ON THE PHYLOGENY OF THE EMBRYONIC APPARATUS OF SOME FORAMINIFERA

BY

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INTRODUCTION.

In the following pages data will be given about the size of the megalospheric embryonic apparatus, and of the size of the shell, of some *Foraminifera*. By comparing these data for a certain species from different samples, the relative ages of which are known, it will be possible, to get an insight into the alterations of the measured characters in geological times. For that purpose samples from geological sections, or otherwise well defined geological formations, were used. A description of each of these sections will be given, in order to discuss the reliability of the determinations of the relative ages of the samples.

I may point out here, that as the layers containing the foraminiferal shells have a certain thickness, and as the sampling has been done over the whole width of the outcropping layer, or over part of it, we may be certain, that the deposition of these shells, must have taken "many years". In my opinion this may be an advantage, as the possible annual or short-periode influence of the environment on the phaenotype may thus have been eliminated.

The size of the embryonic chambers was determined by means of equatorial sections of the shells, projected on a large scale. In these projections the innerwalls of the protoconch and of the deuteroconch were traced and their surfaces afterwards determined with the aid of a planimeter. The square roots of these figures gave a measure for the relative radius of the embryonic chambers, from which the real radius could at once be calculated.

The form of the embryonic chamber is supposed to be globular. Actually this will only be more or less true for the protoconch, but as for the deuteroconch, the deviations may certainly be appreciable, which will lessen the reliability of these measurements.

The large variation of the measurements of the characters, soon made it clear that, statistical methods had to be used, to determine their typical conditions. It will be unnecessary to describe in detail the methods for the reduction of quantitative data, in view of their general currency in experimental work ¹). For this matter we refer to W. JOHANNSEN (19), Elemente der exakten Erblichkeitslehre.

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¹) Much of the following has been taken from H. P. CRAMPTON's Studies on the variation, distribution and evolution of the genus *Partula* (10).

In working out the biometric constants, the numerical variates were combined into classes, which together constituted the frequency distribution of the measurements of a certain character. These frequency distributions which may also be given as curves, form the basis for the calculation of the constants. If however, the number of measurements was less than a hundred, no frequency distributions were used, but each measurement was accounted for separately.

The first constant, the average or mean value (M), is of course the sum of the classified measurements divided by the total number; it indicates the typical condition. The second constant is the standard deviation, or index of variability (σ), which describes the degree of conservatism of the members of a group in relation to the average or mean condition; the individual deviations from the mean are squared and added, and the square root of this sum is the standard deviation. It is expressed in the same units as the average. The measure of absolute variability or coefficient of variation (v) is the index of variability (σ) divided by the mean value (M) and multiplied by 100. It shows the absolute degrees of variability of the character, irrespective of the nature of the concrete dimensions or proportions; thus the variation coefficients of divergent characters may be compared.

In order to judge, whether there is a real statistical difference, between the characters of two samples of the same species, but of a different geological age, it is necessary to determine the standard errors (m) of the descriptive constants. The standard error of the average (M) is σ divided by the square root of the number of cases (n):

$$m_M = \frac{\sigma}{\sqrt{n}}$$

thus:

$$m_\sigma' = \frac{\sigma}{\sqrt{2n}}$$

and:

$$m_v = v \sqrt{\frac{1 + 2\left(\frac{v}{100}\right)^2}{2n}}$$

(according to PEARSON) (23).

Observing a numerical difference between the average values of a character, in two comparable samples, the difference must be judged as to its significance by its own error, which is the squared root of the sum of the squared standard errors of the two average values:

$$m_{\mathrm{diff}} = \sqrt{m_1^2 + m_2^2}.$$

Should the difference in question exceed its error, but fall below twice the error, it is not significant; should it lie between twice and thrice its standard error, then it presumably indicates a real constitutional diversity (in more than 955 out of 1000 chances); when it is greater than three times its standard error, then the existence of a real difference is a statistical certainty (997 out of 1000 chances).

In the tables the standard errors of the differences in mean values are placed in [ ], when these differences are smaller than twice their standard errors.

It remains to be stated, that in computing the constants, fractions were carried out to six decimal places, in order that the second-place index should be as accurate as possible. According to JOHANNSEN (19), two decimal places are always sufficient for the constants.

Though it is not my intention to discuss the frequency distributions here, I will make some remarks concerning them.

The formula used for the calculation of the constants bear upon the "ideal frequency"- or Gauss-curve. When the deviations from this curve become considerable e. g. when two or more tops are prominent, these constants lose their meaning. That is the reason why, instead of the measured surfaces, the relative radius of the embryonic chambers was used as a base for the composition of the frequency distributions. For it appeared, that the latter were much better in harmony with the "ideal" distribution of variates.

The second remark concerns the fact that a considerable number of the many frequency distributions which had to be used, were more or less irregular and gave the impression that the samples used were not homogeneous. Proof for such a supposition, can only be given by a biological analysis of living material.

When the samples were not taken by the author himself, special information regarding their origin is given.

I am greatly indebted to my friend Prof. Dr. I. M. VAN DER VLERK, for the material he put at my disposal and the trouble he took to provide me with the samples from the St. Pietersberg.

At the same time I wish to acknowledge, the helpful assistance of Messrs. BURGERS and MAURENBRECHER, who made a great many of the preparations of the Belgian *Nummulites*.

Prof. Dr. B. G. ESCHER I want to thank, for the hospitality he again accorded to me in the "Rijksmuseum voor Geologie en Mineralogie te Leiden".

DETERMINATION OF THE GEOLOGICAL- AND RELATIVE-AGE OF THE SAMPLES TAKEN FROM LOCALITIES I—VI; AND A STATISTICAL DESCRIPTION OF THE SPECIES INVESTIGATED.

Locality I: St. Pietersberg, province of Limburg, Holland.

Shells of *Lepidorbitoides minor* (SCHLUMBERGER) and *Calcarina calcitrapoides* (LAMARCK) were investigated from four samples taken from the Upper-Cretaceous beds of *Bryozoa* in the Burgerwacht-quarry of the St. Pietersberg, near the town of Maastricht.

There is no need for a palaeontological description of the contents of these beds, as their geological age is well known.

Prof. Dr. I. M. VAN DER VLERK who took the samples, gave me the details of the section (fig. 1).

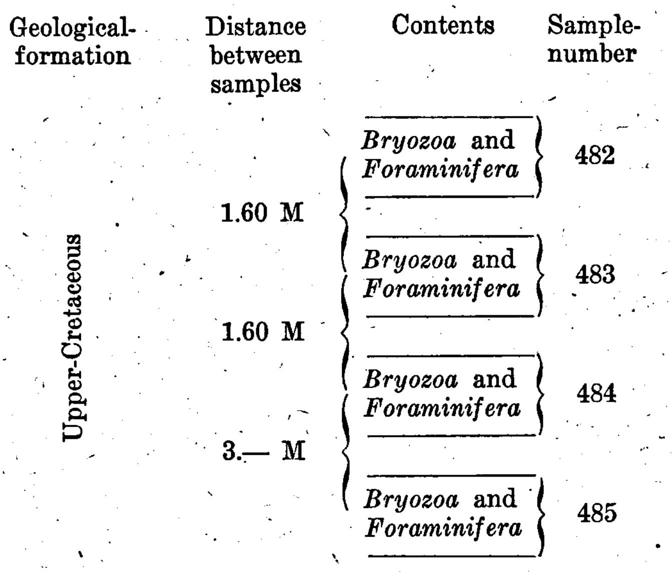

Fig. 1.

The *Bryozoa*-beds are nearly horizontal and rather thin, their thickness being about 10—20 cM. From the section (fig. 1) it appears that, sample 482 is the youngest and 485 the oldest. The *Foraminifera* occurring in the different beds, are very much the same.

For a general description of *Lepidorbitoides minor* (Schlumberger), I refer to: Schlumberger (27), pl. 8, fig. 2, 3, 5; pl. 9, fig. 2 and 3. Douvillé (13), pl. 8, fig. 3 and 4. Rutten (24), pl. fig. 1—4, 8 and 9.

Calcarina calcitrapoides (Lamarck) is described by Hofker (18), fig. 1—14. The older literature is also given in that paper.

The statistical description of these species is given in the tables I and II.

Locality II: Puente Viejo, Spain.

The three samples from this locality derived from an easily crumbling foraminiferal limestone-breccia and marls outcropping along the southern bank of the Quadalquivir, near the old bridge ("Puente Viejo"), marked on the topographical map, sheet 927 Baeza, scale 1:50.000.

A sketch of this section is given in fig. 2.

The general strike of the beds is N 165°, the dip 60°—70° W; thus sample 408 being the oldest and 410 the youngest in the section. R. Douvillé has given a geological description of this locality (15), p. 127. The layers in our section (fig. 2) belong according to him, to the west-flank of an anticline.

As to the geological age of our samples, I mention the occurrence of *Miogypsina (Miogypsinoides) complanata* Schlumberger. Though rare in the oldest sample, this species is abundant in both the younger samples. Thus, in accordance with Douvillé (15), p. 102 ff., the geological age may be taken as Lower-Miocene. I may observe however, that Senn mentions the occurrence of *Miogypsinoides* in the Chattian (Upper-Oligocene) of Morocco (28), p. 90, a statement which is confirmed by Brönnimann (6), p. 106.

