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Associations of Miogypsina and Lepidocyclina at some European localities

By **Cornelis W. Drooger** and **Tom Freudenthal** (Utrecht)

With 8 figures in the text

ZUSAMMENFASSUNG: *Nephrolepidina* Vergesellschaftungen aus zerstreuten europäischen Fundstellen zeigen eine beschränktere morphologische Variation als die Reihenfolge der zusammen mit den Nephrolepidinen vorkommenden Miogypsinen. Im Augenblick scheint es nicht angebracht zu sein, in dem Chatt–Burdigal Intervall auf mehr als zwei spezifische Einheiten zu schliessen, während die *Miogypsina*-Reihenfolge die Annahme von etwa fünf erlaubt.

Wiederholte Messungen derselben Vergesellschaftungen durch verschiedene Personen haben eine Einsicht in das Mass der Genauigkeit von Mittelwerten ergeben. Systematische Unterschiede, die auf den Einfluss von vorgefassten Meinungen bei den Messungen zurückzuführen sind, kommen vor, aber sie sind nicht grösser als die schwankenden Abweichungen. Alle Abweichungen nähern sich einem Standardfehler des Durchschnitts, der für Vergesellschaftungen von kleinem oder mittelmässigem Umfang berechnet wurde.

INTRODUCTION

During the last decade *Miogypsina* assemblages have become known in considerable detail from several European localities. They fit into fairly well-established lineages, which evidently developed according to the principle of nepionic acceleration. Recent work by VAN DER VLERK (1959, 1963) has shown that assemblages of *Nephrolepidina*, subgenus of *Lepidocyclina*, may be treated in a similar manner. They can be arranged according to the same principle.

Some classical European localities are known to contain representatives of both groups. For *Miogypsina* earlier data, gathered by the first author, were available, or he could extend them. For *Nephrolepidina* the second author carried out the investigations on the basis of VAN DER VLERK's methods, though somewhat modified (see below).

Samples from four localities will be considered: Escornebéou, Estoti, Sausset and Rosignano. They were chosen because their Miogypsinids cover the greatest known morphological difference in European *Nephrolepidina*-bearing deposits. The ages are thought to lie in the interval from the Chattian to the Burdigalian.

The purpose of this investigation was to check whether nepionic acceleration in both groups was roughly parallel, and to see how detailed a biostratigraphic zoning would be possible by means of *Nephrolepidina*. Furthermore, the various sets of data from successive periods of observations, and by different workers repeatedly offered the opportunity to get an insight into the degree of subjectivity in measuring and counting. This is of special importance for the evaluation of the calculated means, which are used for taxionomic and stratigraphic conclusions.

The authors gratefully acknowledge the assistance of several colleagues: Mr. G. J. BOEKSCHOTEN (Groningen), who took one of the samples; Messrs. C. C. VERVLOET, R. FELIX, R. C. TJALSMA, AFTAB A. BUTT and N. C. MEIJER DREES (Utrecht), who made many of the sections and delivered a number of independent sets of observations; Messrs. A. VAN DOORN and J. J. VERMAAT (Utrecht), who made the drawings.

Further thanks are due to Drs. P. MARKS and J. E. VAN HINTE (Utrecht) for their critical reading of the manuscript.

COUNTS AND MEASUREMENTS

Miogypsina

In accordance with earlier used methods (DROOGER, 1952, 1963) the median sections of macrospheric *Miogypsina* individuals rendered the following data.

1. For primitive single-spiralled forms (fig. 1):

X = the total number of nepionic chambers, starting to count with the third chamber, i.e. the first principal auxiliary chamber.

Y = the number of nepionic chambers up to and not including the first one with a distal stoloniferous opening; hence, up to the beginning of equatorial growth.

Z = the number of nepionic chambers up to and including the largest one in section.

γ = the angle between the apical-frontal line and the line connecting the centres of both nepionic chambers. Positive and negative values depend on the position of the third chamber relative to the apex (see DROOGER, 1963, fig. 8).

d_I (or simply I) = the diameter of the protoconch, and

d_{II} (or II) = the diameter of the deuteroconch, both diameters including half of the thickness of the walls, and both taken at right angles to the line connecting the centres of these embryonic chambers. The measurements are expressed in μ.

2. For more advanced forms with two nepionic spirals along the outer side of the protoconch (fig. 2) we measured instead of X, Y and Z:

V (or $200\ \alpha/\beta$), which is 100 times the arc length of the protoconch section underlying the smaller spiral (α), divided by half of the arc length underlying both protoconchal spirals (β).

Species have been mainly defined on the basis of M_x or M_v values of the investigated assemblages. For European Miogypsinids the lineages are thought to be as shown in fig. 6.

Nephrolepidina

Measurements and counts were made at the embryonic and nepionic (= peri-embryonic) chambers in median sections of megalospheric specimens. The methods of VAN DER VLERK (1959) are slightly different, but the results are thought to be comparable. Factors A and B we measured from camera lucida drawings with a magnification of 100 and using a shiftable linear scale drawn on paper. Figure 3 shows the features measured.

