal runs obliquely, and all the canals of the whorl together form the „spiral canal". In the meanwhile, the distal part of the toothplate forming the funnel spreads into a thickened plate closing the umbilical cavity from the outer world and situated horizontally, thus forming a typical covering tenon over the umbilical area; all chambers of the whorl do so, so that the „spiral canal" is separated by them from the outer world, except for some passages between the successive toothplates. At the dorsal side of the chamber, just at the margin, one single passage is formed by the toothplate which divides into several passages near to the surface, thus giving rise to several openings at the dorsal suture. So, the different passages found at the septa, in the umbilical area, at the ventral and dorsal sutures, are all formed not „interseptal", as I formerly (1927, 15) believed, but by the folding toothplate; they are all toothplate-foramina, comparable with the toothplate foramen at the dorsal sutures of *Pseudoeponides*; obviously, *Pseudorotalia* is closely allied to *Pseudoeponides* which, as I already stated (1958, 108), is closely allied to *Streblus*.

B. ROTALIA TROCHIDIFORMIS Lamarck (Pl. 15)

In *Rotalia trochidiformis*. the toothplate is distinctly granular; this makes it easy to detect the structure and the situation of the toothplate in each chamber. Each chamberwall itself consists of a dorsal roof, running from the former whorl to the margin, a ventral base forming a porous plate (the margin is poreless) ending towards the centre in a poreless tectal plate, and an oblique apertural face on which the sutural aperture is found. Above the ventral tectum, and at its proximal side, where a slit-like opening exists between the ventral wall and that of the former chamber, so that the tectum does not close the ventral side entirely, near to the middle of that slit. a protoforamen is found, totally surrounded by the toothplate and formed by it. The toothplate, beginning at this protoforamen, here forms a peculiar sacculus which is visible in transverse sections and is then seen to divide the innermost part of the chamber lumen from the rest. From this sacculus an outgrowth runs obliquely towards the innermost part of the chamber and opens into a space running spirally around the central calcitic mass, which space is also connected with the space left free between the proximal wall of the toothplate and the wall of the former chamber. The toothplate is fastened at the distal wall of the chamber running as a thin plate towards the margin till it meets the inner border of the aperture, which is thus a deuteroforamen. At the proximal side of the chamber, the toothplate adheres dorsally from the protoforamen to the distal wall of the former chamber, then runs down obliquely and adheres at the ventral side to the open edge of the ventral chamber wall. so that here it closes the chamber. leaving a ventral canal free which is open ventrally; thus this canal has an open connection through the protoforamen towards the inner part of the chamber, and connects itself with the spiral canal around the central calcitic mass, formed by the tena of former chamber whorls. Later, the streaming protoplasm builds lobular calcitic masses at the brims of the canal, with side-canals between, so that the peculiar structure of the ventral side of the test is formed. The sacculus of the toothplate is closed toward the dorsal side, but more to the margin it forms an open boat-like hollow so that the dorsal wall shows nothing of the toothplate. At the ventral wall the toothplate forms a thin inner lining. running up. proximally to form the wall of the proximal canal, distally to adhere to the inner border of the aperture (deuteroforamen). We here have a toothplate beginning with a true protoforamen. forming a toothplate-foramen which opens into the umbilical cavity. and. moreover. a large part of the inner wall of the chamber.

C. STREBLUS BECCARII (Linné) (Pl. 15)

The toothplate of *Streblus beccarii* (Linné) is of the type of that of *Pseudorotalia schroeteriana* (Parker and Jones), though much simpler. It begins as a small protoforamen which is scarcely visible, at the axial base of the chamber, situated within the proximal canal at the ventral side between the chamber and the former one; it forms a funnel-like structure near the wall of the former whorl, which is situated at the proximal border of the deuteroforamen of the chamber (or the aperture) and proximally forms a narrow canal which opens into the spiral canal between the central calcitic mass and the ventral chamber wall. Along part of the ventral chamber wall, originating from the funnel, and partly surrounding the ventral border of the deuteroforamen, a plate-like part of the toothplate runs alongside the chamber wall towards the margin of the chamber, where it ends (septal flap); this septal flap does not adhere to the distal and dorsal border of the deuteroforamen. In transverse sections of the test the funnel-like part of the tooth-plate can be seen in the inner angle of the chambers, running from the ventral chamber wall towards the axial wall of the chamber (outer wall of a former whorl). No accessory canals are formed by the toothplate other than the canal running from the inner angle of the chamber towards the spiral cavity (canal) in the ventral central chalk mass.

In the smaller species of *Streblus (S.tepidus* (Cushman) and allies) the toothplate is of the same structure, though somewhat simpler.

In horizontal sections parts of the toothplate are seen opposite the septal foramina, protruding from the axial chamber walls as hook-like protuding structures directed towards the outside of the chamber. Barker and Grimsdale (1936) described such hook-shaped structures in *Tremastegina lopeztrigoi* (Palmer), *Helicostegina, Eulinderina.* Especially basing their views on the occurrence of these peculiar hooks at the apertures in horizontal sections they concluded that all three genera are closely related, and that all Lepidocycline Foraminifera should have derived from *Amphistegina.* It is very probable that *Helicostegina* and *Euliderina*, together with *Tremastegina lopeztrigoi* (Palmer) belong to the same stock, to which *Streblus and Pseudorotalia* belong. It is very remarkable, that these peculiar hooks are not formed in *Rotalia trochidiformis* Lamarck.

D. ASTEROROTALIA INFLATA (Millet)

In this species the elongation of the chambers formed by the toothplate-foramen, found in *Rotalia, Pseudorotalia* and *Streblus* obliquely and backward, is directed downward, so that a pointed ventral side is formed. The free folded part of the toothplate, forming the funnel, and here also found axially to the deuteroforamen, is thin-walled. Ventrally from it, a small protoforamen, surrounded by the toothplate, opens into the large canal which separates two chambers at the ventral side. The proximal wall of this canal here is also formed by the toothplate, which continues from the sacculus and bends along part of the lateral wall, forming the whole proximal wall of the canal. Typical for the genus, this sutural canal is partly closed by a porous plate which begins at the toothplate-foramen and runs up covering more than half of the canal. The whole elongation of the chamber itself leading to the toothplate-foramen at the pointed ventral side, is formed by the toothplate; whether the porous plate running from that opening upward. is formed by the toothplate. is not certain; the pores in it make that supposition somewhat doubtful. When the porous plate is formed after the building of the next chamber. the toothplate-foramen opens into the covered canal.

E. ASTEROROTALIA PULCHELLA (d'Orbigny) (Pl. 15)

The species which is common at the coasts of Java (Indonesia) was named by Thalmann (1933) *Rotalia trispinosa,* since there are two different species which were called *pulchella* by d'Orbigny; one of 1826, which according to authors is an *Eponides,* whereas the other of 1839 is, according to Thalmann, a true *Rotalia.* However, already Thalmann's fig. 3, pl. 12 shows at the ventral side the typical covering plates, and thus the species cannot be a *Rotalia;* Hofker (49) made the indonesian species, which certainly is identical with d'Orbigny's figure of 1839, the type-species of a new genus, *Asterorotalia;* in this way Thalmann's name *trispinosa* becomes unnecessary, since the two species *pulchella* do not belong to the same genus and not to *Rotalia* either.

In this species the toothplate shows many affinities to that found in *Pseudorotalia, Streblus* and *Asterorotalia inflata* (Millet). The distal part of the funnel, also situated near the axial chamber wall (wall of a former whorl), forms the distal wall of the canal between two adjacent chambers at the ventral side. In some of the chambers, the sacculus forms the inner hollow of a spine dorsally from the septal foramen;

when this spine is formed near chambers of the first whorl following the proloculus (only in megalospheric specimens), this spine is clearly formed as a tube-form outgrowth of the toothplate; when the spine is formed near chambers of a later whorl (microspheric specimens) the spine is formed by enrolment of the distal wall of the ventral canal, also near to the dorsal side; in this case in horizontal sections the hollow of the funnel of the toothplate distinctly continues in the hollow of the spine. In 1927 I believed that the spines were massive; Thalmann (1933) also believed this; in 1951 (49, p. 506-507) I described the spine as hollow, and already suggested its connection with the toothplate, which was denied by Reiss (1963, p. 11); successive sections through a spine (transversely) gave the certainty that they are connected at their base with the toothplates. Obvious the hollow in the spine is a kind of toothplate-foramen; always the walls of the basal part of spines originate in the dorsal parts of the toothplates.

Thalmann (1933) already mentions the fact that rare specimens have not three spines, but four. It was found, that all megalospheric specimens have three spines, and that spines are formed between each three chambers of the first whorl; in microspheric specimens, the first whorls do not form spines; since the number of chambers in the whorl in which the spines appear is larger than that in the megalospheric form, the number of spines is larger, viz. 4. Especially in these microspheric forms the endchambers are strongly inflated, which is not a degeneration, as Thalman believed, but has to do with the reproduction by „plasmodiospores", as is often the case in the B-form of Foraminifera (broodchambers).

F. ELPHIDIUM CRISPUM (Linné) (Pl. 15)

Since in this species all structures formed by the toothplates are slightly more granular than the very hyaline walls of the chambers, it is relatively easy to describe the very complicated toothplate.

In *Rotalia*, *Streblus* and *Pseudorotalia* in the most ventral corner of each chamber the toothplate forms a curved part which divides the main lumen of the chamber from the spiral canal, formed between that part of the toothplate and the central calcitic mass (umbilical walls of formed whorl). In *Elphidium* we find, at the same outer corner of each chamber, but now at both sides of the planospiral test, this transverse part of the toothplate, equally dividing the main chamber lumen from the two umbilical spiral canals. This can be seen, when we study superficial horizontal tangential sections. Since each chamber in reality has only one toothplate, it is obvious that in each chamber the toothplate thus forms two transversely curved parts at either side of a chamber.

Each bended toothplate connects itself at the former septum, then bends distally from it and runs as a funnel to the next septum, the septum of the chamber to which the toothplate in reality belongs; it runs up towards the margin close to the septal wall of the former septum; where a foramen is found, it attaches itself to the rim of the foramen, but between the foramina (which are found near the suture in a row of round openings) an open space is left by the toothplate, between septum and toothplate, which space connects the hollow between toothplate and septum with the spiral canal. When one gets a horizontal tangential section just along the so called septal canal, one finds that the toothplate (nowadays called in this part of it the septal flap) runs nearly straight parallel to the former septal wall, till it attaches itself close to the marginal part of the chamber wall, where it ends, mostly not smoothly with the septum, but at a distinct angle to it. Horizontal sections taken somewhat closer to the surface often go just through the forking canals of the septal canal, and here the toothplate repeatedly bends down, attaching itself to the septum and forming in this way the forking canals. It is obvious that the whole canal system, the spiral canals as well as the septal canal, are formed by the toothplate, and that the canal openings at the sutures are nothing but toothplate-foramina. This can easily be followed, when one observes the inner wall of the toothplate, the wall which is directed towards the septum or the lumen of the spiral canal; this wall shows fine tubercles, which become larger near to the openings of the sutural canals, forming here small dents. This typical structure may have to do with the flow of the protoplasm through these canals.

Just between two forking canals, the outer wall of the toothplate forms a rounded opening, in such a way, that it closes the septal canal and forms the inner wall of a kind of sacculus, the retral processus. The outer wall of this processus is porous, the side-walls are formed by the walls with dents of the toothplate, and the inner wall is also formed by the toothplate, bending backward to divide the lumen of the retral processus from the septal canal. The inner openings, formed by the toothplate, connect the lumen of the processus with that of the main chamber lumen. It is remarkable that in this way each processus strongly resembles the structure found when the lumen of the sutural canal, covered by the porous plate, is sectioned transversely in *Asterorotalia*. I believe, that the retral processes of *Elphidium* are in reality nothing but successive, or repeated, sutural canals covered by porous plates, as found in *Asterorotalia*. When in *Pseudorotalia* the sutural canals would open into a sutural canal, which obviously would than have been formed by the septal wall at one side and the toothplate at the other side, and that sutural canal would have been closed by a porous plate, intermittently open for the passages of the sutural canal, one would get the primitive pattern of *Elphidium*.

It is thus obvious that the toothplate of *Elphidium*, at least in the type-species, is a highly developed rotaliid toothplate.

In *Elphidiononion poeyanum* (d'Orbigny) on the other hand, there is a primitive toothplate. This toothplate, however, forms at the suture the sutural canals but no retral processes between them as found in *Elphidium;* between the toothplate-openings at the sutures only solid poreless parts of the chamber wall are found, described by the author in 1956 as solid „pillars". Thus, contrarily to what is believed by Wade (1957, p. 333), *Elphidiononion* is not close to *Elphidium*, but to *Nonion*. It is true, that all species of *Elphidiononion* have hyaline walls, whereas in literature the walls of the genus *Nonion* have been described as being granular. But this idea is due to a vague definition of the genus *Nonion;* many species, called *Nonion* in reality belong to *Nonionella*, though they are symmetric on both sides; *Nonionella* has a granular wall structure. Until now not much has been known about the genotype of *Nonion;* when it is really a form from the pliocene of Elba, it should also be found in other localities of the Italian Pliocene; the conspicuous umbilical calcitic bud is not very typical for *Nonion*, but indicates that it is a form which must be of hyaline, not granular structure. *Nonion*, and its genotype, *N.incrassatum* Fichtel and Moll, has one characteristic which differs from granulate *Nonionella:* the chambers very gradually increase in size, whereas typical *Nonionella*, such as „*Nonion" scapha* (Fichtel and Moll), „*Nonion" asterizans* (Fichtel and Moll), „*Nonion" troostae* Visser, show a much faster increase of the breadths of the chambers. When we consider the real *Nonion* which occurs abundantly in the Pliocene-Recent in the North Sea Basin as true *Nonion umbilicatulum* (Walker and Jacob), as Van Voorthuysen (1957) did, the type of the genus *Nonion* has a hyaline, crystalline test with very thin, simple septa and fine but distinct pores. Such a form would be very close to *Elphidiononion* indeed and there would be no reason to separate *Nonion* from *Elphidiononion* on the basis of the structure of the test wall. However, the genotype of *Nonion*, *N.incrassatum*, as found in the collection of Fichtel and Moll at the Zool. Mus. in Vienna, is a *Cibicidoides*.

G. ELPHIDIELLA ARCTICA (Parker and Jones) (Pl. 15)

In this species the toothplate is rather simple. As in *Elphidium*, at both sides of each chamber the folded part of the toothplate is found at the angle where the overlapping chamber-part meets the umbilical region; here it divides the spiral canal from the main lumen of the chamber. But contrarily to *Elphidium*, the toothplate at the proximal septum near both side walls of the chambers only forms a very narrow septal flap, so that this flap is not found at the larger middle part of the septum, nor near the foramen; so, in horizontal sections, the septa are simple. Close to the side walls of each chamber, from the folded part of the toothplate, a narrow plate runs along the chamber suture, separating a narrow canal from the chamber lumen; in that canal, which is triangular in transverse section, the sutural canals open, but it seems that they are not formed by the toothplate. No retral processes are formed either.

The narrow septal canal opens axially into the narrow spiral canal, found between the chamber toothplates and the central chalk mass, and in each folded part of the toothplate a narrow porus leads from the chamber lumen into that spiral canal.

So it must be emphasized that the toothplate of *Elphidiella* is much more simple than that of *Elphidium*. Moreover, the septal canals of both sides in a chamber do not meet at the margin.

We must conclude that *Elphidiella* must be closer to *Elphidiononion* than to *Elphidium*. *Elphidiononion* does not seem to have a real spiral canal, whereas *Elphidiella* has.

H. ASTRONONION

Referring to the description and figures of *Astrononion sidebottomi* (Cushman) from the Bay of Napels (93, p. 137, pl. 20, fig. 5-9), just as in *Elphidium* and *Elphidiella* the transverse section reveals a distinct, though very thin, folded part of the toothplate in the umbilical parts of the chambers. This folded part separates the main chamber lumen from a kind of „spiral canal" which is formed by an extending part of the toothplate, having, as in all rotaliid Foraminifera, a granular structure. This extended part forms an outer granular wall just at the sutures, with a slit-like opening at its marginal end. This structure is clearly seen on my fig. 8, pl. 20, 93, and so we have here an outer part of the toothplate, forming a kind of extension of the main chamber wall, but distinctly connected with the folded part of the toothplate, as in *Bisaccium*. Thus, the openings of the granular „star" at each side of *Astrononion* are nothing but toothplate foramina and the so-called chamberlets are toothplate-canals; they are in some way comparable with the spiral canal, which is also formed in the Rotaliidae by the toothplate.

I. NOTOROTALIA CLATHRATA (Brady) (Pl. 15)

Some good sections and descriptions were already given in Hofker, 93, p. 163, pl. 25, fig. 1-10; many thin sections made recently revealed that the folded part is found at the ventral angle of each chamber; it can be easily detected by the granular structure which contrasts with the hyaline test. This folded part separates the main lumen of the chamber from an irregularly shaped ventral canal between the folded toothplate and the slightly developed umbilical calcitic mass. From this folded part, which attaches itself at the septum of the former chamber and then runs down, the „septal flap" forms a narrow band along the ventral suture and then runs upward along the distal suture of the former chamber over the margin and a small part of the dorsal suture. At the folded part an opening is formed through which the main lumen of the chamber is connected with the spiral canal; this passage is a very narrow one.

The septal flap forms a narrow canal between the proximal chamber suture (the distal wall of the former chamber) and the septum. From this canal, small folds run to the wall and form the beginning of the sutural canals which open somewhat distally from the suture. In this way, the toothplate of *Notorotalia* strongly resembles that of *Elphidiella*, and less that of *Elphidium*. There are no retral processes whatever.

According to the law of Dollo, it is not likely that *Notorotalia* is an offspring of *Elphidium;* it is more likely that it forms a primitive stock, maintaining characteristics which were complicated when the group became planospiral; for in the main features the toothplate is like that of *Streblus* and allies.

K. ELPHIDIOIDES (PARRELLINA) IMPERATRIX (Brady) (Pl. 15)

Parrellina imperatrix very much resembles *Notorotalia*, from which it is distinguishable only by the planospiral arrangement of the chambers and by the spines (some fossil *Notorotalia* show short spines too); apertural conditions, sutural passages, ornamentation of the walls, and the brittle condition of the walls, are all quite similar. The structure of the toothplate is only in so far different, that it is found on either side of the chamber, whereas in *Notorotalia* it is found only at the ventral side. The folded part of the toothplate is found at the umbilical angles of the chambers; here it forms a twisted part which surrounds the fine passage which leads to the „spiral canal" from the main lumen of the chamber. This „spiral canal", however, is more a space between the last formed whorl of chambers and the former whorl; its outer wall consists of parts of the toothplates continuing the main side walls of the chambers, but differing from them by the more granular structure. In this way a structure is formed which strongly resembles the central part of the filling of the umbilical cavity in *Astrononion*. From the folded parts two lamellae of the „septal flap" run over the axial chamber wall and later diverge along both sutures with the former chamber septum. A simple canal is formed between the septal flap and the main former septum close to the suture. From this canal passages diverge, formed also by the toothplate, through the outer chamber wall, forming the sutural openings. When a spine is formed, several of such canals emerge from the septal canal and form the canals in the spine, often ramifying in it and opening into groves over the surface of the spine. In this way, also the spines are formed by the toothplate. At the basal row of foramina, which are always found in deep groves in the apertural face, and also in the secondarily formed areal foramina in the apertural walls between older chambers, the toothplates are not found; the septal flap never reaches them. This might lead to the conclusion, that these foramina are deuteroforamina, since the toothplates do not begin at their borders; this in contradiction to what is found at the row of sutural foramina in *Elphidium*, but similar to what is stated in *Notorotalia*, and in *Elphidiella arctica*. So it seems that *Parrellina*, *Elphidiella* and *Notorotalia* form a group which is very distinct from *Elphidium*.

The toothplates of many other Foraminifera of the rotaliid group have already been studied exhaustively by the author. In *Pseudoeponides* Uchio the toothplate has been studied in the genotype, *P. japonicus* Uchio, as well as in another species found in the Caribean Sea; it only differs from that of *Streblus* in having a kind of septal flap which runs upward to the dorsal side and opens into a toothplate-foramen just where the spiral suture of the chamber meets two sutures of former chambers. This dorsal toothplate-foramen is thus similar to the septal passages of *Pseudorotalia*, which also open at the sutures and are also toothplate-foramina. Thus *Pseudoeponides* is nothing but a *Streblus* in which a dorsal toothplate-foramen is formed. *Pseudoeponides*, *Streblus* and *Pseudorotalia* are closely allied (Hofker, 108, pp. 46-48, fig. 1, 2).

With their free folded parts the toothplates of the asterigerinid Foraminifera form the poreless plates between the main chambers and the so-called chamberlets; quite different groups of Foraminifera have led to these asterigerinid Foraminifera. The basic feature in all these forms is, that the protoforamen, enclosed by the toothplate, is closed by a porous plate. This phenomenon is found in *Reinholdella*, deriving from *Conorboides* (Hofker, 108, pp. 15-29, fig. 1-17); *Asterigerina*, closely allied to *Globorotalia; Asterigerinoides*, derived from *Discopulvinulina* or *Discorbis; Asterigerinata*, derived from *Neoconorbina;* and *Hemingwayina*, which ancestor is uncertain. In all these forms the toothplates thus form the poreless walls between the main chambers and the secondary „chamberlets" (Hofker, 134, pp. 247-265, fig. 1-30).

In *Epistomaria* the toothplate is very much complicated; it forms a basal „septal flap", a toothplate-foramen at the dorsal side, a second one at the ventral side, and a marginal foramen, which may be the former protoforamen. In *Epistomaroides* there are complicated toothplates, and the „canal-systems" in this group are formed by the toothplate outgrowths bending inwardly at the sutures, whereas the dorsal sutural openings are „canals" between toothplates and the septal walls. The ventral plates cover the umbilicus in *Epistomaroides separans* le Calvez and in *E. polystomelloides*, have passages at the sutures, and are comparable with the chamberlets of *Asterigerina* (Hofker, 51).

In *Palmerinella palmerae* Bermudez, the toothplate very much resembles that of *Ceratobulimina*, though it is more complicated by several folds; this species may have derived from *Ceratobulimina* by becoming planospiral; there is, as in *Ceratobulimina*, a loop-shaped protoforamen, but in the septa, which are simple, secondarily formed areal foramina also occur (Hofker, 110, pp. 32-33, fig. A-E).

L. FAUJASINA CARINATA d'Orbigny)

In 1928 the author described the canal system of *Faujasina;* he showed that in megalospheric asymmetrically built specimens there exists a spiral canal system on both sides, connected with the septal canal system. The existence of a more symmetrically built microspheric generation and the fact that in trochoidally built specimens the spiral canal is found at both sides, made the author believed that this species was derived from *Elphidium* and is not its ancestor, which would have been suggested by the statement of d'Orbigny, that he found this species in the Maestrichtian Tuff Chalk of Holland. We known now that this species does not occur in that sediment, and that d'Orbigny's observation must have been caused by contamination. The species is only known from certain Pliocene layers in England (St. Erth), probably also in Holland. A sample recieved from Dr. Mac Fadyen from St. Erth yielded many well-preserved specimens. In transverse section in each chamber, as well at the convex side as at the flat side, there is at the inner corner the contorted part of the toothplate forming the cameral part of the spiral canal, opening at that corner right and left from the margin, and obviously continued by this structure of the next chamber, forming the spiral canal; one or more rounded openings, foramina, close to the suture, connect the former chamber with the next through the septum; moreover, in the septum several other openings are generally found. From the contorted part of the toothplate along both outer walls of the chamber and parallel to the proximal septal wall, runs the „septal flap", forming two canals from the spiral canal towards the margin, and opening into a row of sutural toothplate-foramina at both convex and flat sides.

In this way the whole toothplate-structure does not differ from that found in real *Elphidium*. Only, walls, septa and „septal flaps" are extremely thin (cold water in a shallow sea). The septal flap is not found in the middle part of the septum, is thus restricted to the side-borders of the septum. As there are real retral processes at the sutures (Hofker, 19, fig. 1, 2 and 5), and since the thin walls show between the fine pores the typical calcite knobs found at the surface of many species of *Elphidium*, the species is very close to *Elphidium;* it is a somewhat trochoidally built *Elphidium*, with a microspheric generation which can hardly be distinguished from *Elphidium*. Fig. 9 on pl. 11 1928 is incomplete, since it lacks the contorted toothplate parts; this is set right here.

M. NUMMULITIDAE (Pl. 15)

The toothplate conditions of the Nummulitidae have been studied in recent *Operculina complanata* (Defrance) and *Nummulites variolarius* Sowerby of the Ledian of Bambrugge, Belgium. The latter fossil in this locality occurs in air-filled tests and can be studied in thin sections accordingly (see also chapter XIV, v on *Nummulites* in Pt. II of this paper).

In both species, the aperture is marginal and consists of a single crescent-like opening; and in both species there exists a canal system between the „septal flap" (which is the toothplate) and the main septum. This canal system consists of two main canals which originate from side-canals opening at the marginal chord of a former whorl; they run towards the marginal chord of the chamber itself and give somewhat irregularly side-canals towards the suture which open in that suture where the septum connects with the suture. In *Operculina* they are finer than in *Nummulites*. In both species there is a main basal canal in the marginal chord; in *Operculina* it is seen in a band of calcitic matter protruding in the lumen of each chamber at the margin; in Nummulites only in some parts of the chamberwall it is seen as a protruding band, but not always; moreover, in *Nummulites* this main canal often splits into two canals at the inner base of the marginal chord. From this canal several side-canals run and form the canal system of the marginal chord. Within this chord, in both species canals connect the several canals which run parrallel to the surface; in *Nummulites* there are only few of these connecting canals and, if they occur, they always run obliquely and in the direction of coiling; in *Operculina* they are directed more radially.

The main canal and some of the canals running parallel to the surface originate from the main canals which are found between the main septum and the „septal flap"; this discovery contradicts what I believed to have found in canada-balsam preparations in *Operculina complanata* in Hofker, 25, pl. 33, fig. 1; this connection can also be seen, 25, pl. 32, fig. 2, whereas the main canal and its branches can be seen 25, pl. 32, fig. 7; similar connections between the septal canal system and that of the marginal chord can be seen 25, pl. 34, fig. 6, 5 and 3 in *Heterostegina operculinoides* Hofker, and pl. 35, fig. 9 in *H. suborbicularis* d'Orbigny. It is obvious that these septal canals are the main source for the marginal chord system in the Nummulitidae (See also Bannink, 1948, pl. 3, fig. 22 a and b).

In *Operculina complanata* the septal flap does not reach the border of the foramen in the middle, only at its sides; in *Nummulites variolarius* it reaches this border at all sides.

In transverse sections of the two species no trace of a folding part of the toothplate can be found at the overlapping ends of the chambers and consequently no real umbilical spiral canals are formed in this group of Foraminifera; obviously the chambers do not open into such a canal, and so the protoforamen seems to be lost totally. On the other hand, since the toothplate in *Operculina* does not reach the upper border of the foramen, that foramen cannot be a protoforamen either. But in some specimens of *Nummulites variolarius*, two narrow openings were found right and left of the foramen; these openings are found just where the main canals of the septal canal system begin; it may be that these small openings are in reality homologous with the chamber parts found axially from the folded part of the toothplate in *Elphidium* or in *Streblus*, and that they are reduced protoforamina. When that is correct the chamber lumen here would be connected with the septal canals.

The septal walls show an inner more granular layer; the septal flaps (toothplates) are also slightly granular.

In case that all these observations are correct, the Nummulitidae should be closely allied to the Rotaliidae. They would mainly differ in the forming of a marginal chord system. The remnants of the folded part of the toothplate right and left of the foramen also were observed by Reiss (1958, p. 17, where he states: „The remnants of a toothplate are present in the Nummulitidae, as rather insignificant extensions of the septal flap situated in the deepest inner part of the chambers on both sides of the aperture, coating the axial walls; the same is true of the Elphidiidae, in which the toothplates form, spaces between them and the axial wall of the chambers". It was stated here, that these spaces, though very narrow, also occur in *Nummulites* and in *Operculina*. However, I do not think that Smout and Reiss are correct in believing the Elphidiidae and Nummulidae to be closely related to the Miscellaneidae. For in *Daviesina* and *Pseudosiderolites* no such folded toothplates occur. The Miscellaneidae are related in some way to *Siderolites* and *Calcarina*, which are related to *Pararotalia*. *Elphidium*, however, and *Elphidiella*, we saw, are related to *Streblus* or *Pseudorotalia*, having become planospirally built. This, in some way, has also been the case in the Nummulitidae.

