



Neanic acceleration in *Nephrolepidina* from the Oligo-Miocene Mt. Torretta section (L'Aquila, central Apennines): biometric results and evolutionary, taxonomic and biostratigraphic remarks

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ABSTRACT - A sequence of eighteen *Nephrolepidina* populations, coming from the Oligo-Miocene outcrop of Mt. Torretta (L'Aquila-central Apennines), are investigated applying the biometric analysis on the embryo-nepionic chambers and on the fifth stage of the neanic equatorial chamberlets, supplying additional data about parameters and factors that had already demonstrated to have taxonomic-biostratigraphic significance. The occurrence of the whole sequence of different evolutionary stages, *Nephrolepidina praemarginata*-*N. morgani*-*N. tournoueri*, is confirmed. These chronospecies, characterizing the Mediterranean lineage, follow an evolutionary development according to the principles of "embryonic and nepionic acceleration". The data evidence that the "Degree of stolonistic distalization" (Factor FD5) and the "Shape Index" (Factor SI5), measured at the 5th neanic stage, have a very good fitting with the previously evidenced overall trend to elongate the shape of the equatorial chamberlets, connected with their packing (golden selection) and a gradually more distal position of the radial stolons (Neanic acceleration). However, according to the biometrical investigation of embryo-nepionic apparatuses, there are significant taxonomic issues, hampering an effective application of the genus to high-resolution biostratigraphy. Both the typological and the quantitative specific, phylogenetic and biostratigraphic definitions, could be improved by means of an integration of the embryonic-nepionic-neanic data. In that way, a significant preliminary goal is reached, suggesting two new, tentative, preliminary biometric boundaries between the chronospecies.

Keywords: Biometry; Larger foraminifera; Lepidocyclinidae; Taxonomy; Biostratigraphy; Oligocene; Miocene.

Submitted: 21 July 2016 - Accepted: 19 September 2016

1. INTRODUCTION

The biometric studies of the embryonic and nepionic chambers in *Nephrolepidina*, following the methods introduced by van der Vlerk (1959 a,b, 1963), evidenced frequent phases with a decrease in time of the mean values of the "degree of enclosure" of the protoconch by the deuteroconch (Factor A of van der Vlerk, 1959), and of the "number of adauxiliary chamberlets". Moreover, a statistical discrimination between populations at an intermediate-high evolutionary stage (*N. morgani*-*N. tournoueri*) frequently appeared to be very difficult (Matteucci and Schiavinotto, 1977; Schiavinotto, 1978, 1979; Giovagnoli and Schiavinotto, 1990; Schiavinotto and Verrubbi, 1994 a,b; Giannini et al., 2007). Consequently, these instances of stasis affected the application of *Nephrolepidina* for a detailed biostratigraphy, at least at the level of the intermediate - final development of the Mediterranean *Nephrolepidina* lineage.

This work contributes data on several populations representing these different evolutionary stages, in

order to obtain more reliable indications on the validity of a new biometry of the neanic chambers, introduced by Schiavinotto (1992, 1993a,b, 2010). The first results permitted to hypothesize an evolutionary process based on a "Neanic Acceleration", with a progression of the mean values of the parameters and factors at any rate, in agreement with their stratigraphic sequence. Subsequently, this methodological approach was followed by Benedetti and Pignatti (2013). New data on the neanic apparatus of eighteen previous investigated populations from the Monte Torretta section (Giannini et al., 2007) are added here with the aim to improve the evolutionary, taxonomic, and biostratigraphic significance of the Mediterranean lepidocyclinids. After a review of these materials some published mistakes were evidenced, but the errata do not altered the meaning of the final results and, anyway, they are corrected here.

The final goal is to give new inputs to contribute significantly to a further tentative reassessment of *Nephrolepidina*, focused on the evolutionary development of the chamberlets in the neanic stage, considering the

new perspectives offered by the “Golden Selection” suggested by Benedetti (2014).

2. GEOLOGICAL AND STRATIGRAPHICAL SETTING

Monte Torretta is located in an area that is characterized by the geodynamic evolution of a Triassic carbonatic platform extending along the passive edge of the expanding Tethys. During the Cenozoic, the emersion and break-up of the platform gave rise at first local lacunose phenomena, and then the complete disarticulation of the whole carbonatic unit, with shortening of the structures and the formation of folds and overthrusts with E and NE vergence (Accordi, 1963, 1966; Parotto and Praturlon, 1975).