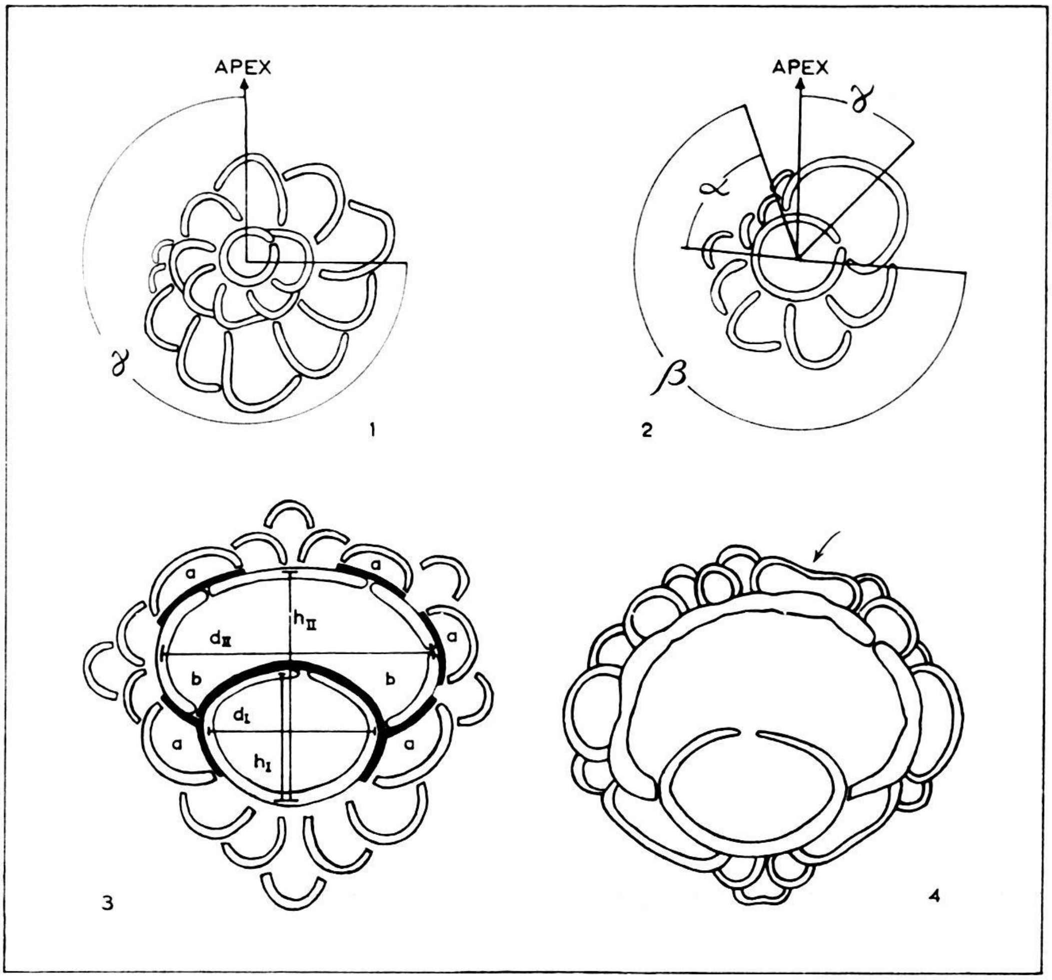

Fig. 1–4. Schematic drawings of median sections of the embryonic-nepionic stage in *Miogypsina* (1, 2) and in *Nephrolepidina* (3, 4).
Fig. 1. $X = 15$, $Y = 4$, $Z = 11$, $\gamma = -270°$.
Fig. 2. $\alpha = 65°$, $\beta = 245°$, $V = 53$, $\gamma = +45°$.
Fig. 3. $A = 47$, $B = 58$, $A + B = 105$, $C = 3$.
Fig. 4. $C = 6$ or 7.

d_I = width of protoconch; d_{II} = width of deuteroconch; h_I = height of protoconch; and h_{II} = height of nucleoconch. d_I and d_{II} are measured at right angles to the line connecting the centres of both embryonic chambers, along which h_I and h_{II} are found. The measurements include half the thickness of the walls, and again they are all expressed in μ.

A is the degree of embracement of the protoconch by the deuteroconch. The part of the outer circumference of the protoconch that is embraced by the deuteroconch is given as a percentage of the whole outer circumference of the protoconch. Hence:

$$A = \frac{100 \times \text{length b}}{\text{outer circumference of protoconch}}$$

A can be measured only when all nepionic chambers are visible. This indicates a good orientation of the section. Unorientated sections often yield too low values of A (see also fig. 5).

Unfortunately, our measurements were made along the outer circumference of the protoconch, whereas VAN DER VLERK (1963) considers the inner side preferable. For one of our samples (A 357) we measured inner and outer walls. The difference in M_A values amounts to less than $2\sigma_M$, the inner side giving lower values.

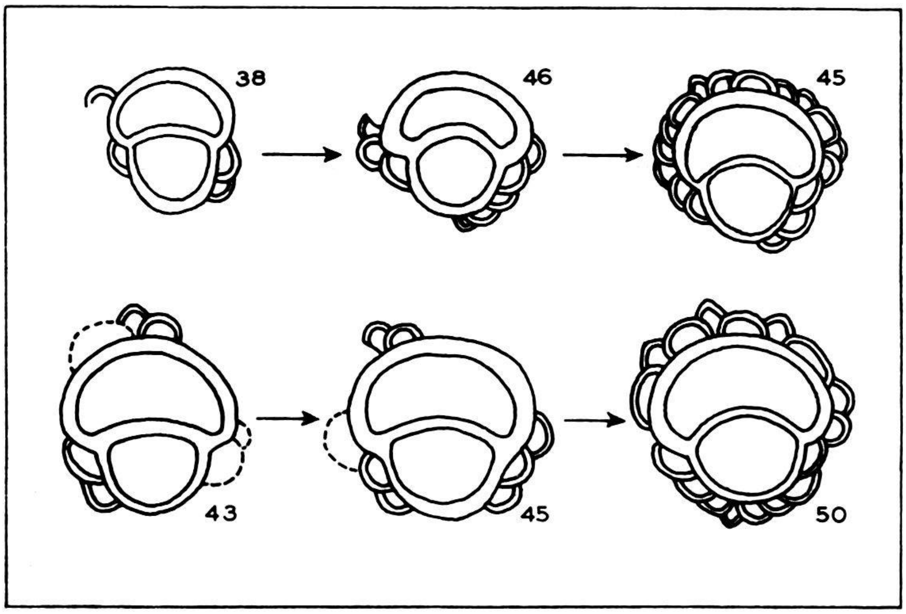

Fig. 5. Change of A value in successive stages of sectioning of two *Nephrolepidina* individuals from sample A 71.

B gives the part of the outer circumference of the nucleoconch which is covered by the auxiliary chambers together, as a percentage of the whole outer circumference of the nucleoconch. Hence:

$$B = \frac{100 \times \Sigma \text{ length a}}{\text{outer circumference of nucleoconch}}$$

A + B has been considered to give information about the stage of evolution of Lepidocyclinids (see also VAN DER VLERK, 1959). In his later paper (1963) VAN DER VLERK abandons the use of B and A + B, since he found these factors to be less reliable than A.

C is found by counting the number of adauxiliary chambers (i.e. on the deuteroconch; AAC II). It is considered to give another value for expressing the stage of nepionic acceleration. According to VAN DER VLERK also this factor is less reliable.

In the *Nephrolepidina* assemblages investigated there are always two (sub) equal primary auxiliary chambers. The number of adauxiliary chambers (AAC II) shows considerable variation in individuals of the same assemblage. Accessory auxiliary chambers on the protoconch (AAC I) are present in a few specimens only; they are not incorporated in the C values.

ESCORNEBEOU, SOUTHWESTERN FRANCE

This well known locality near Saint-Géours-de-Maremme, in the southern part of the Aquitaine basin, has been the subject of many discussions. Even in the more recent literature the deposits visible are placed variously in the Aquitanian, Chattian or Rupelian (DAGUIN, 1948; SZÖTS, 1961, 1964; EAMES et al., 1962).

Both Lepidocyclinids and Miogypsinids have been known to occur at this locality. In 1904 LEMOINE and R. DOUVILLÉ described from these deposits the species *Lepidocyclina (Eulepidina) raulini* and *L. (Nephrolepidina)* cf. *morgani*. H. DOUVILLÉ (1925) listed *L. (E.) raulini, L. (E.) roberti, L. (N.) partita, L. (N.) praemarginata* and *L. (N.) tournoueri*. GRIMSDALE (1952) considered the Eulepidines to belong to *L. (E.) ephippioides;* DROOGER and SOCIN (1959) advanced *L. (N.) morgani* as the correct name for all Nephrolepidines.

The Miogypsinids of Escornebéou were placed in *Miogypsina (Miogypsinoides) complanata* by DROOGER (1955), but not before 1963 did he give sufficient evidence for this determination, which was based on a group of individuals from his sample A 75.

Both the *Miogypsinoides* and the *Nephrolepidina* assemblages from two samples (taken 1954) will be (re)considered. These two samples are A 75 and A 71 (the latter is thought to be the youngest, though the stratigraphic interval in metres is unknown).

Miogypsina (Miogypsinoides) complanata SCHLUMBERGER

Miogypsina complanata SCHLUMBERGER, 1900, Bull. Soc. géol. France, sér. 3, vol. 28, p. 330, pl. 2, fig. 13–16, pl. 3, fig. 18–21; DROOGER, 1955, Verh. Kon. Ned. Ak. Wetensch., afd. Nat., ser. 1, vol. 21, no. 2, p. 18, pl. 1, fig. 28 (not 21–27); DROOGER, 1963, Evol. trends, Elsevier, fig. 4, 6, 9, 13, 16, 24.