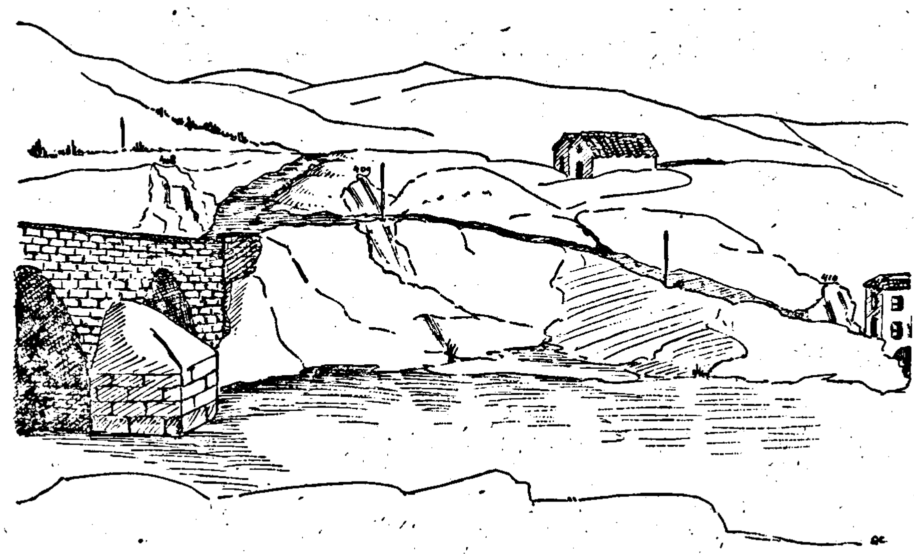

Fig. 2.

The samples 408—410 all yielded shells of *Lepidocyclina tournoueri* Lemoine and R. Douvillé; *Miogypsina (Miogypsinoides) complanata* Schlumberger and *Spiroclypeus margaritatus* (Schlumberger). Shells of these three species were ground and prepared for examination.

For a general description of *L. tournoueri* I refer to: Lemoine and R. Douvillé (21), p. 19, pl. 1, fig. 5, pl. 2, fig. 2, 14, pl. 3, fig. 1; H. Douvillé (14), p. 78, pl. 6, fig. 8—12; J. Flandrin (16), p. 91, pl. 8, fig. 17—33; F. Gómez Llueca (17), p. 352, pl. 33, fig. 1—27; P. Brönnimann (6), p. 47, pl. 3, fig. 3—6, 15, pl. 5, fig. 11, 12, 14.

M. complanata is described by: Schlumberger (25), p. 327 ff, pl. 3, fig. 18; Silvestri (29), p. 7 ff, pl. 1, fig. 19; Checchia-Rispoli (7), p. 1 ff, pl. 2, fig. 2, 5, 6; Bourcart and David (3), p. 52, fig. 6a, pl. 12, fig. 10; Barker and Grimsdale (2), p. 162, pl. 5, fig. 6, pl. 6, fig. 1—6, 8, pl. 7, fig. 1, pl. 8, fig. 6; Brönnimann (6), p. 77 ff, pl. 7, fig. 7—14, pl. 8, fig. 18, pl. 9, fig. 1, 2, pl. 11, fig. 9—17 (described by this author as var. *mauretanica*, though it seems to me, that no essential difference exists, between his figures and the *Miogypsina*-shells of my samples).

S. margaritatus is described by: Schlumberger (26), p. 253, fig. 1—5; Yabe and Hanzawa (32), p. 627, fig. 1—3; Krijnen (20), p. 89, pl. 1, fig. 1—5; Tan (31), p. 182, pl. 2, fig. 12, pl. 3, fig. 9, pl. 4, fig. 6, 7.

The statistical description of the three species is given in the tables III—V.

Localities III. A section along the road from Villajoyosa to Orcheta (province of Alicante, Spain) and an exposure near Jaen (Spain).

The section was surveyed and described by the author (9), p. 10 ff. I quote here the essentials and the geological sketch (fig. 3) from this paper.

The foraminiferal breccia's which are intersected by the road north of the Ermita de S. Antonio, are situated in the northern limb of a syncline, wherein a small secondary fold occurs about 200 M north of exposure 1 (sample 455), after which the layers very soon resume their regular position, dipping in a southerly direction. Thus there is sufficient certainty

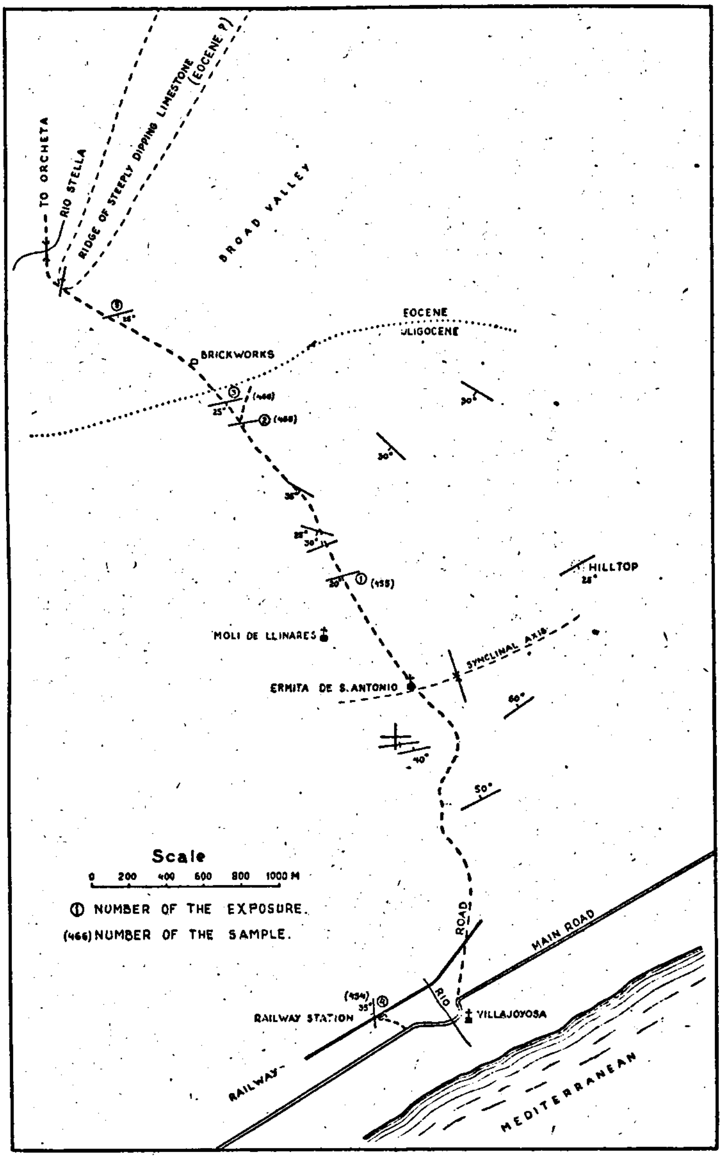

Fig. 3. Geological sketch of the region between Villajoyosa and Orcheta.

to suppose, on the strength of the section-measurements, that exposures 2 (sample 468) and 3 (sample 466), situated close to the boundary of the Eocene, are stratigraphically older than exposure 1 (sample 455).

From the sketch (fig. 3) it appears, that sample 466 must be older than sample 468. According to my fieldnotes, the distance between these samples is only about 10 M (in the sketchmap, fig. 3, it erroneously seems to be more).

As to sample 454 (exposure 4) it is remarked (p. 10, l. c.) that the section measurements allow no decision, with regard to the age of sample 454, with respect to the other exposures.

Comparing the foraminiferal contents of the samples, we note the occurence of the large forms of *Lepidocyclina*, cf. *L. (Eulepidina) elephantina* (MUNIER CHALMAS) in sample 454. H. DOUVILLÉ (14), p. 69 observes about this species, that it is always found in the company of the last small *Camerina's* so, according to DOUVILLÉ, in the Upper-Oligocene, or at the base of the Aquitanian. This description fully applies to sample 454 wherein some small *Camerina*-shells were found, rather in contrast with the abundance of *Camerina's*, belonging to different species, in samples 466 and 468.

As *Lepidocyclina* cf. *elephantina* didn't occur in the other samples of this section, sample 454 is probably younger than these samples.

Sample 228 was collected from an exposure, described by R. DOUVILLÉ (15), p. 156 on the southern edge of the town of Jaen, on the righthandbank of the Arroyo de la Alcantarilla, about 100 M below the bridge, (top. sheet 947, Jaen, scale 1:50.000). The exposure is there situated at the initial letter of the word "Alfareria".

The foraminiferal contents of this sample is mentioned in my paper (9), p. 15. I emphasise here the occurence of some shells of *Miogypsina (Miogypsinoides) complanata* SCHLUMBERGER, a species not found in any of the other samples, and the absence of *Camerina* shells. Although the occurence of *Miogypsina* was not known to him, R. DOUVILLÉ fixed the age of this exposure as Aquitanian, on the negative fact that *Camerinae* are absent, while the upward boundery is sufficiently fixed, as the marly complex is, in many places, regularly covered by a molassus, wherein occur the species: *Pecten beudanti* and *P. praescabriusculus*, characteristic of the Burdigalian (15), pp. 102 ff. Since we have proof that *Miogypsina complanata* is also present in this exposure, the age-determination by DOUVILLÉ is confirmed.

Reviewing our samples, 466, 468, 455, 454 and 228, we conclude: that their relative age is in the order cited here, sample 466 being the oldest and 228 the youngest of the series, leaving only some uncertainty as to the place of sample 454.

All samples mentioned, contained *Lepidocyclina tournoueri* LEMOINE and R. DOUVILLÉ, whereas the three younger samples yielded enough shells of *Cycloclypeus* cf. *guembelianus* BRADY, to permit a statistical examination.

Literature for a general description of *L. tournoueri* has already been given on p. 144; for *C.* cf. *guembelianus* I refer to my paper (9), p. 26, fig. 4a, b and c. The older literature is also given there.

The statistical description of these species is given in the tables VI and VII.

Localities IV: Well Bodjonegoro I, Java (East-Indies) and a dredging-sample near the Kei-islands (East-Indies).

The well-samples put at my disposal by the "Bataafsche Petroleum Maatschappij", and the subrecent sample given to me for examination by Prof. Dr. I. M. VAN DER VLERK, were extensively described in chapter III of my paper (9). The following essentials are quoted from this paper.

The depth of the drilling-samples from the well Bodjonegoro I, is stated as follows:

201—209 M depth
211—215 M „
401—404 M „
604 M „
1007 M „
1627 M „

Samples 201—209 M and 211—215 M were put together because apart, they were too poor in *Foraminifera.* I have indicated these samples as: 208 M, 403 M, 604 M, 1007 M and 1627 M.