The local architecture of the Tethyan palaeomargin from the early Mesozoic rifting greatly influenced the evolution of the Neogene orogenic belt in the studied area. During the Miocene, open neritic platform set up; organogenous formations are transgressive on a large part of the Cretaceous platform. For a detailed review of the geological setting of the area, references are made to Accordi (1963, 1966), Parotto and Praturlon (1975, cum bibl.), Calamita et al. (2002).

3. MATERIALS AND METHODS

3.1. Mt. Torretta Section

Monte Torretta (1097 m) is located 10 km WNW of L'Aquila (42°22'49"N-13°17'18"E; I.G.M. topographic map 1:25,000 - 139 II SW, Scoppito) (Fig. 1).

It is the easternmost offshoot of the highest mountain (Monte Calvo, 1909 m) between the Velino and the Aterno valleys. The sampled succession is about 95 m thick, and starts at 850 m altitude. It consists of red and grey Lepidocyclinidae-bearing marls and marly limestones, and hard limestones with *Miogypsina*. The middle Oligocene-Lower Miocene Monte Torretta section was subdivided by Giannini et al. (2007, Fig. 2) in the following two units from bottom to top:

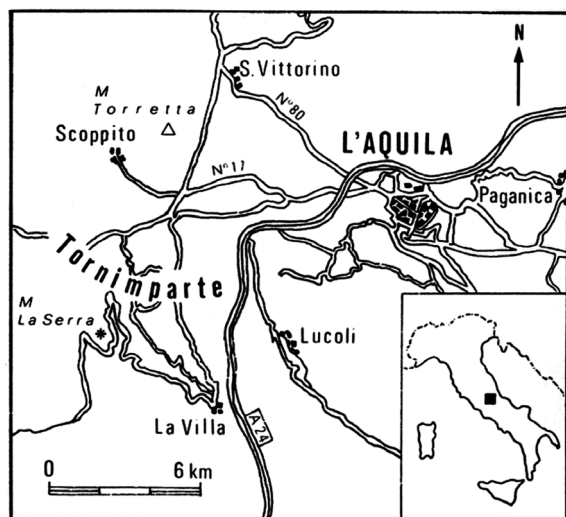


Fig. 1 - Location map of the outcrop.

Unit I: A sequence of larger foraminiferal marls and interbedded coarse-very coarse bioclastic larger foraminiferal packstones.

Unit II: Coarse to-very coarse bioclastic larger foraminiferal packstones.

3.1.1. Material

Eighteen *Nephrolepidina* assemblages were obtained from the samples collected in the Monte Torretta succession. As reported by Giannini et al. (2007), five of these assemblages were obtained from washing residues of marly samples collected in the lower (samples PMT32 - PMT30), middle (sample PMT24) and upper (samples PMT23 - PMT22) part of Unit I; another washing residue provided an assemblage from the lower part of Unit II (sample PMT8).

Total number of measured free specimens (embryo-nepionic chambers) = 394 (mean number per population = 65).

Total number of measured free specimens (neanic chamberlets) = 281 (mean number per population = 46).

Total number of measured neanic chamberlets = 2822 (mean number of chamberlets per individual = 10).

Many thin sections of hard-rock supplied 12 *Nephrolepidina* assemblages from as many layers along the sequence. For the embryo-nepionic chambers, the total number of measured (equatorially sectioned) specimens is = 445; mean number per assemblage = 37; this relatively low number is due to the poor orientation of the tests in some samples.

Total number of measured specimens for the neanic chamberlets = 277 (mean number per population = 23).

Total number of measured chamberlets = 1324 (mean number per specimen = around 4-5).

3.1.1.1. Biometric study

Nephrolepidina Douvillé, 1911 is a lepidocyclinid genus, characterised by a biconvex, lenticular calcareous hyaline test composed of chambers arranged in an equatorial layer between two distinct packs of lateral chamberlets. The megalospheric specimens have a bilocular nucleocoenoch with the protoconch partially enclosed by the subcircular to reniform deuteroconch, slightly larger than the protoconch (Fig. 2). The equatorial chambers are arcuate, ogival, rhombic or hexagonal and were considered as arranged in cyclic annuli. Recently, Benedetti (2014) evidenced the spiral growth of the neanic stage of *Nephrolepidina*. Consequently, the “annuli” are considered as “pseudo-annuli” in the present research.

The Degree of enclosure of the protoconch by the deuteroconch (Factor Ai of van der Vlerk, 1959a,b, 1963, 1964), the number of auxiliary chambers AACII (Parameter C of Drooger and Freudenthal, 1964) and the diameters of the protoconch (DI) and the deuteroconch (DII), were measured on equatorial sections of the megalospheric specimens (Fig. 2).