All these references deal with *M. complanata* from Escornebéou and from the nearby type locality of the species at Saint-Etienne-d'Orthe. *M. complanata* is now used in its restricted sense, i.e. for assemblages with M_X greater than 17 (see DROOGER, 1963, fig. 2).

Countings and measurements of the individuals of A 75, carried out in 1956, were not repeated or extended. Those of A 71 were made in 1963, though of 12 specimens earlier counts of X (1956) were available.

The individuals of both samples are fully and rather evenly pustulated; they have thick side walls and the greatest thickness of the test is in the apical part, which position corresponds with that of the centre of the long, trochoid nepionic spiral. In both samples half or even more of the sectioned individuals appeared to be microspheric; there is no obvious difference in size between the specimens of both generations.

The various internal features of the macrospheric individuals yielded the following counts and measurements. The number of observations (N) is given in parentheses.

A 71	X (17)	Y (16)	Z (17)	γ° (17)	d_I (16)	d_{II} (13)
Range	27–13	12–5	19–9	−450 – −190	75–145	70–155
Mean	18.9	7.4	13.1	−288	111	114
σ_M	0.77			15.4		
A 75	X	Y	Z	γ°	d_I	(N
Range	25–19	10–7	15–12	−435 – −370	75–125	always
Mean	22.5	7.7	13.5	−401	104	10)
σ_M	0.70			6.7		

Comparison of both samples shows the much narrower variation in A 75 for aearly all features measured. However, the relatively low number of observations, und possibly the widely different times at which they were made, preclude any conclusion.

Between the calculated means of Y, Z and d_I differences are too slight to reveal any indication of change. However, the differences of the M_X and the M_γ values are significant, that of M_γ even strongly so. The sample A 75 being considered the older one, the differences would mean changes in accordance with the principle of nepionic acceleration.

Of five specimens of A 71 earlier counts of X existed. They appear to be reasonably close to the later ones (mean of 18.6 against 19.0 for the same group of individuals).

The sectioned microspheric specimens of both samples gave the following results:

A 71 (N = 26)	X	Y	Z	d_I
Range	41–31	27–16	32–25	7–17 (?)
Mean	34.6	21.4	28.9	13
σ_M	0.50		0.35	

A 75 (N = 13)	X	Y	Z	d_I
Range	41–33	24–16	29–19	10–20
Mean	36.2	20.0	25.5	14
σ_M	0.76		0.74	

The width of variation in both samples is not greatly different if we disregard the single Z observation of 19, which extends the range from 29–23 to 29–19 in A 75.

The differences between the M_X and M_Y values are not statistically significant, but they are for the M_Z values. The latter indicates an increase of average Z in the course of time, if the countings can be taken at face value. However, the qualification marks accompanying the individual counts are in general relatively low. This is completely understandable if we consider that the sections were primarily directed towards good observations of the very small protoconch and surrounding chambers, because incorrect observations in this part of the spiral would cause important errors in the counts. The strongly trochoid character of the spiral is the reason why in these sections the later chambers lie well outside the plane of sectioning, which causes guesswork in all counts, especially so if the sectioning started from the ventral side.

For seven of the microspheric individuals of A 71 earlier X counts existed. For two of these specimens they gave differences with the later observations of as many as three chambers less. This gave an average of 32.9 in 1956 against 33.6 in 1963 for the same seven individuals. If we include one, later discarded, specimen, the M_X value in 1956 would even be as low as 32.5. This mean would have given much more reason to consider nepionic acceleration for the development of the microspheric generation in both samples. However, we had better consider bias too great here, so that much greater differences (or more careful observations) would be needed to permit conclusions. For the same reason we may equally refrain from drawing conclusions from the differences between the M_Z values mentioned earlier.

Lepidocyclina (Nephrolepidina) morgani LEMOINE AND R. DOUVILLÉ

Lepidocyclina morgani LEMOINE and R. DOUVILLÉ, 1904, Mém. Soc. géol. France, vol. 12, fasc. 2, p. 17, 18, pl. 1, fig. 12, pl. 2, fig. 4, pl. 3, fig. 2.

Measurements were made on 40 specimens of sample A 75 and on 12 of sample A 71. On account of the good preservation the measurements are reliable to a high degree.

	A		B		A + B	
	Range	Mean $\pm \sigma_M$	Range	Mean $\pm \sigma_M$	Range	Mean
A 71	42–63	49.5 ± 2.0	48–65	58.2 ± 1.6	96–129	107.7
A 75	36–54	43.3 ± 0.5	43–72	55.4 ± 1.0	87–120	98.8

	C		h_I		d_I	
	Range	Mean $\pm \sigma_M$	Range	Mean $\pm \sigma_M$	Range	Mean $\pm \sigma_M$
A 71	3–8	4.83 ± 0.45	170–290	219 ± 8.5	200–340	264 ± 13.5
A 75	2–7	3.78 ± 0.20	104–230	180 ± 4.5	128–360	248 ± 7.7

	h_{II}		d_{II}	
	Range	Mean $\pm \sigma_M$	Range	Mean $\pm \sigma_M$
A 71	330–490	400 ± 13.0	370–550	461 ± 16.0
A 75	280–464	364 ± 8.0	260–500	377 ± 9.4

The difference of 1.05 between the means of C is rather significant. This increase in number of AAC II demonstrates the principle of nepionic acceleration. The A factor also increases considerably, and the difference between the mean values for both samples is again significant. As to the B factor the increase of 2.8 is of little importance. With regard to the other measurements increase in size of the embryonic chambers is manifestly evident.

Apart from the material of these two samples, specimens of sample A 79a (Saint-Etienne-d'Orthe) and of sample A 76a (Escornebéou) were measured also.

	N	$M_A \pm \sigma_M$	$M_B \pm \sigma_M$	M_{A+B}	$M_C \pm \sigma_M$
A 79a	19	47.2 ± 1.2	55.9 ± 1.1	103.1	4.05 ± 0.28
A 76a	23	45.3 ± 0.7	55.9 ± 1.4	101.2	3.82 ± 0.22

The values are all very close to those of samples A 75 and A 71. The same is true for the Miogypsinids, where we again have to do with *M. complanata* s. str.

For sample A 76a, approximately two metres above A 75, some observations could be made about the reliability of measurements. Twenty specimens were measured by VERVLOET and afterwards measured again by the author (FREUDENTHAL). The results are:

	A		C	
	Range	Mean	Range	Mean
VERVLOET	35–49	42.2	2–5	3.76
FREUDENTHAL	38–51	45.3	2–7	3.82

The difference between the M_C values is negligible, that between the M_A values is much greater and exceeds the average standard error of the means. From these data it would appear that the average AAC II number is rather constant if computed by several authors. But counts by DROOGER (1956), and by the author on the same specimens from other samples, showed greater differences:

	A 75		A 71		A 79a	
	N	M_C	N	M_C	N	M_C
DROOGER	15	3.9	12	4.54	30	3.67
FREUDENTHAL	15	3.8	12	4.83	19	4.05

ESTOTI, SOUTHWESTERN FRANCE

This is a less well known locality in the southern part of the Aquitaine basin, situated some 4 km NW of Saint-Paul-les-Dax and 11 km ENE of Escornebéou. The abandoned quarry is found on the right side of the Herrère valley, immediately south of the secondary road, and under the farmhouse with the name of Estoti, which is marked on the topographic map: Mont-de-Marsan SO, 1:50000. The locality is approximately 1 km east of the classical locality Abesse, where the original outcrops are completely gone today. The description of sediment and fauna of Abesse seemingly indicates little difference with the deposits of Estoti.