There seem to be two different groups of rotaliform higher organised Foraminifera; both have emerged from ancient forms already present in the lower Senonian. One of these groups is allied to *Rotalia trochidiformis* Lamarck, with distinct folded part of the toothplate forming an umbilical foramen (toothplate foramen) at the axial angle of each chamber with the axial wall. To this group may belong *Streblus*, *Pseudorotalia*, *Asterorotalia*, *Operculina*, *Nummulites*, *Elphidium*, *Notorotalia*, *Faujasina*, *Parrellina*, *Elphidiella*.

The second group descends from *Pararotalia* and does not show a distinct toothplate, but in some cases forms double septa by bending in the successive walls of the chambers at the sutures, not forming real canals; all the canals in this group have been formed by these septa or by fusing pores into canals in thickened walls or spines. To this group belong *Siderolites* (with *Pseudosiderolites*), *Daviesina*, *Pellatispira*, possibly *Lafitteina*.

There are, however, still more groups with toothplates in the rotaliform Foraminifera. They all seem to descend from *Conorboides*, and find their utmost development in *Asterigerina* and *Amphistegina*, with closing porous plates over the protoforaminal area. In case they do not build these plates, they result in *Neoconorbina*, *Discorbis*, *Discopulvinulina*. They are, through *Reinholdella*, related to the Epistomariidae, as well as to the more buliminid Robertinidae.

I have shown that there must be some relationship between the primitive Globigerinidae and Globotruncanidae and the Conorbiidae. Toothplates are also found in these planktonic groups, forming free folded parts spreading out into umbilical covering tecta, just as is found in *Lamarckina*. They distinctly show protoforaminal parts and deuteroforaminal parts of the aperture, between which the toothplate is situated, as it is the case with the „tenon" of so many discorboid Foraminifera. On the other hand, the conditions of the pores and the poreless margin in *Globotruncana* and *Globorotalia* strongly suggest some allience to *Pararotalia* (Hofker, 91, p. 314, fig. 1).

N. THE EVOLUTION OF THE TOOTHPLATE OF REUSSELLA

(Pl. 16, 17)

Many groups of dentate Foraminifera during the evolution of the group also show an evolution of the toothplate. A fine instance of such an evolution is found in the genus *Reussella*.

In my paper on the Foraminifera of the upper Cretaceous of Northwestern Germany and Holland (105), I have given the descriptions of many species of *Reussella*; we will confine ourselves to those forms which are very minute and may form a special group (*R. buliminoides* Brotzen to *R.cimbrica* (Troelsen)) and only give attention to the larger species with distinctly angled sides, *R. cushmani* Brotzen, *R. pseudospinulosa* Troelsen, *R. truncata* Hofker, *R. szaj-*

nochae (Grzybowski) and *R. pyramidalis* Hofker. They more or less show the outer form of the type-species, *R. spinulosa* Reuss from the Miocene; often they develop spines at the angles, and all these forms show minute pores in the chamber walls. In all these forms, the toothplates are rather simple, each toothplate has an attached part to the axial wall, and a thick free folded part the back of which is often slightly curved. The aperture is simple too, being always a loop-shaped opening at the axial sutures of the last formed chamber.

Such forms continue for some time up into the Tertiary; well-known is the common species *Reussella limbata* (Terquem) from the Eocene of France and elsewhere; it also has fine pores in the chamber walls, all over the outer wall and the toothplate is a simple one, though it seems to be much thinner than that of the Cretaceous forms. The aperture consists of a small opening which, however, is somewhat more areal, near to the axial part of the apertural face; the latter is distinctly depressed and around the aperture there are blunt dents all over the apertural face; this apertural face is poreless.

Also in the Eocene, we find for the first time a species which shows much coarser pores, piercing the whole outer chamber wall except for the thick sutures between the successive chambers. The toothplates are thin and simple, with curved free folded part *(Reussella terquemi* Cushman).

From the Oligocene no species of *Reussella* are known to me. But in the Miocene, *Reussella* is common in Europe, with *Reussella pulchra* Cushman and *R. spinulosa* Reuss, both in the Miocene of Vienna.

R. pulchra Cushman has distinct pores especially at the distal and marginal parts of the chamber walls, a smooth apertural face with depressed part around the loop-shaped sutural aperture. The toothplate is rather simple. *Reussella spinulosa* Reuss, the type-species of *Reussella*, has rather coarse pores in a single row along the sutures of the chambers; the apertural face is smooth, deeply depressed, with a sutural loop-shaped aperture. The toothplate is very thin, with slightly curved free folded part.

In the Miocene of Cabanes near Dax, France, *Reussella miocenica* Cushman is found which, contrary to the foregoing species, has smooth angles. It shows two kinds of pores in the chamber walls: very fine, closely set pores and much coarser pores between, especially near the margins. The apertural wall has the same blunt dents as found in Eocene *R. limbata*, but the toothplate is more complicated. It consists of an attached part running from the foramen over the axial wall of the chamber and forming a highly contorted free folded part, yet with smooth border. The aperture is rounded and found, as in *R. limbata*, as an areal opening in the axial part of the depressed apertural face. It may be that this species is closely related to *R. limbata*.

In the Pliocene of Millas, France, at least two different species of *Reussella* are known to me. One of them has a hyaline, smooth wall with irregular spinose angled side, small pores all over the chamber walls and very coarse pores along the sutures, and a smooth apertural face which has a deeply depressed part in which the loop-shaped axial sutural aperture lies. The toothplate is broad, partly totally free from the inner chamber wall, with a peculiarly curved free folded part. The second species, *Reussella glabrata* (Cushman) is somewhat more robust, with only dentated angles and small blunt pustules not only on the apertural face, but also over the chamber walls; the pores are not so coarse as those found in the former species, and only restricted to a single row along the sutures of the chambers. The toothplate is somewhat simpler, one side attached to the axial wall, the other side with a narrow free folded part, slightly curved backward.

In the recent seas many species of *Reussella* occur. In the Philippines *Reussella armata* Cushman is found, with strong sharp dents at the angles and relatively small, but distinct pores scattered all over the surface of the chamber walls. Often a long spine is found at the initial end. The aperture opens wide in the depressed apertural face that is characterized by a somewhat protruding free part of the toothplate, which forms the deeper part of the axial indentation. The toothplate runs from the former foramen towards the next as a broad cap with a slightly curved back, and is wholly covered by fine pustules which are characteristic of this species.

In the sea around Cuba, Caribbean, an elongate species occurs which also shows strong spines at the angles and pores which are very distinct are found in the earlier chambers along the sutures only, but in the later chambers scattered all over the walls *(Reussella atlantica* Cushman). The toothplate is a very large plate, very thin, but lacks the pustules as found in *R. armata*. It is extremely complicated.

In the whole Mediterranean *Reussella neapolitana* Hofker is found with strong dents at the angles and one row of large pores at the proximal suture of each chamber, whereas the whole wall is pierced by fine pores. The apertural face is smooth, except for some strong dents which are found at the slightly protruding free border of the toothplate. This plate is very bulky, with strongly curved back, and the plate has round openings all over it (Hofker, 138, p. 248, fig. 84, 90; 93, pl. 5, fig. 2).

A very stout *Reussella* is *R. mortensi* Hofker from the deeper Caribbean. It has distinct spines at the angles, coarse pores mostly only around the sutures, and some small pustules at the apertural face. The toothplate is relatively small, with strongly bent back, and distinct blunt dents at the slightly protruding free folded part, at its border.

Reussella weberi Hofker from Indonesia has hardly any spines at the angles, coarse pores in a single row along the sutures of the chambers, and a toothplate which forms the larger part of the apertural face and is covered with blunt pustules; often in this toothplate several large openings are found (Hofker, 49, pp. 170-175, fig. 107-109).

Reussella simplex (Cushman) also found in the deeper water of the Pacific, has only some very conspicuous spines at the last formed chambers, whereas the more initial part of the angles is smooth. There are only some very coarse pores at the marginal chamber wall along the angle, and in the apertural face some blunt pustules are formed at the border of the depressed indentation in which the sutural aperture lies. The toothplate is not large, with smoothly bent back and at the border of the free folded part a peculiar sharp dent.

In the very elongate *Reussella aequa* Cushman and McCulloch with its smooth angles (Hofker, 49, p. 169, fig. 105) the pores are very coarse and scattered over the surface of the chamber walls, mostly near the sutures. The apertural face is smooth, the toothplate thin with narrow free folded part and some oval openings in its side. Between the large pores, very fine pores could be observed.

These descriptions clearly show that in the earlier forms the pores are fine and the toothplates simple; then Tertiary species are found with much coarser pores, mostly together with the fine pores, but also with a relatively simple toothplate. In the Pliocene and Recent the species with coarse pores are mainly distinguishable by the different toothplates which are much larger and much more complicated than those in the earlier forms.

The Upper-Cretaceous *Reussellae* from North-Western Europe have got an exhaustive treatment by the author (105, pp. 201-222); all the species with a distinctly triangular transverse section were gathered in this genus. In the course of time some of the smaller forms have gradually shown the tendency to close the basal sutural part of the aperture so that this aperture becomes in the end a terminal one. Therefore it seemed to be impossible to distinguish between *Reussella* and Brotzen's genus *Pyramidina*. There are two groups of *Reussella* in the Upper Cretaceous: a group with large species and one with small species. The small species tend to get a terminal aperture, the large species never do. Tertiary *Angulogerina* may have developed from the small group with terminal aperture *(„Pyramidina")*. All Cretaceous forms have a simple toothplate and walls pierced by fine pores. To the group with large species belong *R. cushmani, R. pseudospinulosa, R. truncata, R. szajnochae, R. pyramidalis;* to the group with small species belong *R. buliminoides* Brotzen, *R. prolixa* (Cushman and Parker), *R. paleocenica* Brotzen, *R. uvigeriniformis* Hofker, *R. rugosa* (Brotzen), *R. cimbrica* Troelsen; only the latter group may have end-stages as *„Pyramidina"*. In the Paleocene and the Eocene there are several species which in reality belong to the Cretaceous types, the latest occurring form being *Reussella limbata* (Terquem) from the Lutetian.

In the Oligocene and Miocene a more developed group starts; all species have the same characteristics as found in the Cretaceous, triangular from the beginning, but now large pores are introduced, mostly arranged along the initial suture, often also elsewhere; the proloculus always maintains the primitive fine pores, and often several of the initial chambers do so too. The toothplate becomes more flaring, till in some of the Recent and sub-Recent species this toothplate gives rise to a complicated structure. This structure is characterised by many openings in the wall, and may often be seen within the then large aperture from above;

this characteristic induced Loeblich and Tappan (1964) to separate these latest forms of *Reussella* forming a new genus, *Fijiella;* they took this toothplate for an aperture consisting of supplementary openings; since this seems to be a wrong observation, as the figures here show, *Fijiella* becomes a synonym of *Reussella*. The type-species of *Reussella, R. spinulosa* Reus from the Tortonian of Austria, shows all the characteristics of Tertiary and Recent *Reussella;* the later chambers show the larger pores, the toothplate already is more flaring than that of the Upper Cretaceous forms. The Upper Cretaceous *Reussellae* have been seperated by Loeblich and Tappan (Treatise. 1964. p. 546) as the genus *Pyramidina* Brotzen from the Tertiary forms; the characteristic. given by Brotzen for his genus, has been neglected by Loeblich and Tappan, since they mention that the Cretaceous forms have the tendency to close the basal part of the aperture; this is only the case in late-Cretaceous forms of the group with small species; the group with species with large size never shows this tendency. They placed this Cretaceous genus *Pyramidina* in the Family Turrilinidae, of which they state that the wall is formed of lamellar radial calcite; it is certain that the wall of Cretaceous *Reussella* is radial. *Reussella* and *Fijiella* were placed by these authors in the Family Buliminidae, which also has a radial wall. Their descriptions of the two genera *Pyramidina* and *Reussella* thus only differ in the pores, *Pyramidina* having fine pores, *Reussella* having large pores. The closing of the basal part of the aperture cannot be taken as a characteristic separating the two genera so far from each other. that they should even belong to separate families! Moreover, Loeblich and Tappan state, that this closing only occurs in the Cretaceous forms as a „tendency". Moreover, *Pyramidina* is stated to occur from Santonian to Danian, whereas we saw that a form with all characteristics of the Cretaceous forms, occurs in the Lutetian, Eocene.

So, there is only one genus, gradually changing some of its characteristics, especially the form of the toothplate and the diameter of its pores, namely *Reussella,* of which *Fijiella* and *Pyramidina* are synonyms. It is very probable, that the genus *Chrysalidinella* is an end form of *Reussella*. and that its closing end-plate with large openings is the plate of the toothplate with large openings as found in „*Fijiella*". *Chrysalidinella* was described by the author in 1951 (Hofker, 49, pp. 175-178, fig. 110-112). In the case that the genus *Pyramidina* is maintained, it can only be used for the group of small Cretaceous species mentioned above, for only that group has apertures „tending to become areal". The group of large Cretaceous species never shows this characteristic.

CHAPTER VII

ON PLANKTONIC FORAMINIFERA

Are all the forms, believed nowadays to have or have had a planktonic life, really planktonic? Discoveries by Christiansen and by the present author make it plausible that some forms, especially those with thicker tests, are benthonic. Forms with keels cannot have developed from differenciated forms without keels. Moreover, quite different groups (genera) tried to attain the planktonic environment. Changes during time within a gens have been found; changes in the life-cycle during a geologic period also are observed. Changes in the direction of coiling may be due to changes in temperature. Many examples of monolamellar planktonic Foraminifera occur, though they are believed to be bilamellar up till now. The distribution of the pores on the tests and the size of these pores are constant features within a biologic unit of planktonic Foraminifera; but the several species differ from each other in this respect. Yet, in planktonic Foraminifera the product of pore size and density of the pores is a constant one. The aperture of *Globotruncana* shows to be a foramen compositum. Such forms as *Globigeraspis*, *Globigerinatheca* and *Porticulasphaera* cannot have the value of genera but are development stages within a species, due to more or less optimum environments. Special attention got the finer structure of the tests of *Globorotalia*. *Planomalina buxtorfi* Gandolfi was not a planktonic species but may belong in the vicinity of *Gavelinella*.

VIIa General remarks

In samples with plankton-nets planktonic Foraminifera are well-known. They consist of two groups, one with globular chambers throughout, the other with dorso-ventrally compressed tests. The globular forms have simple septa, globular chambers; they may be divided into two groups: one group in which the chambers are primarily bent down over the ventral side, with few chambers in a whorl, so that the whole test becomes more or less globular; the second have more than three chambers in a whorl and have a more flattened test; secondarily in some forms the tests may become planospiral. It is a remarkable fact, that many species with globular tests show coarse pores in the recent species, or there is a honeycomb-structure, whereas the pores open in the centre of the honeycombs (this group has been distinguished by Brotzen and Pozaryska as *Subbotina*), whereas all the forms with more flattened tests and more chambers to a whorl have very fine pores with only pustules between the pores. The latter group may be more primitive than the former.

The much compressed group is placed around *Globorotalia tumida* Brady. A poreless marginal keel is always present, and there is a tenon between a protoforaminal part and a deuteroforaminal part of the aperture. The pores are evenly distributed over the surface and in all species they are of the same shape and pattern. The septa between the chambers are simple, though in several species the outer walls, especially at the dorsal side, may be thickened by secondary layers of calcite. It was found by the author in the Siboga-material that in plankton hauls from to about 1300 m depth the walls are simple, whereas in bottom samples specimens often occur which show secondary thickened outer walls (Hofker, 166; p. 111, fig. 43; p. 112, fig. 44,45). These thick walls do not point to a planktonic life and probably in the life-cycle of many so-called planktonic species a benthonic stage exists. (See Chrisiansen, 1965, Publ. Staz. Zool. Napoli, Vol. 34, p. 197-202). There are many other groups of Foraminifera mentioned by authors as planktonic, such as fossil *Globotruncana;* many species, such as *Globotruncana (Marginotruncana) contusa* Cushman show very thick walls in many of the forms; it will be obvious that these forms were not planktonic but lived benthonically. Such a doubt as to their planktonic life was already expressed by Brotzen (1959, p. 35), where he puts planktonic in quotation marks. De world-wide distribution of such forms cannot be held as proof for planktonic life, since many typically benthonic Foraminifera also show a world-wide distribution; these thick-shelled forms may have other life-cycle-stages which are really planktonic and, moreover, many Foraminifera propagate in one of the stages of the life-cycle by means of microspores, which may be spread with the stream of the water.

The two groups of „planktonic" Foraminifera, the one without poreless keel, the other with distinct poreless keel, must belong to quite different groups of Foraminifera. Those with distinct keels always show closely and densely set pores in the hyaline test walls, which pores always have very distinct borders and never open into real pits or honeycomb structures.

Moreover, the walls, sutures excepted, are very smooth, but for some pustules which may appear near the umbilical cavity. In the group with globular chambers, on the other hand, in which, at least originally, no keels are found at the margin, so that the margin is always porous, the pores in the walls are not at all densely placed, the walls show tubercles and ridges between the pores, often fusing; the pores often open into pits which, when strongly developed, may give rise to a honeycomb structure, which is never found in real *Globorotalia*.

It may be, that some groups of real *Globorotalia* developed in the end of the Cretaceous from the latest *Globotruncanae;* in the Upper Maastrichtian there are species, such as *Globotruncana (Marginotruncana) citae* Bolli, which already show features which could be interpreted as globorotaline; it is also possible, that they started from *Pararotalia; Globorotalia praepseudobulloides* Hofker from the Lower Paleocene of Holland suggests such a development. In many species of true *Pararotalia* the margin is poreless, and the pores are placed in exactly the same way as found in *Globorotalia*. The difference is that in *Pararotalia* an umbilical plug is formed (but not in all species). *Pararotalia*, becoming planktonic, had to reduce that plug in order to get a ligther test. Bolli, Loeblich and Tappan (1957) and after them many other authors believe to have found forms in the Lower Cretaceous *(Praeglobotruncana* Bermudez) which they consider to be the forefathers of *Globotruncana* as well as of *Globorotalia;* but the distribution of the pores of those forms is that of *Globigerina*, with pustules between the pores, and they do not show marginal keels, except for some forms which obviously do not belong to this group and have to be removed to their genus *Planomalina*, which was not planktonic.

Some attempts have been made to prove that forms without definite keels, gathered into the artificial genus *Turborotalia*, in some forms developed poreless keels; Banner and Blow (1959) named such keels, which are sharp and have pores, pseudocarinae. In some groups the tests tend to become compressed; in *Globigerina compressa* Plummer, this tendency may be studied during the Danian and lower Paleocene; some authors believe, that the most compressed stage has a poreless keel (see Gohrband, 1963, pl. 6, fig. 8 who figured a typically compressed stage with pores at the margin); it is not found in the topotype specimens from the Wills Point Formation. Though Banner and Blow (1959, p. 6) give as genus-characteristic of *Globorotalia:* „test with an imperforate peripheral carina, at least in part", such species as *Globigerina compressa* Plummer and *Globigerina pseudobulloides* Plummer are mostly gathered into *Globorotalia*, though erroneously. Banner and Blow thus give as appearance for *Globorotalia* Danian to Recent, whereas in the Danian of Denmark no forms with imperforate carina occur. Only species with a true imperforate carina belong to *Globorotalia*, since the genotype, *G. tumida* (Brady), is characterized by a distinct imperforate carina. Bolli, Loeblich and Tappan (1957, p. 41), believe *Truncorotalia* Cushman and Bermudez and *Turborotalia* Cushman and Bermudez to be synonyms of *Globorotalia*, though Banner and Blow (1959) emphasize that *Turborotalia*, with the type-species *Globorotalia centralis* Cushman and Bermudez (see also Hofker, 166, pp. 106-108, who also showed that the type-species does not possess a carina) has not an imperforate carina. Recent *Globorotalia truncatulinoides* d'Orbigny, the type of *Truncorotalia*, on the other hand, has a true imperforate carina, and thus should be placed in synonymy with *Globorotalia*, which is done by Bolli c.s. Much more attention should be given to the pores of planktonic Foraminifera; for then such controversies would not have taken place; moreover, the shape of the finer structure of the walls, changing orthogenetically during time, should have been taken into consideration. That would have led to a much more reliable definition of the species of planktonic genera too, as has been proved by the author in boreal Oligocene species (Hofker, 182).

In many groups of planktonic Foraminifera there is a tendency to develop sutural openings which has even lead to the establisment of a genus, *Globigerinoides*. This feature is found in many different series of planktonic Foraminifera, and among the group „*Truncorotalia*" *(Acarinina)* it has also lead to sutural openings in the „genus" *Truncatulinoides* Brönnimann and Bermudez. In reality we observe that during the evolution of one single gens, viz. *Globigerina daubjergensis* Brönnimann (Hofker, 136, p. 83, fig. 4) and *Globigerina quadrilobata (triloba)* d'Orb., (Hofker, 160, pp. 64-68), these sutural openings develop gradually; in the gens *Globigerina daubjergensis* even several openings per chamber suture appear in the end, in *Globigerina kozlowskii* Brotzen and Pozaryska, in the higher Lower Paleocene. These sutural openings cannot be considered as genus-characteristics, since they develop gradually in primarily closed forms; they have to do with the steady increase of the volume of the tests during time, as is found in so many Foraminifera, and the smallness of the primary aperture which becomes too small to let pass enough pseudopodia towards the outer world.

Other planktonic groups develop so-called „bullae". They have given rise to the creation of different „genera" as *Catapsydrax, Globigerinita*, (see Hofker, 130, pp. 1-9) and *Globigerinatheca, Globigerinapsis, Porticulasphaera* (see: Hofker, 166, pp. 89-92). Whether those bullae are developed to close sutural openings, as is the case in *Globigerina rubra* d'Orbigny (Hofker, 130, p. 5, fig. 7, 8) or that they are closing the apertural hollow (l.c., p. 6, fig. 9-12; fig. 13-16), or moreover, in case they are covering most of the ventral side of the test, as in *Candorbulina*, or even surrounding the whole test as in *Orbulina universa* d'Orbigny, when found, they are always met with specimens of the same species without these bullae. In *Globigerina daubjergensis* Brönnimann the author could prove, that they are only found in the later part of the evolution series, so that bullae are also found in the latest stage of this gens which Brotzen and Pozaryska called *Globigerina kozlowskii* Brotzen and Pozaryska, 1961. So is obvious that, though the real meaning of these bullae is not yet known, it is a characteristic that developed in several different lineages and thus cannot be a genus-characteristic, so that all these „genera" have to be dropped; nor are sutural openings genus-characteristics, and the different genera based on these openings, neither have taxonomic meaning. Both features, sutural openings and bullae, have developed in different lineages and in different times in the Tertiary. In most cases they have no stratigraphic use as „genus"; only in case that the orthogenesis of one definite species is fully known, and that in the end it developed a typical bulla in some of its specimens, can such a case be used as a time-marker. This has been done for *Globigerina daubjergensis*, which developed these bullae for the first time at the very end of the Danian stage, and it can be done with those species of *Globigerina* which developed into *Candorbulina* and *Orbulina*; it may be done in the case of *Globigerina turgida* Finlay, which developed into „*Globigerinapsis*" and „*Globigerinatheca*", to end into „*Porticulasphaera*". Such developments are of stratigraphic significance and can be used for the purpose; but it is meaningless to gather such forms, which, to some extent, may be repeated in different lineages in different times, into distinct „genera". They are always endforms of such lineages, and may be compared with the end-chamber of *Eponides repandus* Fichtel and Moll, which is in the collection of these authors, a real *Eponides*, but which often forms, in good surroundings, a voluminous chamber with many large pores on the apertural face, which gave rise to the „genus" *Poroeponides;* or the „broodchambers" of *Orbitolites*, large chambers at the periphery quite different from the normal chambers or, the „bulla"-like chamber of *Tetromphalus bulloides* (d'Orbigny) which, as a benthonic form does not show that chamber and develops it in a certain generation when it becomes planktonic; or, even, the mud-cysts as I described them from *Quinqueloculina* and *Streblus* (Hofker, 25, p. 82, figs. 17, -20; p. 89, fig. 26); or, may be, the fistulose chambers of the Polymorphinidae, as I described them in detail in *Pseudopolymorphina acuta* (Roemer), 22, pp. 7-12. Bullae-like chambers are not at all restricted to Tertiary and Recent planktonic Foraminifera; they are found in several end-forms of planospirally coiled Globigerines of the Cretaceous, where they gave rise to „*Biglobigerinella*"; they are found, often commonly, in some end-stages of the *Globigerina cretacea*-gens.

We do not know what the ancestors were of the group of the Globigerinidae; the most primitive species of the Globotruncanidae *Rotalipora, Thalmanninella*, show distinct protoforamina and deuteroforamina; the author has suggested that these characteristics might point to Jurassic *Conorboides*, which group is also found in the Lower Cretaceous (Hofker, 91, p. 314, fig. 1). This suggestion was denied by Bolli, Loeblich and Tappan, but not on serious grounds.

Several groups of Foraminifera which are certainly or probably planktonic, have derived from quite different sources. *Globigerinatella* is certainly not a Globigerine species, but belongs, with its only species *G. insueta* Cushman and Stainforth, to the group of the Cassidulinidae; (Hofker, 130, p. 3); the same is the case with *Cassigerinella* Pokorny (Hofker, 184, pp. 321-324); *Candeina nitida* d'Orbigny, also forming with this only species a genus, seems to have derived from ancestors which are related to *Virgulinella pertusa* (Reuss) (Hofker, 93, pp. 98-99, pl. 12, figs. 5-17). It is remarkable, that all these species are also the genoholotype; obviously it was not at all easy to attain the planktonic state and the attempt was not continued by other offsprings of each species. In the case of fossil *Cassigerinella*, only one species developed and soon after it extinguished (only Oligocene).

In case that in planktonic Foraminifera keels are formed, these keels are always connected with a poreless area in the apertural face and this poreless area is connected with the poreless plates over the umbilical area, which plates in Tertiary and Recent Globigerines are often very much reduced, but are found in what is called „*Globoquadrina*" and in Upper Cretaceous *Globigerina*. There is some evidence that the whole poreless structure of the tests is a toothplate (Hofker, 185, text fig. 1-9); in this respect we must remember that in the genus *Laticarinina* the toothplate also forms part of the poreless apertural face and also the poreless carina; I have given an exhaustive analysis of *Laticarinina pauperata* (Parker and Jones), 49, pp. 408-412, and suggested in 1956, 93, pp. 189-206, that the whole family Marginolamellidae, to which I reckoned *Globotruncana*, *Globorotalia* and *Cancris*, have some connection in respect of the margin-forming toothplates with *Laticarinina* as well as with the Pulvinulinidae. There are many characteristics which are typical for this group Marginolamellidae: the density and clearness of the pores; the poreless margin; the tenon-like toothplate separating a protoforamen from a deuteroforamen, or, in the case that a foramen compositum has been developed, separating the protoforaminal part of the aperture from the deuteroforaminal part. In case this supposition is true, the poreless keels cannot be derived from forms in which the test was compressed in such a way that the keel resulted from it, but they are structures sui generis, connected with keel-forming parts of the toothplates, as is found in *Laticarinina*. Since *Discopulvinulina* also has strong affinities with this group, and seems to have derived from *Conorboides*-like forefathers, the suggestion that at least the Globotruncanidae also derived from that group, here finds support again.

Planktonic Foraminifera have been used intensively for stratigraphic purpose since in 1951 Grimsdale showed that Tertiary planktonic Foraminifera can be used in a world-wide scale. This topic has fascinated students in such a way, that benthonic Foraminifera were neglected more and more, and nowadays many investigators only study the planktonic species of the faunas for stratigraphic purposes. They even totally neglect the fact that previously benthonic Foraminifera were used successfully; they moreover neglect the fact that planktonic Foraminifera, when fossil, represent the tests of living organisms and that in reality they can only be used in case all data about their variation, lifecycle, sensitiviness for outer circumstances and, last not least their orthogenetic change during time, are fully known. Neglecting those fundamental facts, students made more and more species, genera, families, etc., used characteristics which later turned out to be unreliable, and a chaotic state of our knowledge of planktonic Foraminifera was the result, in which no one who is not a specialist can find his way. Especially the orthogenetic trends have to be studied beforehand if a good reliable system of species and genera should give us the base on which finer stratigraphic studies can be built. Knipscheer (range of *Globotruncana elevata-stuarti, 1956)*, Bukowa (lower Tertiary Globigerines, 1960) v. Hillebrandt (lower Tertiary *Globorotalia*, 1964) and the author *(Globigerina daubjergensis* Brönnimann, *Globigerina pseudobulloides* Plummer, *Globigerina cretacea* d'Orbigny, *Globigerina triloba* Reuss, (see Hofker, 143, 160, 166) gave examples of the change of tests during time, showing that only when these changes are known, planktonic Foraminifera can be used for stratigraphic purposes. The ignorance of such data was the cause of Brotzen's „cri de coeur", when he wrote (1959, p. 35): „Even Loeblich and Tappan in 1957 (a and b) studied some samples of the Swedish and Danish Danian which resulted in world-wide correlation of the Danian. The important new results for correlating the Calcaire pisolithique and the Danish-Swedish Danian (noted already by Desor in 1846 and before him by de Beaumont) are based on two foraminifera which would have a vertical distribution from the Lowermost Danian to the Eocene (according to the same authors in the same paper!). The correlation between the Danish-Swedish Danian with the type Montian is also based on two „planktonic" foraminifera in common in one sample of Mons and some samples from the Danian. With the same methods the correlations of the Paleocene were fullfilled, on a world-wide scale. Apart from the good descriptions and figures of „planktonic" foraminifera by Loeblich and Tappan, their statigraphical correlation of the Danian lacks all background for a discussion".