For a description of the biometric method and the techniques used to obtain the various measurements,

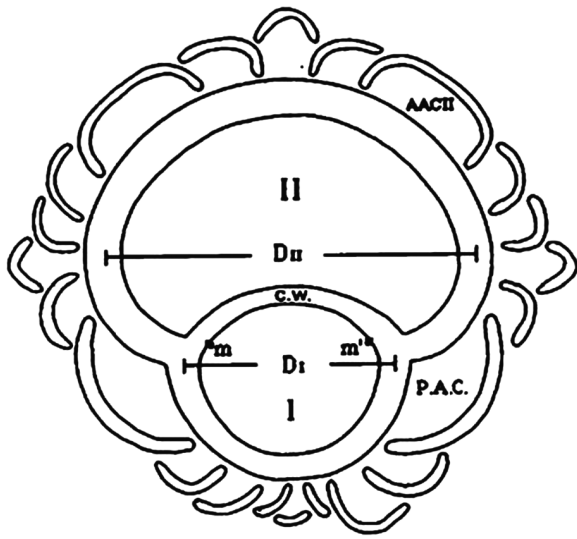


Fig. 2 - Schematic drawing of the internal features counted and measured on the horizontally sectioned embryonic-nepionic stage of megalospheric *Nephrolepidina*. I = protoconch; II = deutoconch; PAC = principal auxiliary chamber; AACII = adauxiliary chamber.

reference is made to the above-mentioned works and to de Mulder (1975).

The diameters were measured including half thickness of the wall, to increase the number of comparisons with data in the literature. On the contrary, recently, Benedetti et al. (2010), and Benedetti and Pignatti (2013), measured DI and DII both considering and excluding the thickness of the wall, because there are evidences of environmental control on this feature (e.g., Beavington-Penny and Racey, 2004).

The neanic equatorial chamberlets in *Nephrolepidina* are commonly considered as arranged in concentric annuli, connected through annular, oblique and lateral stolons, without a canal system.

Schiavinotto (1992), starting from some observations reported by Eames et al. (1962), evidenced the connection between the sequence of morphologies of the neanic equatorial chambers and the type of stolons as visible in the median plane of *Nephrolepidina*. The chamberlet shape varies from simple arcuate (not in lateral contact) and simple arcuate in lateral contact, to rhombic-ogival-exagonal. Subsequently, Adams (1987) confirmed the observations of Eames et al. (1962). The arrangement of the chamberlets is closely linked to the length of the common walls between contiguous chamberlets of the same cycle (or "annulus").

A greater extent of these walls is connected with a more distal position of the intercytic stolons. Similar observations were done on Cretaceous orbitoidids (van Gorsel, 1975, 1978). Consequently, Schiavinotto (1992), starting from the observations reported by Eames et al. (1962), introduced indexes of "stolonic distalization", measuring the tendency through time of the chamberlets to become more elongated, suggesting

the statistical usefulness of the number of chamberlets in the fifth annulus. On the contrary, after the fifth annulus the growth becomes more irregular, possibly due to environmental factors (Schiavinotto, 2010).

Schiavinotto (1993 a,b) delineated a "neanic acceleration" as the tendency to increase in time of the connections between the contiguous chambers (stolon system).

Recently, Benedetti (2014) suggested the concept of "golden selection", evidencing the spiral growth of the neanic chambers of *Nephrolepidina*, rather than annular-concentric, and rephrased the neanic acceleration as the tendency through time of the equatorial chamberlets to achieve more efficient packing. This approach depicts a new fascinating path, but it is very difficult to follow proceeding on material coming only from thin sections of hard rocks; therefore, in this study the following measurements introduced by Schiavinotto (1992, 1993a,b) are used (Fig. 3), as related to the chamberlets belonging to the "pseudo-annuli":

c = "lateral length" of the common wall between contiguous chamberlets; since each chamberlet generally has unequal length of the two common walls with adjacent chamberlets, a mean value between the two measurements is calculated.

d = "protruding length" of the chamberlets, starting from the line joining the bases of the lateral walls; the front wall of the chamberlets is included.

h = "front height" of the chamberlets.

w = "front width" of the chamberlets, taken along the line connecting the distal ends of the common walls.

$FD5 = c/d \times 100$ = "degree of stolonic distalization"; this factor is a quantitative expression of the "crowding" of the chamberlets of a single cycle, according to the shape-growth relations described in Eames et al. (1962).