For various reasons one placed Abesse stratigraphically at a level higher than those of Escornebéou (H. DOUVILLÉ, 1925). In 1955 DROOGER (p. 19) reported a few specimens of *M. complanata* s.l. found in museum material from Abesse. They are more highly developed – at present they are determined as *M. bantamensis* – than the assemblages from Escornebéou, and characteristic because of a peculiar surface ornamentation consisting of distinct ridges on the individual median chambers.

Five sectioned individuals of the accompanying Nephrolepidinids (range C: 3–8; M_C = 4,6) revealed no notable difference with those which occur together with *M. complanata* s. str. at Escornebéou and Saint-Etienne-d'Orthe.

No new material from Abesse being available, one of the samples from Estoti (A 357, coll. 1954), obtained from a stratigraphic level that is probably higher than those of Escornebéou, and from the same restricted geographic area, was investigated for comparable data. Miogypsinids appeared to be numerous and Nephrolepidinids less frequent. All were of excellent outer preservation but showed considerable recrystallisation internally.

Miogypsina formosensis-bantamensis

The individuals are strongly variable in shape; they are broad to very narrow, but always distinctly fan-shaped because of the protruding apical portion. The diameter of the test ranges up to 2.5 mm, the thickness varies from 0.3–0.7 mm.

Relatively thin specimens are most common; they are thickest at the apical portion, usually unequally biconvex to concavo-convex. Especially the later median chambers are distinctly visible from the exterior, with ridges as surface ornamentation – commonly one ridge per chamber in longitudinal direction. Broken specimens of this type show compact but thin lateral walls; hence, the wall structure of the subgenus *Miogypsinoides*.

At the other end of the variation, thicker variants have a more normal pustulate surface and their greatest thickness is farther removed from the apex towards the centre of the entire test. Some transverse sections show thick side walls with prominent horizontal structures and some irregularly placed cavities, suggesting the beginning of the development of lateral chambers. Many intermediate types exist in between both extremes.

At one end of the variation we thus find numerous individuals resembling those found at Abesse, and at the other end specimens which show already faintly the features of the subgenus *Miogypsina* s. str. The assemblage might therefore also be determined as *M. formosensis-basraensis* (see fig. 6).

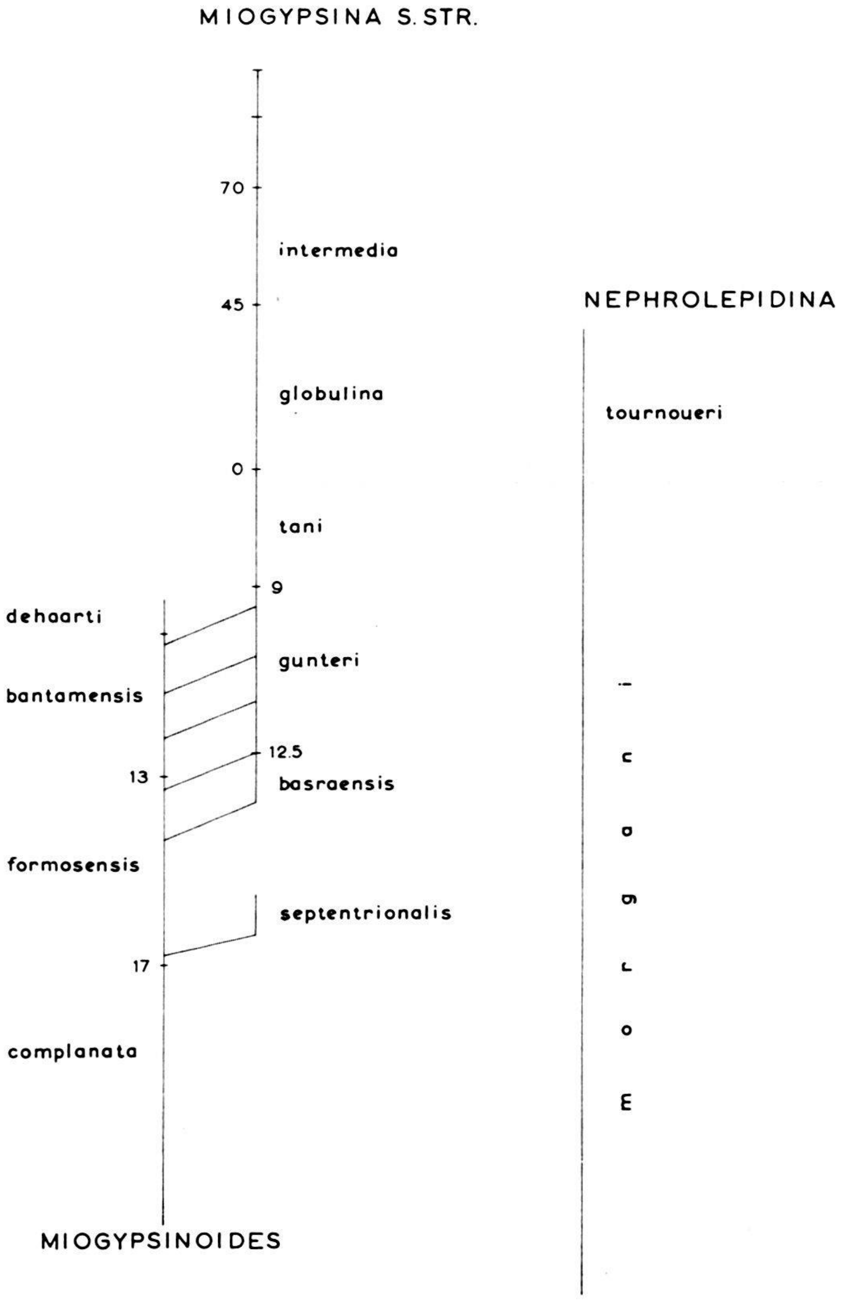

Fig. 6. Assumed phylogenetic relationship of the European *Miogypsina* and *Nephrolepidina* species discussed in the text.

It was considered worthwhile to check whether the extremes differed in internal features. One might expect that the thick *Miogypsina*-like specimens were also more advanced in other characteristics. Groups of extreme variants were selected for sectioning. The results are shown below:

A 357		X		Y		Z	
	N	Range	Mean $\pm \sigma_M$	Range	Mean $\pm \sigma_M$	Range	Mean $\pm \sigma_M$
Thick	12	18–11	13.5	7–1	3.7	12–7	9.1
Thin	14	19–8	12.7	7–2	4.4	14–4	8.1
Total	26	19–8	13.1 ± 0.56	7–1	4.0 ± 0.34	14–4	8.6 ± 0.42

		γ°		d_I	
	N	Range	Mean $\pm \sigma_M$	Range	Mean $\pm \sigma_M$
Thick	12	−270– −140	−176	80–145	112
Thin	14	−340– −60	−191	100–170	133
Total	26	−340– −60	-184 ± 12.3	80–170	124 ± 4.6

There is no evidence that the thicker specimens are more advanced in internal features. The assumption that the total is a homogeneous group without differences between the extremes cannot, or hardly, be disproved. It is possible that a greater number of observations may change these negative results, but they might as well diminish the few minor differences visible now. One of these differences is the greater range of variation in X, γ and Z for the thin specimens, the other is that the average protoconch size of the thin ones seems to be greater. The latter feature might point to a more favourable habitat, as might follow also from the greater number of thin specimens. Whether this fits in with the idea that thicker specimens lived in shallower water (DROOGER, 1955, p. 34) is hard to see.