The strata in the well are lying flat to a depth of 1400 M, thus the samples above that depth, no doubt represent a normal stratigraphical section. The connection between sample 1627 M and the higher ones, is not so clear, though most probably this sample will represent the oldest in the section.

As no *Lepidocyclinae* or *Miogypsinae* occur in these drilling-samples, they are probably of a Pliocene age.

The youngest sample involved in this examination is of course the subrecent sample, dredged near the Kei-islands (Dutch East-Indies), by the Danish expedition of 1922 under the leadership of Dr. TH. MORTENSEN.

All the samples mentioned from these localities contained the shells belonging to the group of forms known as: *Globorotalia menardii* (D'ORBIGNY) — *G. tumida* (BRADY). As in all samples both forms occurred, with all their transitions, a result also reached by SCHMID (30), p. 51, we will unite them under the name of *Globorotalia menardii* (D'ORB.).

As far as could be judged, no microspheric shells were found in these populations.

As for classification and description, I refer to SCHMID (l. c.), pp. 50—53, fig. 1 and 2.

The statistical description of *G. menardii* is given in table VIII.

Localities V: Suburbs of Brussels (Schaerbeek, Heysel and Helmet), Belgium.

The three samples which will be described here, belonged to a collection lend by the "Musée Royal d'Histoire naturelle de Belgique" to the "Rijksmuseum voor Geologie en Mineralogie" at Leyden. Prof. Dr. I. M. VAN DER VLERK was so kind to put them at my disposal.

The samples were labelled as follows:

collection: van den Broek nr. 4
locality : Helmet
geol. age: Wemmelian

collection: van den Broek nr. 5599
locality : Heysel (Laeken)
geol. age: Ledian (Laekenian)

collection: Storms nr. 8084
locality : Schaerbeek (V. Josaphat)
geol. age: Ypresian.

Thus the geological age ranges from Lower-Eocene (Ypresian) to Upper-Eocene (Wemmelian). From the geol. map (carte géol. d. l. Belgique, scale 1:40.000 nr. 88) it appears, that the strata in this region are lying flat.

The samples consisted exclusively of the shells of *Camerina planulata* (LAMARCK) and her megalospheric companion, known as, *Camerina elegans* (SOWERBY).

A general description of the megalospheric shell is given by: **Boussac** (4), pp. 13 ff, pl. 1, fig. 9. (The literature older than 1911 is also given here); **Douvillé** (12), p. 49, fig. 6, 7; **Gómez Llueca** (17), p. 76, pl. 1, fig. 7—18; Mme **de Cizancourt** (8), p. 747, pl. 44, fig. 2, 9; **Flandrin** (16), p. 33, pl. 1, fig. 7, 8; **Arni** (1), p. 130, pl. 6, fig. 2.

The statistical description of this *Camerina* is given in table IX.

Locality VI: Cabo Oriambre (Spain).

The three samples we will discuss here, derived from a section through the steep layers of Cape Oriambre, some kilometers east of San Vicente de la Barquera, on the north coast of Spain. This section, with the fossil-contents of its layers, is described by **Mengaud** (22), pp. 237 ff. A reproduction of his profile is given in fig. 4.

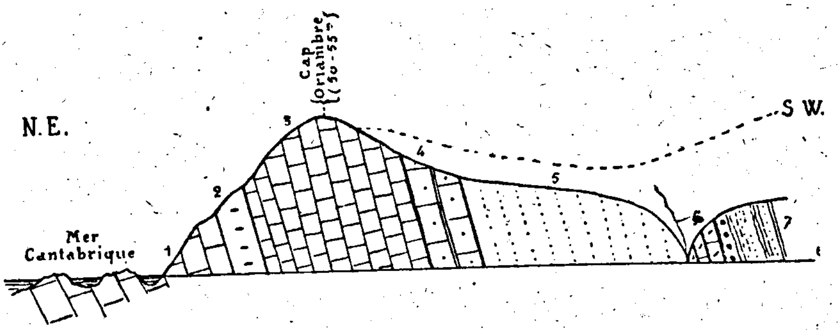

Fig. 4. Profil-coupe des falaises du Cap Oriambre.

1) Calcaire à Alvéolines, *Num. atacicus, N. globulus.*
2) Grès et bancs calcaires à *Num. atacicus, N. globulus, N. Lucasi, Assilina granulosa-Leymeriei.*
3) Calcaire compact avec même faune que 2), mais sections se rapportant probablement à *Num. planulatus* ou *N. aquitanicus.*
4) Lumachelle de Nummulites, Assilines, *Orthophragmina,* avec *N. atacicus, N. irregularis, Assilina exponens, A. mamillata.*
5) Grès tendre gris clair sans fossiles.
6) Calcaire gréseux jaunâtre à *Num. aturicus-Rouaulti.*
7) Conglomérats, grès et marnes rouges de l'Oligocène.

Sample 379 which I took about 50 M to the southwest of the top of the cape, probably belongs to the upper part of complex 3) and the samples 380 and 381 to complex 4). Thus 379 is the oldest- and 381 the youngest sample in this series. The distance between the samples (379—380 and 380—381) is about 20 M. According to **Mengaud** the geological age is Cuisian (Ypresian).

Assilina exponens (J. **de** C. **Sowerby**) which occurred in these samples was selected for examination. **Mengaud** (l. c.), p. 238 mentions the couple *Assilina granulosa* (**d'Archiac**) and *A. Leymeriei* (**d'Archiac**) in the strata 2), whereas *A. exponens* and her megalospheric companion *A. mamillata* (**d'Archiac**) would no sooner appear, than in the stratigraphically higher complex 4). **Mengaud** agrees however with the view expressed by **Boussac** (4), pp. 104 and 105, and **Douvillé** (12), p. 73, that transitions in form always exist between *A. granulosa* and *A. exponens,* so that a clear distinction seems impossible (l. c.), p. 250.

Flandrin (16), p. 78, gives the same interpretation of this question, and as a result of the statistical examination of my samples, I can only affirm the views of the above mentioned authors.

Though the megalospheric companion of *A. exponens* is often called *A. mamillata* (d'Archiac) I will follow Boussac in his uninominal denomination of the B- and A-forms of the same species.

Flandrin gives a good description of this species (16), p. 80, pl. 8, fig. 6—16. The statistical description is given in the table X.

DISCUSSION OF THE DATA FURNISHED BY THE TABLES I—X.

Mean values for the size of the shell and the diameter of the protoconch.

As the mean values for the different characters are the most valuable figures the tables produce, we will discuss these in the first instance. The differences in mean values with their standard errors, given in the tables, determine the reliability of these figures, as has been explained in the introduction.

The following table (p. 150) gives the data for the mean size of the shell and the protoconch, for each species in chronological sequence, and from left to right, in ascending order according to the size of the protoconch.

When we examine the figures for the mean radius of the protoconch given in table fig. 5, we see that the range in size is very large (7.69—222.28 μ) and, taking into consideration the small number of species examined, we must expect this range to be much larger still in reality. On the other hand, when we consider the species separately, it appears that the changes during geological times are rather small, indeed no more than 10—25 %. Moreover we will try to show, that these changes are not haphazard, as might be thought at first sight, but regular.

From table fig. 5 we see that, with four species: *Calc. calcitrapoides, Lepidorb. minor, Cycl.* cf. *guembelianus,* and *Cam. planulata,* the size of the protoconch increases from old to young, whereas three other species (*Miogypsina complanata, Spiroclyp. margaritatus,* and *Lepidoc. tournoueri*) show a decrease in size with time. The protoconch of two species, i. e. *Glob. menardii* and *Ass. exponens* at first increases in size, and then follows the reversed order of development.

When the cause of these changes is put to the question, three possibilities offer themselves: the effect of the surrounding agencies; some inherent law of phylogeny; and as a third possibility, both these causes might have exercised their influences jointly.

Considering the first possibility, we are forced to accept in the majority of cases, a constant influence of the environment, acting during a very long time, in one direction or the other. Although such a long-period-effect, imposed by the surroundings, would not be easily conceivable, there are other objections which, in my opinion, make it improbably that the milieu factor could be responsible for these regular changes.

Changes in the mean radius of the protoconch and the mean diameter of the shell.

Globorotalia-menardii		*Calcarina-calcitrapoides*		*Lepidorbitoides-minor*		*Cycloclypeus* cf. *guembelianus*		*Miogypsina-complanata*	
radius protoconch in μ	diam. shell in mm.	radius protoconch in μ	diam. shell in mm.	radius protoconch in μ	diam. shell in mm.	radius protoconch in μ	diam. shell in mm.	radius protoconch in μ	diam. shell in mm.
VIII		II		I		VII		IV	
9.26 ↓	↑ 0.86	47.51 ↑	↑	56.74 ↑	↑ 3.70	71.17 ↑		56.72 ↓	↓
9.48	0.54	39.20		56.37	2.67	63.71		60.49	
9.64	0.43			54.10	↓ 1.98	57.68		79.39	
9.64 ↑	↑ 0.53			50.39	3.15				
8.11	0.37								
7.69	0.36								

Spiroclypeus-margaritatus		*Lepidocyclina-tournoueri*		*Lepidocyclina-tournoueri*		*Camerina-planulata*		*Assilina-exponens*	
radius protoconch in μ	diam. shell in mm.	radius protoconch in μ	diam. shell in mm.	radius protoconch in μ	diam. shell in mm.	radius protoconch in μ	diam. shell in mm.	radius protoconch in μ	diam. shell in mm.
V		VI		III		IX		X	
111.50 ↓	↓	112.99 ↓	↑ 2.69	103 56 ↓	↓ 1.63	161.72 ↑	↓ 2.33	200.51 ↓	↓ 5.64
115.69		120.66	2.65	108.73	1.75	154.51	2.91	222.28	6.41
129.79		123.86	2.11	127.87	2.46	152.63	3.17	156.52 ↑	↑ 4.78
		130.25	↓ 2.06						
		130.71	2.31						

Directions of arrows coincide with an increase in size.
Roman figures refer to the tables from which the data were taken.