Since it is know that the two species discriminated above, *Globigerina daubjergensis* Brönnimann and *G. pseudobulloides* Plummer, have both a range from uppermost Maastrichtian up into the Danian or even later, they cannot be used for finer stratigraphic purposes, if their gliding change in teststructure and in test-shape are not known and carefully studied; this was done by the author, and he proved that the correlations made by Loeblich and Tappan are untenable. Especially when we try to date the age of a certain bed more accurately, it is absolutely necessary to study the tests with high magnification (at least x 300) and in transmitted light in a clarifier; only in this way we can get results (Hofker, 182, pp. 197-206, figs. 1-14). In case we neglect this finer structure, we get the results to which Banner and Blow came (Eames, Banner, Blow, Clarke, 1960, Mid-Tertiary stratigraphical correlation). Another characteristic result in this direction, based on the methods introduced by Bolli, Loeblich and Tappan (1957) is the paper, issued by Berggren (1962, critisized by the author in 1963, 183, pp. 208-288)

There is another remarkable change in planktonic Foraminifera during time. In two cases already, viz. in *Globigerina aspera* Ehrenberg and in *Globigerina daubjergensis* Brönnimann the author could establish a gradual change in the mean diameter of the proloculus, obviously caused by a change in the reproduction-cycle (105, p. 418; 165, p. 122); since this change often occurs together with a change in the whole form of the test (in *G. aspera* from trochoid to planospiral; in *G. daubjergensis* from low-spiral to high-spiral) this change may be of utmost importance. (see pl. 18, fig. 2; pl. 5, fig. 12).

Remarkable also is the change in coiling-direction, first noticed by Bolli (1950, pp. 82-88; 1951, pp. 139-143). Bandy (1960) stated in the case of *Globigerina pachyderma* (Ehrenberg) that there is a relation between the temperature of the water and the direction of coiling; dextral species are dominant in warm water, and the reverse in cold water. This gave him the opportunity to compare the temperatures during the last 30.000 years. The author checked the direction of coiling during the Danian stage in Denmark by means of two species; in *Globigerina daubjergensis* Brönnimann is a steady change from left coiling specimens towards right coiling specimens which, according to Bandy, might indicate a change of temperature from colder to warmer (Hofker, 165, p. 125; see pl. 18, fig. 1); however, *Globigerina pseudobulloides* Plummer did not change the direction of coiling during the same time. It is suggestive that occultists believe that for sensitive persons a right coiling spiral of metal produces the suggestion of warm, left coiling spirals the suggestion of cold. This then would point to an adaption of the organisms to the temperature as well. It would be worth while to study more of such changes in long-living gentes, such as in the gens *Globigerina cretacea* d'Orbigny (Hofker, 159, p. 118) and to compare the result with what has been found by Emiliani and others about the change in temperature during that time of the Cretaceous. Special attention should be paid to the grouping of planktonic Foraminifera as given by Bolli, Loeblich and Tappan (1957) and by Banner and Blow (1959, 1960). I could show that planospiral forms like *Planomalina* (not a planktonic genus) from the Lower Cretaceous, and so-called *Globigerinella* from the Upper Cretaceous and the Lower Tertiary are typically planospiral, at least in their end-forms; on the other hand so-called planospiral *Globigerina siphonifera* d' Orbigny and *G. aequilateralis* Brady are in essence trochospiral, and cannot belong to *Hasterigerina*; *Hasterigerina pelagica* (d' Orbigny), with its very thin wall and triangular spines, is planospiral throughout and obviously belongs to quite a different series of Foraminifera (Hofker, 166).

Reiss (1957, 1963), Ayala Castanares (1954), Loeblich and Tappan (1964) and several other authors have postulated that the bulk of the planktonic Foraminifera are bilamellar. Not only the septa between the chambers should be double, but there also was a double wall even in the last formed chamber. Contrary to this postulate, the author has shown, that planktonic Foraminifera are monolamellar and that only in some forms double and trifold lamellae are formed secondarily; this is even not a constant phenomenon within a single species, since in *Globorotalia tumida* Brady the dwellers near the surface have a single outer wall whereas those specimens living near or at the bottom of the ocean have thickened outer walls, especially at the dorsal sides (see also Bé, 1965, pp. 81-97).

The author could prove with photographs (185) that the septa of *Globotruncana* and *Globorotalia* are simple without any trace of a second lamellum, and that at the protoforaminal part of the foramen compositum a reduced toothplate begins, running along the border of the aperture and ending in the umbilical plate which partly covers the umbilical hollow. This toothplate forms a gutter along the foraminal border, the inner hollow of which can often be seen in transverse sections, forming a kind of canal (pl. 18, fig. 12; pl. 19; pl. 20).

Reiss especially believed that in *Globotruncana* there was a lamellation over the whole test wall, growing per instar, and he demonstrated this in a figure (1957, text fig. 3); if the photographic reproduction of this figure is compared with photographs taken transversely through air-filled well-preserved tests of *Globotruncana linneiformis* Hofker and *Marginotruncana globigerinoides* (Brotzen), it is proved that the figure given by Reiss does not agree with reality: over the whole test no secondary thickening by means of lamellae has been formed and nowhere a second lamellum can be traced (pl. 21, figs. 1, 2).

Yet several photographs published by authors suggest double walls and also double septa; the majority of these photographs have been taken from specimens filled with rock-material. There may be two causes for the „doubling" of the septa in such sections:

1. Grinding with tension will also cause a tension on the tiny septum now fastened to rock; the result will be that just in the middle of the brittle wall a rupture occurs which suggests bilamellation;

2. recrystallisation, attacking the thin wall from both sides will cause fine crystals which will meet just in the middle of the wall; here a dark line will appear at the junction of the crystals.

Yet it is remarkable that Reiss obviously did not observe that in his figures of Globigerines, 1957, pl. 20, 5, 6, 9, the outer wall of the last formed chamber is distinctly monolamellar.

Sections of *Globigerinelloides eaglefordensis* (Moreman) clearly show (pl. 19, figs. 1,2) that in all chambers a primary monolamellar wall exists, which is the only wall in the last formed chamber and which continues in the monolamellar septa; moreover, the whole outer wall is strengthened secondarily by a second layer, except for the last formed chamber. Since planktonic Foraminifera cannot use fine particles of foreign material, the primary wall, contrarily to so many benthonic forms, is quite hyaline, and radial crystalline.

In the Treatise of Foraminifera (1964) Loeblich and Tappan describe the Superfamily Globigerinacea as having „double walls of lamellar hyaline calcite". The first family they mention is that of the Heterohelicidae, in the new scope they use, only containing planktonic forms. Sections of *Heterohelix* reveal that the tests are monolamellar, only with secondary thickening in some cases as can be seen from the photographs (pl. 19, figs. 3,5; pl. 20, fig. 4). However, in fossil specimens penetration of rock matter from both sides may suggest lamination in the middle of the pores. Even in the more initial chambers, where the outer walls may be thicker than those in the distal chambers, this thickening here seems not to have occurred by distinct layers. No such layers could be detected in air-filled well-preserved specimens, as the photograph of *Guembelina (Heterohelix) striata* (Ehrenberg) shows.

In 1962, 166, the author gave many details of several planktonic Foraminifera. All tests of *Hantkenina*-species showed to be monolamellar; a photograph of a horizontal section here shows this characteristic in detail (pl. 19, fig. 4). Moreover, the author showed that series of transverse sections through *Globotruncana* revealed that the so-called canals in the keel are formed by overlap of adjacent chambers (166, fig. 46). *Globorotalia menardii* (d'Orbigny) from a plankton sample shows a monolamellar test, whereas specimens from a deep bottom sample show tests with double outer walls (166, fig. 44, 45). *Globigerina aequilateralis* Brady from a plankton sample shows simple walls (fig. 32), whereas later chambers from the deep-sea form *G. siphonifera* d'Orbigny show double walls only in the outer chamber whorl. *Hastigerina pelagica* (d'Orbigny) from a plankton sample shows simple test walls throughout.

The same can be said about *Globigerina aspera* (Ehrenberg) from the Upper Cretaceous, *Globigerina micra* (Cole) from the Eocene and *G. danvillensis* Howe and Wallace, also from the Eocene (166, fig. 18-20).

We have to redefine the Superfamily Globigerinacea:

Test enrolled, planispiral or trochospiral or modified from such; chambers basically globular, later they may be compressed or variously modified; simple walls originally as primary walls, in some cases with lamellar thickening only at the outside, often only at the dorsal side, which thickening is secondary. Walls of radial hyaline calcite, perforate except for the umbilical flaps and often except for the apertural face; some groups have massive keels which are not perforate. Aperture in most cases a foramen compositum, often with distinct proto-and deuteroforamen separated by a platelike toothplate. In some cases also dorsal sutural openings. Habitat: commonly planktonic, but it may be that specimens with extremely thick walls have a more benthonic life. See also Christiansen, 1965.

VIIb Pores of planktonic Foraminifera

The author has laid stress on the shape, distribution over the wall, and the size of the pores in many occasions. As to the size of the pores, the present author could prove that in the species which can be gathered in the Gavelinellidae, the pores increase in size during time (see also chapter on Evolution). In the planktonic Foraminifera within each species, different from what has been found in the Gavelinellidae, the size of the pores is very constant, though during time within a gens or species gradual thickening of walls may lead to outer wall structures which may give rise to pits and honeycomb structures in which the pores open. In the genus *Globotruncana* and in *Globorotalia* pores are always of the same type in the different species: clearcut, distinct, densely placed and relatively small in size. But in the genus *Globigerina*, especially in the Tertiary and the Recent species, the size of the pores may differ greatly in the different species. However, each species as such maintained the size of pores during geologic time. This constant size of pores whithin the species, but differing from species to species, made the author consider the size of pores as an important characteristic of the species of *Globigerina*; in this idea he was followed by Berggren (1960, Acta Univ. Stockholmensis, Stockholm Contr. Geol., vol. V, pt. 3, pp. 60-65, fig. 4, 5). The present author could use the pore-index (pore pattern) to prove the Oligocene age of the lower part of the Cipero Formation of Trinidad (182, especially p. 105).

In reality we may observe that geologically older species of *Globigerina* often have smaller pores than geologically younger species. *Globigerina daubjergensis*, Brönnimann the first species with globular test, has very small pores; later species with such a test may develop coarser pores; the late-Tertiary and Recent species with globular test may even belong to the species with very coarse pores. It is a remarkable fact that species with a flat trochoidal test (with about 5-6 chambers in the last formed whorl) mostly have fine pores, even the Recent species, such as *G. eggeri* Rhumbler, *G. bulloides* d'Orbigny. On the other hand, species with globular tests (number of chambers in the last formed whorl less than 5) often show much coarser pores such as *G. sacculifera* Brady, *Sphaeroidinoides dehiscens* (Parker and Jones), *G. conglobata* Brady. There are remarkable exceptions to this rule: *Globigerina bradyi* Wiesner from the North Atlantic, though this species shows only three chambers in the last formed whorl, has very fine pores. Just this exception may lead us to an explanation of the function of the pores. In the author's opinion it is a wrong conception to regard the pores of the Foraminifera as openings through which the pseudopodia run towards the outer world; in many cases (viz. Lagenidae) pores are too fine to let the dense protoplasm pass; moreover, Le Calvez, Jahn and the present author found that coarser pores possess sieve plates with extremely fine openings. The function of pores must be quite different: to make respiration possible. It is obvious, that the surface of a globular test forms a less favourable ratio with the volume of the protoplasm than in more trochoidally built tests (tests with 5 chambers or more in the last formed whorl). In the case of *Globigerina bradyi* the extremely long axis of the test gives a much larger surface for respiration than in globular tests; hence the very fine pores. Metabolic processes in planktonic Foraminifera are of very much importance for this group of animals since they mostly live in combination with Zooxantellae.

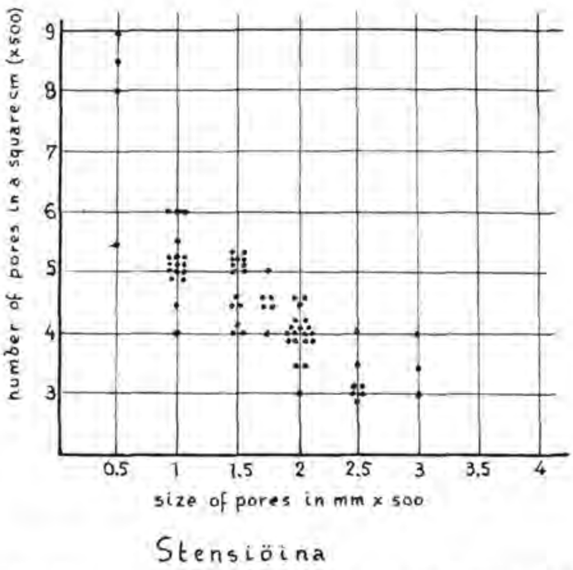
In this respect the author has given a method to measure the size of pores together with the density in which they are placed in the test wall, the so-called pore-index; the pores of a species (not to be confused with the pits or honeycomb structures in which the pores may open) are drawn with a camera lucida with a magnification of x 500; the number of pores (in a mean) which in the drawing are found within a square cm forms the first number of the index; mean diameter of the pores in the drawing forms the second number; in such a way we find the following indices:

1	*Globigerina bulloides* d'Orbigny	9-0,5
2	*Globigerina bradyi* Wiessner . .	11-0,5
3	*Globigerina pachyderma* (Ehrenberg)	5-1
4	*Globigerina eggeri* Rhumbler . .	9-0,5
5	*Globigerina glutinata* Egger . .	40-0,1
6	*Globigerina inflata* d'Orbigny . .	6-2
7	*Globigerina rubra* d'Orbigny . .	3-2
8	*Globigerina conglobata* Brady .	3-5
9	*Globigerina sacculifera* Brady . .	2-3
10	*Sphaeroidinoides dehiscens* (Parker and Jones)	1-6

The instances 1 to 5 show fine pores with a high first index number; instances 6 to 10 show coarse pores with a low first index number. Of the first mentioned species only no. 2 has 3-4 chambers in the last formed whorl. The instances 6-10 all belong to the globular type of test.

A large number of species has been measured by the author in this way, fossil as well as recent ones. It was found that when the first number of the index increases, the second number decreases (Textfig. 14). Just the same phenomenon has been found in different species of the genus *Stensiöina*, in which genus, since it belongs to the Gavelinellidae, the size of the pores increased during geologic time (Textfig. 13). With the idea in mind that pores serve respiration, it will be easy to understand that there must be a negative correlation between the number of pores per surface unity and the size of the pores, in so as to make respiration assured. (See Textfigure 14).

There are some instances in which two forms, occurring in different parts of the recent sea, show nearly similar outer characteristics; yet they may differ in the pore-index; in such cases it will be worth while studying such species occurring in the same time-level more accurately; they may also differ in other characteristics.



Textfig. 13. Correlation between the size of pores and the number of pores in a square cm (x 500) in *Stensiöina*. In this correlation different species from different stratigraphic levels are analysed. The correlation shows that there exists a negative correlation between the two variants considered, and that in this way the total of respiration openings remains constant.

Remarkable are the very large pores found in *Sphaeroidinoides:*

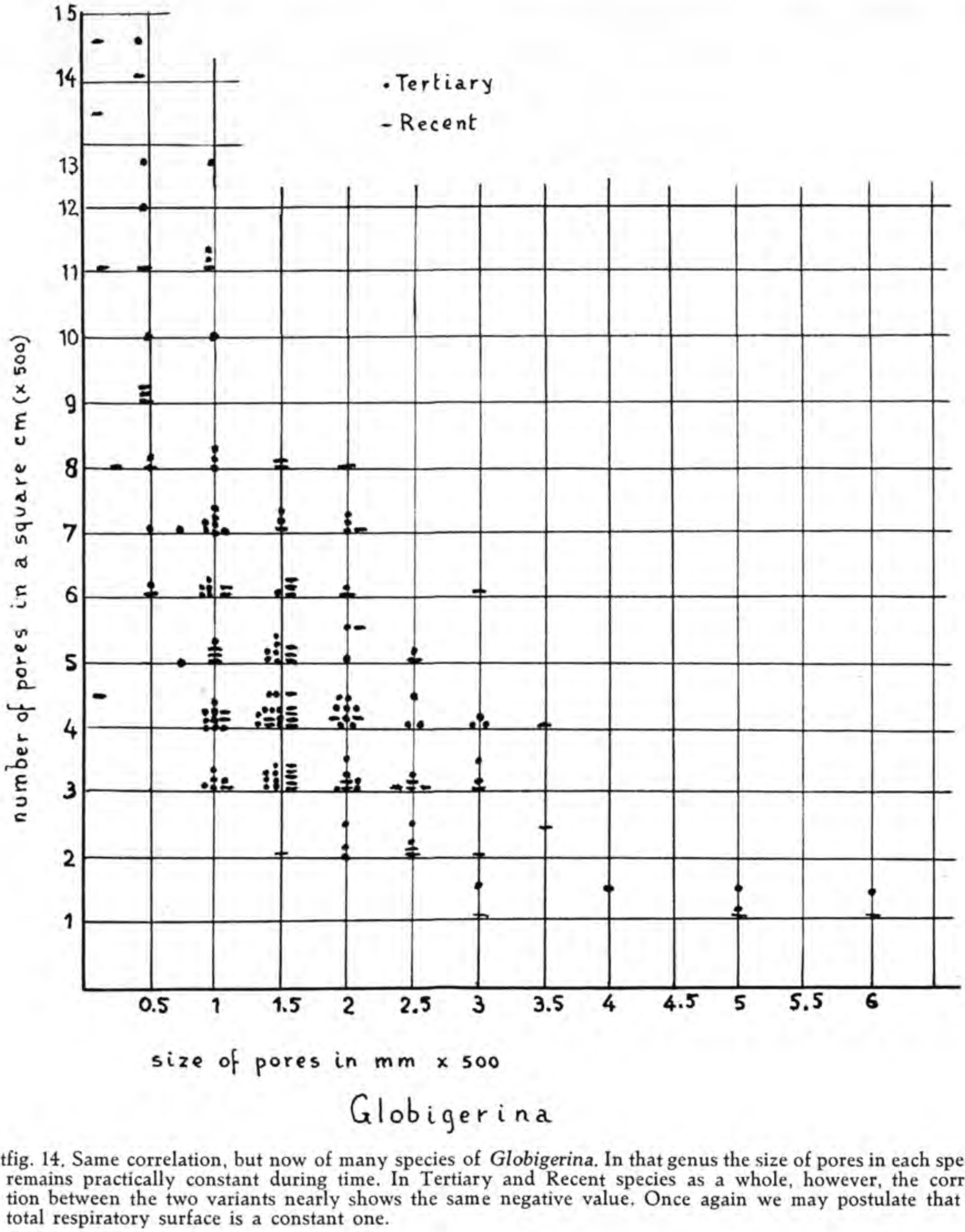
Oligocene Trinidad:
Sphaeroidinoides grimsdalei
(Keyzer) 2-4; 1,5-6
Miocene Trinidad:
Sphaeroidinoides seminulina
(Schwager) 1.5-4
Recent Caribbean:
Sphaeroidinoides dehiscens
(Parker and Jones) . . 1-6

Large pores are found in the globular group *venezuelana:*

Upp. Eocene Trinidad:
Globigerina venezuelana
Hedberg 4-2
Ecuador Oligocene-Miocene:
Globigerina cf. venezuelana
Hedberg 4-3; 5-2,5; 4-2

VIIc. Monolamellar planktonic Foraminifera

In a paper (1964, 185) the author showed that there is a large difference in structure between *Globotruncana* and *Globorotalia* on the one side, and *Gavelinella* on the other. In Ga-



Textfig. 14. Same correlation, but now of many species of *Globigerina*. In that genus the size of pores in each species remains practically constant during time. In Tertiary and Recent species as a whole, however, the correlation between the two variants nearly shows the same negative value. Once again we may postulate that the total respiratory surface is a constant one.

velinella the septa are double, which characteristic was called by Reiss „bilamellar"; in the planktonic groups studied no trace of a bilamellar structure of the septa could be found. All the specimens studied were taken from material in excellent preservation.

The study of tests of *Globigerina (Globigerinelloides) eaglefordensis* in very thin horizontal sections revealed that in older chambers the outer wall may become double by means of secondary thickening, but that the last formed two chambers had simple outer walls; moreover, in all the chambers the septa showed to be the continuation of the inner primary wall and consequently are simple.

Globigerina aspera shows simple walls throughout, though in some places a trace of doubling by secondary calcite at the outer walls could be observed; the septa, however, are always the continuation of the primary inner wall and are consequently simple (pl. 18, fig. 2).

Guembelina striata (Ehrenberg) from different localities may show different structures with respect to the outer walls; some specimens show very thin outer walls and no secondary doubling is found, neither in the outer wall, nor in the septa. Other specimens may get a double outer wall, and it may be that even two successive stages of growth can be observed. In one specimen in the first part, consisting of 8 chambers, the whole wall was double; the septa in the initial chambers were simple, but the whole outer wall of two later chambers, also the apertural walls were doubled by a secondary layer of calcite. Then a new period of growth seems to have started, and three new larger chambers were added. The oldest of these chambers showed a double outer wall, but the septum is simple. The two apertural walls of the last formed chambers, and also the outer walls of them, are simple throughout. This case may illustrate the possibility that some authors got the idea that the septa of *Guembelina* are double. We must, however, conclude that also in *Guembelina* the septa are simple in the majority of cases and that only when growth is restarted in some individuals after a period of rest, septa (apertural walls) can be doubled secondarily (pl. 19, fig. 3, 5). In Hofker, 166, Ueber Hantkeninen, pp. 126-129, figs. 65-85, the author stated that the walls in later chambers may be thickened by secondary calcite, but that the septa as well as the wall of the spines are simple (pl. 19, fig. 4). I give here some other instances of monolamellar walls in planktonic Foraminifera, though these walls may be thickened secondarily at the outside. *Globigerinatella insueta* Cushman and Stainforth, which the author showed to belong to the Cassidulinidae (59; 130, p. 3), has monolamellar walls and septa; the same can be said about *Cassigerinella boudecensis* Pokorny (184). All Cassidulinidae, and also their planktonic species, have simple walls.
Globigerina yeguaensis Weinzerl and Applin from the Cocoa sands has secondarily thickened outer walls (pl. 19, figs 7,8); but the end of the walls, the poreless septa, are monolamellar, as are the inner walls of the initial chambers.
Globigerina cretacea d'Orbigny from the Campanian of Folx-les-Caves in Belgium has slightly thickened outer walls, but the septa and the wall of the last formed chamber are monolamellar (pl. 20, fig. 2).
Very thin sections were made of *Globigerina daubjergensis* Brönnimann and studied in normal and polarisized light with magnification x 500. Not the slightest trace of bilamellar structure could be observed; even the slightly thicker walls of the initial chambers showed a totally simple wall, as were the poreless septa within the test (pl. 18, fig. 5). Lately this *Globigerina* was transferred to a new genus, *Globoconusa* Khalilow, 1956; this new name was based by Khalilow, according to Loeblich and Tappan (Treatise, p. 670) on the more conical form of the initial part of the test. The author, however, could prove that this conical form was reached in the later stages of the evolution of this species and that mainly tests beginning with a small proloculus show this characteristic; it is continued in *Globigerina kozlowskii* Brotzen and Pozaryska in the higher Paleocene. So this characteristic is due to the forming of smaller proloculi in some of the generations of *Globigerina daubjergensis* and so it has no specific and even less generic meaning. So *Globoconusa* Khalilow is a younger synonym of *Globigerina* and must be dropped. The author could prove in *Globigerina rubra* d'Orbigny, that in that species specimens also develop with higher spire and smaller proloculus (see Hofker, 166, pp. 122-124, fig. 61, 62, 63; 1956, 93, pp. 231-234(Diagram 20).

Another planktonic group of species is *Stainforthia (Chiloguembelina);* the author analysed this group in 1963, 187; the toothplates, the loop-shaped apertures, the triserial initial part are characteristics which point to *Virgulina;* the calcareous radial crystalline microstructure does not mean much here; planktonic forms of microgranular ancestors must change their microstructure from granular into crystalline. Since this group is related to *Virgulina*, the structure of the test walls must be monolamellar; thin sections substantiate that view; no trace of bilamellation can be found (pl. 18, fig. 6). The simple septa in *Stainforthia (Chiloguembelina)* were also stated by Reiss (1963) and consequently Reiss placed *Chiloguembelina* in the Buliminidae (a family with toothplates). Loeblich and Tappan (1964, Journ. Geol. Soc. India, vol. 5, p. 26) denies the occurrence of a toothplate in *Chiloguembelina*. They state: „The 'toothplates' illustrated by Hofker (1963, p. 151) for *Chiloguembelina* (as *Stainforthia midwayensis* (Cushman), *S. morsei* (Kline) or *S. parallela* (Beckmann) are in reality only this external lip, which becomes covered only by addition of a later chamber. The toothplate of true *Stainforthia (S. concava* Höglund) is internal in the final chamber as well as in all previous ones, and is not represented as an external lip". The author, when defining toothplates, always wrote: a toothplate is a structure, beginning at the border of the aperture of a former chamber, and running through the chamber itself towards the protoforamen of that chamber adhering to its border. The free-folded part may protude from the foramen. When we study the „lips" of *Chiloguembelina* they begin at the attached part of the former „lip" and the axial border of the former, loop-shaped aperture; they then run through the chamber, along the axial border of the former chamber, and run towards the opening of the foramen of the next chamber, forming free folded parts slightly protruding from the loop-shaped foramen of that chamber and adhering to the axial border of that foramen. So, the „lip" is, for its larger part, surrounded by the wall of the chamber which formed it, and is not „external". Loeblich and Tappan concur with Reiss in placing *Chiloguembelina* in the Buliminidae; but, obviously, they ignore the fact that all members of that family have loop-shaped apertures and true toothplates.

Photographs, published by Bé (1964, pp. 823-824) distinctly show, that the septa of *Globorotalia truncatulinoides* d'Orbigny are simple.

VIId. The aperture of Globotruncana

In my paper on Globotruncanidae of North Western Germany (91) I tried to give a taxonomic analysis of the Globotruncanidae, mainly based on the apertural conditions and the structure of the ventral side corresponding with those apertural conditions.

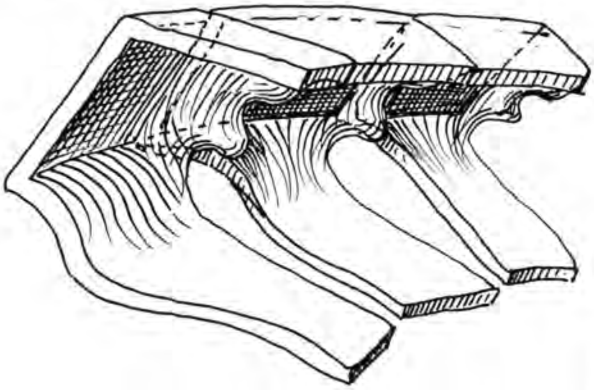
In 1957, Bolli, Loeblich and Tappan gave a new description of the genus *Globotruncana*, in which they describe the aperture as follows (p. 44):

„primary apertures interiomarginal, umbilical, in well preserved specimens covered by tegilla, which are perforated by accessory infralaminal and intralaminal apertures, which are then the only openings to the exterior, the tegilla are commonly partially or wholly broken out during the process of fossilisation, or may be preserved only as scalloped fragments."