From the data given it is clear that the whole assemblage from Estoti is much more highly developed than that from Escornebéou. Only the mean protoconch size and the relation M_{II}/M_I ($= 1.03$) are about equal.

Lepidocyclina (Nephrolepidina) morgani LEMOINE and R. DOUVILLÉ

Altogether 22 specimens were measured with the following results:

	A	B	A + B	C	h_I	d_I	h_{II}	d_{II}
Range	43–58	44–70	93–124	2–6	150–250	200–350	280–520	315–570
Mean	50.5	62.5	113.0	3.9	196	259	381	411
σ_M	0.9	1.4	1.4	0.23	6.5	11.1	14.6	15.0

Comparing these data with those from the Escornebéou samples, stratigraphically probably lower, the most striking result appears to be the very low M_C value, which is distinctly lower than that found in A 71, the higher sample from Escornebéou. However, the slight increase in the average values of A, B and A + B is in better accordance with the development expected from the change in the accompanying Miogypsinids. There is no notable change in the dimensions of the embryonic chambers.

SAUSSET, SOUTHEASTERN FRANCE

The coastal strip in between the villages of Carro and La Redonne, west of Marseille, shows nearly continuous exposures of Early Miocene sediments. The deposits are partly of shallow marine and partly of continental origin. Individual lithostratigraphic units vary rapidly from east to west both in character and in thickness. There are several stratigraphic gaps, and finally there are numerous faults, sometimes with obscure displacement. The sediments are usually considered to be of Aquitanian-Burdigalian age because of their transgressive character and their molluscan fauna.

In 1907 R. DOUVILLÉ described the following Lepidocyclinids from the Anse Grand Vallat, near Sausset: *L. marginata*, *L. cottreaui*, *L. tournoueri*, and the latter's variety *concentrica*. He also mentioned the presence of *Miogypsina*. DOUVILLÉ considered this association to be of Helvetian age. In 1963 DROOGER described as *Miogypsina bantamensis-dehaarti* a number of specimens from a sample (FR 475) taken west of Sausset in the area of DOUVILLÉ's locality.

Fieldwork done by BOEKSCHOTEN in 1956 showed that Lepidocyclinids occur at several places. BOEKSCHOTEN's sample 62 (49) was also taken in the vicinity of the Anse Grand Vallat. The two samples FR 475 and 62 (49) cannot be far apart stratigraphically, but the exact interrelation is not known. According to the field notes, FR 475 is probably from a somewhat higher level.

Miogypsina bantamensis-gunteri

Miogypsina bantamensis-dehaarti, DROOGER, 1963, Evol. trends, Elsevier, fig. 4, 6, 9, 13, 16.

The earlier published measurements of the individuals of FR 475 were repeated in but one instance (see below). Those of 62 (49) were made later, in 1963.

Miogypsinids in FR 475 appeared to be fairly rare. The specimens are usually small, 1.0–1.8 mm in diameter, only occasionally measuring up to 2.5 mm. They are of about equal length and breadth, and with a thickness of 0.4–0.6 mm. The apical portion is distinctly visible since it protrudes, but it is not of greater thickness. Pustules are generally present; they are of about constant size, and often low and indistinct. Preservation is fairly bad, especially in the sections.

The frequent specimens of sample 62 (49) are much better preserved and more often of greater size, but otherwise of the same general shape and ornamentation. Especially among the bigger specimens the side walls contain distinct lateral chambers, occasionally as many as three, irregularly placed on top of one another. Other specimens, mainly but not exclusively the smaller ones, did not show such chambers. In this respect they resemble the fewer and smaller specimens of FR 475.

As a whole, the group therefore (see fig. 6) had rather be considered as intermediate between *M. bantamensis* TAN SIN HOK and *M. gunteri* COLE, than being on its way to development of *M. dehaarti* VAN DER VLERK.

Counting and measuring of the internal features produced the following results for the megalospheric specimens. The number of observations is 13 for FR 475 and 45 for 62 (49).

FR 475	X	Y	Z	γ°	d_I	d_{II}
Range	13–8	7–0	10–4	−250– −20	67–183	67–167
Mean	10.0	2.8	6.2	−89	108	108
σ_M	0.49	0.50	0.41	14.8	8.8	

62 (49)	X	Y	Z	γ°	d_I	d_{II}
Range	17–8	7–1	12–4	−280– −30	90–332	85–295
Mean	11.3	3.7	7.1	−130	164	165
σ_M	0.34	0.23	0.28	8.3	7.8	

If the assumed relative position of the samples is correct, the differences in the M_X and M_γ values point to nepionic acceleration, but the significance hardly reaches the 90% level. The changes in M_Y and M_Z are of still less significance.

Most remarkable is the change of the average protoconch diameter from 164 μ to 108 μ, which is statistically the most significant. It is opposed to the general idea of increase of protoconch size in the course of time. It is well known that such an increase is true only in a very general way. Our two samples furnish evidence that these diameters can be influenced to a considerable extent by other factors, in this case of unknown character.

As a check on these earlier data, the measurements of protoconch diameters of the specimens of FR 475 were repeated in 1963 with a different microscope. This time M_I was found to be 105 μ, which admits of confidence in the accuracy of the earlier measurements.

Other checks could be made on the material of 62 (49). The sections of the *Miogypsina* specimens were made by Messrs. Vervloet, Felix and Tjalsma. These colleagues made their own counts, each of them for about one third of the total number of 45 sections. The deviations in the three sets of partial means from the corresponding ones calculated from the author's observations are:

M_X	M_Y	M_Z	M_γ	M_I	M_{II}
−0.30	+0.67	−1.27	+2.7	0	−9
−0.14	+0.19	−0.66	+5	+10	0
−0.20	+0.08	−0.50	−1.5	+18	+3

In order to be able to evaluate these deviations, the author's means and corresponding standard errors (but based on $N = 45$) are repeated as a reference:

M	11.3	3.7	7.1	−130	164	165
σ_M	0.34	0.23	0.28	8.3	7.8	

The accuracy of M_X values is especially important, because this feature is primarily used for specific determinations. The X means of the partial collections calculated by our colleagues differ from 0.14 to 0.30 from those of the author Drooger, but all in the same sense, the author's being always highest. However, they are all smaller than the corresponding standard error of the mean. The average systematic deviation of single observations between any two of the four persons involved, was found to be maximally 0.2, which is thought to be very low.

Apart from the satisfactory comparison of the X counts, the measurements of γ seem also to allow considerable accuracy. Single observations, as well as the means, appear to show only slight deviations.

This is not true for Y, Z and their means. Considerable discrepancies occur, which are probably related to the fact that these counts contain far more guesswork than those of X and γ. Consequently, they may easily be subject to systematic errors. Bias seems to play a less important part in the measurements of the diameters of the embryonic chambers. The inaccurate position of the middle of the walls may account for the numerous fluctuating deviations in the sets of individual measurements. Occasional errors in scale reading may have caused some very great discrepancies.

As a whole X and γ seem to give the most reliable and most accurate data, though possibly not entirely unbiased.