Table fig. 5.

From the fourth and seventh column of table fig. 5 it appears, that the mean size of the protoconch of *Cycloclypeus* cf. *guembelianus* and *Lepidocyclina tournoueri* is changing in an opposite direction. As both species occurred together in each of the samples 455, 454 and 228 (see the tables VI and VII), we should be obliged to accept a contrary effect on the alteration of the size of the protoconch of these species, caused by the same surrounding agencies.

Accepting for a moment the environment as the cause for our regular changes, we should expect that under the influence of a different milieu, the same species would show a different phylogenetic development. Although the very few facts we have to go on in this respect, are far from conclusive, they don't seem to confirm this conception.

The shells of *Lepidocyclina tournoueri* from the spanish localities II and III (tables III, VI), situated some three hundred kilometers apart, on the west- and east-side of the Andalusian mountain-range, showed the same retrogressive evolution for the size of the protoconch. On the other hand, the alterations in the mean diameter of these shells, a character which is known to be very sensitive as to its environment, showed a contrary development, thus demonstrating the difference of the surrounding agencies in the two localities (table fig. 5, columns 7 and 8).

For the above mentioned reasons, we consider it improbable that environment is the ruling factor at the back of our regular changes in the mean size of the protoconch.

When we consider again the data for the size of the protoconch in our table fig. 5, we may as we saw already, bring the different species into three groups: those with an-, from old to young, -increasing, and those with a decreasing-size of the protoconch, leaving as a third group two species, which show a reversal in their mode of phylogeny, i. e. at first increasing, and then decreasing the mean volume of their protoconch (table, fig. 6).

I		II		III	
Calcarina-calcitrapoides	↑	*Miogypsina-complanata*	↓	*Assilina-exponens*	↓
Lepidorbitoides-minor		*Lepidocyclina-tournoueri*		*Globorotalia-menardii*	↑
Cycloclypeus cf.-*guembelianus*		*Spiroclypeus-margaritatus*			
Camerina-planulata					

direction of arrows coincides with an increase in size of the protoconch.

Table fig. 6.

But besides the mode of phylogenetic development of their protoconch, these groups show other pecularities.

The first group contains four species all of them characterised by the fact that, from a phylogenetic point of view, they are "young". In this way the three species of the second group are "old", whereas the species of the last group are, more or less, indifferent in this respect. This categorical statement needs some explanation for each separate species.

The genus *Calcarina* is known from Upper-Cretaceous -till recent times. According to HOFKER (18), p. 17 the Upper-Cretaceous *Calcarina calcitrapoides* is only slightly different from the recent *Calcarina spengleri.* Though the data about *C. calcitrapoides* are not conclusive in this respect, we probably won't be wrong when stating that this species is still in the prime of its life in Upper-Cretaceous times.

Much the same may be said about *Lepidorbitoides minor.* The occurrence of this species is limited to the Upper-Cretaceous. Being one of the oldest *Orbitoids,* its last descendants lived in the Miocene. Thus *L. minor* stands at the beginning of the phylogenetic development of its genus.

Cycloclypei appear for the first time in the Oligocene and are still living in the present time. Our samples with *C.* cf. *guembelianus,* a species still living in our present oceans, range from Oligocene to Lower-Miocene. It is obvious that they are still in their progressive mode of phylogeny.

Camerina planulata is characteristic for the Lower-Eocene, being one of the oldest *Camerinae* known. The genus becomes extinct in the Upper-Oligocene. In our samples they range from Ypresian to Upper-Eocene (Wemmelian), so the beginning of its phylogeny will certainly be included in this range.

Miogypsina (Miogypsinoides) complanata belongs to the second group. It is the most primitive species of its genus, proving its descent from *Rotalia* by the initial spire of its test and its canal-system, as has been shown by WRIGHT BARKER and GRIMSDALE (2), pp. 161 ff. According to these authors this evolution probably took place in the Middle-Oligocene. So much may be said for certain, that this species doesn't outlive the Miocene. As our samples with *M. complanata* are of a Miocene age, it is most probable that this species is already in its old age in this period of its phylogeny.

Our samples with *Lepidocyclina tournoueri* range from Lower-Oligocene to Miocene. This species is one of the last of the long living family of *Orbitoids* of which *Lepidorbitoides minor,* a species of our first group, was one of the first living. As the *Lepidocyclinae* nowhere outlive the Miocene, we may expect our *L. tournoueri* to be in the "old" age of its phylogeny.

Spiroclypeus margaritatus is found from Eocene to Miocene. As our samples with this species all belong to the Miocene, it is therefore obvious, that she must be in her last evolutional stages here.

Remains the discussion of the two species of the third group. *Assilina exponens* is a relatively short living species, only known from the Lower- and Middle-Eocene (Ypresian and Lutetian). Our samples of this species belong according to MENGAUD (see also p. 148) to the upper part of the Ypresian. The shells, particularly the microspheric ones, being very large and abundant, we get the impression that *A. exponens* is here in the optimum of its phylogenetic development, thus being neither "old" nor "young".

Not much can be said about *Globorotalia menardii.* It is a pelagic foraminifer living in great abundance in our present oceans. According to CUSHMAN (11), p. 268, the genus is known from Upper-Cretaceous to Recent. BRADY (5), p. 691 gives in his Challenger report the same phylogenetic period for the species. Thus, nothing more definite can be said about the phylogenetic age of this foraminifer in our Pliocene till Recent samples.

It is true, that for some of our species, the description given above of their phylogeny, lacks the necessary details, to be sure of their group-place in table fig. 6. This is due to the fact, that we have to little data about the beginning or (and) the end of their existence as a species. However, on the whole I think that the place they have been given in the table is satisfactory.

Now looking over the characteristics of the three groups of table fig. 6, we tried to make it plausible, that the species of the first group are more or less at the beginning of their phylogeny, showing at the same time a progressive state of phylogenetic development for the size of their protoconch. The species of the second group show the reversed phylogenetic conditions for both these characters, whereas the third group, contains the species constituting, so to say, a connecting link between those two.

This has led us to drawing up the following hypothesis:

The foraminiferal protoconch goes through a phylogenetic development that is characterized by a gradual increase of the average volume, followed, after a maximum has been reached, by a period wherein the reversed phylogenetic picture is passed through, during which, the average volume is gradually reduced.

This hypothesis has already been advocated, though on lesser facts, in the authors thesis of 1938 (9).

Keeping in mind what has been said about the possible cause of the regular changes in the mean size of the protoconch (p. 149—151), it will be needless to say, that in the manner in which the facts have been interpreted here, they agree with the conception of an inherent law of necessary phylogenetic development.

Remains the discussion of the last raised possible cause, i. e.: that apart from an inherent law of necessary phylogenetic development, the surrounding agencies will exercise their influence simultaneously. The lack of data prevent us from giving a well-based opinion in this matter, but a priori, nothing can be said against such an influence, though nothing could be traced of it.

Passing on to a discussion of the diameter of the shell, we see at once from the data of table fig. 5, that here no such regular changes are found as could be traced for the protoconch. But notwithstanding this far more irregular conduct, five out of nine cases show a parallel phylogenetic development for both these characters, i. e. the columns 2, 5, 6, 8 and 10. In column 9 the changes are contrary, whereas the columns 1, 3 and 7 show an irregular phylogenetic development, in parts parallel or contrary.

As has been said before, it has often been demonstrated, that the size of the shell reacts upon the agencies of her surroundings, and thus we may be convinced, that these agencies will be more or less responsible for the sometimes erratic phylogenetic development of the size of the shell.

At the end of this paragraph I want to mention the fact, that probably there exists a relation between the size of the protoconch and the size of the shell. For some populations, for which the greatest number of measurements were available, the correlation-coefficient for these features has been calculated. The following table fig. 7, shows these coefficients with their standard errors.

Correlation coeff. for the characters: diam. shell — radius protoconch.

Globorotalia menardii ...	sub-recent	+ 0.11 ± [0.07]	(196)
„ „ ...	201—205 M	+ 0.18 ± 0.09	(99)
„ „ ...	1627 M	+ 0.23 ± 0.08	(128)
Camerina planulata	no. 8084	+ 0.17 ± 0.06	(281)

Table fig. 7.

From the table we see that the correlation is positive, which means that, speaking in terms of means, a larger shell has also a larger protoconch. As the values for the correlation-coeff. always lie between 0 and 1, the correlation is small. In some cases not mentioned in the table even negative, but then the standard error indicated that the correlation-coeff. was too small to be of any significance.

We have also to bear in mind, that shells which have not yet reached their full growth, lessen the positive correlation-coeff., as they tend to exaggerate the number of variates in the negative part of the correlation-field. Thus we may be sure that the values given in our table are somewhat too small.

Mean values for the size of the protoconch and the deuteroconch.

From the table fig. 8 it appears that, in seven out of nine cases, the size of the protoconch and the deuteroconch change in the same way, either increasing or decreasing in time. It is a pity we have no data for the deuteroconch of *Globorotalia*; being one of the first species we investigated, the importance of this feature was overseen at that time.

Changes in the mean radius of the protoconch and the deuteroconch.