$Re5 = h/w \times 100$ = "curvature index of the front wall.

$SI5 = FD5/Re5 \times 100$ = "Shape Index" of the chamberlets.

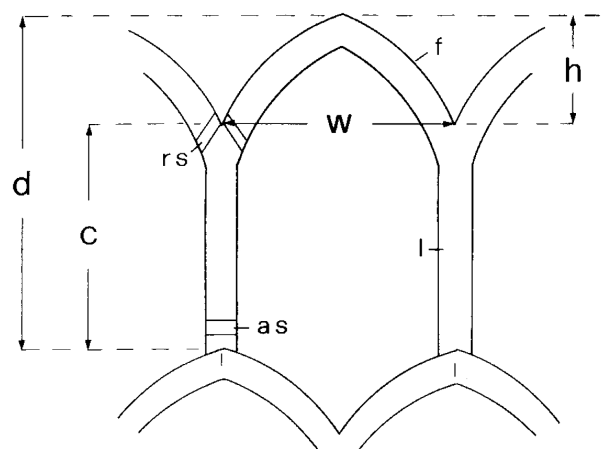


Fig. 3 - Schematic drawing of the internal features measured on the horizontally sectioned neanic equatorial chamberlets of *Nephrolepidina*. f = frontal wall; l = lateral (common) wall; rs = radial (intercyclic) stolons; as = annular (concylic) stolons; c = lateral length; d = protruding length; h = front height; w = front width.

Many populations were obtained from thin sections of hard rocks. In such a condition, the specimens show frequently an incomplete equatorial plane. Consequently, to investigate the equatorial plane, a subdivision in 120° sectors may be suitable in few cases. Therefore, when it was unavoidable, the measurements were taken on the segments of the 5th annulus in a random well preserved area of the equatorial plane.

Also, in thin sections of hard rocks, incomplete annuli as described in Schiavinotto (2010) are difficult to be detected; in these cases, only a full, regular development of the visible chamberlets is a guarantee of reliable measurements, although Benedetti (2014) suggested that incomplete annuli are not growth anomalies, but they are due to the natural spiral pattern of growth of the equatorial plane of *Nephrolepidina*, reflecting the packing of the equatorial chamberlets.

Considering the time consuming methodology, and the difficulty in obtaining complete “annuli” from thin sections of rocks, Benedetti and Pignatti (2013) took these measures only for a single well-preserved chamberlet of the fifth “annulus”, similarly to what is routinely used for orthophragmines by Less (1987), that is in only one equatorial chamber at 0.5 mm from the embryonic chambers.

Picking only one representative chamberlet may be difficult and subjective, because the frequent irregular/asymmetric growth of the neanic equatorial chamberlets

in *Nephrolepidina*, maybe related also to the pseudo-annular arrangement.

This simplified data collection was tested by Schiavinotto (2010), giving evidence that more reliable results are obtained measuring at least three chamberlets per pseudo-annulus, but also in the present case, only one-two chamberlets for some specimens were measured frequently, because of the incomplete preservation of the neanic apparatus.

The measurements were done on microphotographs, with the software Autocad™.

The statistical comparison between the means of the variables obtained in the PMT populations and the data from the previous works, was done by means of the Student's t-test. The normality of the distributions was checked by means of the Kolmogorov-Smirnov test (K-S), at a probability level P=95%.

4. RESULTS

The results of counts and measurements on the embryonepionic stages are in Tables 1-4, replacing those listed in Tables 1 and 2 of Giannini et al. (2007). This revision was necessary since some digital files were computer-processed erroneously. Consequently, mistakes in the text, tables and figures are corrected here, before their use for further research. The corrected data do not change the substance of the previous results but allow new

FACTOR Ai							
POPULATIONS	N	R	M	S	SM	K-S	K-SC
PMT8/80	18	34.84-64.02	48.00	6.52	1.53	0.159	0.309
PMT8	58	37.68-59.00	47.49	5.20	0.68	0.055	0.175
PMT16	29	36.21-59.33	44.57	6.10	1.13	0.100	0.246
PMT18	17	29.89-55.65	46.15	5.92	1.43	0.160	0.318
PMT20	28	30.01-56.80	42.93	6.83	1.29	0.082	0.250
PMT21	58	34.82-60.11	46.91	5.40	0.70	0.052	0.175
PMT22	64	33.50-60.45	45.06	5.45	0.68	0.071	0.167
PMT23	77	36.06-59.60	46.39	4.68	0.53	0.043	0.153
PMT23/6	47	37.61-55.52	45.26	4.51	0.65	0.103	0.194
PMT23/7	68	30.68-57.25	44.21	4.74	0.57	0.074	0.162
PMT23/8	56	28.53-55.30	43.41	5.50	0.73	0.069	0.178
PMT24	57	34.10-58.20	44.04	4.80	0.63	0.102	0.177
PMT24B	48	29.66-54.05	43.01	4.75	0.66	0.123	0.192
PMT24C	32	29.14-54.25	42.48	6.23	1.10	0.074	0.234
PMT24D	17	35.67-55.46	43.32	6.31	1.53	0.208	0.318
PMT24E	27	33.19-50.60	43.69	3.92	0.75	0.105	0.255
PMT30	70	31.61-53.08	40.34	3.99	0.47	0.066	0.160
PMT32	68	31.42-47.79	40.12	4.01	0.48	0.121	0.162