Lepidocyclina (Nephrolepidina) morgani Lemoine and Douvillé

Measurements were made on 22 specimens of sample 62 (49) and on 19 of sample FR 475. They rendered the data mentioned below:

	A		B		A + B	
	Range	Mean ± σ_M	Range	Mean ± σ_M	Range	Mean
FR 475	39–62	47 ± 1.2	49–67	57 ± 1.3	90–119	104.5
62 (49)	40–51	46 ± 0.6	50–64	55 ± 0.7	95–108	100.8

	C		h_I		d_I	
	Range	Mean ± σ_M	Range	Mean ± σ_M	Range	Mean ± σ_M
FR 475	3–7	4.4 ± 0.24	140–300	186 ± 9.6	190–390	244 ± 12.0
62 (49)	2–6	4.1 ± 0.22	145–235	190 ± 5.0	210–295	270 ± 5.0

	h_{II}		d_{II}	
	Range	Mean ± σ_M	Range	Mean ± σ_M
FR 475	285–575	352 ± 17.0	280–590	377 ± 17.0
62 (49)	365–455	390 ± 7.0	275–470	390 ± 9.6

The M_C values give the impression that sample FR 475 has the higher stratigraphic position. However, the differences in A, B and C factors are not statistically significant.

It is remarkable that, if sample FR 475 is indeed the younger one, the diameters of protoconch and deuteroconch seem to decrease in the course of time. Similar and even more distinct observations were made on the Miogypsinids of these samples.

It must be emphasized that these *Nephrolepidina* assemblages do not show a higher level of evolution than those of the locality Escornebéou. As to the features measured, all can easily be placed in between the assemblages of samples A 71 and A 75. Again these observations are not in accordance with those made on the accompanying *Miogypsina* assemblages, which clearly represent a higher level of evolution than those of Escornebéou.

ROSIGNANO, NORTHERN ITALY

The village of Rosignano is approximately central in the outcrop area of the so-called Pietra da Cantoni, a complex of 40–80 metres of more or less marly calcarenitic limestone (de Alessandri, 1897; Elter, 1956; Drooger and Socin, 1959). They locally contain well preserved Lepidocyclinids, and their age has been determined variously within the interval Oligocene-Helvetian.

Lemoine and R. Douvillé (1904) mentioned several species, the most important of which is *L.* (*N.*) *tournoueri* with its type locality at Rosignano. *L. tournoueri* was described in more detail by Drooger and Socin (1959) from several samples of the Pietra da Cantoni. These authors found the species to be usually accompanied by *Miogypsina globulina*, for which reason the deposits were considered to be of Burdigalian age.

The collection of DROOGER and SOCIN, stored in Utrecht, was used once more without new sections being added. The stratigraphic interrelation of the various samples is generally unknown. Only samples CM 2, 1 and 3 are spaced from bottom to top in a single outcrop at intervals of approximately one metre, while sample CM 9 must be younger than that of CM 10.

Miogypsina (Miogypsina) globulina (MICHELOTTI)

Nummulina globulina MICHELOTTI, 1841, Mem. Soc. Ital. Sci. Modena, vol. 22, p. 297, pl. 3, fig. 6.

Miogypsina globulina (MICHELOTTI), DROOGER and SOCIN, 1959, Micropaleont., vol. 5, p. 420, pl. 1, fig. 5, 6, table 2.

Miogypsina irregularis (MICHELOTTI), DROOGER, 1952, Study Amer. Miog., p. 54, pl. 2, fig. 25–29; DROOGER, 1955, Verh. Kon. Ned. Ak. Wetensch., ser. 1, vol. 21, no. 2, p. 24, pl. 1, fig. 6–10.

All the assemblages of Miogypsinids (1959, table 2) appear to belong to a single group of highly developed *M. globulina* with a tendency towards *M. intermedia*. The number of observations for the separate samples is too low to warrant a subdivision. M_V values range from 32 to 49, the extremes from samples CM 1 and CM 9 indicating nepionic acceleration, which is probably in accordance with the relative stratigraphic position of these samples. All M_γ values are positive and range between $+18°$ and $+39°$. The average diameter of the protoconch ranges from 150 μ to 178 μ, while the deuteroconch is always considerably larger than the protoconch: M_{II}/M_I ranging from 1.27 to 1.39.

Lepidocyclina (Nephrolepidina) tournoueri LEMOINE and R. DOUVILLÉ

Lepidocyclina tournoueri LEMOINE and R. DOUVILLÉ, 1904, Mém. Soc. géol. France, Paléont., vol. 12, fasc. 2, p. 19, pl. 1, fig. 5 (not pl. 2, fig. 2, 14, pl. 3, fig. 1); DROOGER and SOCIN, 1959, Micropaleont., vol. 5. p. 417, pl. 1, fig. 1–4, pl. 2, fig. 1–6.

The specimens used by DROOGER and SOCIN were measured again. Altogether 91 specimens supplied details on B, C, d_I, d_{II} and h_{II}. The number of observations per sample is given as N_1. Only 41 of them (under N_2) rendered information about the A factor and h_I, because in the other specimens the wall between protoconch and deuteroconch is lacking. As a consequence, for each sample A + B is equally based on these smaller numbers. In the following table the samples are arranged on the basis of increasing values of M_B.

Sample	N_1	N_2	A		B	
			Range	Mean $\pm \sigma_M$	Range	Mean $\pm \sigma_M$
CM 13a	15	7	47–60	53.1 ± 1.9	45–85	69.9 ± 2.9
CM 13b	18	8	40–66	53.6 ± 2.9	53–77	68.4 ± 1.4
CM 10	12	6	47–58	53.8 ± 1.6	56–82	67.3 ± 2.4
CM 3a	22	7	49–69	53.7 ± 1.4	57–77	66.4 ± 1.3
CM 3b	12	5	49–57	52.1 ± 1.3	56–74	65.6 ± 1.7
CM 2	12	8	43–52	49.5 ± 1.1	54–76	62.3 ± 2.2

	A + B		C		h_I	
	Range	Mean ± σ_M	Range	Mean ± σ_M	Range	Mean ± σ_M
CM 13a	92–140	122.2 ± 6.0	4–8	6.13 ± 0.41	180–320	233 ± 17
CM 13b	106–136	121.2 ± 3.6	4–9	6.22 ± 0.34	220–335	260 ± 12
CM 10	104–128	118.0 ± 4.0	3–9	6.16 ± 0.60	240–350	280 ± 15
CM 3a	110–127	119.1 ± 2.5	4–9	6.18 ± 0.33	220–310	280 ± 11
CM 3b	112–128	119.3 ± 2.6	4–9	6.00 ± 0.41	180–340	273 ± 28
CM 2	103–123	111.9 ± 2.5	5–9	5.75 ± 0.39	250–400	320 ± 17

	d_I		h_{II}		d_{II}	
	Range	Mean ± σ_M	Range	Mean ± σ_M	Range	Mean ± σ_M
CM 13a	220–450	321 ± 17	340–580	478 ± 19	360–650	515 ± 18
CM 13b	245–425	354 ± 13	410–710	527 ± 15	450–750	567 ± 18
CM 10	250–450	380 ± 17	440–700	564 ± 23	430–710	613 ± 30
CM 3a	280–500	385 ± 12	430–770	601 ± 15	480–750	612 ± 14
CM 3b	190–490	377 ± 26	290–650	543 ± 27	350–700	591 ± 28
CM 2	350–565	427 ± 18	500–850	619 ± 27	510–820	630 ± 26

From these data it is clear that the assemblages of Rosignano form a homogeneous group. None of the differences between mean values can be considered of high statistic significance. Only for the assemblage CM 2 does the mean of A + B differ so much from those of the other samples that CM 2 might be considered the oldest. If true, it is remarkable that the average dimensions of the embryonic chambers seem to be greatest for this older sample. However, there is no field evidence that supports our relative age assumption.