Globorotalia menardii		*Calcarina-calcitrapoides*		*Lepidorbitoides minor*		*Cycloclypeus* cf. *guembelianus*		*Miogypsina-complanata*	
radius protoconch in μ	radius deutero-conch in μ	radius protoconch in μ	radius deutero-conch in μ	radius protoconch in μ	radius deutero-conch in μ	radius protoconch in μ	radius deutero-conch in μ	radius protoconch in μ	radius deutero-conch in μ
VIII		II		I		VII		IV	
9.26		47.51 ↑	↑ 51.28	56.74 ↑	↑ 75.23	71.17 ↑	↑ 66.28	56.72	52.61
9.48		39.20	40.38	56.37	74.06	63.71	59.90	60.49	54.27
9.64 ↓				54.10	71.88	57.68	55.82	79.39 ↓	↓ 72.28
9.64 ↑				50.39	68.78				
8.11									
7.69									

Spiroclypeus margaritatus		*Lepidocyclina-tournoueri*		*Lepidocyclina-tournoueri*		*Camerina planulata*		*Assilina exponens*	
radius protoconch in μ	radius deutero-conch in μ	radius protoconch in μ	radius deutero-conch in μ	radius protoconch in μ	radius deutero-conch in μ	radius protoconch in μ	radius deutero-conch in μ	radius protoconch in μ	radius deutero-conch in μ
V		VI		III		IX		X	
111.50	92.62	112.99	152.31	103.56	145.31	161.72 ↑	118.03	200.51 ↓	↓ 131.46
115.69	95.23	120.66	↓ 163.82	108.73	154.91	154.51	123.49	222.28	137.55
129.79 ↓	↓ 102.50	123.86	144.82	127.87 ↓	↓ 169.49	152.63	↓ 123.98	156.52 ↑	↑ 121.09
		130.25	↑ 149.28						
		130.71 ↓	140.19						

Directions of arrows coincides with an increase in size.
Roman figures refer to the tables from which the data were taken.

Table fig. 8.

In the case of *Lepidocyclina tournoueri* from the seventh column, the changes for the deuteroconch appear to be irregular. The standard errors for the differences between the first and the second sample, and that between the second and the fourth (reckoned from the uppermost downwards), prove, that these differences are almost a statistical certainty (see also table VI). Leaving the third sample unconsidered for a moment, we would have from old to young, first an increase and then a decrease in the mean volume of the deuteroconch. As to the third sample, this certainly breaks such a supposed regular development, but we have to bear in mind, that on account of the more or less irregular shape of the deuteroconch the deviations from the globular form may be appreciable, which will lessen the reliability of these data. This possibility mentioned also in our introduction, may eventually account for the deviating conduct of the third sample.

That a simultaneous contrary development of the proto- and the deuteroconch may occur with *Foraminifera*, is proved by the conduct of the samples of *Camerina planulata* (column 9). Here, however, the protoconch increases and the deuteroconch decreases from old to young.

Differences in the mean radius of the proto- and deuteroconch.

From the upper part of the table fig. 9 we see, that in most cases, there is a regular increase or decrease in time, of the differences in the mean radius of the proto- and the deuteroconch. These differences may be positive or negative, according to the mean protoconch being larger or smaller than the mean deuteroconch.

Differences in the mean radius of the proto- and the deuteroconch.

Calcarina-calc.	*Cyclo-clypeus guemb.*	*Miogypsina-compl.*	*Lepidor-bitoides minor*	*Spiroclypeus marg.*	*Lepido-cyclina-tourn.*	*Lepido-cyclina-tourn.*	*Camerina-plan.*	*Assilina-exp.*
− 3.77 ↑ − 1.18	+ 4.89 ↑ + 3.81 + 1.86	+ 4.11 ↓ + 6.22 + 7.11	− 18.49 ↑ − 17.69 − 17.78 − 18.39	+ 18.88 ↓ + 20.46 + 27.29	− 39.32 ↓ − 43.16 − 20.96 − 19.03 − 9.48	− 41.75 ↓ − 46.18 − 41.62	+ 43.69 ↑ + 31.02 + 28.65	+ 69.05 ↓ + 84.73 + 35.43 ↑
p.c. $\gtrless$ d.c.	p.c. $\gtrless$ d.c.	p.c. $\gtrless$ d.c.	p.c. < d.c.	p.c. > d.c.	2 upper samples: p.c. < d.c. exc. 0 °/₀ 3 lower samples p.c. $\gtrless$ d.c.	2 upper samples: p.c. < d.c. exc. 0 & 1 °/₀ lower most sample p.c. < d.c. exc. 4 °/₀	p.c. > d.c. exc. 1 °/₀	p.c. > d.c. exc. 0 °/₀

Directions of arrows coincides with an increase of the protoconchal radius.
p.c. and d.c. stands for proto- and deuteroconch.

Table fig. 9.

An increasing difference in time, appears to be characteristic for some species which are phylogenetically "young" (columns 1, 2 and 8), whereas the "old" species (columns 3 and 5) show a decreasing difference. Responsive to this conduct, *Assilina exponens* which is perhaps neither "old" nor "young" as we saw (see p. 152), first shows an increasing, and then a decreasing difference.

It is, however, remarkable that the *Orbitoids* appear to differ in this respect. In the case of *Lepidorbitoides minor,* probably a "young" species, the difference remains practically the same, whereas *Lepidocyclina tournoueri,* an "old" species, shows an *increasing* difference in time. This deviating conduct accounts for the difference in the general appearance of the horizontal section of the embryonic apparatus of *L. tournoueri,* compared with other *Foraminifera.* This general appearance led to the distinction of an isolepidinal-, nephrolepidinal- and trybliolepidinal-embryonic apparatus. The composition of our samples prove, that these different shapes find their origin in a phylogenetic series of forms. Thus, our Lower-Oligocene samples yielded a number of shells of *L. tournoueri* with an embryonic apparatus that was strongly reminiscent of that of *Lepidocyclina* s. str. (*"Isolepidina"*). H. DOUVILLÉ (14), p. 60 and 61, fig. 62, 63, described this type as *L. praetournoueri.* The larger part of the shells from these samples, however, showed the nephrolepidinal-type.

In the same way our Miocene samples contained a number of variates with an trybliolepidinal embryonic apparatus, whereas the isolepidinal type was totally absent here. Between these two extremes, a gradual series of transitional forms was found in the interjacent samples. It is hardly possible to give figures about this question, as the limitation of the different types is arbitrary, which prevents a statistical examination.

In the lower part of the columns of table fig. 9, the individual conduct of the variates is indicated. From the columns 1—3 it appears, that the protoconch (p.c.) may be larger or smaller than the deuteroconch (d.c.). The number of variates of either type, can be estimated by the magnitude of the mean difference and its token, given in the same columns. Thus e.g. with *Cycloclypeus* cf. *guembelianus,* this difference is small and positive in the oldest sample, which means, that there will be a good many variates, — but at any rate less than 50 % —, with a d.c. larger in size than the p.c., (36 % in this case). This percentage will however decrease in the younger samples, as the mean differences in size of the p.c. and d.c. become larger here.

In the three lower samples of column 6, resp. 21-, 13- and 7 % of the variates have a p.c. which is larger than the d.c. The shells of *Lepidorbitoides minor* and those of the younger samples of *Lepidocyclina tournoueri* (columns 6 and 7) are characterised by the fact that the p.c. is practically always smaller than the d.c.

Spiroclypeus margaritatus, Camerina planulata and *Assilina exponens* have a p.c. which is, in almost every variate, larger than the d.c. As for *C. planulata* this statement may probably be extended to the genus *Camerina.* I have never seen an equatorial section of a *Camerina* sp., figured in literature or elswhere, showing a d.c. which was larger than the accompanying p.c., though I made a special search for it.

From table fig. 10 we see that the correlative variability between the size of the proto- and deuteroconch is rather small, or in other words, the correlation coefficient for these charcters is large.

Correlation-coeff. for the characters: p.c. — d.c.

Camerina planulata	sample 4	+ 0.63 ± 0.03 (405)
„ „	„ 5599	+ 0.71 ± 0.02 (466)
„ „	„ 8084	+ 0.65 ± 0.03 (405)
Cycloclypeus cf. *guembelianus*	„ 455	+ 0.74 ± 0.03 (186)
Lepidocyclina tournoueri	„ 410	+ 0.79 ± 0.02 (295)
Miogypsina complanata	„ 409	+ 0.89 ± 0.01 (196)

Table fig. 10.

Biometric investigation has shown that total correlation ($r = 1$) doesn't exist in nature.

Coefficient of variation.

The further discussion of our tables I—X, now brings us to consider the data furnished by the coefficients of variation. These data have been brought together in table fig. 11. As the standard errors of this constant are relatively high, it is not possible to go into details, a general review of the data must suffice and deviations from possible regularities may be expected.

A comparison of this constant for the different characters shows, that in general the variation coefficient for the diameter of the shell is larger than that for the deuteroconch, whereas for the protoconch it is, in the main, smaller than for the deuteroconch. Thus *v*, shell > *v*, d.c. > *v*, p. c. There are exceptions however: In all populations of *Lepidorbitoides minor* *v*, p.c. > *v*, d.c. This is also the case with *Assilina exponens*, though here the differences are insignificant, being of the order of their standard errors. In the oldest populations of *Lepidocyclina tournoueri* and *Camerina planulata* *v*, p.c. is also larger than *v*, d.c. In the same way there are some species which have, for one or more samples, a *v*, shell which is smaller than *v* for the other characters (*Globorotalia menardii, Lepidocyclina tournoueri, Camerina planulata*).

When we try to trace a possible connection between the phylogenetic age of the species and the coefficient of variation, we get the impression, that an increasing phylogenetic age, results in a decreasing variation-coeff., though many deviating fluctuations appear to exist. In the columns for *Cycloclypeus, Lepidocyclina, Camerina, Miogypsina* and *Spiroclypeus,* this development is more or less evident, though the diameter of the shell shows a contrary process with *Camerina*. *Assilina* too shows an opposite trend of phylogeny, even for all characters.

Range of measurements.

The measurements at both ends of the frequency-distribution of variates determine the breadth of variation. It will be obvious, that this measure must be very unreliable, as it depends in a large degree, on the total number of variates. An increase of measurements, will always tend to enlarge the breadth of variation.

Notwithstanding this drawback, we gave the figures concerning this measure in the tables I—X, as they show, that the breadth of variation is often very large, a fact not always rated at true value, but which may be useful having in mind, when describing a possible new species, which only slightly differs from one already known.

Coefficients of variation (v).