This description of the apertural conditions in *Globotruncana* is superficial and even untrue. When we study series of sections of *Globotruncana*, and especially the Maestrichtian forms with single keels, we find that each chamberwall forms a rounded lip directed towards the dorsal side bordering the large aperture towards the umbilical hollow, provided with a distinct tenon (why the term „tegillum" where Brotzen has given the name of „tenon" to all such homologous structures?), which tenon, always poreless, covers part of the umbilical hollow. These tena never fuse totally, but when they are very large, as is the case in most undamaged specimens, they may overlap each other, giving rise to a totally covering „plate"; in those cases secondary openings often occur, or rather here and there the tena show irregular borders giving rise to those openings. At the proximal end of the rounded rim of the umbilical aperture, the rim is attached to the former chamberwall, whereas at the distal part it is attached with a protruding part to the wall of the next chamber. The latter attachment is narrow, for the septal foramen is found just dorsally to this place, mostly an arched opening, not even mentioned by Bolli, Loeblich and Tappan. This foramen opens into the lumen of the next chamber.

In this way, each chamber shows two apertures, one leading into the next chamber, the other, totally separated from it, leading into the umbilical hollow. These conditions very much resemble those of *Discopulvinulina*, *Rotalia*, *Gavelinella*, and we must consider the umbilical aperture as a protoforamen, and the septal foramen, always much more dorsally placed, as a deuteroforamen.

In many forms of Globotruncanidae, especially the more bulky forms with a poreless mar-



Textfig. 15. Reconstruction of the apertural conditions of *Globotruncana linneiformis* Hofker.

gin with two rims, the protruding part of the rim bordering the umbilical aperture does not reach the wall of the next chamber, and in this way a foramen compositum is formed, as observed in those forms by the author in 1956 (91). Moreover it was stated, that in most tests observed in oil, the tena over the umbilical hollow were not broken away as was suggested by Bolli, Loeblich and Tappan; on the contrary, in most species observed these tena are well-preserved, especially in those cases in which the hollows of the tests are filled with calcite material, and when they are studied in oil with high magnification.

The rounded margin of the septal foramen, and the whole structure of the rim around the umbilical protoforamen show that those foramina are not secondary buildings, but that they are preformed when the chamber was formed. In several specimens of *Marginotruncana pauperata* Hofker, of which the author could study tests without interior calcite-fillings, the septal deuteroforamen, at the last formed chamber could be clearly seen.

Bolli, Loeblich and Tappan emphasize that *Globotruncanae* were planktonic organisms. But were they? In any case there are strong indications that the whole group with poreless rims at the margin and two foramina, a protoforamen opening into the umbilical hollow and the deuteroforamen openings into the lumen of the next chamber, which foramina often fuse together into a foramen compositum, together with the so typical tena over the protoforamina, had, together with *Gavelinella, Discopulvinulina, Conorboides*, etc, one single ancestral group in common. The poreless tena were in connection with the poreless rim on the margin. This group I gave the name of Marginolamellidae. It is believed that Globotruncanidae were very wide-spread organisms thus giving rise to very fine guiding-fossils; hence the suggestion that they were planktonic organisms. But are they so widely spread? The author has compared many thousands of samples from different regions, and of comparable age, the *Globotruncanae*, even when determined as identical species, showed quite different features when studied with high magnifications or in sections. They seem to form only regional guides, and the different appearences of several species as given by some authors strongly suggest that these authors in reality did not study the same species, though they gave the same name. There are at least 5 species known to the author mentioned by authors as *G. arca* (Cushman); even Cushman himself described and figured at least two of them; four species are known by the author called *G. stuarti* (De Lapparent); the number of species which goes under the name of *G. marginata* (Reuss) is legio; *G. stuarti* and similar forms in Europe and in Northern Africa seem to be restricted to the Maestrichtian; but Bolli describes it from the Lower Campanian and younger strata from Trinidad; Cita cites *G. arca* from Santonian to Lower Maestrichtian, whereas Bolli found it only in the Middle and Upper Maestrichtian; the same can be said of *G. cretacea*. So it seems that either the concepts of the geologic stages, or the determinations of the Globotruncanae do not correspond. Types received by the author from several authors indicate the latter probability. Only a much more accurate study of the fossils involved can lead us to sharp definitions of the species; but they have to be studied in sections, with high magnifications, and in oil or other clarifiers. And in that case we shall find that these fossils can only be guides for restricted regions, and are not more wide-spread than many benthonic Foraminifera.

I here give the results from series of sections obtained from:

a. *Globotruncana stuarti* (de Lapparent), Gerhardsreuter Graben, Siegsdorf, Bavaria, Lower Maestrichtian; the protoforamen and the deuteroforamen are separated, the tenon is distinct (pl. 18, fig. 11).

b. *Marginotruncana paraventricosa* Hofker, drill-hole in Holland, Lower Campanian; the wide foramen compositum opens into the umbilicus, and only a small deuteroforamen opens sidewards into the lumen of the next chamber; the tena are wholly covering the umbilical hollow (pl. 18, fig. 8).

c. *Globotruncana pura* Hofker, drill-hole near Hannover, Lower Campanian; the much smaller foramen compositum opens obliquely into the umbilical hollow, the tena are small, only covering the border of the umbilical hollow (pl. 18, fig. 9).

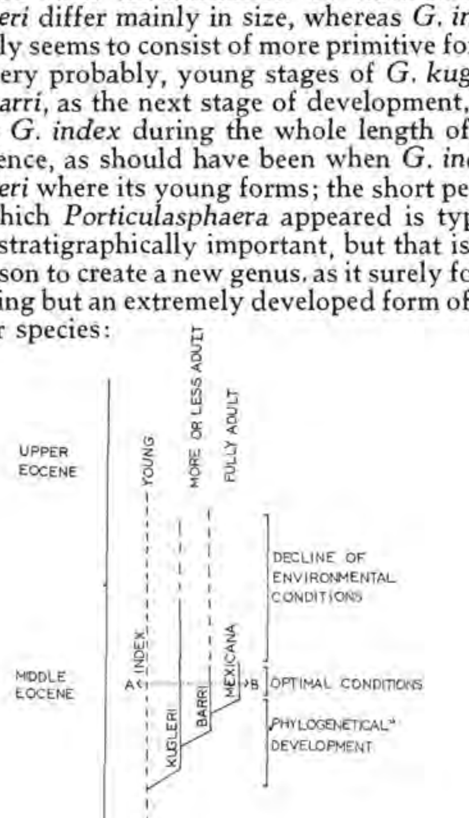
See for more figures: Hofker, 1961, 156; when comparing the transverse sections with those of *Discorbis vesicularis* Lamarck, 1963, 186, the resemblance is striking.

VIIe. Globigeraspis, Globigerinatheca, Porticulasphaera.

In a previous study (1962, 166) the author decribed several stages of development in a series of samples from the so-called Stockletten in Bavaria, Germany. It was found that there are small specimens with the characteristics of *Globigerina turgida* Finlay, larger specimens with the characteristics of *Globigeraspis kugleri* Bolli, Loeblich and Tappan, and still larger specimens with the characteristics of *Globigerinatheca barri* Brönnimann; the author suggested that in more favourable environments the end-stage, called *Porticulasphaera mexicana* (Cushman) could also be attained. All specimens have the same surface-structure: a relatively smooth surface when seen with small magnification, and the pores are mostly not surrounded by a honeycomb structure. Sections revealed that all these forms show the same inner structures, only more differentiated by growth and by additional bullae-shaped chambers. In *Porticulasphaera* the last formed chambers show rows of additional openings along the sutures, whereas in *Globigerinatheca* and *Globigeraspis* these openings are mostly found at places where several sutures meet. The author emphasized (1962, 166, pp. 89-92) that all these forms obviously belong together and that the name of this group of forms should be the oldest name, viz. *Globigerina mexicana* Cushman 1925, in the case that in better environment *Porticulasphaera mexicana* could also be found together with the other forms, and *Globigerina turgida* Finlay 1939 in the case in which *Porticulasphaera mexicana* should prove to have a quite different surface structure and inner structure. Loeblich and Tappan in the Treatise (1964, pp. 675, 676) place *Globigeraspis* and *Porticulasphaera* together in the subfamily Sphaeroidinellinae, whereas *Globigerinatheca* is placed in the Catapsydracinae. So, according to these authors, not only four different genera are found which in reality belong together, but they would also belong to two different subfamilies!

The author got a good sample from Trinidad from the type-locality indicated by Bolli, Loeblich and Tappan in 1957 for *Porticulasphaera mexicana*, viz, Brasso-Tamana Road, 12¾ km milepost, Trinidad. In that sample, just as was found in the Stockletten, the smallest specimens with the typical surface-structure do not differ from *Globigerina turgida* Finlay; slightly larger specimens have at least one bulla-chamber with some openings (*Globigeraspis kugleri* Bolli, Loeblich and Tappan); still larger specimens show several of these chambers together with one very large end-chamber (*Globigerinatheca barri* Brönnimann); the largest specimens, with quite the same surface-structure after all, show several chambers which have some sutural openings at the meeting-point of several sutures, whereas the last formed chamber, forming the larger half of the whole test, shows the typical row of openings along the suture. A transverse section made it clear that this *Porticulasphaera mexicana* in reality forms the end-stage of development of all the former stages and that we do not deal with two subfamilies nor with four different genera but with one single species, of which the end-stage of development got the first-mentioned name in literature, viz. *Globigerina mexicana* Cushman. So we have to speak of *Globigerina mexicana* which has the peculiarity to develop different stages, first with an umbilical aperture and with three or four chambers, closely coiled, highly inflated towards the ventral side, with a pore-index 4-2 and a smooth or slightly honeycombed surface (in older chambers). The wall is thick. The second stage is somewhat larger, has one bulla-like chamber covering the umbilicus with several small openings at the sutures with former chambers; the third stage has several of these bulla-like chambers and large end-chambers; the last-formed stage not only has the normal and the additional chambers developed with the already mentioned openings, but also a very large end-chamber with many openings along the suture with the former chambers. Since all these stages have been taken as genotypes of the genera *Globigeraspis*, *Globigerinatheca* and *Porticulasphaera*, these names become synonyms of *Globigerina*.

From a biologic point of view these genera have to be dropped; from a stratigraphic standpoint we find that *Globigerina turgida* Finlay is found in the Lower Eocene and the lower part of the Middle Eocene, where it changes into its adult form, *Globigeraspis index* Finlay. In Trinidad *Globigerinatheca barri* begins slightly later than *G. index* and *G. kugleri*, and ends together with *G. index* in the lower part of the Upper Eocene. Most favourable for the development of the full-grown form *Porticulasphaera mexicana* seems to have been the upper part of the Middle Eocene in the Caribean region, where it is found for a short time; it is not impossible that in other parts of the world the last mentioned form appears later or earlier, due to other circumstances. *G. index* and *G. kugleri* differ mainly in size, whereas *G. index* mostly seems to consist of more primitive forms, or, very probably, young stages of *G. kugleri*. *G. barri*, as the next stage of development, follows *G. index* during the whole length of appearence, as should have been when *G. index-kugleri* where its young forms; the short period in which *Porticulasphaera* appeared is typical and stratigraphically important, but that is not a reason to create a new genus. as it surely forms nothing but an extremely developed form of one other species:



The steady increase of the tests during time as well as during individual development is a characteristic which is found in many gentes of Foraminifera; the sections do not differ (but for the sutural openings which in the latest and most developed forms are easily met with in the sections) from those of the less developed stages made and published bij the author. Beckmann (1953, Ecl. geol. Helv., vol. 46, p. 393, fig. 18 19) also showed these openings; the sections reveal that these openings are formed secondarily, since some pores have been cut through by the openings, as was also found by Beckmann. The author fully agrees with Beckmann, when he says: „Auf einer spezifischen oder gar generischen Abtrennung der vorliegenden *Globigerinatheka*-artigen Exemplare von *G. mexicana* kann jedenfalls verzichtet werden". This warning by Beckmann has been flung to the winds by Bolli, Loeblich and Tappan (1957, U. S. Nat. Mus., Bull. 215).

VIIf. The structure of Globorotalia

The material for this study consisted of specimens of *Globorotalia tumida* (Brady), *G. menardii* (d'Orbigny) and *G. truncatulinoides* (d'Orbigny), all three already described by the author from off Santa Cruz, Virginia Archipelago, West-Indies. *Globorotalia tumida* is the genotype of the genus *Globorotalia*. (See Hofker, 93, pp. 192-199, pl. 29, figs. 15-26, pl. 29, fig. 27-33; pl. 30, fig. 1-14).

Sections were made transversely through the proloculus, horizontally through the keel, below and above the keel, and some sections tangentially. These sections revealed that:

1. in *Globorotalia* the septa are extremely thin;
2. the septa often are strongly twisted and strongly obliquely placed in respect to the axis of the test;
3. the septa are partly built by the septum of a former chamber and by the septum of the next one, in such a way that each next chamber wall bends inward along the former septum;
4. the dorsal part of each septum is only formed by the chamber found proximally to the septum;
5. the dorsal part of each septum is simple, monolamellar;
6. axially from the thickened lip of the foramen compositum the toothplate, covering

part of the umbilical hollow, forms part of the septum and adheres to the lip of the foramen;

7. the „double" parts of the septa are porous; the monolamellar part of them is always poreless.

The strongly twisted septa make it difficult to get a good idea of their structure; only several sections which have to be very thin, taken on different heights of the axis, give a true idea of their structure.

In that part of the septa which is not accompanied by the inwardly bent part of the next chamber, it may be seen that it is formed by a continuation of the primary outer wall; this may especially be seen near below the dorsal side of the test; here the septum also bends backward before it adheres to the spiral of the former whorl; this indentation can also be seen in *Globorotalites* and in *Gyroidinoides*. The last formed chamber in all cases observed has a wall consisting solely of the primary wall. Later chambers, at least in forms found in deeper water, have secondary thickenings over the primary outer walls. The poreless parts of the septa never show such secondary thickenings.

Contrarily to these results are those obtained by Reiss, who believed the Globorotalidae to be bilamellar, with double septa; (Reiss, 1960, Geol. Survey Israel. Bull. 29, p. 17): „*Truncorotalia* is a bilamellid and belongs definitely to the Globigerinaceae as redifined by Banner and Blow". Reiss, 1958, pp. 51-70, who placed *Globorotalia* in his Superfamily Bilamellidae: „this Superfamily has been erected for those members of the superfamily Discorbidae Smout (1954) that show primarily formed double septa". In reality we saw that the poreless parts of the septa of *Globorotalia* are simple. Septa are always poreless; when parts of septa show pores, they are not real septa but parts of outer walls covered by the next chamber. Only the outer walls of chambers before the last one may be covered by layers of secondary calcite; these thickenings may in some instances consist of one single layer, but in others, especially at the dorsal side, many more thickening layers may be added *(G. truncatulinoides, G. tumida)*.

The test wall is hyaline, radial in polarised light. In most cases the outer walls are pierced by very regularly placed pores which mostly show the same diameter all along the wall; but in initial chambers which are later covered by thicker secondary layers, on the dorsal side, the primary small pores suddenly get much larger diameters in the secondary layer or layers. In this way, at the outer side, all chambers show the same diameter of pores. The outer porous surface of the test is mostly very smooth; only close to the umbilical hollow protuberances of a different kind may have developed.

VIIg. Planomalina buxtorfi (Gandolfi)

In 1942, Gandolfi described a planospiral species as *Planulina buxtorfi*. In 1946, Loeblich and Tappan described *Planomalina apsidostroba*, which they made the genotype of *Planomalina;* Bolli, Loeblich and Tappan (1957, l.c.) redescribed this species as a planktonic species. They believed it to be a planktonic species, though they mention the fact that the pores are more coarse or distinct than in most planktonic species. The type-species has a distinct poreless peripheral keel and possesses „supplementary relict apertures". These supplementary apertures do not in reality differ from the open parts of foramina covered by lips as found in planospiral forms related to *Gavelinella* known now as *Gavelinonion* Hofker.

Horizontal sections through tests from the Cenomanian of Les Rontins, Alpes Romanes, Switzerland, show that one of the typical features encountered in all real planktonic species, viz. the small proloculus, is missing in „*Planulina*" *buxtorfi*. The proloculus is relatively large, with a diameter of about 40-70μ. Moreover, contrary to many planktonic Foraminifera, the septa are distinctly double, with an inner granular primary wall and an outer calcareous radial one, whereas the inner granular layer continues in the outer walls of the chambers. The outer hyaline layer also forms the keel of the test which is strong and thick, and also is found at the inner whorls of the test. For comparison I have also given sections of *Planomalina apsidostroba* (pl. 20, figs. 5-6); here also the inner granular layer is conspicuous.

The relatively coarse pores, the granular inner layer of the wall (never found in real planktonic forms) and the voluminous calcareous peripheral keel do not show that the species is a planktonic form; without any doubt the large proloculus in the megalospheric form contradicts this planktonic life. The species obviously belongs to the *Gavelinella*-group; in *Gavelinonion* the lips on both sides of the planospiral test are also found. The species is a benthonic form of *Gavelinonion*, in so far as the test structure shows a more primitive stage of development than is found in the later species of *Gavelinonion*, where the granular layer is mostly the middle layer found between two hyaline layers in the septa. In polarized light the test does not seem to be one single spherical crystal, as the outer more hyaline wall consists of many fine crystals.

Bolli, Loeblich and Tappan (1957, p. 24) described another species which they incorporated with the genus *Planomalina* Loeblich and Tappan, *P. carseyae*, from the Albian of England. Very fine specimens, often filled with air, were found by the author in the Albian of Holland, not differing in any respect from those, described by Bolli, Loeblich and Tappan from the Albian of England. This species has a much thinner test, much finer pores, more inflated chambers, and lacks the keel at the periphery. However, in 1961 (Micropal., vol 7, p. 268) Loeblich and Tappan named this species *Globigerinelloides eaglefordensis* (Moreman), and in their Treatise in 1964 they give the typefigure of *Planomalina carseyae* from 1957 as figure 526, 7, for *Globigerinelloides eaglefordensis* (Moreman). In the present paper (pl. 19, figs. 1, 2) I show, that in the microspheric form this species shows a proloculus with diameter of about 7μ and in the megalospheric generation with diameter of about 20μ; the test walls are thin, the pores fine; the septa and the last formed chamber have simple walls; later a second thickening layer is formed at the outer walls in some specimens, but the walls remain thin. This may be a true planktonic species, since there is no trace of a granular inner wall. In 1961 Loeblich and Tappan considered this species a synonym of *Globigerinelloides eaglefordensis* (Moreman). Yet they place it in the Family Planomalinidae Bolli, Loeblich and Tappan which, in respect of the quite different inner structure of *Planomalina buxtorfi*, cannot be correct. The fact that only one species is known belonging to *Planomalina* Loeblich and Tappan, makes this genus rather suspicious. In the Treatise, 1964, Loeblich and Tappan do not mention any other species belonging to this genus. It should be removed from the planktonic species and placed into the benthonic species surrounding *Gavelinella*, of which it has most of the characteristics, though it is nearly planospiral, showing, as in *Gavelinonion*, lips at both umbilici.

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Plates 1 – XXIV

Pl. 1. Figs. 1-8. *Angulogerina danvillensis* Howe and Wallace, from the Cocoa Sands, Alabama, Upper Eocene, U.S.A. 1-6 x 190; 7, 8 x 236.
1, 5. Megalospheric.
2, 3, 4. Microspheric.
6. Section.
7, 8. Toothplates.

Pl. 1, Figs. 9-11. *Euuvigerina gardnerae* Cushman, from the Cocoa Sands, Alabama, Upper Eocene, U.S.A. x 190.
9, 10. Megalospheric.
11. Microspheric.

Pl. 1. Figs. 12-16. *Hanzawaia danvillensis* (Howe and Wallace), from the Cocoa Sands of Alabama, Upper Eocene, U.S.A.
12, 13, 14. Ventral, dorsal and apertural sides, x 190.
15. Transverse section, x 190.
16. Diagram showing correlation between diameter of proloculus and diameter of tests; numbers indicate number of chambers; there are three generations.

Pl. 1, Figs. 17-20. *Parrelloides cocoaensis* (Cushman), from the Cocoa Sands, Alabama, Upper Eocene, U.S.A.
17, 18, 19. Ventral, apertural and dorsal sides, x 240.
20. Transverse section, x 240. All megalospheric.

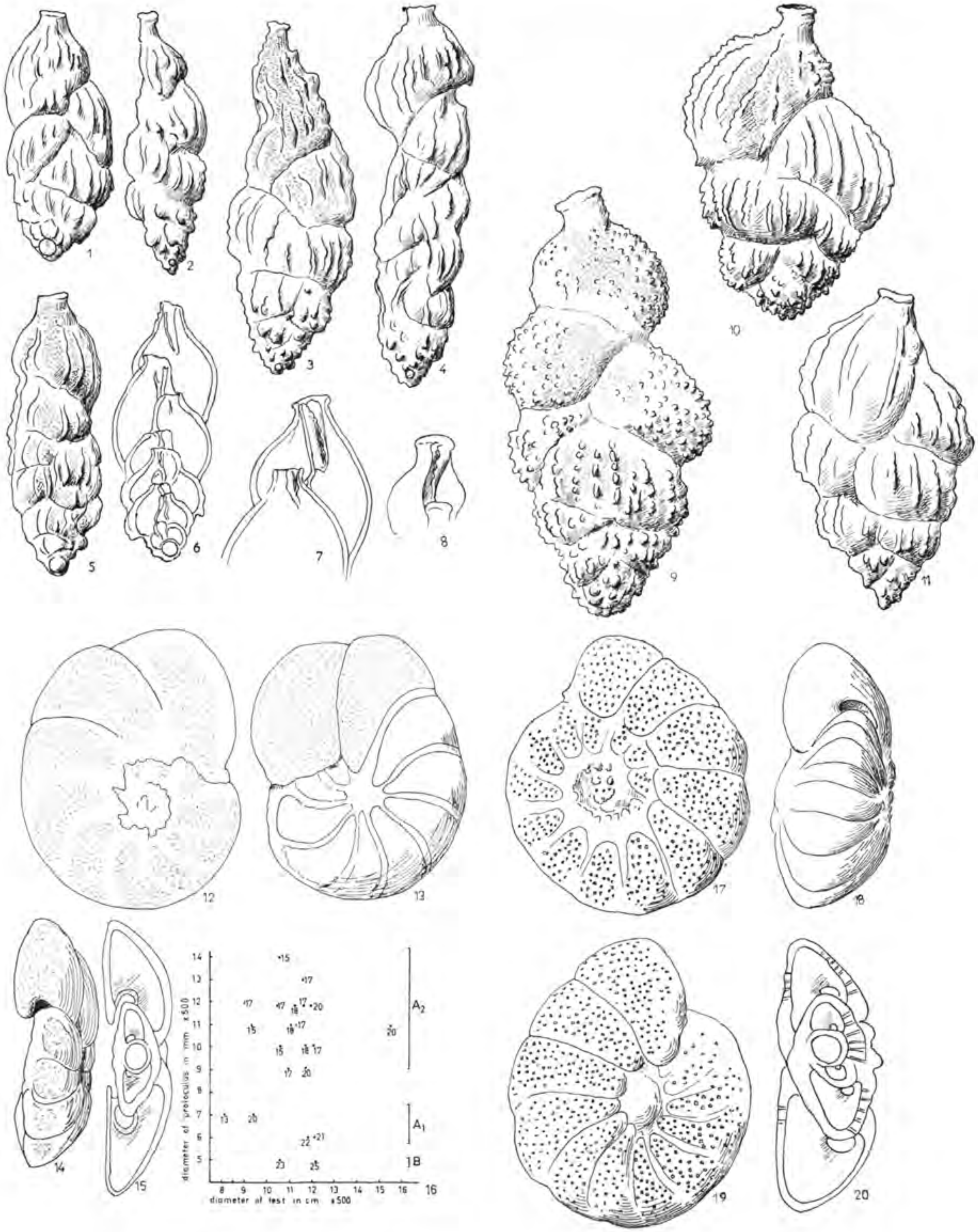
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
diameter of proloculus in mm x500
diameter of test in cm x500
14
13
12
11
10
9
8
7
6
5
8
9
10
11
12
13
14
15
16
A2
A1
B
15
17
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Plate 1

Pl. 2, Figs. 1-4. *Parrelloides cocoaensis* (Cushman), from the Cocoa Sands of Alabama, Upper Eocene, U.S.A.
1, 2. Ventral and dorsal sides, x 210.
3. Transverse section.
4. Diagram showing correlation of diameter of proloculus and diameter of tests; numbers indicate number of chambers. There are three generations.

Pl. 2, Figs. 5-11. *Globigerina yeguaensis* Weinzerl and Applin, from the Cocoa Sands of Alabama. All figs. x 210.
5, 6, 7. Three sides of small individual.
8, 9. Two sides of larger individual.
10. Dorsal side of very large individual.
11. Diagram showing correlation between diameter of proloculus and length of tests. Numbers indicate number of chambers; d and l indicate the direction of coiling.

Pl. 2, Figs. 12-17. *Globigerina pseudobulloides* Plummer, from the Upper Cretaceous, Danian and Lower Paleocene of Denmark. Only the ventral sides have been figured.
12. From the Upper Maestrichtian.
13. From the lowest Danian.
14. Lower Danian.
15. Middle Danian.
16. Uppermost Danian.
17. Lower Paleocene. The increase of size is conspecuous, and with this increase the walls became thicker and the pores more and more opened into pits in the walls, till in the end of the evolution a honeycomb structure was reached. All x 210.

Pl. 2, Figs. 18-25. Evolution of *Globigerina daubjergensis* Brönnimann. Fig. 18 from the Upper Maestrichtian of Denmark (Stevnsian), Fig. 25 from the Lowest Paleocene of Denmark.
19. Lowest Danian.
20. Lower Danian.
21. Middle Danian.
22, 23. Middle Danian.
24. Uppermost Danian.
25. Lowest Paleocene with bulla over the umbilical region. All x 190. The smallest specimens up to the Middle Danian (typelocality of the species in Daubjerg, Fig. 21) show no sutural openings; in the Uppermost Danian and the Lowest Paleocene the species develops bullae.