Furthermore there is no doubt that our Italian assemblages differ considerably from those of southern France in some of the features measured. The specimens from Rosignano have distinctly larger embryonic chambers and a much greater average C factor. The calculated values are as much as 0.92–1.39 higher than M_C in sample A 71 from Escornebéou, in this respect highest among the French assemblages. The increase in mean A and B values is much smaller; these means differ not so much from those in A 357 or A 71.

Again some remarks can be made about the reliability of measurements, because our results can be compared with those of Drooger and Socin (1959, p. 418, table I) made on the same groups of specimens. However, in every sample the author (Freudenthal) measured a smaller number of specimens. In the next table, N_3 is the number of specimens on which measurements of the nucleoconch were made; N_4 is the number of specimens in which the AAC II (factor C) was counted. For each sample the measurements by Drooger and Socin are listed first. Those of the author are placed below on the second line. δ_1 shows for each sample the difference between the M_C values, calculated by Drooger and Socin (1959), and those calculated by the author. δ_2 gives the differences if the observations of the author are compared with the counts of Drooger and Socin on the corresponding specimens only.

From these data it appears that the averages of h_{II} and d_{II} are fairly close. The mean values of h_{II} found by the author (Freudenthal) differ from -12 μ up to $+16$ μ from those of Drooger and Socin. For the mean values of d_{II} these differences are from $+1$ μ to $+29$ μ. Evidently the average measuring error, to whatever reason it may be due, is of the same order of magnitude as the standard error of the means.

	N_3	$M_{hII} \pm \sigma_M$	$M_{dII} \pm \sigma_M$	N_4	Range C	$M_C \pm \sigma_M$	δ_1	δ_2
CM 10	42	548 ± 15	594 ± 13	27	2–9	5.69 ± 0.34	0.47	0.50
	12	564 ± 23	613 ± 30	12	3–9	6.16 ± 0.60		
CM 3a	59	587 ± 10	611 ± 9	28	4–10	6.11 ± 0.27	0.07	0.05
	22	601 ± 15	612 ± 14	22	4–9	6.18 ± 0.33		
CM 3b	21	555 ± 21	580 ± 21	14	4–7	5.71 ± 0.32	0.29	0.17
	12	543 ± 27	591 ± 28	12	4–9	6.00 ± 0.41		
CM 2	20	608 ± 17	601 ± 17	13	4–8	5.62 ± 0.35	0.13	0.36
	12	619 ± 27	630 ± 26	12	5–9	5.75 ± 0.39		
CM 13a	25	480 ± 12	513 ± 13	21	4–8	5.60 ± 0.26	0.53	0.23
	15	478 ± 19	515 ± 18	15	4–8	6.13 ± 0.41		
CM 13b	32	512 ± 13	541 ± 14	26	3–9	5.87 ± 0.32	0.35	0.09
	18	527 ± 15	567 ± 18	18	4–9	6.22 ± 0.34		

More interesting are the differences found in the computed M_C values. The author's means are from +0.07 up to +0.53 greater than those given by Drooger and Socin, being greatest for those samples in which the number of observations between both sets differ most. For this reason an attempt was made to find out whether the differences could be narrowed down if only the observations on the same specimens were compared. This appeared to be hardly possible; the new series of differences (δ_2) shows a completely comparable range of variation. Moreover, the means found by the author appear to remain always greater than those of Drooger and Socin.

This proves that bias during the observations cannot be denied. Some of it could be retraced. Evidently there do exist differences of appreciation in counting the number of AAC II. For instance, in fig. 4 (after Drooger and Socin, 1959, pl. 2, fig. 3) the lumen on the top of the deuteroconch was counted as two AAC II by Freudenthal and as one by Drooger. Such clear cases do not fully account for the bias. Some of it remains, especially in groups of nepionic chambers that are not too well visible. Here appreciation evidently plays another part.

BIAS

The various double sets of counts and measurements in both *Miogypsina* and *Nephrolepidina* yield information about the degree of accuracy in the observations of the separate features. Furthermore, they give some notion of to what extent the calculated means in small to moderate size assemblages are affected by personal factors.

In general, it appears that the range of such differences does not exceed that of the corresponding standard error of the means. Whether this is thought satisfactorily low or not, it provides a criterion in evaluating the means, and especially a warning against drawing too detailed phylogenetic or stratigraphic conclusions from differences of means, which are not so far apart. The correctness of the application of parameters from statistics is hardly ever tested for paleontological material; here we have another reason for caution.

Especially in the *Miogypsinidae* we found that the better visible features (X, γ) allow much smaller discrepancies than the vaguer ones (Y, Z). The latter offer more opportunity for bias during the observations. Such bias also occurs in