Lepidorbitoides minor			*Cycloclypeus* cf. *guembelianus*		*Globorotalia menardii*		*Lepidocyclina tournoueri*			*Lepidocyclina tournoueri*		
diam. shell	radius p.c.	radius d.c.	radius p.c.	radius d.c.	diam. shell	diam. p.c.	diam. shell	radius p.c.	radius d.c.	diam. shell	radius p.c.	radius d.c.
I			VII		VIII		III			VI		
34.93	15.66	12.16	9.25	12.61	15.13	15.89	27.05	18.28	20.01	22.33	18.61	19.31
38.40	15.89	13.79	14.99	17.73	18.36	14.56	29.62	18.69	20.68	11.25	17.06	20.01
44.76	17.43	12.78	16.10	16.46	17.62	14.20	24.89	18.10	18.17	18.77	20.26	23.78
26.57	14.34	12.86			12.25	15.31				27.99	23.87	27.77
					17.48	16.56				23.58	21.28	16.78
					17.37	13.85						

Camerina planulata			*Miogypsina complanata*		*Spiroclypeus margaritatus*		*Assilina exponens*			*Calcarina calcitrapoides*	
diam. shell	radius p.c.	radius d.c.	radius p.c.	radius d.c.	radius p.c.	radius d.c.	diam. shell	radius p.c.	radius d.c.	radius p.c.	radius d.c.
IX			IV		V		X			II	
30.02	13.21	16.05	21.07	23.67	16.49	22.74	23.13	17.08	16.03	15.80	13.99
15.49	16.66	18.12	25.68	27.87	15.89	17.62	21.02	15.15	14.57	14.22	14.36
9.75	18.14	16.67	25.85	30.15	17.91	18.18	11.91	14.27	14.01		

p.c. and d.c. stands for proto- and deuteroconch.

Roman figures indicate the tables the data were taken from.

Table fig. 11.

Range of measurements.

Lepidorbitoides minor			*Lepidocyclina tournoueri*			*Lepidocyclina tournoueri*			*Globorotalia menardii*		*Cycloclypeus* cf. *guembelianus*	
diam. shell	radius p.c.	radius d.c.	diam. shell	radius p.c.	radius d.c.	diam. shell	radius p.c.	radius d.c.	diam. shell	radius p.c.	radius p.c.	radius d.c.
I			III			VI			VIII		VII	
1.3—6.3	38—85	55—102	0.5—2.5	61—171	76—242	1.6—4.6	25—57	35—86	0.5—1.3	6—13	20—32	16—29
1.3—6.8	38—85	51—98	0.5—2.5	61—195	76—266	1.6—4.4	28—61	35—93	0.3—0.8	5—13	13—28	13—29
0.8—5.8	34—82	51—102	0.5—5.5	76—211	92—298	1.4—3.4	25—79	28—75	0.3—0.7	7—13	13—29	13—33
1.3—4.8	38—66	55—94				1.1—4.9	21—82	28—97	0.4—0.7	6—14		
						1.1—3.6	32—82	32—82	0.3—0.5	5—14		
									0.3—0.5	6—11		

Camerina planulata			*Miogypsina complanata*			*Assilina exponens*			*Spiroclypeus margaritatus*		*Calcarina calcitrapoides*	
diam. shell	radius p.c.	radius d.c.	radius p.c.	radius d.c.		diam. shell	radius p.c.	radius d.c.	radius p.c.	radius d.c.	radius p.c.	radius d.c.
IX			IV			X			V		II	
0.8—3.8	102—229	60—176	30—93	30—93		2.8—8.4	116—305	74—179	71—145	49—133	36—79	36—68
1.8—4.6	60—229	50—197	36—99	30—93		2.0—8.4	147—316	95—179	89—164	70—133	26—58	31—58
1.6—5.4	71—229	60—176	36—137	30—131		3.6—6.0	105—221	84—147	80—183	69—126		

p.c. and d.c. stands for proto- and deuteroconch.

Roman figures refer to the tables the data were taken from.

Table fig. 12.

From table fig. 12 we see, that the largest shell has 3—11 times the diameter of the smallest shell. The first figure concerns *Globorotalia,* the second *Lepidocyclina tournoueri.* It is self-evident that shells of young individuals tend to enlarge this relation beyond proportion.

As to the radius of the embryonic chambers, the table shows, that the radius of the largest protoconch is 2.5—4 times that of the smallest. This means that the protoconchal chamber of a species may vary between 1 and 15—64 volume units.

For the deuteroconch the figures are very much the same.

CONCLUSIONS.

This brings us to the end of the discussion of the data, which the measurements of some characters of the shells of a number of foraminiferal species, have yielded.

It has been my intention to show, that in this manner it is possible, to gain some insight in the phylogeny of these characters.

The principle results of the investigation may be summed up as follows:

1) The regular phylogenetic changes of the size of the protoconch led to the drawing up of the hypothesis that: these changes are characterized by a gradual increase of the average volume, followed, after a maximum has been reached, by a period wherein the reversed phylogenetic picture is passed through, during which, the average volume is gradually reduced.

2). An inherent phylogenetic law seems to be the cause of the regular changes in the size of the protoconch.

3) No data came to the for, showing the influence of the surrounding agencies on the size of the protconch.

4) Though in some cases a small positive correlation could be traced, between the size of the protoconch and the diameter of the shell, the phylogeny of these characters didn't always progressed in the same sense. Thus, a phylogenetic increase of the protoconchal volume, was sometimes accompanied by a decreasing size of the shell.

In my opinion this conduct demonstrates that different causes are at the back of these changes. On the one hand a phylogenetic law regulating the changes in the mean volume of the protoconch, apparently not influenced in a disturbing measure by the surrounding agencies, and on the other hand, probably the same phylogenetic law, controlling the alterations of the average size of the shell, but now largely modified by the surrounding agencies, which may strengthen, annul or even reverse the effect of the phylogenetic law.

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TABLE I.

Statistical description of the megalospheric shell of *Lepidorbitoides minor* (SCHLUMBERGER) from locality I: Burgerwacht-quarry, St. Pietersberg; province of Limburg, Holland. (Samples arranged chronologically).

Samples	Distance between samples	Shell	Embryonic apparatus	
		Diameter in mm	Protoconch radius in μ	Deuteroconch radius in μ
		Range (class values).		
482	1.60 M	1.30 — 6.30 (117)	38.07 — 85.45 (118)	54.99 —102.37 (117)
483	1.60 M	1.30 — 6.80 (94)	38.07 — 85.45 (96)	51.04 — 98.42 (94)
484	3.00 M	0.80 — 5.80 (101)	34.12 — 81.50 (101)	51.04 —102.37 (101)
485		1.30 — 4.80 (74)	38.07 — 65.71 (74)	54.99 — 94.47 (73)
		Mean value (*M*).		
482	1.60 M	3.70 ± 0.12 (117)	56.74 ± 0.82 (118)	75.23 ± 0.85 (117)
483	1.60 M	2.67 ± 0.11 (94)	56.37 ± 0.91 (96)	74.06 ± 1.05 (94)
484	3.00 M	1.98 ± 0.09 (101)	54.10 ± 0.94 (101)	71.88 ± 0.91 (101)
485		3.15 ± 0.10 (74)	50.39 ± 0.84 (74)	68.78 ± 1.03 (73)
		Standard deviation (σ).		
482	1.60 M	1.29 ± 0.08 (117)	8.88 ± 0.58 (118)	9.14 ± 0.60 (117)
483	1.60 M	1.02 ± 0.07 (94)	8.96 ± 0.65 (96)	10.21 ± 0.74 (94)
484	3.00 M	0.89 ± 0.06 (101)	9.42 ± 0.66 (101)	9.18 ± 0.65 (101)
485		0.84 ± 0.07 (74)	7.22 ± 0.60 (74)	8.84 ± 0.73 (73)
		Coefficient of variation (v).		
482	1.60 M	34.93 ± 2.55 (117)	15.66 ± 1.04 (118)	12.16 ± 1.36 (117)
483	1.60 M	38.40 ± 3.19 (94)	15.89 ± 1.18 (96)	13.79 ± 1.03 (94)
484	3.00 M	44.76 ± 3.73 (101)	17.43 ± 1.26 (101)	12.78 ± 0.91 (101)
485		26.57 ± 2.33 (74)	14.34 ± 1.28 (74)	12.86 ± 1.08 (73)
		Differences in mean values.		
482 485	6.20 M	0.55 ± 0.15	6.35 ± 1.17	6.45 ± 1.34
483 485	4.60 M	0.48 ± 0.14	5.98 ± 1.24	5.28 ± 1.48
482 484	3.20 M	1.72 ± 0.15	2.64 ± 1.25	3.35 ± 1.25

Figures placed in ( ) indicate the number of shells examined.

TABLE II.

Statistical description of the megalospheric shell of *Calcarina calcitrapoides* (LAMARCK) from locality I: Burgerwacht-quarry, St. Pietersberg; province of Limburg, Holland.

(Samples arranged chronologically).

Samples	Distance between samples	Embryonic apparatus	
		Protoconch radius in μ	Deuteroconch radius in μ
Range (class values).			
482	3.20 M	36.47 — 78.58 (46)	36.47 — 68.06 (45)
484		25.94 — 57.53 (51)	31.21 — 57.53 (47)
Mean value (M).			
482	3.20 M	47.51 ± 1.11 (46)	51.28 ± 1.07 (45)
484		39.20 ± 0.78 (51)	40.38 ± 0.85 (47)
Standard deviation (σ).			
482	3.20 M	7.51 ± 0.78 (46)	7.18 ± 0.76 (45)
484		5.57 ± 0.55 (51)	5.80 ± 0.60 (47)
Coefficient of variation (v).			
482	3.20 M	15.80 ± 1.69 (46)	13.99 ± 1.50 (45)
484		14.22 ± 1.44 (51)	14.36 ± 1.51 (47)
Differences in mean values.			
482 484	3.20 M	8.31 ± 1.35	10.90 ± 1.36

Figures placed in ( ) indicate the number of shells examined.

TABLE III.