Tab. 1 - Statistical results for the factor Ai measured in the *Nephrolepidina* populations from the Mt. Torretta section (N= number of measured specimens; R = range; S = standard deviation; SM = standard error of the mean; K-S = experimental value for the Kolmogorov-Smirnov test; bold type = significant values at P = 95%; K-SC= Kolmogorov-Smirnov critical value (95%).

PARAMETER C							
POPULATIONS	N	R	M	S	SM	K-S	K- SC
PMT8/80	18	4-8	6.20	1.20	0.27	0.224	0.309
PMT8	54	3-9	5.64	1.36	0.18	0.199	0.182
PMT16	20	3-8	5.00	1.30	0.28	0.200	0.294
PMT18	22	3-9	5.45	1.26	0.26	0.242	0.281
PMT20	37	3-8	5.20	1.40	0.22	0.177	0.218
PMT21	54	3-7	4.74	1.08	0.14	0.236	0.182
PMT22	59	2-7	4.57	1.07	0.13	0.212	0.174
PMT23	75	2-9	4.65	1.32	0.15	0.215	0.153
PMT23/6	66	2-7	4.30	0.98	0.12	0.260	0.165
PMT23/7	106	3-7	4.53	0.99	0.10	0.204	0.130
PMT23/8	65	3-7	4.30	1.00	0.12	0.249	0.167
PMT24	57	2-7	4.28	1.11	0.14	0.266	0.212
PMT24B	54	2-6	4.00	1.00	0.14	0.211	0.182
PMT24C	42	2-9	4.40	1.70	0.26	0.175	0.205
PMT24D	19	2-7	3.80	1.50	0.34	0.187	0.301
PMT24E	32	2-6	3.90	1.00	0.18	0.206	0.234
PMT30	67	1-5	3.14	0.85	0.10	0.315	0.164
PMT32	62	1-6	3.04	0.99	0.12	0.229	0.170

Tab. 2 - Statistical results for the parameter C measured in the *Nephrolepidina* populations from the Mt. Torretta section (Symbols as in Tab. 1).

DI							
POPULATIONS	N	R	M	S	SM	K-S	K-SC
PMT8/80	19	318-545	414.70	69.67	15.98	0.131	0.301
PMT8	58	199-629	362.58	84.16	11.05	0.128	0.175
PMT16	33	239-568	393.00	94.51	16.45	0.176	0.231
PMT18	23	239-568	368.26	96.39	20.10	0.140	0.275
PMT20	39	216-511	361.40	77.21	12.36	0.102	0.213
PMT21	58	210-466	326.31	59.96	7.87	0.135	0.175
PMT22	64	187-454	331.26	59.99	7.49	0.087	0.167
PMT23	77	210-551	336.59	69.74	7.94	0.103	0.153
PMT23/6	72	204-551	327.00	69.39	8.18	0.119	0.158
PMT23/7	109	210-511	337.10	56.38	5.40	0.069	0.129
PMT23/8	70	204-511	326.70	58.92	7.04	0.105	0.161
PMT24	57	233-483	346.36	52.24	6.91	0.099	0.177
PMT24B	57	170-415	266.73	55.85	7.40	0.150	0.177
PMT24C	51	193-568	301.10	70.12	9.82	0.158	0.186
PMT24D	18	210-386	283.80	55.78	13.15	0.123	0.309
PMT24E	36	165-568	296.30	75.52	12.59	0.124	0.221
PMT30	71	165-449	272.14	47.38	5.62	0.130	0.159
PMT32	69	176-381	272.82	40.43	4.86	0.108	0.161

Tab. 3 - Statistical results for the parameter DI measured in the *Nephrolepidina* populations from the Mt. Torretta section (Symbols as in Tab. 1).