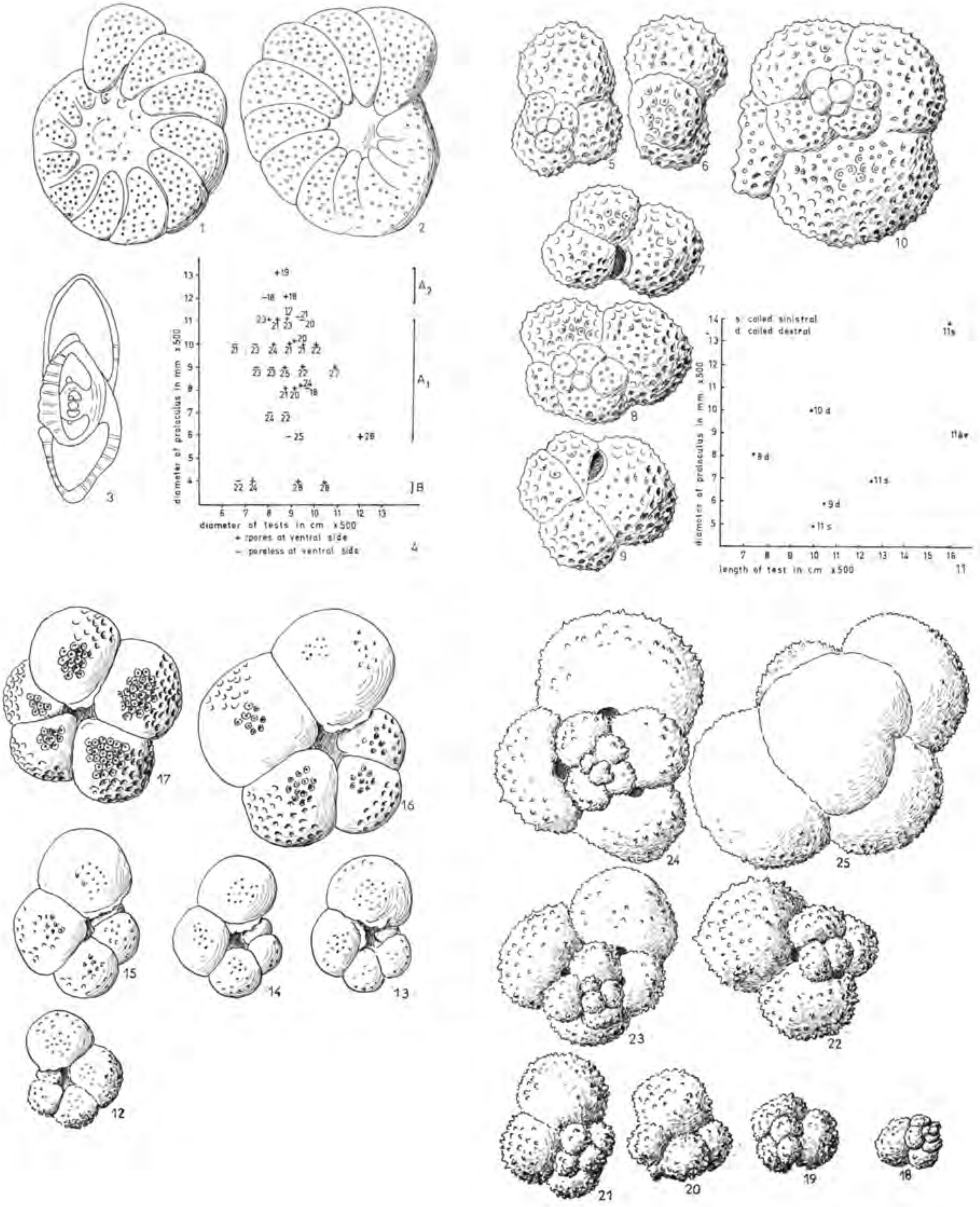

1
2
3
diameter of proloculus in mm x500
diameter of tests in cm x500
+ pores at ventral side
– poreless at ventral side
A2
A1
B
4
5
6
7
8
9
10
s coiled sinistral
d coiled dextral
diameter of proloculus in mm x500
length of test in cm x500
10 d
8 d
11 s
9 d
11 s
11 s
11a
11
17
16
15
14
13
12
24
25
23
22
21
20
19
18

Plate 2

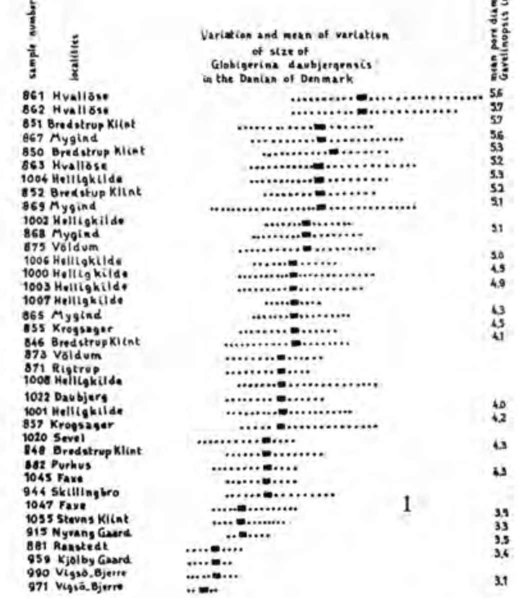
Pl. 3, Fig. 1. Evolution ot size of *Globigerina daubjergensis* Brönnimann during Uppermost Maestrichtian (Vigsö-Bjerre 971), Danian and Lowermost Paleocene (Hvallöse 861). During that period another species increased the diameter of its pores from a mean of $3{,}1\mu$ up to $5{,}6\mu$ (*Gavelinopsis involuta* (Reuss)). The gliding increase of the size of *G. daubjergensis* runs parallel to the increase of pores in *G. involuta*.

Pl. 3, Fig. 2. Evolution of the size of tests in the *Globigerina cretacea* d'Orbigny gens, from the Aptian up into the Maestrichtian. The gens is known by different names successively, but the gliding increase strongly points to one biologic unit.

P. 3, Figs. 3-9. The evolution of *Coleites reticulosus* (Plummer) during the Upper Maestrichtian up into the Paleocene. The size increases, and with this increase the ornamentation of the tests increases, as to strengthen the test. Moreover, the situation of the aperture changes from sutural into areal.

3. Upper Maestrichtian.
4. Upper Maestrichtian.
5. Uppermost Maestrichtian.
6. Top of Maestrichtian.
7. Lowermost Tuff Chalk of Maestricht.
8. Lowermost Paleocene.
9. Lower Montian.

Pl. 3, Fig. 10. Increase of the number of pustules in the last formed chamber of *Bolivinoides decorata-australis-gigantea* gens from the lowest to the upper layers in the large quarry of Hallembaye, Belgium; the samples 206-226 are from the Upper Campanian; between the samples 226 and 229 lies a hard ground, indicating a hiatus in sedimentation; then the Middle-Upper Maestrichtian starts, but in sample 247 the uppermost Maestrichtian is not reached. The distinct leap in the gliding increase at the hard ground is remarkable (mean from 4,2 to 5,7). During that time the gens gradually increased the size of its tests and together with this increase the number of pustules increased, thus more and more strengthening the test wall.


sample number
localities
Variation and mean of variation
of size of
Globigerina daubjergensis
in the Danian of Denmark
mean pore diameters
Gavelinopsis involuta
861 Hvallöse
862 Hvallöse
851 Bredstrup Klint
867 Mygind
850 Bredstrup Klint
863 Hvallöse
1004 Helligkilde
852 Bredstup Klint
869 Mygind
1002 Helligkilde
868 Mygind
875 Völdum
1006 Helligkilde
1000 Helligkilde
1003 Helligkilde
1007 Helligkilde
865 Mygind
855 Krogsager
846 Bredstrup Klint
873 Völdum
871 Rigtrup
1008 Helligkilde
1022 Daubjerg
1001 Helligkilde
857 Krogsager
1020 Sevel
848 Bredstrup Klint
882 Purhus
1045 Faxe
944 Skillingbro
1047 Faxe
1055 Stevns Klint
915 Nyvang Gaard
881 Raastedt
959 Kjölby Gaard
990 Vigsö_Bjerre
971 Vigsö_Bjerre
5,6
5,7
5,7
5,6
5,3
5,2
5,3
5,2
5,1
5,1
5,0
4,9
4,9
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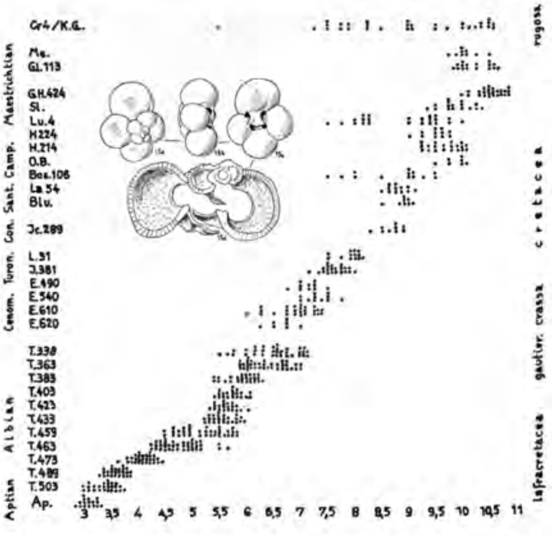
3,4
3,1

1


Gr4/K.G.
Me.
GL.113
G.H.424
Sl.
Lu.4
H224
H.214
O.B.
Bos.106
La 54
Blu.
Jc.289
L.31
J.381
E.490
E.540
E.610
E.620
T.338
T.363
T.383
T.403
T.423
T.433
T.459
T.463
T.473
T.489
T.503
Ap.
Aptian
Albian
Cenom.
Turon.
Con.
Sant.
Camp.
Maastrichtian
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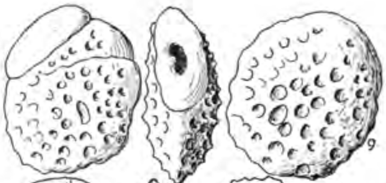
10
10,5
11
rugosa
cretacea
gaultier. crassa
Infracretacea

2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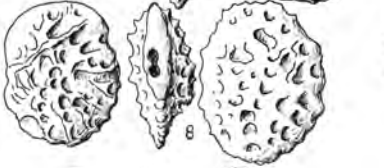
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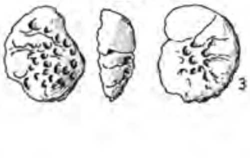
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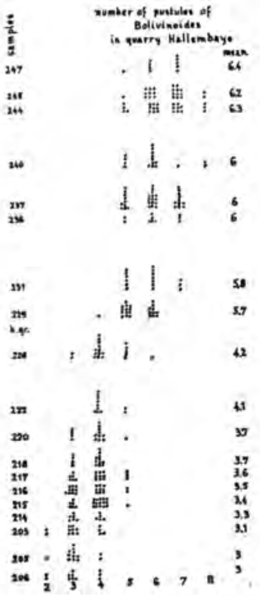

samples
number of pustules of
Bolivinoides
in quarry Hallembaye
mean
247
245
244
240
237
236
231
229
h.gr.
228
222
220
218
217
216
215
214
205
207
206
6,4
6,2
6,3
6
6
6
5,8
5,7
4,2
4,1
3,7
3,7
3,6
3,5
3,4
3,3
3,1
3
3
1
2
3
4
5
6
7
8

10

Plate 3

Pl. 4. Gliding change of the *Bolivinoides*-gens in the chalk of the quarry at Hallembaye, Belgium, as demonstrated in Pl. 3, Fig. 10. The plate consists of 4 quadrants; lower quadrant to the left: samples 203-205; lower quadrant to the right: samples 218-220; upper quadrant to the right: sample 229; upper quadrant to the left: sample 244. Both lower quadrants show the characteristics of *Bolivinoides decorata* (Jones); both upper quadrants show the features of *B. australis* Edgell; typical *gigantea* is not yet reached. The numbers of pustules in the specimens figured are:

lower left	lower right	upper right	upper left	
2 18 5	6 16 0	0 9 7	5 4 7 1	specimens
2 3 4	3 4 5	4 5 6	5 6 7 8	pustules
203-205	218-220	229	244	samples

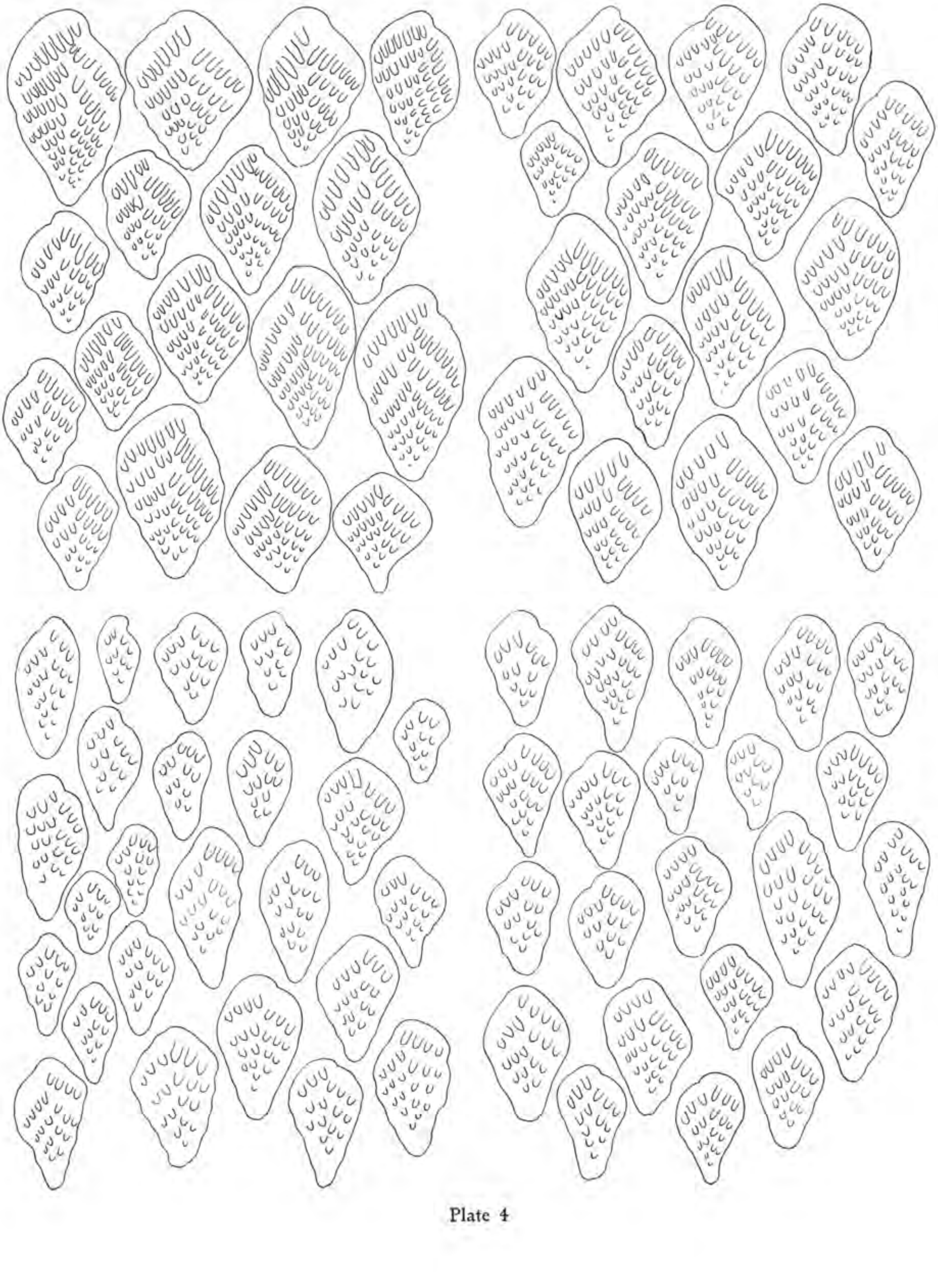


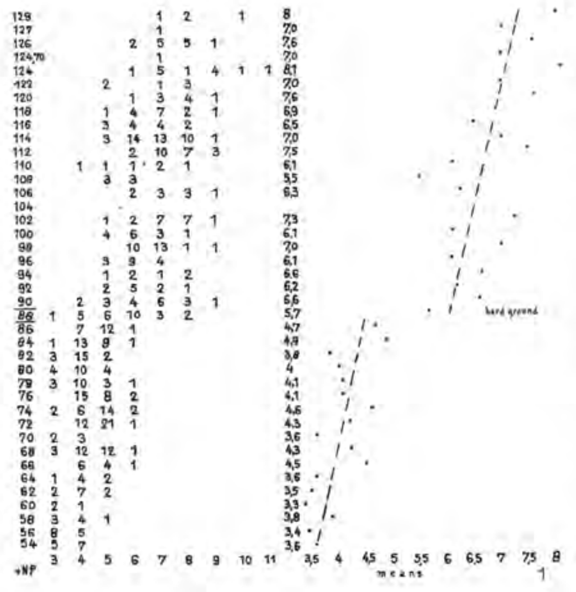
Plate 4

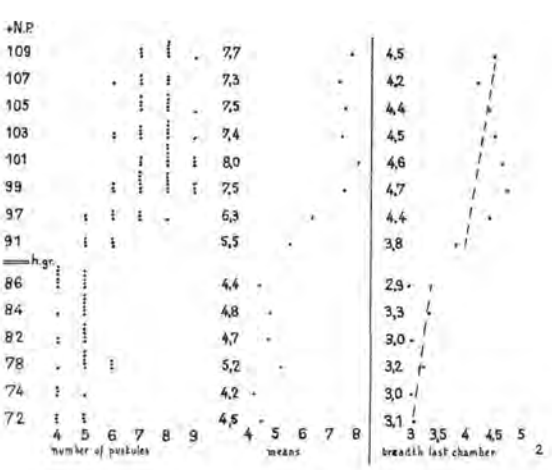
Pl. 5, Fig. 1. Gliding change of the number of pustules of *Bolivinoides decorata-australis-gigantea* gens in the drill-hole and quarry above it at Glons, Belgium.
At 88 m + NP the same hard ground is found between Campanian and Maestrichtian as found in Hallem-Baye (Pl. 3, Fig. 10). The sudden leap in the means at this hard ground once again is remarkable. It shows that when sedimentation started again, the evolution of the gens in the meantime had continued elsewhere.

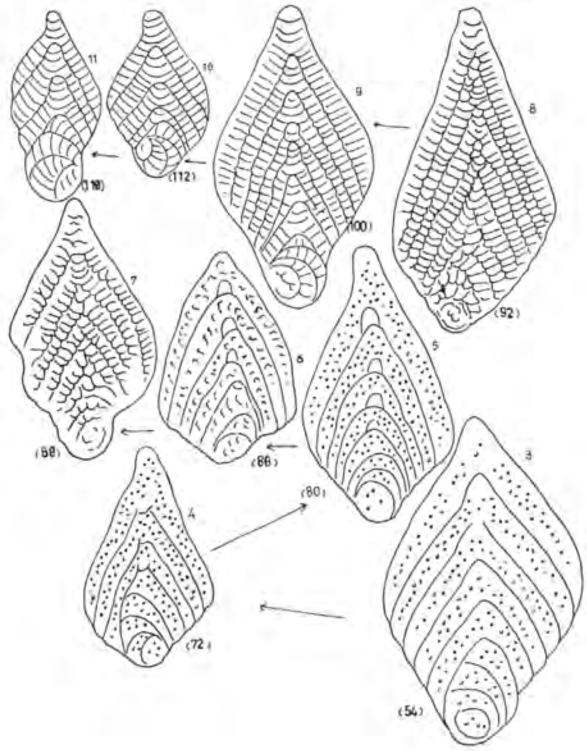
Pl. 5, Fig. 2. Gliding change of the number of pustules in *Bolivinoides decorata-australis-gigantea* gens in the quarry at Boirs. Between 86 and 91 m the hard ground occurs. When we compare the diagrams Pl. 5, Figs. 1, 2 with the diagram from the quarry at Hallembaye (Pl. 3, Fig. 10), we see that at Glons and Boirs a higher part of the Upper Maestrichtian is reached than at Hallembaye; in fact, at Glons the highest Maestrichtian is reached; in Boirs this highest part of the Maestrichtian is just touched; at Hallembaye the quarry ends at its top below the highest Maestrichtian; this is indicated by the number of pustules, for in Boirs and Glons the forma*gigantea* is reached: mean of top at Hallembaye is 6,4; mean of top at Boirs is 7,7; mean of top ot Glons is 8.

Pl. 5, Figs. 3-11. Evolution of the *Neoflabellina leptodisca-praereticulata-reticulata-postreticulata* gens. The specimens are taken from samples of the drill-hole and quarry at Glons, north eastern Belgium. The figures indicate the level above NP, in metres. The change here is found in a gradual increase of the ornamentation on the test walls.
3, 4, 5. Are called *N. leptodisca* (Wedekind).
6, 7. Are *N. praereticulata* Hiltermann and Koch.
8. *N. reticulata* (Reuss).
9, 10, 11. Are *N. postreticulata* Hofker.
The highest observed specimens (10, 11) distinctly show the appraoching end of the gens.

Pl. 5, Fig. 12. Change in the correlation between number of chambers and diameter of proloculus during Danian and Lowest Paleocene in Denmark of *Globigerina daubjergensis Brönnimann*. The roman figures indicate the levels in the Danian as given by Wind. There is an increasing spreading in the size of proloculus, indicatin a change of modus of reproduction. Typical B-individuals appear for the forst time in III and more common in V and Pal. These individuals show a high spiralled test. They forcast the appearance of high-spiralled *G. koszlowskii* Brotzen and Pozaryska. On the other hand it seems that in the end of the evolution also an A_2-generation is formed, which can be seen in Pal., where three distinct groups can be traced. *G. daubjergensis* thus forms a typical instance of the change in mode of reproduction during time.


+NP
means
hard ground
1


+N.P.
109 7,7 4,5
107 7,3 4,2
105 7,5 4,4
103 7,4 4,5
101 8,0 4,6
99 7,5 4,7
97 6,3 4,4
91 5,5 3,8
h.gr.
86 4,4 2,9
84 4,8 3,3
82 4,7 3,0
78 5,2 3,2
74 4,2 3,0
72 4,5 3,1
number of pustules
means
breadth last chamber
2


11
10
9
8
(118)
(112)
(100)
(92)
7
6
5
(88)
(86)
(80)
4
3
(72)
(54)

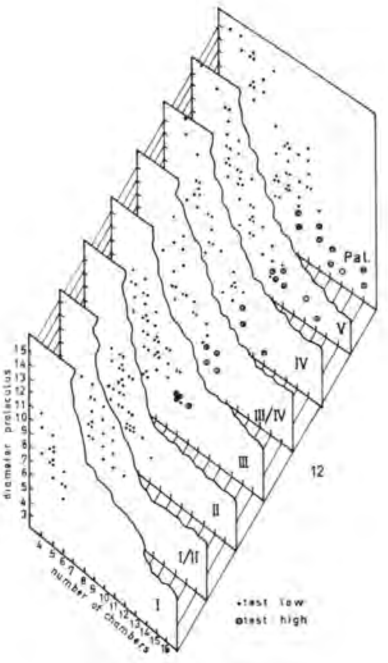

diameter proloculus
number of chambers
Pal.
V
IV
III/IV
III
II
I/II
I
12
• test low
○ test high

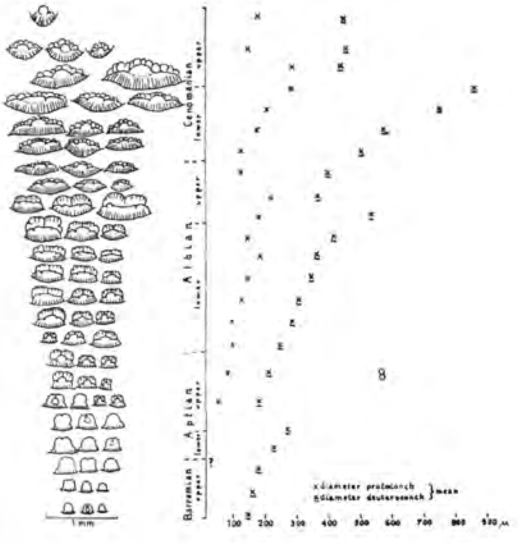
Plate 5

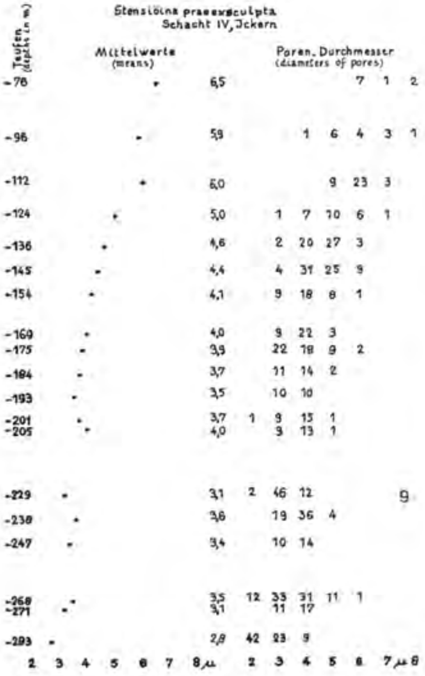
Pl. 6, Figs. 1-7. Trimorphism in *Marginulina decorata* (Reuss) from the Miocene of Malta. From each generation the whole test (1, 4, 6), x 15; the initial part (2, 5, 7), x 190, are given. Moreover, Fig. 3 shows the peculiar aperture of the microspheric generation (x 190). The generations (B, A_1, A_2) are indicated. The B-generation shows 7 coiled chambers, the A_1 shows 3 of them, whereas in the A_2-generation there is only one chamber which shows a coiled appearance.

Pl. 6, Fig. 8. Evolution of the embryonic apparatus of the *Orbitolina lenticularis* gens (after J. Hofker Jun., Leidse geol. Mededeel., vol. **29**, 1963, Chart X). The enlargement of the proloculus during time compelled the gens to change the structure of the embryonic apparatus as has been described in the text. In the end of the evolution the development of an A_1-generation and the suppression of the much too large B-generation led to the extinction of the gens.

P. 6, Fig. 9. Increase in the pore-diameter of *Stensiöina praeexculpta* (Keller) during time.

Pl. 6, Fig. 10. Increase of pore diameter of *Stensiöina exsculpta* (Reuss) and *S. pommerana* Brotzen during time.





Stensiöina praeexsculpta
Schacht IV, Jckern

Teufen (depths in m)	Mittelwerte (means)	Poren-Durchmesser (diameters of pores) 2	3	4	5	6	7	8 µ
-78	6,5					7	1	2
-96	5,9			1	6	4	3	1
-112	6,0				9	23	3	
-124	5,0		1	7	10	6	1	
-136	4,6		2	20	27	3		
-145	4,4		4	31	25	9		
-154	4,1		9	18	8	1		
-169	4,0		9	22	3			
-175	3,9		22	18	9	2		
-184	3,7		11	14	2			
-193	3,5		10	10				
-201	3,7	1	9	15	1			
-205	4,0		9	13	1			
-229	3,1	2	46	12				
-238	3,6		19	36	4			
-247	3,4		10	14				
-268	3,5	12	35	31	11	1		
-271	3,1		11	17				
-293	2,8	42	23	9				

Poren-Durchmesser (diameters of pores)
Bohrung Höllviken I, Schweden (Sweden)

Stensiöina pommerana

Teufen (depths in metres)	Poren-Durchmesser	Mittelwert
260	2 8 7 1	6,2
350	1 10 12 7 3	5,3
401	1 8 19 2 6	5,1
450	3 7 2	5,1
505	3 12 4 1	4,1
550	1 3 8 2 1	4,1
600	2 7 16 12 5	4,1
658	3 9 13 7 2	3,9
700	1 2 8 7 3	3,8
749	1 5 14 13 6 2	2,8
800	2 8 5 1	2,2
850	10 18 9 3 1	2,1
800	6 9 8 4	2,3

Stensiöina exsculpta

Teufen	Poren-Durchmesser	Mittelwert
1010	1 6 12 14 4	5,6
1020	2 8 14 7 1	4,9
1030	5 18 6 1	4,0
1040	2 6 3	3,5
1050	1 6 15 21 5	3,7
1060	2 8 3 1	3,1
1070	2 7 1	2,5
1080	4 8 3 2	2,5
1090	1 9 11 13 4	2,6
1100	2 8 8	2,1

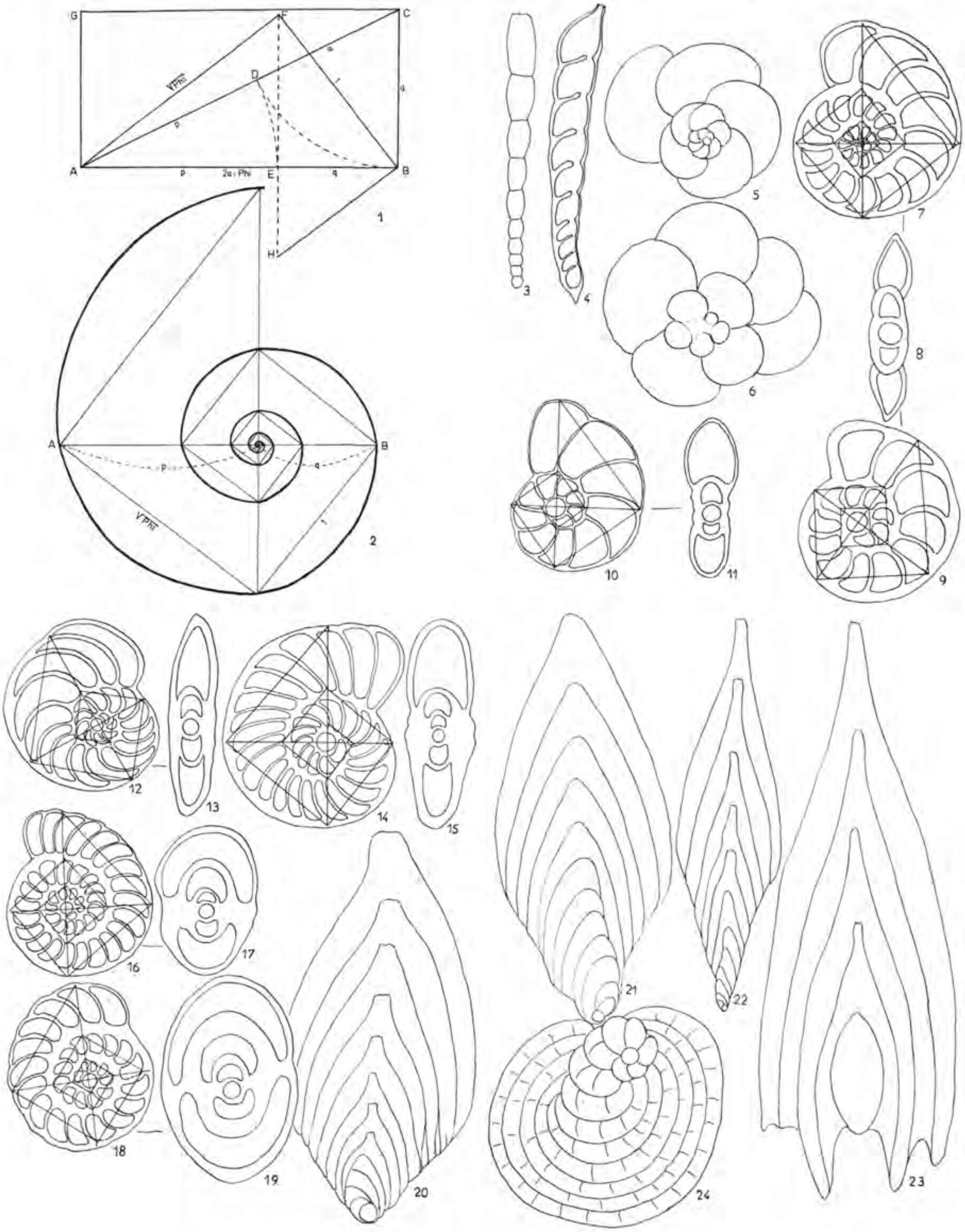
Plate 6

Pl. 7, Figs. 1, 2.
1. Shows the construction of the Sectio Divina as done by Imhotep while constructing the complex of the Pyramid of Sakkara. In this drawing a rectangular triangle has been constructed with sides in proportion of resp. Phi: $\sqrt{\text{Phi}}$: 1. In that triangle AE:EB = 1,618:1 (Great Pyramid of Gizeh).
2. By means of the triangle AFB a gnomon can be constructed; the angles of this gnomon give a spiral, Goethe's „Spirale des Lebens", a spiral which can be found in Foraminifera, especially in flat planospiral species. In the case that such a species has overlapping chambers, the spiral becomes narrower.