Statistical description of the megalospheric shell of *Lepidocyclina tournoueri* Lemoine and R. Douvillé from locality II: Puente Viejo (Spain).

(Samples arranged chronologically).

Samples	Distance between samples	Shell	Embryonic apparatus	
		Diameter in mm	Protoconch radius in μ	Deuteroconch radius in μ
		Range (class values).		
410	60 M	0.5 —2.5 (222)	60.63—171.17 (295)	76.42—242.24 (294)
409	20 M	0.5 —2.5 (212)	60.63—194.86 (219)	76.42—265.93 (219)
408		0.5 —5.5 (762)	76.42—210.65 (760)	92.21—297.51 (758)
		Mean value (M).		
410	60 M	1.63 ± 0.03 (222)	103.56 ± 1.10 (295)	145.31 ± 1.70 (294)
409	20 M	1.75 ± 0.04 (212)	108.73 ± 1.37 (219)	154.91 ± 2.17 (219)
408		2.46 ± 0.02 (762)	127.87 ± 0.84 (760)	169.49 ± 1.12 (758)
		Standard deviation (σ).		
410	60 M	0.44 ± 0.02 (222)	18.95 ± 0.78 (295)	29.08 ± 1.20 (294)
409	20 M	0.52 ± 0.03 (212)	20.32 ± 0.97 (219)	32.07 ± 1.53 (219)
408		0.61 ± 0.02 (762)	23.15 ± 0.59 (760)	30.79 ± 0.79 (758)
		Coefficient of variation (v).		
410	60 M	27.05 ± 1.37 (222)	18.28 ± 0.78 (295)	20.01 ± 0.86 (294)
409	20 M	29.62 ± 1.66 (212)	18.69 ± 0.92 (219)	20.68 ± 0.99 (219)
408		24.89 ± 0.68 (762)	18.10 ± 0.48 (760)	18.17 ± 0.48 (758)
		Differences in mean values.		
410 408	80 M	0.83 ± 0.04	24.31 ± 1.39	24.18 ± 2.03
410 409	60 M	0.12 ± 0.05	5.17 ± 1.76	9.60 ± 2.75
409 408	20 M	0.71 ± 0.04	19.14 ± 1.61	14.58 ± 2.44

Figures placed in ( ) indicate the number of shells examined.

TABLE IV.

Statistical description of the megalospheric shell of *Miogypsina (Miogypsinoides) complanata* Schlumberger from locality II: Puente Viejo (Spain).

(Samples arranged chronologically).

Samples	Distance between samples	Embryonic apparatus	
		Protoconch radius in μ	Deuteroconch radius in μ
Range (class values).			
410		29.57 — 92.76 (209)	29.57 — 92.76 (175)
409	60 M	35.89 — 99.08 (224)	29.57 — 92.76 (197)
408	20 M	35.89 — 136.99 (223)	29.57 — 130.68 (178)
Mean value (*M*).			
410		56.72 ± 0.83 (209)	52.61 ± 0.94 (175)
409	60 M	60.49 ± 1.04 (224)	54.27 ± 1.08 (197)
408	20 M	79.39 ± 1.37 (223)	72.28 ± 1.63 (178)
Standard deviation (σ).			
410		11.95 ± 0.58 (209)	12.46 ± 0.67 (175)
409	60 M	15.53 ± 0.73 (224)	15.12 ± 0.76 (197)
408	20 M	20.52 ± 0.97 (223)	21.79 ± 1.16 (178)
Coefficient of variation (*v*).			
410		21.07 ± 1.07 (209)	23.67 ± 1.33 (175)
409	60 M	25.68 ± 1.29 (224)	27.87 ± 1.51 (197)
408	20 M	25.85 ± 1.30 (223)	30.15 ± 1.74 (178)
Differences in mean values.			
410 408	80 M	22.67 ± 1.60	19.67 ± 1.89
410 409	60 M	3.77 ± 1.33	1.66 ± [1.43]
409 408	20 M	18.90 ± 1.50	18.01 ± 1.96

Figures placed in ( ) indicate the number of shells examined.
Figures placed in [ ] indicate that the "difference" is less than twice the standard error.
The mean value for the diameter of the shell decreases from old to young.

TABLE V.

Statistical description of the megalospheric shell of *Spiroclypeus margaritatus* Schlumberger from locality II: Puente Viejo (Spain).

(Samples arranged chronologically).

Samples	Distance between samples	Embryonic apparatus	
		Protoconch radius in μ	Deuteroconch radius in μ
		Range (no class values).	
410	60 M	71.22 — 145.13 (22)	49.43 — 132.94 (21)
409	20 M	88.93 — 164.08 (38)	69.52 — 132.71 (38)
408		80.12 — 183.27 (17)	68.84 — 126.39 (16)
		Mean value (*M*).	
410	60 M	111.50 ± 3.92 (22)	92.62 ± 4.60 (21)
409	20 M	115.69 ± 2.98 (38)	95.23 ± 2.72 (38)
408		129.79 ± 5.63 (17)	102.50 ± 4.66 (16)
		Standard deviation (σ).	
410	60 M	18.39 ± 2.77 (22)	21.06 ± 3.25 (21)
409	20 M	18.37 ± 2.11 (38)	16.78 ± 1.92 (38)
408		23.23 ± 3.98 (17)	18.62 ± 3.29 (16)
		Coefficient of variation (v).	
410	60 M	16.49 ± 2.55 (22)	22.74 ± 3.69 (21)
409	20 M	15.89 ± 1.87 (38)	17.62 ± 2.08 (38)
408		17.91 ± 3.17 (17)	18.18 ± 3.32 (16)
		Differences in mean values.	
410 408	80 M	18.29 ± 6.86	9.88 ± [6.54]
410 409	60 M	4.19 ± [4.92]	2.61 ± [5.34]
409 408	20 M	14.10 ± 6.37	7.27 ± [5.39]

Figures placed in ( ) indicate the number of shells examined.

Figures placed in [ ] indicate that the "difference" is less than twice the standard error.

The mean value of the diameter of the shell of sample 410 is probably less than that of both the olden samples.

TABLE VI.

Statistical description of the megalospheric shell of *Lepidocyclina tournoueri* LEMOINE and R. DOUVILLÉ from localities III: Villajoyosa-Orcheta (prov. of Alicante, Spain) and Jaen (Spain). (Samples arranged chronologically).

Samples	Geological formation	Shell	Embryonic apparatus	
		Diameter in mm	Protoconch radius in μ	Deuteroconch radius in μ
		Range (class values).		
228	Miocene	1.6 — 4.6 (98)	24.6 — 57.0(102)	35.4 — 85.8(102)
454	Oligocene	1.6 — 4.4 (63)	28.2 — 60.6 (98)	35.4 — 93.0 (98)
455	Lower-Oligocene	1.4 — 3.4 (118)	24.6 — 78.6(118)	28.2 — 75.0(118)
468	" "	1.1 — 4.9 (68)	21.0 — 82.6 (98)	28.2 — 96.6 (97)
466	" "	1.1 — 3.6 (30)	31.8 — 82.6 (65)	31.8 — 82.2 (64)
		Mean value (*M*).		
228	Miocene	2.69 ± 0.06 (98)	112.99 ± 2.08(102)	152.31 ± 2.65(102)
454	Oligocene	2.65 ± 0.04 (63)	120.66 ± 2.08 (98)	163.82 ± 3.31 (98)
455	Lower-Oligocene	2.11 ± 0.04 (118)	123.86 ± 2.31(118)	144.82 ± 3.17(118)
468	" "	2.06 ± 0.07 (68)	130.25 ± 3.14 (98)	149.28 ± 4.21 (97)
466	" "	2.31 ± 0.10 (30)	130.71 ± 3.45 (65)	140.19 ± 2.94 (64)
		Standard deviation (σ).		
228	Miocene	0.60 ± 0.04 (98)	21.02 ± 1.47(102)	29.41 ± 2.06(102)
454	Oligocene	0.30 ± 0.03 (63)	20.59 ± 1.47 (98)	32.78 ± 2.34 (98)
455	Lower-Oligocene	0.40 ± 0.03 (118)	25.09 ± 1.63(118)	34.43 ± 2.24(118)
468	" "	0.58 ± 0.05 (68)	31.08 ± 2.22 (98)	41.45 ± 2.98 (97)
466	" "	0.54 ± 0.07 (30)	27.81 ± 2.44 (65)	23.52 ± 2.08 (64)
		Coefficient of variation (*v*).		
228	Miocene	22.33 ± 1.67 (98)	18.61 ± 1.35(102)	19.31 ± 1.40(102)
454	Oligocene	11.25 ± 1.02 (63)	17.06 ± 1.25 (98)	20.01 ± 1.49 (98)
455	Lower-Oligocene	18.77 ± 1.26 (118)	20.26 ± 1.37(118)	23.78 ± 1.63(118)
468	" "	27.99 ± 2.58 (68)	23.87 ± 1.80 (98)	27.77 ± 2.14 (97)
466	" "	23.58 ± 3.21 (30)	21.28 ± 1.95 (65)	16.78 ± 1.52 (64)
		Differences in mean values.		
228 454	Miocene-Oligocene	0.04 ± [0.07]	7.67 ± 2.94	11.51 ± 4.24
454 468	Olig.—Lower-Olig.	0.59 ± 0.08	9.59 ± 3.77	14.54 ± 5.35
455 466	Lower-Oligocene	0.20 ± 0.10	6.85 ± [4.15]	4.63 ± [4.32]
468 466	± 10 M (Lower-Oligocene)	0.25 ± 0.12	0.56 ± [4.66]	9.09 ± [5.13]

Figures placed in ( ) indicate the number of shells examined.
Figures placed in [ ] indicate that the "difference" is less than twice the standard error.
"Differences" 454—455 and 455—468 are less than twice their standard errors.

TABLE VII.

Statistical description of the megalospheric shell of *Cycloclypeus* cf. *guembelianus* Brady from localities III: Villajoyosa-Orcheta (prov. of Alicante, Spain) and Jaen (Spain).

(Samples arranged chronologically).