DII							
POPULATIONS	N		M	S	SM	K-S	K-SC
PMT8/80	22	483-898	639.30	106.10	22.62	0.111	0.281
PMT8	58	312-981	556.93	132.25	17.36	0.069	0.175
PMT16	36	375-953	595.02	148.85	24.80	0.198	0.221
PMT18	26	364-833	581.96	133.61	26.20	0.112	0.259
PMT20	40	256-841	561.20	135.20	21.38	0.069	0.210
PMT21	58	369-731	517.93	81.87	10.75	0.085	0.175
PMT22	64	301-685	508.71	78.56	9.82	0.125	0.167
PMT23	77	329-814	522.53	97.10	11.06	0.075	0.153
PMT23/6	76	312-740	503.60	89.02	10.21	0.081	0.154
PMT23/7	118	346-694	511.70	72.09	6.63	0.083	0.124
PMT23/8	71	369-759	491.60	77.10	9.15	0.082	0.159
PMT24	57	392-687	532.12	70.74	9.36	0.058	0.177
PMT24B	59	261-602	411.80	87.29	11.36	0.129	0.174
PMT24C	52	267-851	451.70	134.20	18.61	0.138	0.185
PMT24D	20	284-666	456.20	121.70	27.20	0.128	0.294
PMT24E	35	261-740	444.30	107.10	18.11	0.115	0.224
PMT30	71	244-721	382.11	76.13	9.03	0.108	0.159
PMT32	69	227-500	387.28	59.22	7.12	0.107	0.161

Tab. 4 - Statistical results for the parameter DII measured in the *Nephrolepidina* populations from the Mt. Torretta section (Symbols as in Tab. 1).

comparisons with more recent research.

The results of the biometric investigation of the neanic apparatus are summarized in Tables 5-7.

4.1. Homogeneity of the assemblages

The histograms of Giannini et al. (2007, Figs. 5 and 6) contain errors and are replaced here with Figures 4 and 5.

Bimodalities appear in the histograms for DI in PMT18 and PMT16 populations; for DII, there are more frequent bimodalities starting from the population PMT24D.

A check of the normality of the distributions was made by applying the Kolmogorov-Smirnov test (KS). Many results in Giannini et al. (2007, p. 110, Tab. 2) are wrong and they are replaced here, by the recalculated values in Tables 1-4.

Significant differences from the normal distribution were found for parameter C in a large part of the populations from PMT32 to PMT21, not in only three populations (PMT 23/8, PMT 23/7, PMT 23/6) as reported in Giannini et al. (2007), affecting slightly also their conclusive considerations about PMT22 population (see Taxonomy).

For the PMT populations coming from thin sections of hard rocks, the results reported in Table 1 of Giannini et al., (2007) present some wrong significant mean values, as for Ai in three populations (PMT24D, PMT24C, PMT16) and for C in PMT24D. Moreover, in the same Table 1, the maximum values of “monster”, or “jumbo” specimens with Ai = 82.01% or Ai = 70.18% do not exist. Consequently, Table 1 in Giannini et al. (2007) is useless and the recalculated counts and measurements are

summarized here, in Tables 1-4.

The embryo-nepionic data have quite normal distributions, considering the experimental values of the K-S test, all under the critical values. The “nephrolepidine-type” specimens (Ai ranging between 40 and 45%) predominate up to PMT23/6 population, then reappearing only in PMT20 and PMT16 (Fig. 6b). The specimens with Ai below 40% are definitely subordinate, being prevalent only in PMT30 population (Fig. 6a). Large nucleococonches tending towards the “trybliolepidine-type”, with Ai above 50% (Fig. 6c) are always subordinate, increasing in stratigraphically higher populations.

The specimens with a “degree of distalization” (FD5) measuring about 50% (Fig. 7) are predominant.

Specimens with rather primitive equatorial chamberlets (FD5 between 15 and 25%), always subordinate, tending to rare in the uppermost populations (Fig. 8).

Specimens with FD5 around 60%, from bottom to top, tend to become more frequent, although they are always subordinate (Fig. 9).

5. DISCUSSION

5.1. Embryonal-nepionic trends

The graphs in Figure 10 result from the re-evaluated mean values of selected indexes after Giannini et al. (2007). The mean values of Ai, C, DI and DII tend to increase from the bottom to the top of the investigated section, although some deviations from the expected trend occur.