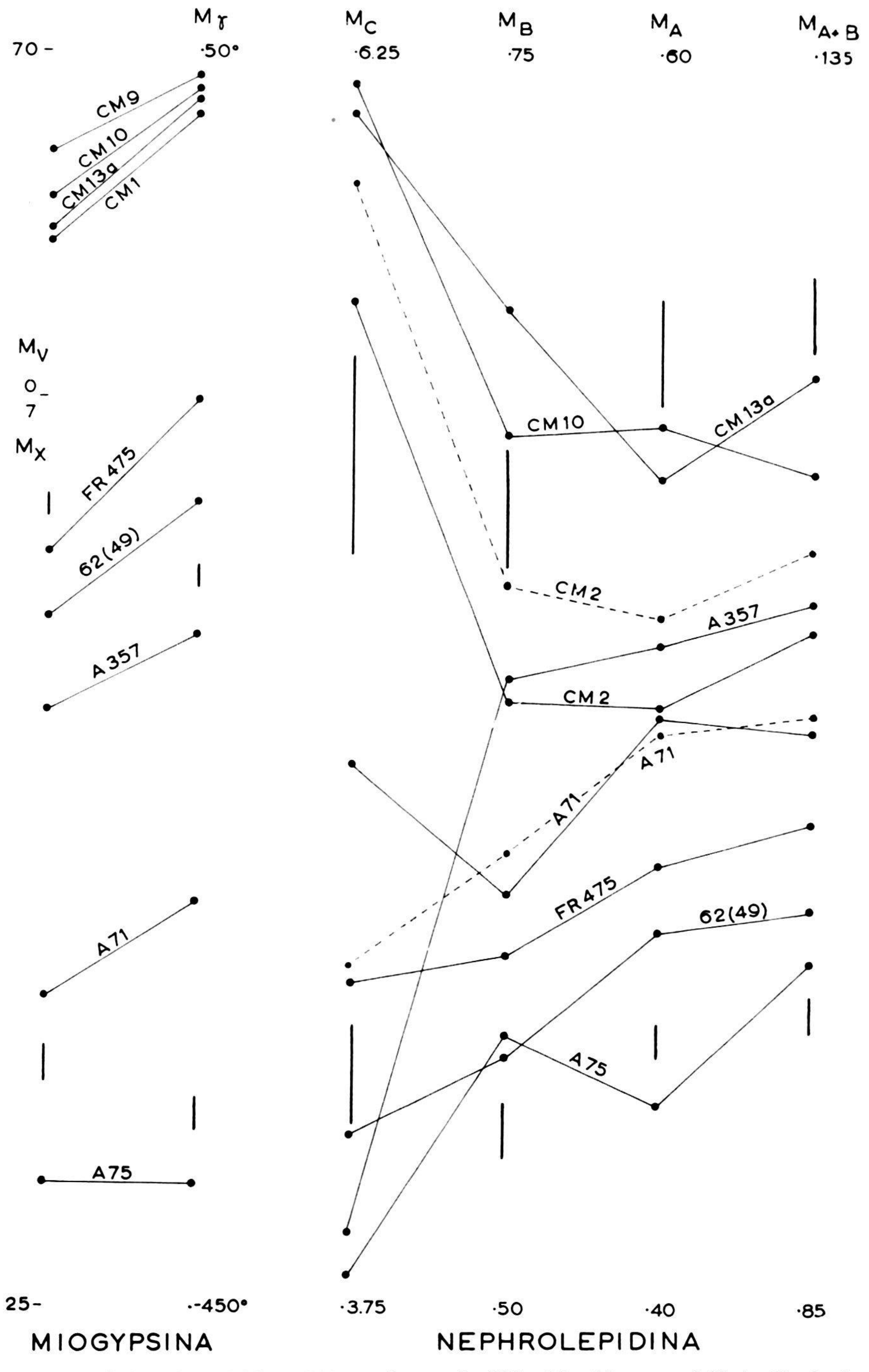

Fig. 7. Values of M_X, M_V and M_γ in *Miogypsina*, and of M_A, M_B, M_{A+B} and M_C in *Nephrolepidina* from Escornebéou (A 75, A 71), Estoti (A 357), Sausset (62 (49), FR 475) and Rosignano (CM 1–13a). For each feature average values of one σ_M have been entered twice as vertical lines. A second set of means is given for CM 2 and A 71 (dash lines).

the counting of AAC II in the Nephrolepidinids, where it is caused only partly by not so well preserved specimens. Even if the material is of good preservation we have to be careful in comparing mean values of different authors. The tolerance limit has to be widened with approximately one σ_M to account for bias. As a rule the limits set between the species of the *Miogypsinidae*, and also the number of specific units recognized in *Nephrolepidina*, are sufficiently far apart and with enough restrictions for use so that practically none of the earlier determinations will be affected.

PHYLOGENETIC AND STRATIGRAPHIC CONCLUSIONS

The main evolutionary features of our *Miogypsina* and *Nephrolepidina* assemblages are repeated in fig. 7 by means of their mean values. As has been shown before (DROOGER, 1963, fig. 10) the M_X and M_γ values of the Miogypsinids appear fairly well correlated. These characteristics admit a splitting of the group into several adjoining specific units. It is thought acceptable that the order from bottom to top, as given in the figure, corresponds with a succession in time.

Unfortunately the Nephrolepidinids give no support to the latter hypothesis. If we regard the – very large – standard errors (σ_M) in this group it becomes clear that they allow for much less diversification. However, this may account for only a part of the irregularities.

If we assume that the stratigraphic order of the *Miogypsina* assemblages is correct, none of the four evolutionary factors in *Nephrolepidina* shows a satisfactory order; they even show highly variable combinations.

Both *Nephrolepidina* samples from Escornebéou clearly demonstrate the principle of nepionic acceleration for all four of the characteristics. The third sample from the Aquitaine basin (Estoti, A 357) – from an assumedly higher stratigraphic level – fits in well as to the factors A, B and A + B, but C shows a distinct setback compared with assemblage A 71. Both samples from Sausset, though closely resembling one another, come in much lower than expected (fig. 7). Finally the most highly developed assemblage from Rosignano (CM 13a) stands well apart at the top, but the most primitive one (CM 2) comes again within the province of the older assemblages as for the A, B and A + B factors.

Since the means calculated for CM2 and A 71 were based on very low numbers of specimens, additional data were gathered on A, B and C factors:

	N	$M_A \pm \sigma_M$	$M_B \pm \sigma_M$	M_{A+B}	$M_C \pm \sigma_M$
CM 2	34	51.0 ± 0.73	64.3 ± 1.1	115.3	6.00 ± 0.21
A 71	32	49.3 ± 1.00	59.1 ± 1.2	108.4	4.44 ± 0.22

Although both samples come farther apart now, the new means differ no more than one standard error from the earlier ones (see fig. 7).

Many of the irregularities in fig. 7 may be unreal, but the jumping pattern probably is correct. Although no sound theory can be based on insufficient data, the most likely solution seems to be that the principle of nepionic acceleration for this already highly developed group of Lepidocyclinids had become less rigorous, allowing much local and haphazard variation. Regional and local stocks, comparable with races, had each their own pattern of development, variously expressed in A, B or C, and in its rigidity variable with time. Figure 8 illustrates two different ways of change, both in accordance with the principle of nepionic acceleration.

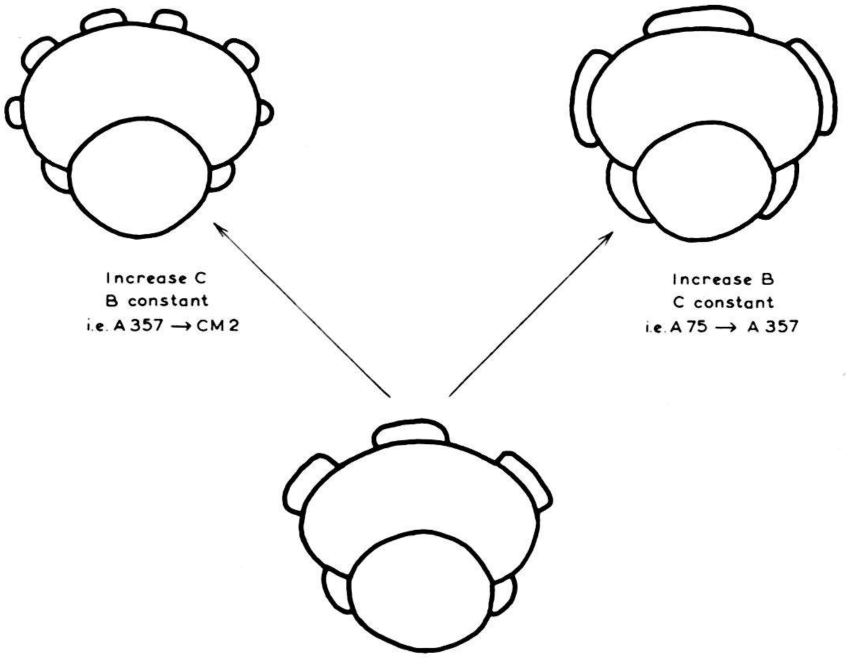

Fig. 8. Two different changes in the adauxiliary chambers of *Nephrolepidina*, both in accordance with the principle of nepionic acceleration.

Development of many population groups within a single evolving plexus is thought to fit better than assuming a number of completely independent and different lineages. The latter assumption might find support in the three separate geographic areas under consideration, and in, for instance, the close resemblance of both assemblages from Sausset in fig. 7. However, the anomalies within the group of assemblages from southwestern France (fig. 7) should make us cautious in looking for such an unwarranted mental simplification and taxionomic complication, like splitting into many completely different lineages.

In former papers two specific units were applied to our entire group: *L. tournoueri* for the assemblages from Rosignano and *L. morgani* for all others. They were primarily based on M_C values. This differentiation seems again permissible from our new data and it is therefore proposed to retain these two specific units, though it must be admitted that they cannot be nicely disentangled on the basis of A and B factors. As a consequence we may expect that in Europe a Chattian-Aquitanian species and a Burdigalian one can be separated, but nothing more, and we postpone the decision on the possibility of recognizing a boundary between the species to future research.

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