Samples	Geological formation	Embryonic apparatus	
		Protoconch radius in μ	Deuteroconch radius in μ
		Range (class values).	
228	Miocene	19.8 — 31.8 (27)	16.2 — 29.4 (27)
454	Oligocene	12.6 — 28.2 (42)	12.6 — 29.4 (42)
455	Lower-Oligocene	12.6 — 29.4 (185)	12.6 — 33.0 (185)
		Mean value (*M*).	
228	Miocene	71.17 ± 1.27 (27)	66.28 ± 1.61 (27)
454	Oligocene	63.71 ± 1.47 (42)	59.90 ± 1.64 (42)
455	Lower-Oligocene	57.68 ± 0.68 (185)	55.82 ± 0.67 (185)
		Standard deviation (σ).	
228	Miocene	6.59 ± 0.89 (27)	8.36 ± 1.16 (27)
454	Oligocene	9.55 ± 1.04 (42)	10.62 ± 1.16 (42)
455	Lower-Oligocene	9.29 ± 0.48 (185)	9.17 ± 0.48 (185)
		Coefficient of variation (v).	
228	Miocene	9.25 ± 1.27 (27)	12.61 ± 1.74 (27)
454	Oligocene	14.99 ± 2.06 (42)	17.73 ± 1.99 (42)
455	Lower-Oligocene	16.10 ± 0.86 (185)	16.46 ± 0.88 (185)
		Differences in mean values.	
228 454	Miocene—Olig.	7.46 ± 1.94	6.38 ± 2.30
454 455	Olig.—Lower-Olig.	6.02 ± 1.62	4.08 ± 1.77

Figures placed in ( ) indicate the number of shells examined.

TABLE VIII.

Statistical description of the megalospheric shell of *Globorotalia menardii* (D'ORBIGNY) from localities IV: Well Bodjonegoro I Java and a dredging sample near the Kei-islands (East-Indies).

(Samples arranged chronologically).

Samples	Distance between samples	Shell measures	Embryonic apparatus
		Length in μ	Protoconch Diameter in μ
		Range (class values).	
sub-recent	> 201 M	534. — 1302. (235)	11.5 — 26.5 (201)
201—215 M	± 195 M	288. — 828. (127)	9.5 — 26.5 (103)
401—404 M	± 200 M	282. — 690. (192)	13.5 — 26.5 (143)
604 M	403 M	354. — 714. (178)	11.5 — 28.5 (160)
1007 M	620 M	258. — 546. (139)	10.5 — 27.5 (135)
1627 M		258. — 546. (136)	11.5 — 21.5 (133)
		Mean value (*M*).	
sub-recent	> 201 M	863.87 ± 8.53 (235)	18.51 ± 0.21 (201)
201—215 M	± 195 M	541.70 ± 8.82 (127)	18.97 ± 0.27 (103)
401—404 M	± 200 M	433.13 ± 5.51 (192)	19.28 ± 0.23 (143)
604 M	403 M	531.57 ± 4.88 (178)	19.28 ± 0.23 (160)
1007 M	620 M	370.23 ± 5.49 (139)	16.23 ± 0.23 (135)
1627 M		357.53 ± 5.33 (136)	15.37 ± 0.18 (133)
		Standard deviation (σ).	
sub-recent	> 201 M	130.69 ± 6.03 (235)	2.94 ± 0.15 (201)
201—215 M	± 195 M	99.43 ± 6.34 (127)	2.76 ± 0.19 (103)
401—404 M	± 200 M	76.33 ± 3.89 (192)	2.74 ± 0.16 (143)
604 M	403 M	65.12 ± 3.45 (178)	2.95 ± 0.17 (160)
1007 M	620 M	64.71 ± 3.88 (139)	2.69 ± 0.16 (135)
1627 M		62.12 ± 3.77 (136)	2.13 ± 0.13 (133)
		Coefficient of variation (*v*).	
sub-recent	> 201 M	15.13 ± 0.71 (235)	15.89 ± 0.81 (201)
201—215 M	± 195 M	18.36 ± 1.19 (127)	14.56 ± 1.04 (103)
401—404 M	± 200 M	17.62 ± 0.93 (192)	14.20 ± 0.86 (143)
604 M	403 M	12.25 ± 0.66 (178)	15.31 ± 0.88 (160)
1007 M	620 M	17.48 ± 1.08 (139)	16.56 ± 1.04 (135)
1627 M		17.37 ± 1.08 (136)	13.85 ± 0.87 (133)
		Differences in mean values.	
sub-recent 201—205 M	> 201 M	322.17 ± 12.27	0.77 ± 0.31
201—205 M 401—404 M	± 200 M	108.58 ± 10.40	
401—404 M 604 M	± 200 M	98.45 ± 7.36	0.00 ± [0.32]
604 M 1007 M	403 M	161.34 ± 7.35	3.05 ± 0.33
1007 M 1627 M	620 M	12.70 ± [7.65]	0.86 ± 0.30

Figures placed in ( ) indicate the number of shells examined.
Figures placed in [ ] indicate that the "difference" is less than twice the standard error.
"Differences" subrecent — (201—205) and (201—205) — (401—404) are less than twice their standard errors.

TABLE IX.

Statistical description of the megalospheric shell of *Camerina planulata* (Lamarck) from localities V: Schaerbeek, Heysel and Helmet (Belgium).

(Samples arranged chronologically).

Samples	Geological formation	Shell	Embryonic apparatus	
		Diameter in mm	Protoconch radius in μ	Deuteroconch radius in μ
		Range (class values).		
4	Wemmelian	0.80 — 3.80 (319)	102.37 — 228.61 (405)	60.16 — 175.97 (407)
5599	Ledian	1.80 — 4.60 (409)	60.16 — 228.61 (466)	49.63 — 197.02 (468)
8084	Ypresian	1.60 — 5.40 (377)	70.69 — 228.61 (406)	60.16 — 175.97 (406)
		Mean value (*M*).		
4	Wemmelian	2.33 ± 0.04 (319)	161.72 ± 1.06 (405)	118.03 ± 0.94 (407)
5599	Ledian	2.91 ± 0.02 (409)	154.51 ± 1.19 (466)	123.49 ± 1.03 (468)
8084	Ypresian	3.17 ± 0.02 (377)	152.63 ± 1.37 (406)	123.98 ± 1.03 (406)
		Standard deviation (σ).		
4	Wemmelian	0.70 ± 0.03 (319)	21.37 ± 0.75 (405)	18.95 ± 0.66 (407)
5599	Ledian	0.45 ± 0.02 (409)	25.75 ± 0.84 (466)	22.34 ± 0.73 (468)
8084	Ypresian	0.31 ± 0.01 (377)	27.69 ± 0.97 (406)	20.66 ± 0.73 (406)
		Coefficient of variation (*v*).		
4	Wemmelian	30.02 ± 1.29 (319)	13.21 ± 0.47 (405)	16.05 ± 0.58 (407)
5599	Ledian	15.49 ± 0.55 (409)	16.66 ± 0.56 (466)	18.12 ± 0.61 (468)
8084	Ypresian	9.75 ± 0.36 (377)	18.14 ± 0.66 (406)	16.67 ± 0.60 (406)
		Differences in mean values.		
4 8084	Wemm.-Ypresian	0.84 ± 0.04	9.09 ± 1.74	5.95 ± 1.39
4 5599	Wemm.-Ledian	0.58 ± 0.04	7.21 ± 1.59	5.46 ± 1.40
5599 8084	Led.-Ypresian	0.26 ± 0.03	1.88 ± [1.82]	0.49 ± [1.46]

Figures placed in ( ) indicate the number of shells examined.
Figures placed in [ ] indicate that the "difference" is less than twice the standard error.

TABLE X.

Statistical description of the megalospheric shell of *Assilina exponens* (SOWERBY) locality VI: Cabo Oriambre (Spain).

(Samples arranged chronologically).

Samples	Distance between samples	Shell	Embryonic apparatus	
		Diameter in mm	Protoconch radius in μ	Deuteroconch radius in μ
		Range (class values).		
382	± 20 M	2.8 — 8.4 (108)	115.81 — 305.31 (111)	73.70 — 179.38 (111)
381	± 20 M	2.0 — 8.4 (106)	147.39 — 315.84 (106)	94.75 — 179.38 (102)
379		3.6 — 6.0 (49)	105.28 — 221.09 (52)	84.22 — 147.39 (52)
		Mean value (*M*).		
382	± 20 M	5.64 ± 0.13 (108)	200.51 ± 3.25 (111)	131.46 ± 2.00 (111)
381	± 20 M	6.41 ± 0.13 (106)	222.28 ± 3.27 (106)	137.55 ± 1.98 (102)
379		4.78 ± 0.08 (49)	156.52 ± 3.10 (52)	121.09 ± 2.35 (52)
		Standard deviation (σ).		
382	± 20 M	1.30 ± 0.09 (108)	34.25 ± 2.30 (111)	21.06 ± 1.41 (111)
381	± 20 M	1.35 ± 0.09 (106)	33.68 ± 2.31 (106)	20.04 ± 1.40 (102)
379		0.57 ± 0.06 (49)	22.34 ± 2.19 (52)	16.96 ± 1.66 (52)
		Coefficient of variation (*v*).		
382	± 20 M	23.13 ± 1.70 (108)	17.08 ± 1.18 (111)	16.03 ± 1.10 (111)
381	± 20 M	21.02 ± 1.51 (106)	15.15 ± 1.06 (106)	14.57 ± 1.04 (102)
379		11.91 ± 1.22 (49)	14.27 ± 1.43 (52)	14.01 ± 1.40 (52)
		Differences in mean values.		
382 379	± 40 M	0.86 ± 0.15	43.99 ± 4.49	10.37 ± 3.09
381 379	± 20 M	1.63 ± 0.15	65.76 ± 4.51	16.46 ± 3.08
382 381	± 20 M	0.77 ± 0.18	21.77 ± 4.61	6.09 ± 2.82

Figures placed in ( ) indicate the number of shells examined.