FACTOR FD5								
POPULATIONS	N	nc	R	M	S	SM	K-S	K-SC
PMT8/80	11	49	47.38 – 74.54	56.78	7.31	2.20	0.236	0.391
PMT8	35	366	32.08 – 69.81	55.15	10.12	1.71	0.127	0.224
PMT16	19	57	42.56 – 62.75	54.04	6.04	1.38	0.158	0.301
PMT18	8	41	29.30 – 64.60	52.46	13.14	4.64	0.236	0.454
PMT20	21	83	40.32 – 73.06	55.72	8.35	1.82	0.135	0.288
PMT21	41	219	33.66 – 70.34	53.97	7.36	1.14	0.064	0.208
PMT22	31	310	33.61 – 69.10	54.88	9.23	1.65	0.200	0.238
PMT23	54	655	34.49 – 71.18	52.71	9.31	1.26	0.080	0.182
PMT23/6	32	126	30.15 – 63.66	47.40	9.99	1.76	0.131	0.234
PMT23/7	35	163	26.27 – 69.77	45.34	10.73	1.81	0.095	0.224
PMT23/8	28	135	17.96 – 63.46	45.93	9.53	1.80	0.184	0.250
PMT24	56	619	15.94 – 69.23	45.54	12.36	1.65	0.084	0.178
PMT24B	33	158	15.56 – 63.45	46.86	11.50	2.00	0.160	0.231
PMT24C	19	124	27.77 – 64.85	46.18	9.74	2.23	0.112	0.301
PMT24D	14	77	32.90 – 64.44	47.71	9.17	2.45	0.106	0.349
PMT24E	16	92	21.86 – 64.59	41.20	12.82	3.20	0.111	0.327
PMT30	53	617	9.63 – 60.27	38.95	10.57	1.45	0.091	0.183
PMT32	52	534	2.14 – 66.70	39.14	13.47	1.86	0.069	0.185

Tab. 5 - Results of measurements on the factor FD5 (5th pseudo annulus) in *Nephrolepidina* from Mt. Torretta section. N= number of measured specimens; nc= total number of measured chambers; R= Range of the individual mean values; M= Mean value; S= Standard deviation; Sm= Standard error of the mean; K-S= Kolmogorov-Smirnov test; bold type = significant values at P = 95%; K-SC= Kolmogorov-Smirnov critical value (95%).

FACTOR RE5								
POPULATIONS	N	nc	R	M	S	SM	K-S	K-SC
PMT8/80	11	49	31.53 – 42.90	36.06	3.45	1.04	0.159	0.391
PMT8	35	366	23.87 – 48.51	33.93	4.47	0.75	0.171	0.224
PMT16	19	57	26.51 – 49.97	38.94	5.31	1.21	0.165	0.301
PMT18*	8	41	32.09 – 45.36	37.37	5.22	1.84	0.197	0.454
PMT20	21	83	25.41 – 47.67	35.42	5.75	1.25	0.128	0.288
PMT21	41	219	28.12 – 48.34	38.55	5.06	0.79	0.062	0.208
PMT22	31	310	25.86 – 47.20	35.54	4.74	0.85	0.164	0.238
PMT23	54	655	26.89 – 54.80	37.86	5.94	0.80	0.069	0.182
PMT23/6	32	126	26.59 – 57.85	41.02	7.46	1.31	0.087	0.234
PMT23/7	35	163	25.72 – 55.44	40.60	6.50	1.09	0.098	0.224
PMT23/8	28	135	31.74 – 51.22	40.78	5.42	1.02	0.155	0.250
PMT24	56	619	29.02 – 51.53	40.62	5.74	0.76	0.069	0.178
PMT24B	33	158	24.54 – 56.06	37.69	6.84	1.19	0.093	0.231
PMT24C	19	124	26.66 – 49.51	38.38	5.70	1.30	0.080	0.301
PMT24D	14	77	28.68 – 50.31	38.55	6.58	1.75	0.159	0.349
PMT24E	16	92	25.08 – 57.73	42.64	8.67	2.16	0.116	0.327
PMT30	53	617	28.49 – 52.47	38.96	4.93	0.67	0.121	0.183
PMT32	52	534	23.08 – 53.69	39.27	6.07	0.84	0.070	0.185

Tab. 6 - Results of measurements on the factor Re5 (5th pseudo annulus) in *Nephrolepidina* from Mt. Torretta section (symbols as in Tab.5).