Pl. 7, Figs. 3-11. Species of Foraminifera in which the Sectio Divina ratio can be detected.
3. *Stilostomella* sp., Tegel of Baden, Soosz, Austria.
4. *Dentalina* spec. Ingolf Exp. St. 90, Recent.
5. *Globorotalia canariensis* (d' Orbigny), Juan Fernandez, Challenger Exp. St. 300.
6. *Globigerina* sp., Same locality.
7, 8, 9. *Hyalinea baltica*, (Schroeter), Ammontatura, Bay of Napels, Recent.
10, 11. *Elphidiononion poeyianum* (d' Orbigny), Caribbean Sea, Recent.
Analysis in the text.

Pl. 7, Figs. 12-20. Species of Foraminifera in which the spirals are typical for Goethe's spiral and others in which overlapping chambers resulted in a narrower spiral. Moreover, *Vaginulina lata* Hofker from the Lower Campanian of drill-hole Lathwehren 11 is given (Fig. 20).
12, 13. *Elphidium macellum* (Fichtel and Moll), Mediterraneum, Recent.
14, 15. *Elphidiononion oregonensis* (Cushman), Pliocene, California.
16, 17. *Elphidiononion schencki* (Cushman and Dusenbury), Avon Park, U.S.A., Florida, Eocene.
18, 19. *Elphidiononion striatopunctatum* (Fichtel and Moll), Red Sea, Recent.

Pl. 7, Figs. 21-24.
21. *Neoflabellina* sp. Lower Campanian.
22, 23. *Frondicularia sagittula* van den Broek, Carribean, 22. microspheric; 23. megalospheric, Recent.
24. *Puteolina discoidea* (Flint), Carribean, Recent.


G
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C
√Phi
D
a
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2a : Phi
E
q
B
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H
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q
B
√Phi
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Plate 7

Pl. 8, Figs. 1-3.

1. *Sorites orbitolitoides* (Hofker), Carribean, Recent.
2. *Plectofrondicularia dentifera* Cushman and Stainforth, Eocene, Ecuador.
3. Graphes of size of chambers in *Plectofrondicularia, Sorites* and *Neoflabellina*, showing curves which very much resemble the ideal curves given in Textfig. 12.

Pl. 8, Fig. 4. Ends of septa of Foraminifera just at the septal foramen. The numbers correspond with those given in the text; the names of the species will be found there.

Pl. 8, Fig. 5. See Fig. 4.

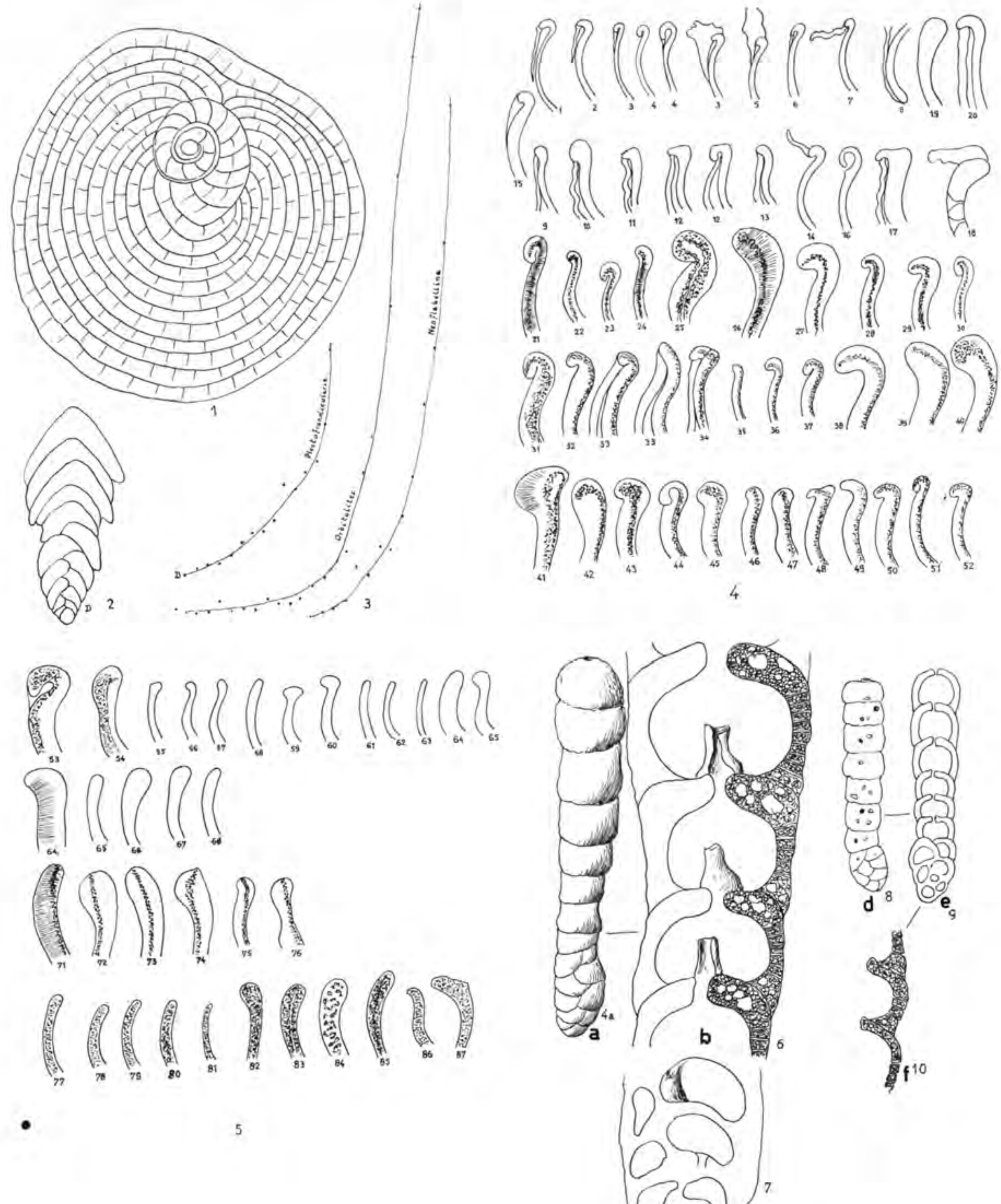
Pl. 8, Figs. 6-10. *Martinotiella* spec. from the Oligocene of Ecuador.

4a. Whole test, x 40.

6. section of upper part, with the pores in the agglutinated wall and the bases of toothplates, x 160.

7. Initial part, showing a toothplate which is not free but attached, proving that in this agglutinated form the structure of the toothplate and ots situation is similar to those found in calcareous forms, and that in fossil forms the plate also can be detected.

8, 9, 10. Another test, x 25, Fig. 9 x 65.


1
D
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Plectofrondicularia
Orbitolites
Neoflabellina
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87
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4a
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b
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c
7
d
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e
9
f
10

Plate 8

Pl. 9, Figs. 1-4. Parts of sections through agglutinated Valvulinidae.
1, 2. *Valvulina oviedoina* d'Orbigny, Carribean, In the initial chambers (Fig. 1) the toothplates are normal, in the later chambers (Fig. 2) they flare out.
3, 4. *Clavulina tricarinata* d'Orbigny, Carribean. 3. initial part with typical toothplates; 4. later chambers, whith more areal and free toothplates, which can be compared with those of *Martinottia* (Pl. 8, Fig. 5).

Pl. 9, Other figures. Several kinds of toothplates; the names of the species are given with the figures.

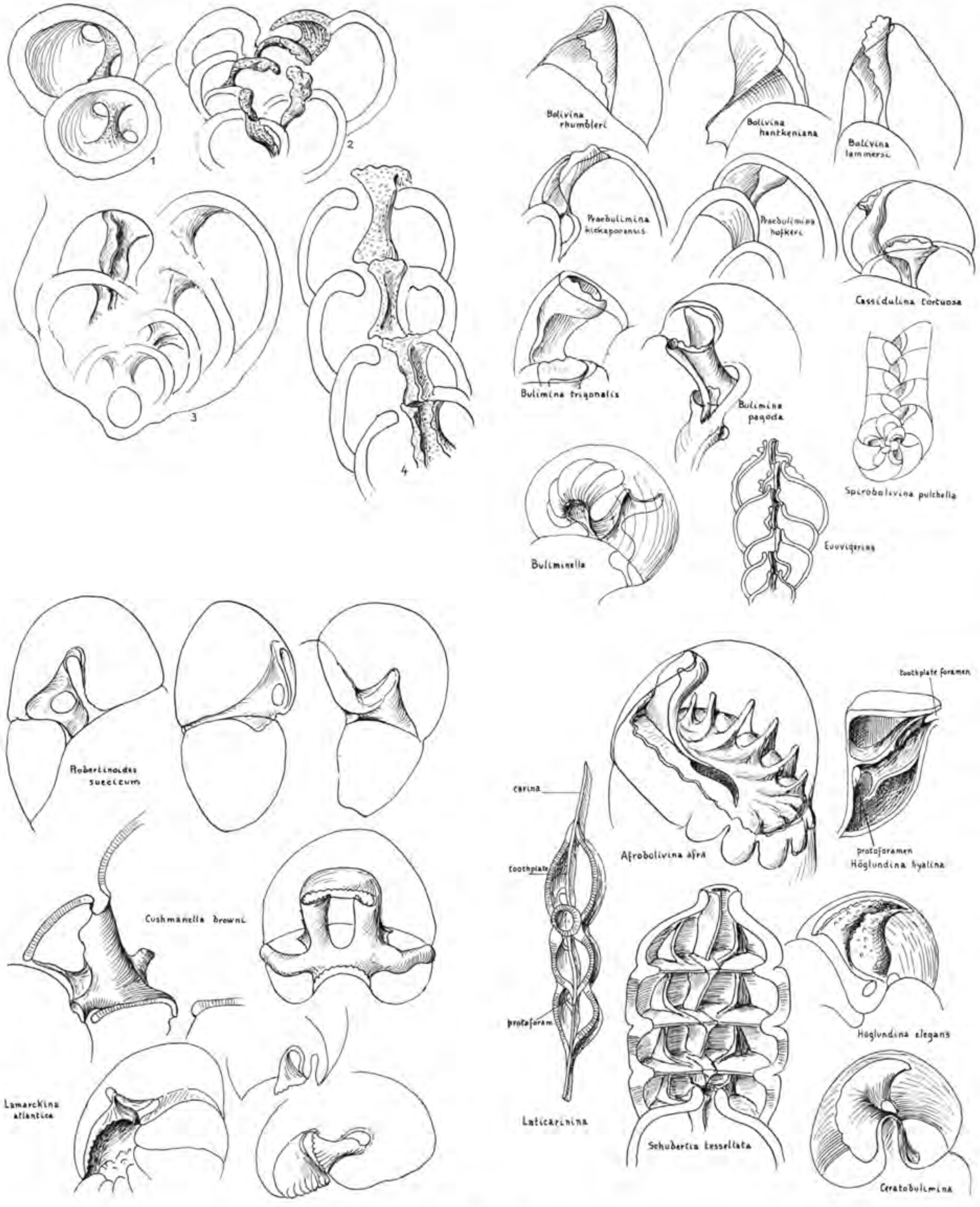

1
2
3
4
Bolivina rhumbleri
Bolivina hantkeniana
Bolivina lammersi
Praebulimina kickapoorensis
Praebulimina hofkeri
Cassidulina tortuosa
Bulimina trigonalis
Bulimina pagoda
Spirobolivina pulchella
Buliminella
Euuvigerina
Robertinoides suecicum
Cushmanella browni
Lamarckina atlantica
toothplate foramen
carina
Afrobolivina afra
protoforamen
Höglundina hyalina
toothplate
protoforam
Höglundina elegans
Laticarinina
Schubertia tessellata
Ceratobulimina

Plate 9

Pl. 10, Figs. 1-5. Sections through species of *Cibicides*.

1. *Cibicides excavatus* Brotzen, x 125; the septa are simple and granular; Lower Campanian.

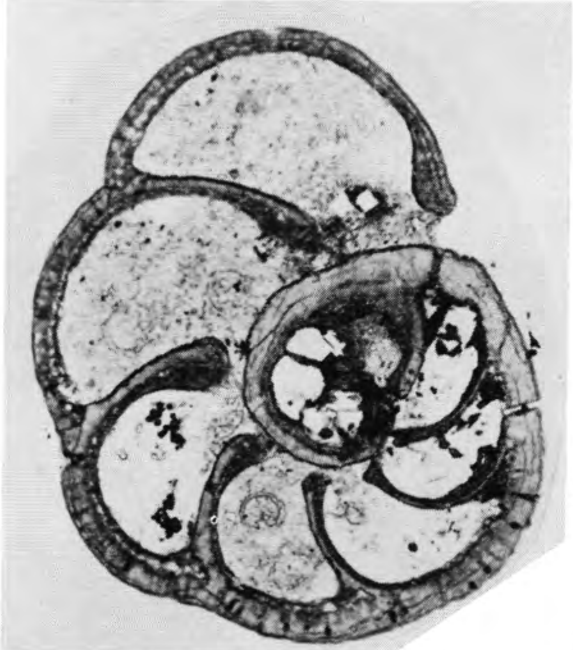
2, 5. *Cibicides lobatulus* (Walker and Jacob), x 125; the septa show a primary granular wall with at the inside a hyaline radial lining; Recent.

3. *Cibicides beaumontianus* d'Orbigny, x 125. Septa with inner and outer hyaline lining, so that the primary granular wall lies in the middle; Maestrichtian.

4. *Cibicides subbosqueti* Hofker, x 125. Septa simple, consisting only of the granular primary wall; Lower Maestrichtian.


1


2


3


4


5

Plate 10

Pl. 11, Figs. 1-6.

1, 2. *Cibicides refulgens* Montfort, Recent, North Atlantic.

1. Two specimens have fused, section, x 50.

2. Part of test, horizontal section; the primary granular wall can be seen as a dark lining; in the septa, moreover, an inner and an outer lining of radial calcareous material, x 300.

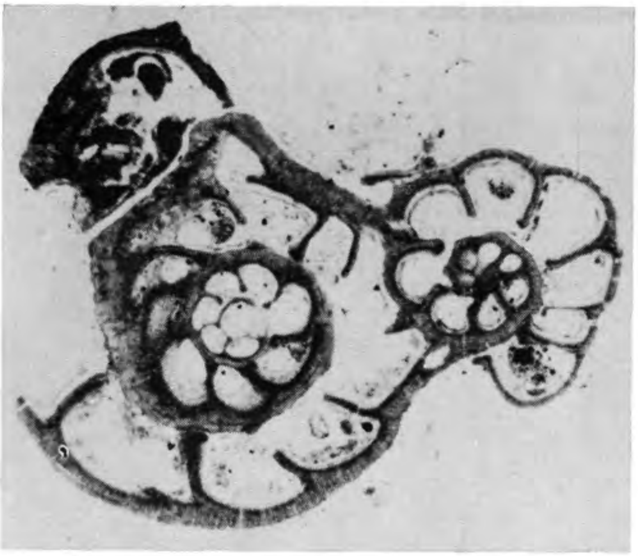
3-6. *Gyroidina* (or *Gyroidinoides,* see Chapter IX, d).

3. *Gyroidina nitida* Reuss, Turonian, x 150. The septa are simple, granular (an inner lining seen at the inner side of some chambers in reality consists of secondary fillings of chalky material).

4. *Gyroidina nitida* (Reuss), Turonian. Septa and walls are simple, granular, x 100.

5. *Gyroidina gracillima* Ten Dam, Albian. Septa and walls are simple, granular. x 100.

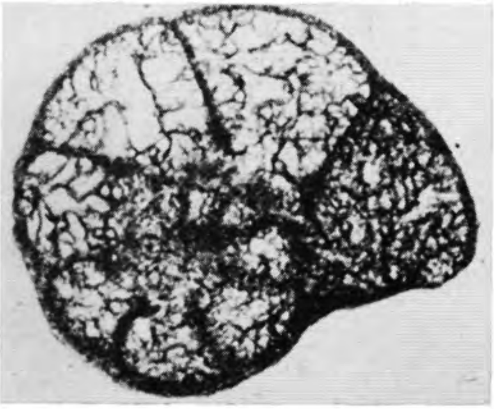
6. *Gyroidina nitida* (Reuss), Santonian of Folx -les -Caves, Belgium. Air filled specimen. x 100. The septa and walls are simple, granular.



1

2

3



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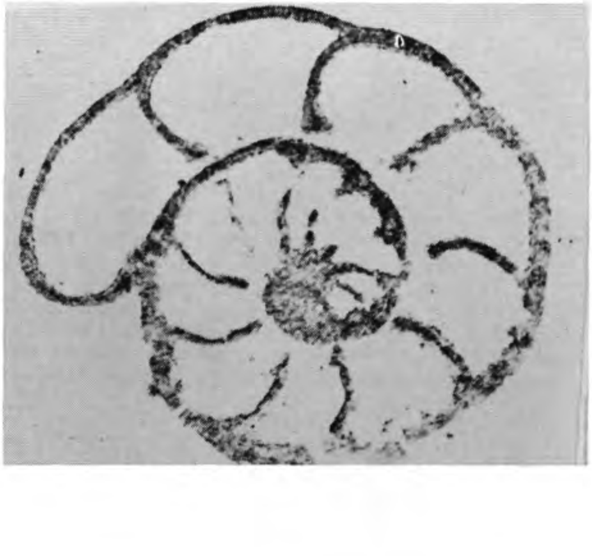


6

Plate 11

Pl. 12, Figs. 1-5. *Gyroidina.*

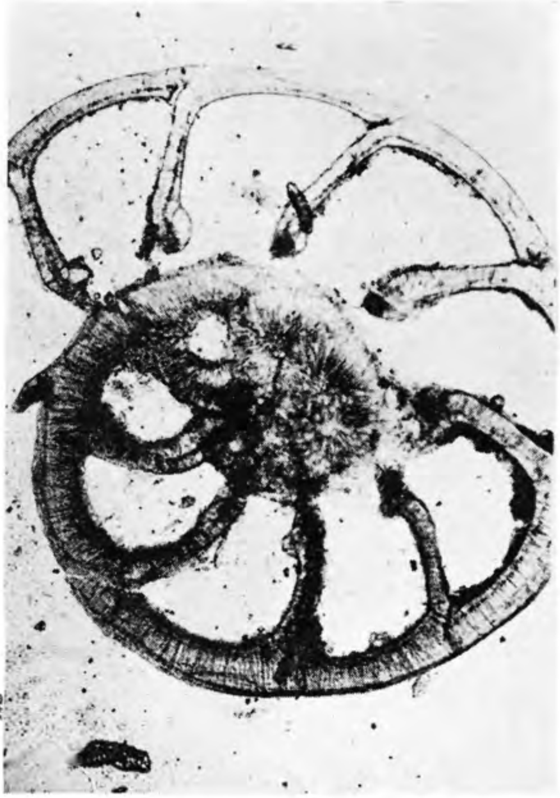
1. *Gyroidina girardana* (Reuss), Miocene. x 300. The primary wall, microgranular, is seen as a layer of granules within two layers which are radial crystalline.

2. The section of which Fig. 1 is a part. x 100.

3. *Gyroidina nitida* (Reuss). This is the forma *octocamerata.* Lower Campanian, Folx -les-Caves. x 300. The outer walls, and the main part of the septa are microgranular in structure; only near to the septal foramen the septa show an inner hyaline lining.

4, 5. *Gyroidina nitida* (Reuss), forma globula Hagenow. Maastrichtian. The primary granular wall is clearly seen as a dark lamellum, at the outside of the septa and the walls, showing that the first hyaline lamellum is the inner one and that, in case an inner and an outer lamellum are formed, the outer one is the later one. 4, x 300; 5, x 100.

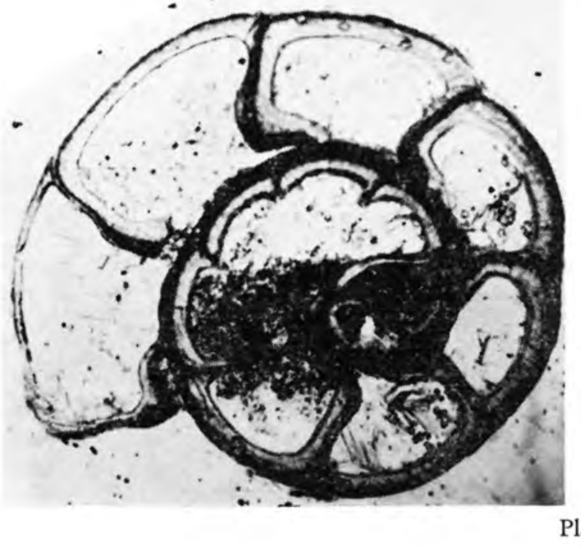
1



2

3

4



5

Plate 12

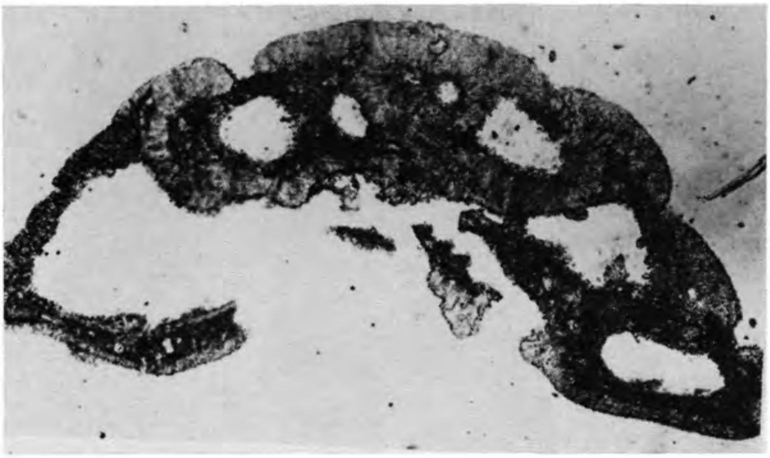
Pl. 13, Figs. 1-5. *Mississippina.*

1. *Mississippina binkhorsti* (Reuss), from the Danian of Denmark, Faxe. x 150. This transverse section shows the agglutinated inner wall (dark) and an outer fibrous calcareous wall only at some places.

2. Horizontal section through *Mississippina binkhorsti* (Reuss), Danian of Denmark. The inner agglutinated primary wall continues in the septa; especially at the margin the outer wall has secondary thickenings in the form of fibrous calcareous matter. x 150.

3, 4. *Mississippina concentrica* (Parker and Jones), from the Caribbean, Recent. 3, x 100; 4, x 150. The main structure of the test wall is the same as in *M. binkhorsti*, but the secondary thickenings are heavier, the agglutinated wall thinner and the agglutination is finer, more granular in structure. The granular wall is the primary wall, and the thickening outer parts are fibrous radial. There are no real pores. The septa (Fig. 3) consist mainly of the agglutinated primary wall, and thus the species is monolamellar.

5. Transverse section of *M. binkhorsti*, from the Maastricht Tuff Chalk. The coarse agglutination of the primary wall can easily be observed; x 150.



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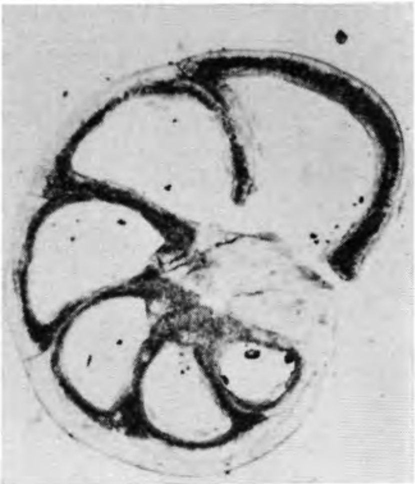

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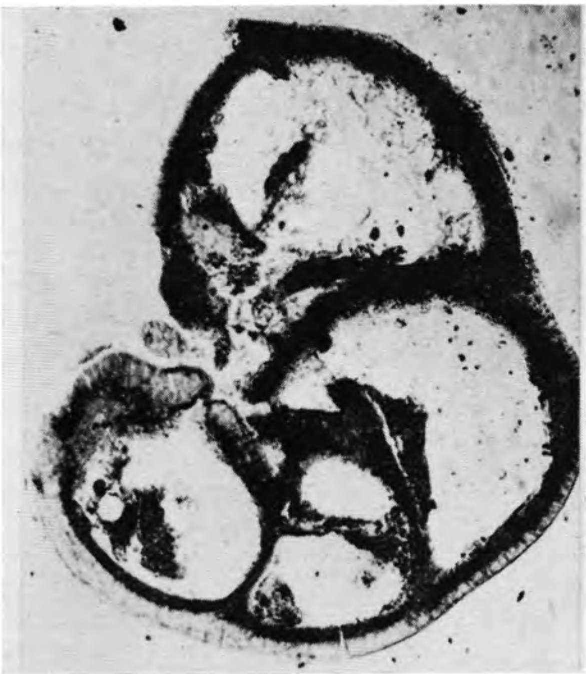

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Plate 13

Pl. 14, Figs. 1-8.

1. *Cymbalopora martini* (Brotzen), Santonian. The whole test is agglutinated; there are at least two layers; pores in the dorsal side; x 100.

2. *Cymbalopora radiata* Hagenow, Maastricht Tuff Chalk, Danian. The wall is thicker, with several layers at the outside, all agglutinated or granular with larger particles between. Pores at the dorsal side only, x 75.

3, 4. *Cymbalopora hemiglobosa* Ten Dam, from the Thanetian of Belgium. 3, transverse section, showing finely agglutinated walls thickened by several layers at the outside. Pores also in the ventral walls; x 100. 4, horizontal section, showing the simple septa of the chambers with secondary chamberlets at the outer wall and sigma-formed inner walls opening in the central space. The agglutination of the walls is obvious.

5, 6. *Cymbaloporetta poeyi* (d'Orbigny). The walls are double at the outside, in reality showing a mediane primary microgranular layer and two granular (or lightly fibrous) outer and inner layers. Pores mostly at the outer wall, but also in the ventral chamber walls. The septal walls are double and form the same sigma-like outgrowths as found in *Cymbalopora;* a central hollow consists in which the chambers open. According to Reiss (1963) it is possible that *Cymbaloporetta* and *Cymbalopora* are related. In that case the wall has changed considerably.

7. *Pulsiphonina prima* Brotzen, Lower Paleocene. Transverse section showing the granular walls, x 150.

8. *Siphonina pulchra* Cushman, Caribbean, Recent, showing the fibrous radial walls, x 150.

Both genera are closely allied, and it is possible that *Siphonina* developed from *Pulsiphonina;* the change of wall structure then is evident.

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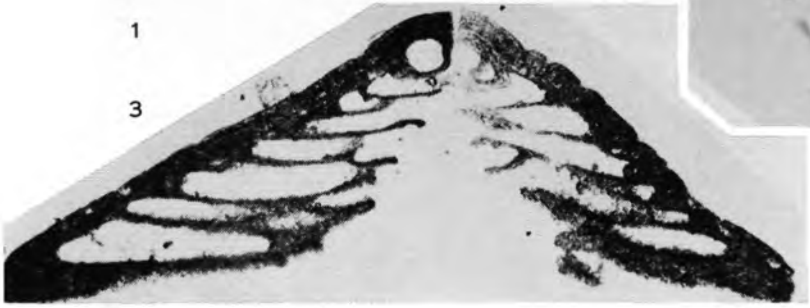

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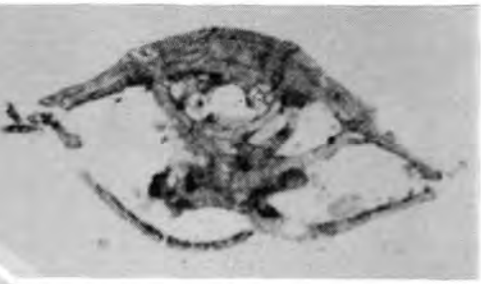

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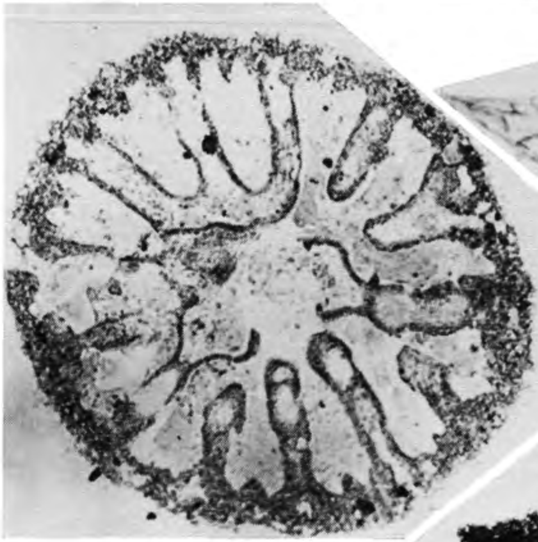

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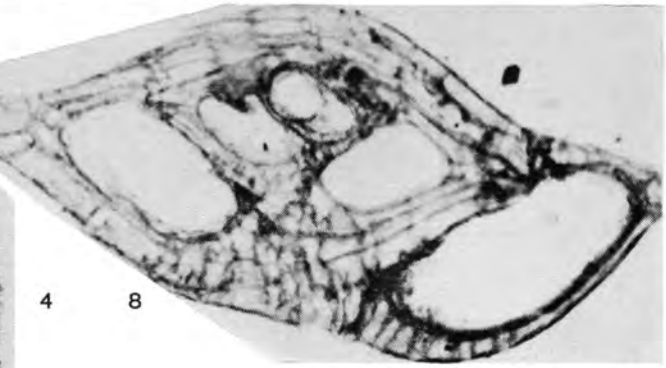

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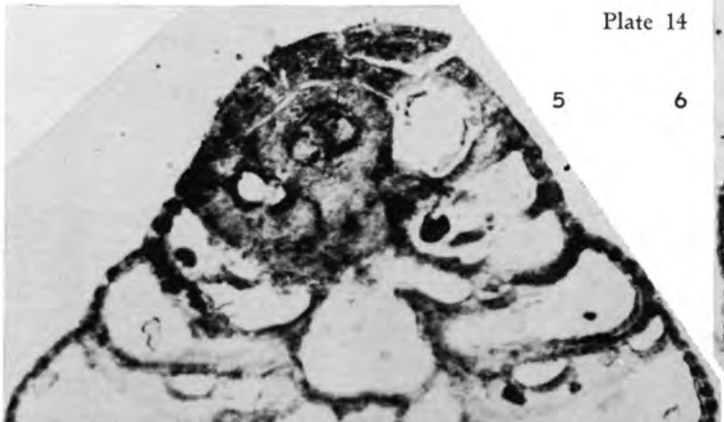
Plate 14



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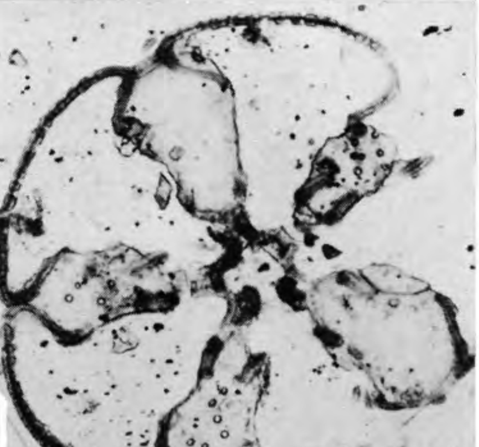

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Pl. 15. Toothplates of different species of Foraminifera. The names of the species as well as the different parts of the test and the different toothplate foramina formed are assigned in the drawings.

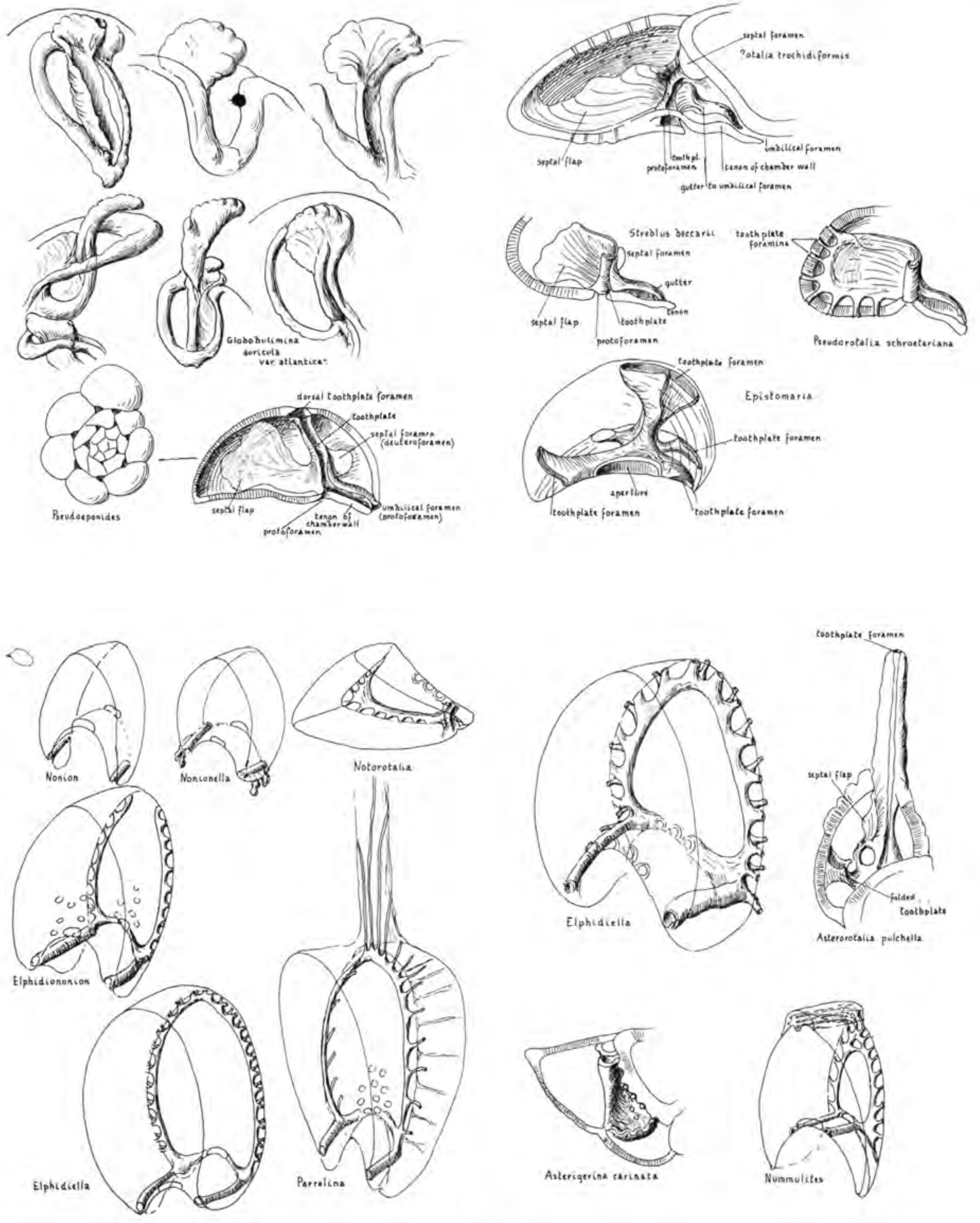

septal foramen
Rotalia trochidiformis
septal flap
tooth pl.
protoforamen
umbilical foramen
tenon of chamber wall
gutter to umbilical foramen
Globobulimina auricula var atlantica*
Streblus beccarii
septal foramen
gutter
tenon
septal flap
toothplate
protoforamen
tooth plate foramina
Pseudorotalia schroeteriana
dorsal toothplate foramen
toothplate
septal foramen (deuteroforamen)
Pseudoeponides
septal flap
tenon of chamberwall
protoforamen
umbilical foramen (protoforamen)
toothplate foramen
Epistomaria
toothplate foramen
aperture
toothplate foramen
toothplate foramen
Nonion
Nonionella
Notorotalia
toothplate foramen
septal flap
folded toothplate
Elphidiella
Asterorotalia pulchella
Elphidiononion
Elphidiella
Parrelina
Asterigerina carinata
Nummulites

Plate 15

Pl. 16. Different species of *Reussella;* the Cretaceous species *(R. szajnochae* Grzybowski, *R. pseudospinulosa* Troelsen) do not belong to Brotzen's genus *Pyramidina*, but are real *Reussella*. Of each species the three sides of the test (x 75) and the toothplates (mostly x 225), and in some cases the aperture (x 225) are drawn. In some Miocene and Pliocene species the complication of the toothplates already begins; in the older forms the toothplates are simple. Of each species the name and the stratigraphic level are given.

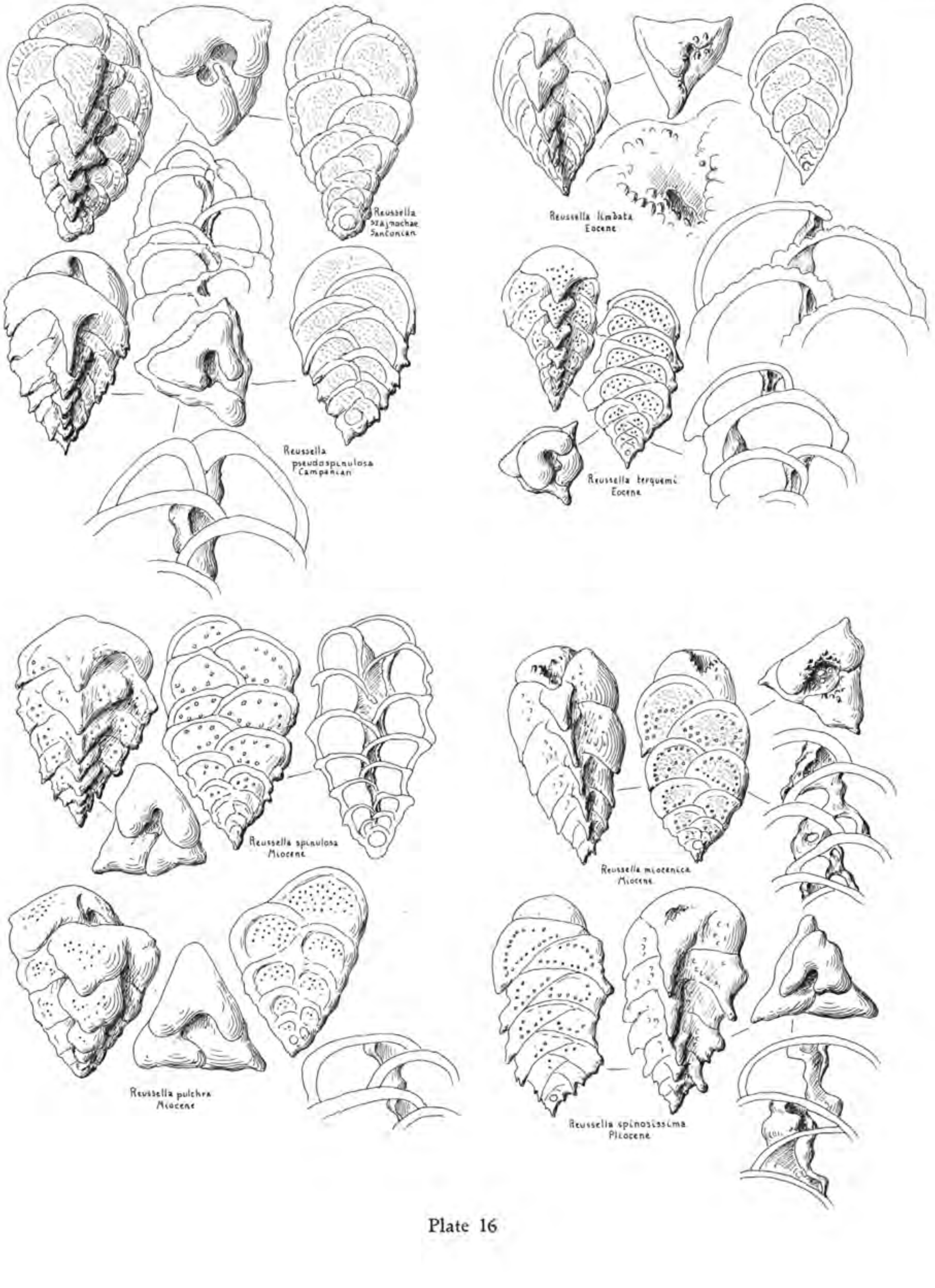
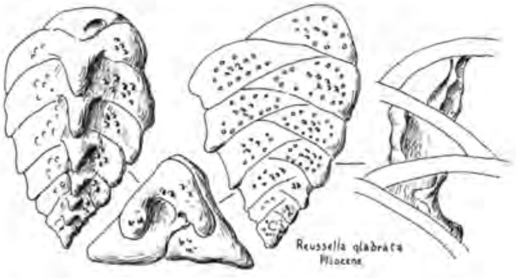
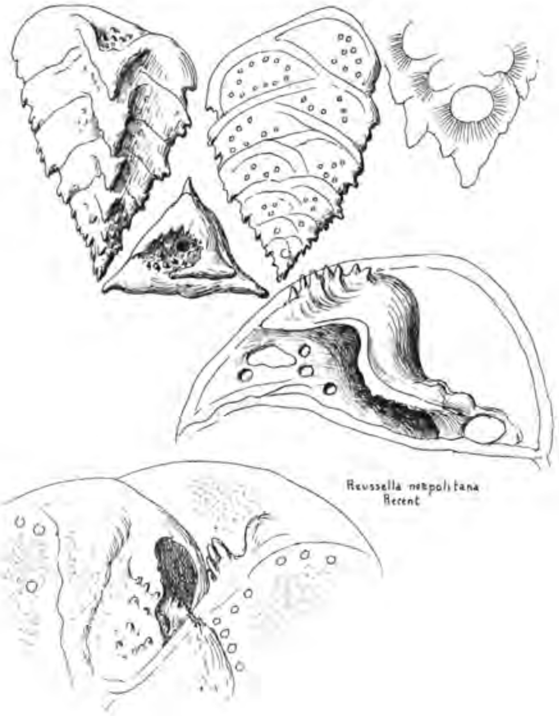

Reussella szajnochae Santonian
Reussella limbata Eocene
Reussella pseudospinulosa Campanian
Reussella terquemi Eocene
Reussella spinulosa Miocene
Reussella miocenica Miocene
Reussella pulchra Miocene
Reussella spinosissima Pliocene

Plate 16

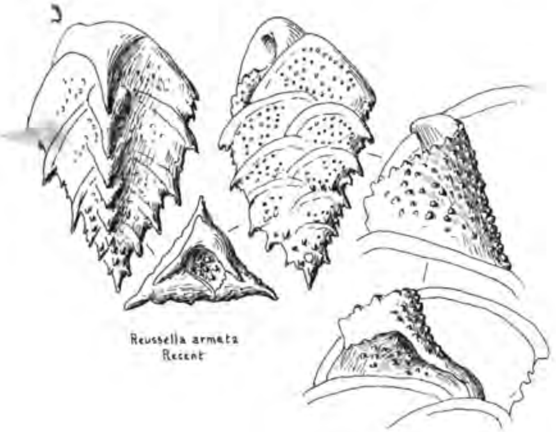
Pl. 17. Different species of *Reussella*. The complication of the toothplates here is obvious; often the toothplates get pustules, dents and openings and in the case that the aperture is wide open, as it is in *R. neapolitana* Hofker, *R. atlantica* Cushman, *R. simplex* Cushman, *R. aequa* Cushman, *R. weberi* Hofker, the toothplate is seen within the aperture, forming the characteristic which led Loeblich and Tappan to create a new genus, *Fijiella;* this genus must be synonym with *Reussella*.



Reussella glabrata
Pliocene

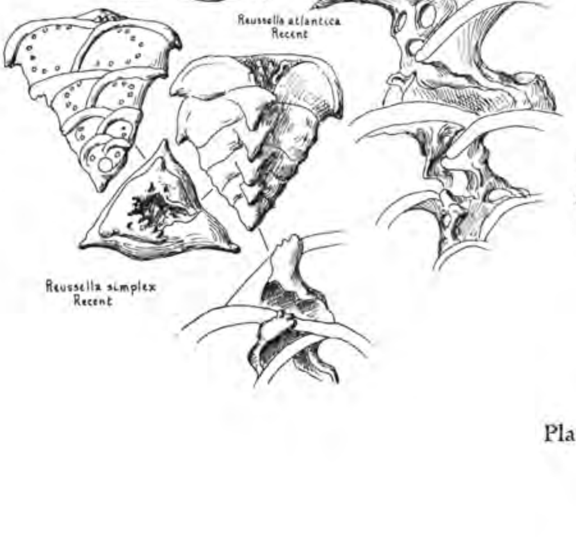


Reussella neapolitana
Recent



Reussella armata
Recent

Reussella atlantica
Recent



Reussella simplex
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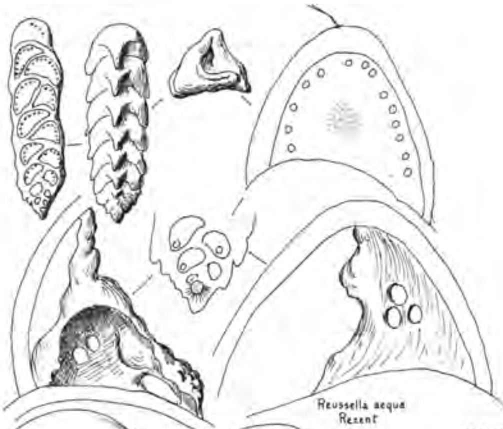

Reussella aequa
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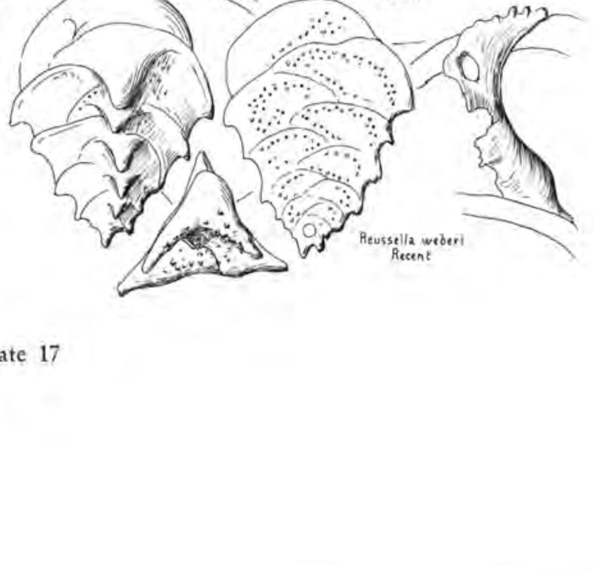


Reussella weberi
Recent

Plate 17

Pl. 18, Fig. 1. During the Uppermost Cretaceous-Danian-Lowermost Paleocene the percentages of specimens of *Globigerina daubjergensis* Brönnimann change from left coiling to right coiling. This would mean, according to Bandy, that the temperature of the surface water got warmer during that time.

Pl. 18, Fig. 2. Evolution of the *Globigerina aspera* (Ehrenberg) gens. In the Turonian the species is distinctly trochoidal; during Coniacian-Santonian it becomes more and more planospirally coiled; during the Campanian the species is nearly planospiral; in the Maestrichtian the specimens tend to form two symmetrically placed apertures instead of one marginal one. Walls and septa are simple.

Pl. 18, Figs. 3-6.

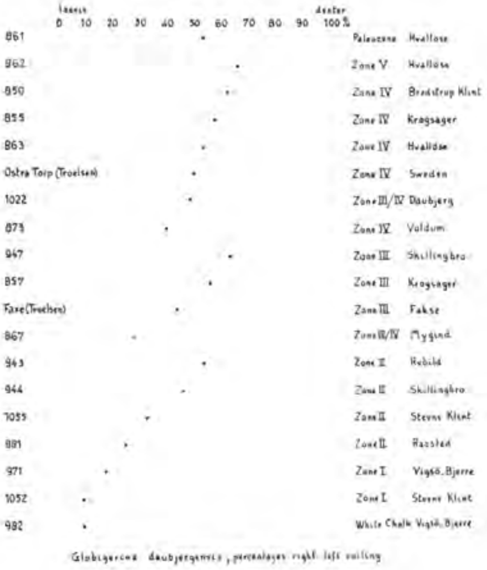
3, 4. Horizontal sections through the walls and septa of *Globigerina eaglefordensis* Moreman from the Albian. The septa are simple and there is a secondary thickening only of the outer wall. x 265.

5. Section through *Globigerina daubjergensis* Brönniman from the Danian. The section clearly shows that the septa and the walls are monolamellar. x 220.

6. Longitudinal section through *Chiloguembelina (Stainforthia) morsei* (Kline) from the Danian. The toothplates running from one foramen to the next one are clearly seen; septa and walls are monolamellar.

Pl. 18, Figs. 7-12. Reconstructions and sections of species of *Globotruncana*.

7. Apertural conditions of *Globotruncana stuarti* (Lapparent).
8. Apertural conditions of *Marginotruncana paraventricosa* Hofker.
9. Apertural conditions of *Marginotruncana pura* Hofker.
10. Horizontal section of *Globotruncana*, showing part of the folded toothplate.
11. Oblique section showing the flap of the toothplate attached to the septum.
12. Reconstruction of the apertures with toothplate of *Globotruncana*.



Globigerina daubjergensis, percentages right-left coiling

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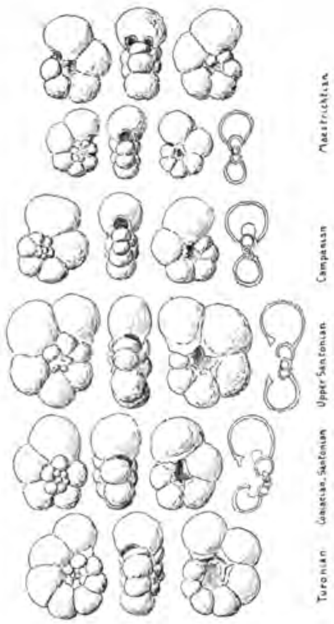
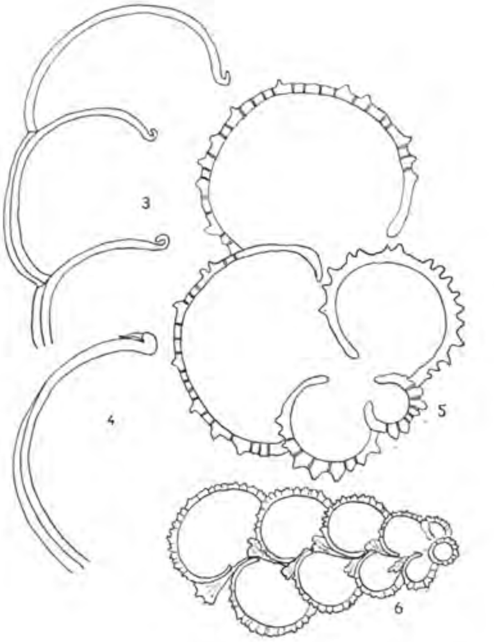




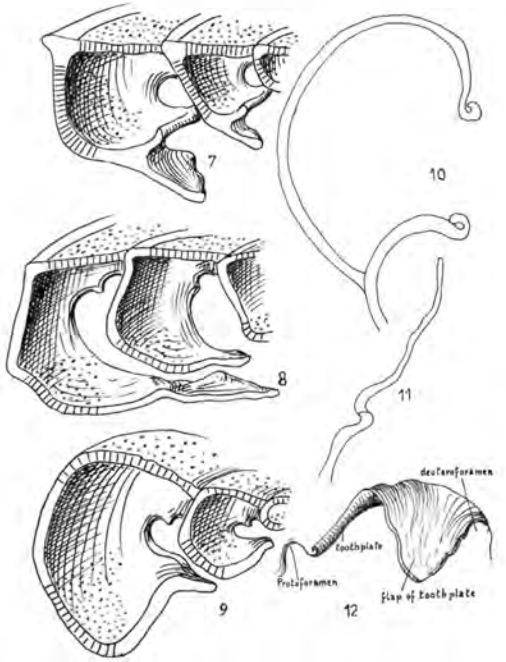


Plate 18

Pl. 19, Figs. 1-8.

1, 2. *Globigerina eaglefordensis* Moreman, from the Upper Albian of a drill-hole in Holland. x 150. The simple septa and the doubling of the outer wall can easily be seen.

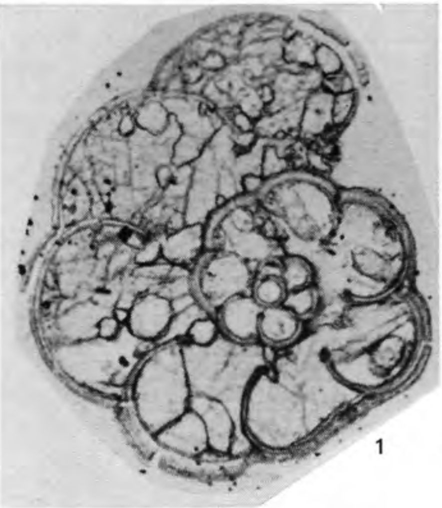
3. *Guembelina striata* (Ehrenberg); Port Gentil, drill-hole, Campanian. x 150. Septa and outer walls are simple throughout.

4. *Hantkenina alabamensis* Cushman, from the Cocoa Sands, Eocene, U.S.A., x 125. The septa are simple, as is the outer wall of the last formed chamber; older outer walls show secondary doubling.

5. *Guembelina striata* (Ehrenberg), from the Lower Campanian of Folx-les-Caves, Belgium. x 200. The septa of all initial chambers are simple some later chambers have the whole wall double, but the walls and septa of the two last formed chambers are simple.

6. *Globigerinatella insueta* Cushman and Stainforth. Section, x 100. All the walls are simple; this is in agreement with the supposition given by the present author that this species belongs in the vicinity of *Cassidulina*.

7, 8. *Globigerina yeguaensis* Weinzerl and Applin, Cocoa Sands, Eocene. x 100. The outer walls are double, but the poreless walls of the initial chambers and the poreless wall parts (septa) of later chambers are simple.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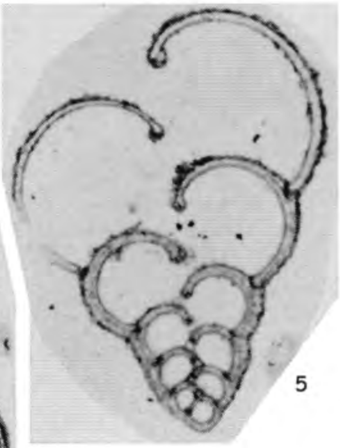
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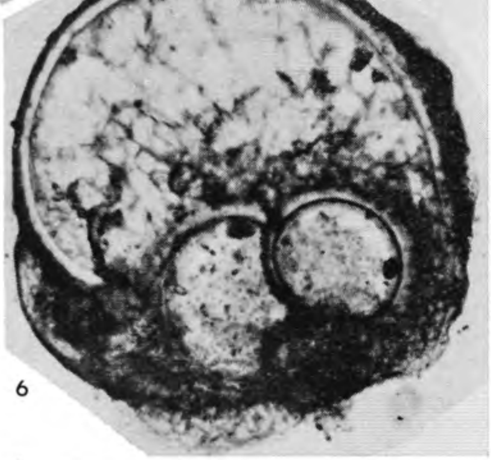
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Plate 19

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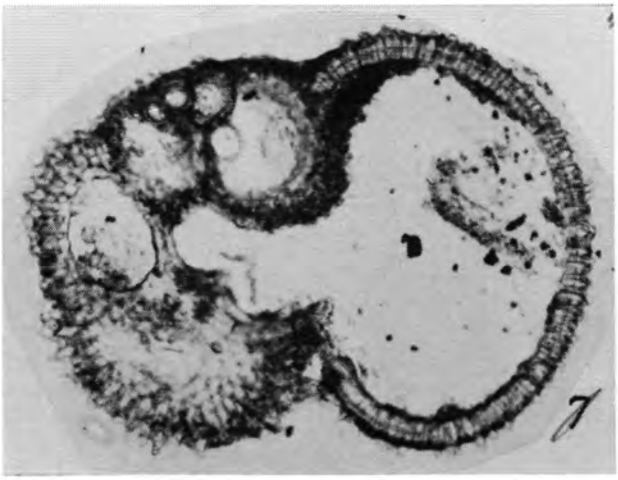

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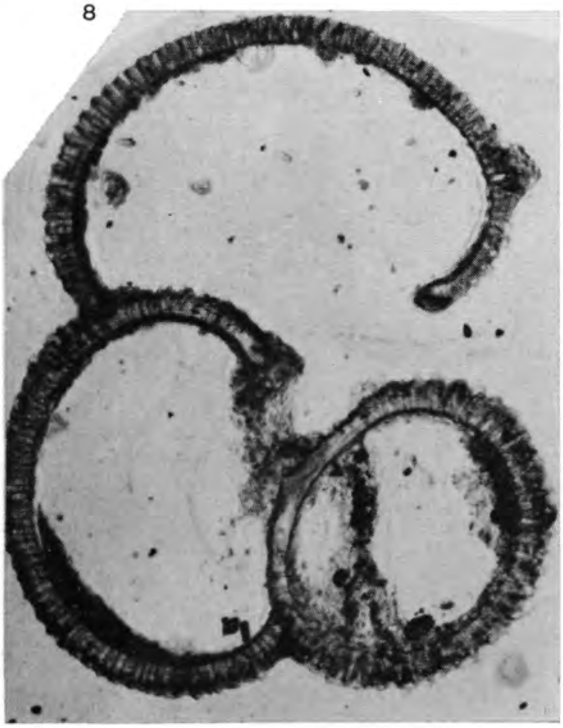
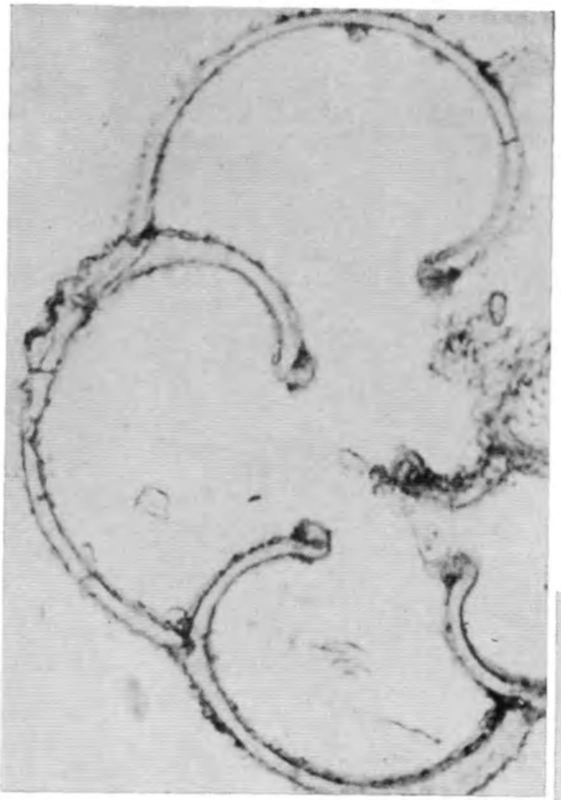


Pl. 20, Figs. 1-4.

1. Horizontal section through *Globotruncana (Marginotruncana) globigerinoides* Brotzen, Folx-les-Caves, Belgium, Lower Campanian. x 300. The septa are simple.
2. *Globigerina aspera* (Ehrenberg). Port Gentil, Campanian. x 150.
The septa are simple, older chamberwalls may be double at the outside.
3. Horizontal section of *Globotruncana (Marginotruncana) paraventricosa* Hofker, from the Lower Campanian of Folx-les-Caves, Belgium. x 300.
The septa are distinctly simple.
4. *Heterohelix navarroensis* Loeblich and Tappan. Navarro-Formation, U.S.A. x 400. The inner walls of the initial chambers (spirally arranged) and the later septa are simple. Outer walls may be double, but the whole wall of the last formed chamber is distinctly simple.

Plate 20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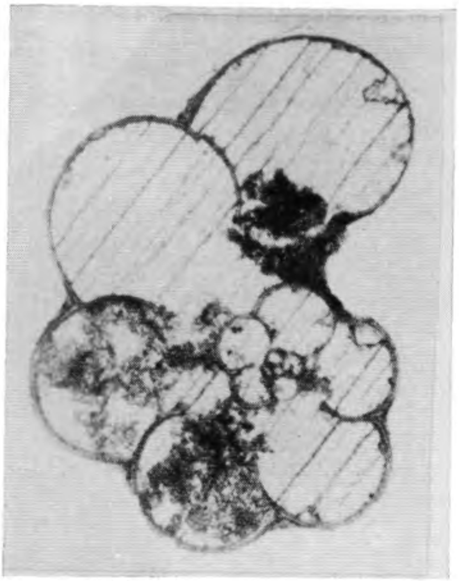
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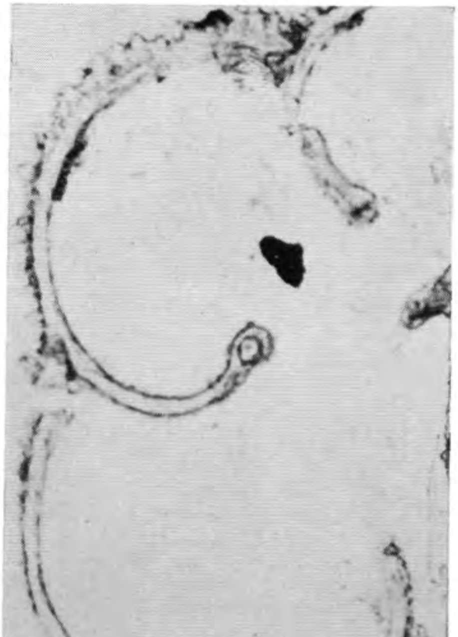
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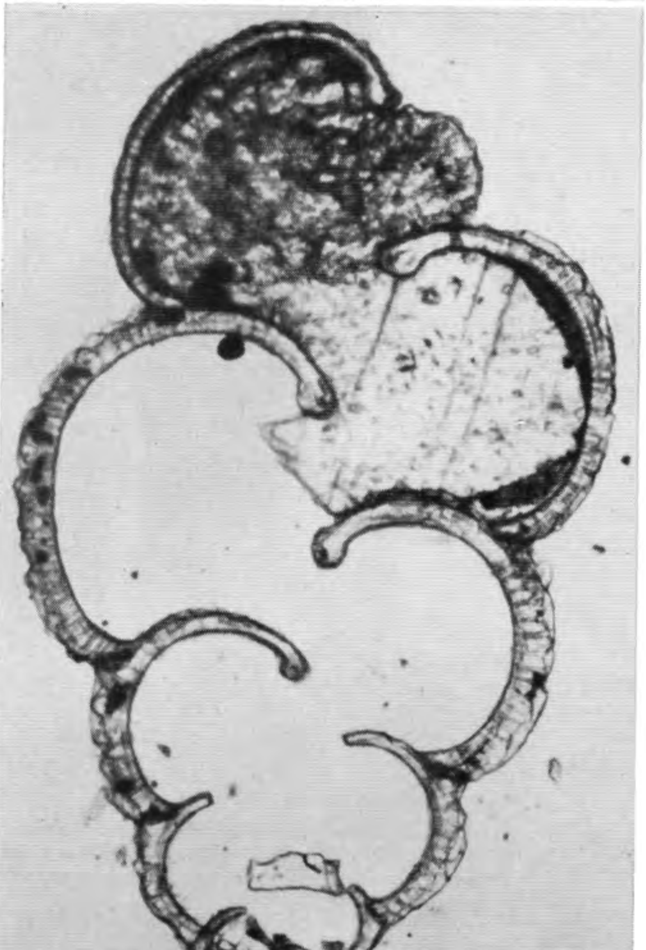
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P. 21, Figs. 1-6.

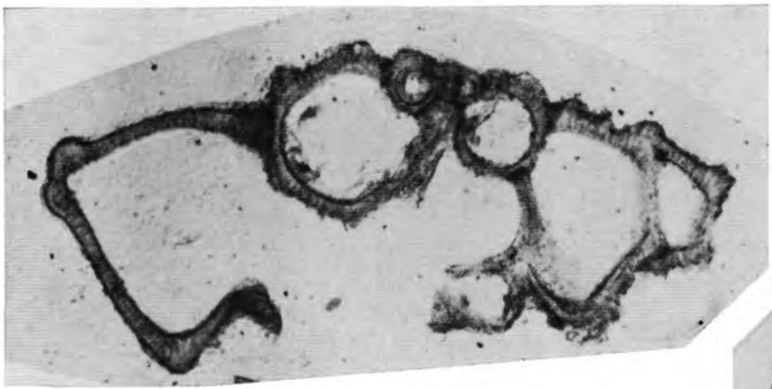
1. Transverse section through *Globotruncana linneiformis* Hofker, from the Lower Campanian of Folx-les-Caves, Belgium. Nothing can be seen of the heavy secondary thickenings as given by Reiss. x 200.

2. Transverse section through *Marginotruncana paraventricose* Hofker, same locality. Here all the walls are distinctly simple. x 100.

3. Horizontal section of *Globotruncana linneiformis* Hofker, same locality. x 200. Septa and walls are simple.

4. *Planoguembelina eggeri*. x 150. All the walls of the inner chambers are simple.

5, 6. Sections through *Planomalina apsidostrobus* Loeblich and Tappan from the Lower Cretaceous of Trinidad. The walls show an inner layer of granular microstructure; the outer walls are fibrous radial. This cannot have been a planktonic species. x 150.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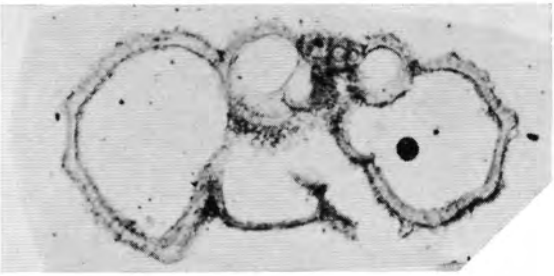
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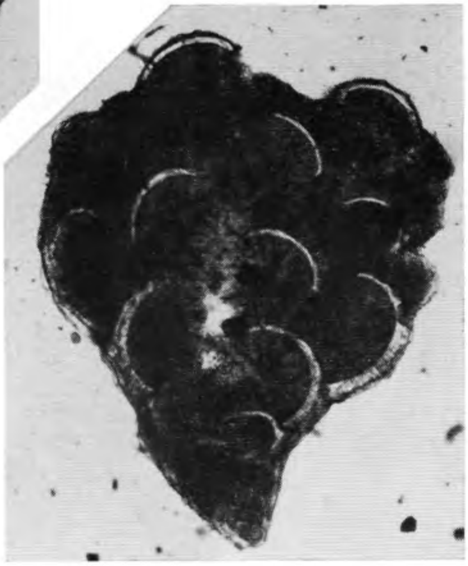
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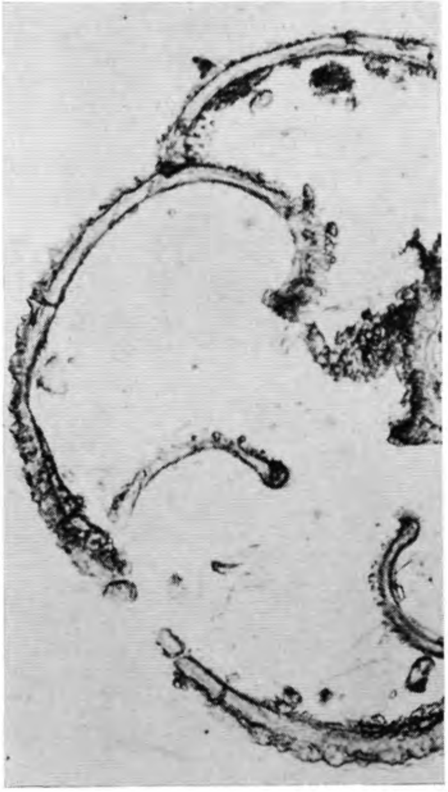
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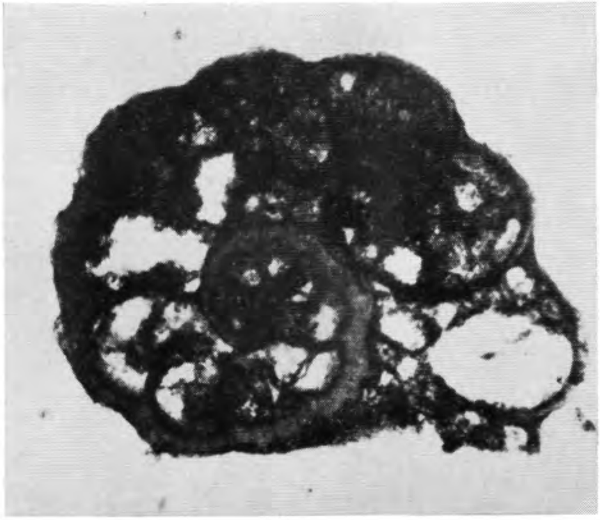
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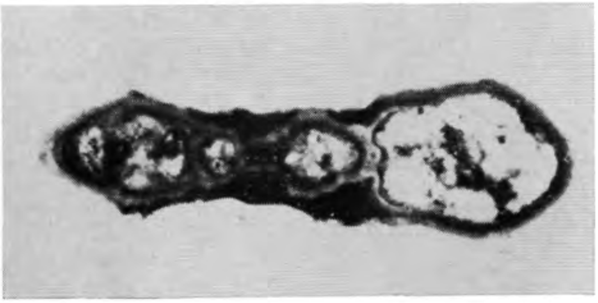
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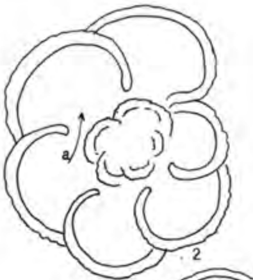
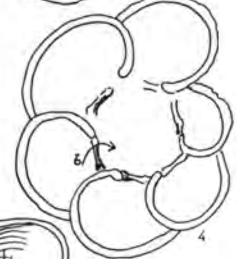
Plate 21

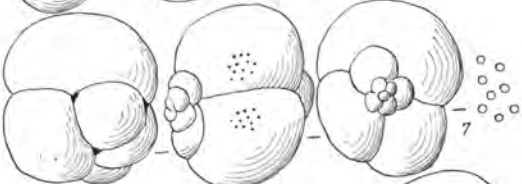
Pl. 22, Figs. 1-5. Successive horizontal sections through *Globotruncana stuarti* (Lapparent), from dorsal toward ventral side.

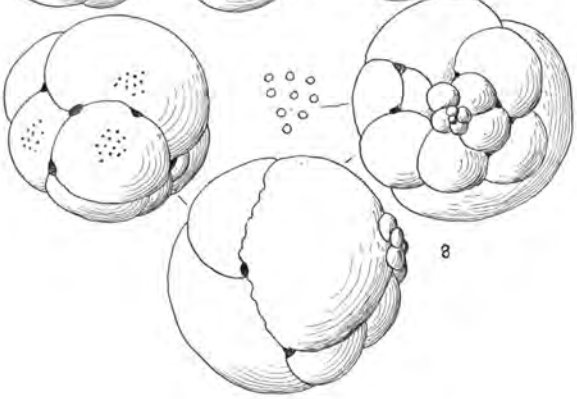
Pl. 22, Figs. 6-11. Evolution and ontogenesis of *Globigerina mexicana* Cushman. Brasso-Tamana Road, 12 ¾ km milepost, Trinidad; type-locality of *Porticulasphaera mexicana* Zone. All x 75.

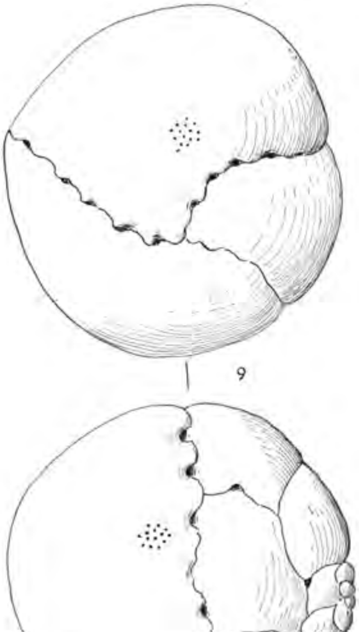
6. Young specimen in the form of *Globigerina turgida* Finlay.
7. Specimen in the form of *Globigeraspis kugleri* Bolli.
8. Specimen in the form of *Globigerinatheca barri* Brönnimann.
9-10. Specimen in the form of *Porticulasphaera mexicana* (Cushman).
11. Longitudinal section through the *P. mexicana* form, showing the thin walls of the initial chambers and the openings at the dorsal sutures distinctly formed by resorption. The walls of the initial chambers are monolamellar.











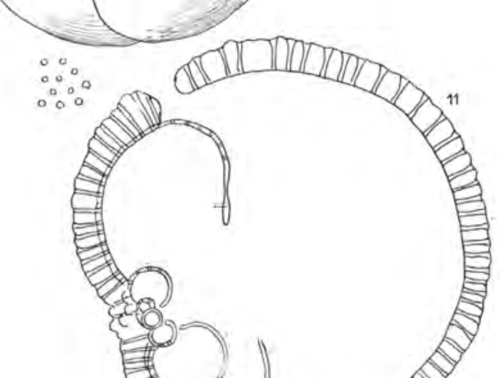


Plate 22

Pl. 23, Figs. 1-6. *Globorotalia.*

1. *Globorotalia truncatulinoides* d'Orbigny, transverse section, x 100.
2. Idem, x 100, horizontal section near the dorsal side; some septa seem double by bending of the chamber walls.
3. Idem, x 150, horizontal section more towards the ventral side; septa are simple.
4. Idem, x 100, most septa are simple, but one of them, ground near to the ventral side, seems double.
5. Idem, x 100. Section grasing the dorsal side; most septa seem double.
6. Transverse section of *Globorotalia menardii* d'Orbigny, x 75. Walls of initial chambers are simple; those of later chambers show secondary thickened outer walls, but the last formed chamber has simple walls.

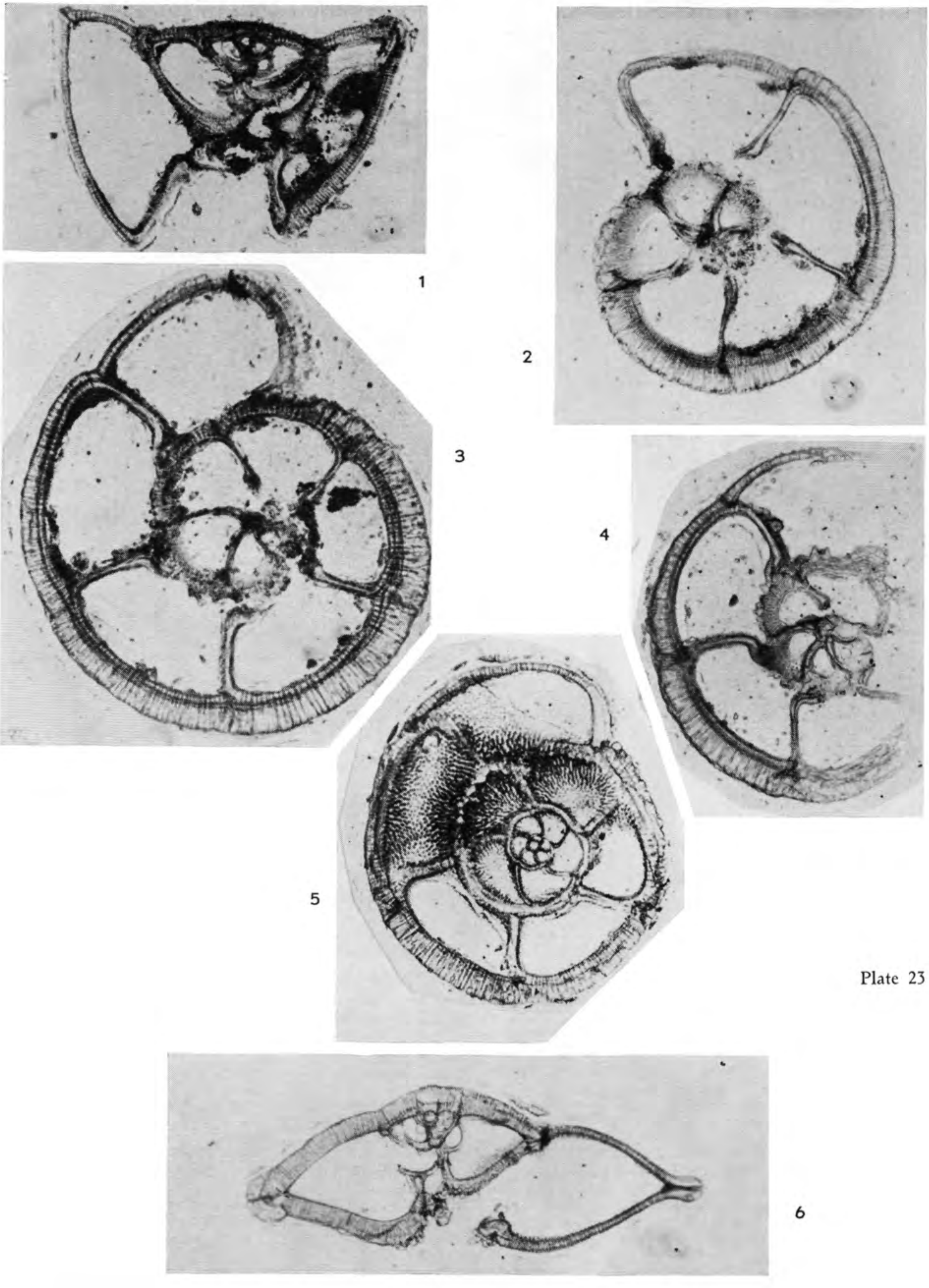


Plate 23

Pl. 24, Figs. 1-4.

1. Transverse section of the sea-floor form of *Globorotalia tumida* (Brady). The outer walls are much thickened by at least one layer; the initial chambers have simple walls inwardly; this also can be seen in Fig. 4, in which an enlargement of the initial part is given; 1, x 75, from near Frederiksted, Carribean; 4, x 225.

2. Initial part of *Globorotalia truncatulinoides* (d'Orbigny), showing simple septa but secondarily thickened outer walls in the later chambers; x 75.

3. *Globorotalia menardii* ('Orbigny), sea-floor specimen with thickened out walls, x 75.

Pl. 24, Figs. 5-7.

5. *Globorotalia tumila* (Brady); tangential transverse section of sea-floor specimen. The bending of the chamber wall against the septum of the next chamber can be seen; horizontal sections thus often show double walls. x 225.

6. Horizontal section through the middle of the test of *G. truncatulinoides* (d'Orbigny), showing nearly simple septa but secondary thickened outer walls. x 75.

7. Horizontal section through the same species, but now close to the dorsal wall, showing so-called bilamellar septa which in reality are simple septa together with the walls of next chamber bending down. x 75.

Pl. 24, Figs 8-10.

8. Slightly oblique horizontal section through *Globorotalia tumida* (Brady) from Frederiksted, 500 fathoms, Caribbean. The simple septa are seen with at the end the beginning of the flap of the toothplate which forms a tectum over the aperture. x 75.

9. Part of section as in Fig. 8, but the slide remained thicker, so that a larger part of the wall, the twisting of the septa and the toothplates can be seen, x 75.

10. Transverse section through *Globorotalia truncatulinoides* (d'Orbigny) showing the simple outer wall of the end chamber and the secondary thickened outer walls of the older chambers. x 75.

Pl. 24, Figs. 11, 12.

11. *Planomalina buxtorffi* (Gandolfi), horizontal section, showing the large megalospheric proloculus, the rim at the margin, and the septa which show an inner granular primary wall and an outer calcareous radial thickening. x 140.

12. *Planomalina buxtorffi* (Gandolfi), transverse section, showing the granular primary walls and the openings of the last formed chambers at the dorsal and ventral central parts. x 140.

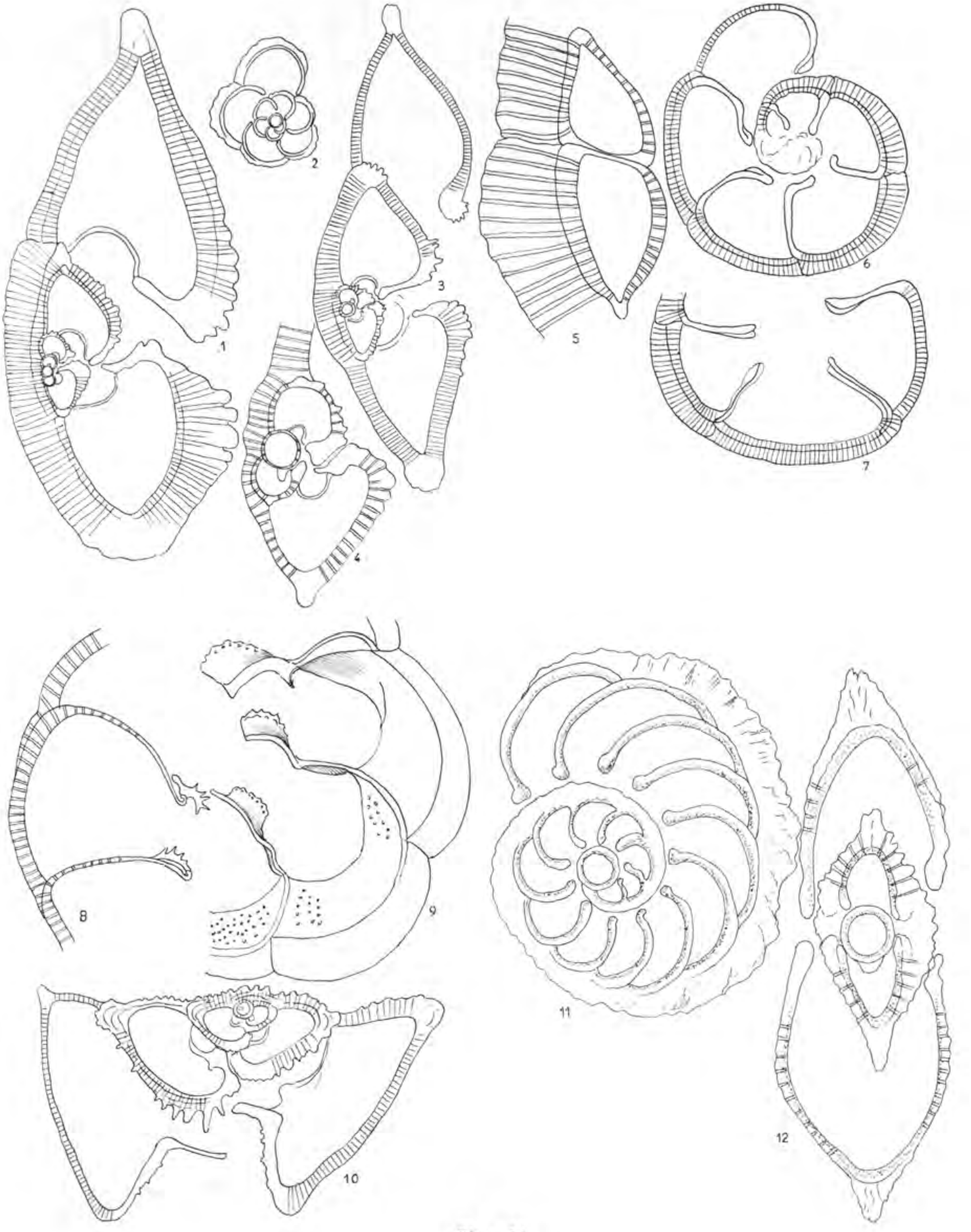


Plate 24

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