FACTOR SI5								
POPULATIONS	N	nc		M	S	SM	K-S	K-SC
PMT8/80	11	49	122.85 – 225.28	162.48	28.75	8.66	0.173	0.391
PMT8	35	366	97.58 – 284.28	174.28	45.67	7.71	0.091	0.224
PMT16	19	57	86.84 – 260.97	147.08	35.81	8.21	0.192	0.301
PMT18	8	41	65.66 – 207.23	150.97	51.39	18.16	0.248	0.454
PMT20	21	83	90.75 – 284.13	167.24	51.47	11.23	0.169	0.288
PMT21	41	219	73.02 – 256.76	148.50	35.42	5.53	0.093	0.208
PMT22	31	310	83.05 – 220.37	164.98	38.35	6.88	0.155	0.238
PMT23	54	655	78.41 – 280.54	150.54	46.13	6.27	0.092	0.182
PMT23/6	32	126	54.08 – 286.90	129.63	52.45	9.27	0.144	0.234
PMT23/7	35	163	55.08 – 296.43	120.15	46.96	7.93	0.121	0.224
PMT23/8	28	135	41.00 – 186.53	120.37	35.92	6.78	0.134	0.250
PMT24	56	619	44.78 – 230.90	120.44	44.20	5.90	0.072	0.178
PMT24B	33	158	36.52 – 232.37	136.13	49.89	8.68	0.069	0.231
PMT24C	19	124	75.08 – 211.24	129.38	36.68	8.41	0.208	0.301
PMT24D	14	77	81.27 – 211.23	135.59	45.58	12.18	0.174	0.349
PMT24E	16	92	49.68 – 259.77	110.80	55.89	13.97	0.172	0.327
PMT30	53	617	21.83 – 213.29	107.24	36.23	4.97	0.075	0.183
PMT32	52	534	6.42 – 281.23	109.65	52.52	7.28	0.158	0.185

Tab. 7 - Results of measurements on the factor SI5 (5th pseudo annulus) in *Nephrolepidina* from Mt. Torretta section (Symbols as in Tab.5).

Overall, the trends in accordance with the principle of the “embryonic acceleration” (Drooger and Freudenthal, 1964) can be clearly seen.

5.1.1. Deviations from the overall evolutionary pattern

Some irregularities are superimposed to the trends. About possible causes and meaning of the deviations, something may be added to what was indicated in Giannini et al. (2007). Maybe, the occurrence of twin embryos, detected in samples PMT23/6 (Fig. 11) and PMT18 (Fig. 12), could be related to the extreme depths of the total distribution range of a larger foraminiferal taxon, where asexual reproduction and adaptive r-strategy dominate far from the ecological optimum. So, these environmental conditions were unfavourable for the regular evolutionary development of the embryonic-nepionic stages (Benedetti, 2015).

5.1.1.1. Evolutionary stages

The PMT populations are plotted in the $\bar{A}i - \bar{C}$ scatter diagram of Figure 13, based on Drooger and Rohling (1988), and including also recent additional data about populations from central Apennines, Sicily and Turkey (Benedetti et al., 2010; Benedetti and Pignatti, 2013; Özcan and Less, 2009; Özcan et al., 2009a,b, 2010; Schiavinotto, 2010, 2015).

The mean values of the Monte Torretta populations fall mainly within the sequence of intermediate-high fields that characterize the Mediterranean lineage. In these

fields, many statistic comparisons are possible without significant differences.

Some PMT populations are not in tune with the expected position; anyway, the overall increase of the mean values may be interpreted at least as a slightly weak significance of $\bar{A}i$ and \bar{C} for the definition of the intermediate evolutionary stages.

Moreover, primitive populations from Majella (S. Spirito Formation) studied by Benedetti et al. (2010) and from Sicily (Benedetti and Pignatti, 2013), are at a very low evolutionary stage for both $\bar{A}i$ and \bar{C} and very significant differences result from comparisons with the lower populations studied here. In the higher part of the distribution, PMT populations have a drop in the \bar{C} values, along some populations from Turkey. As a tentative suggestion, it seems that a slight differentiation of the overall trend took place.

5.1.1.1.1. Embryo-size. The insertion of the data in the $\bar{C} - \bar{D}I$ and $\bar{D}I - \bar{D}II$ scatter diagrams (Figs. 14 and 15) (see also de Mulder, 1975; van Heck and Drooger, 1984; Schiavinotto, 2010), permits a simple comparison with the embryo sizes of the most Mediterranean populations. The mean values of PMT populations are among those that are related to the same embryo-nepionic evolutionary degree, and PMT8/80 reaches the “jumbo” mean values detected in populations from Mt. La Serra and Rosignano.

Populations from Sicily, Majella, Turkey are in somewhat separated fields.

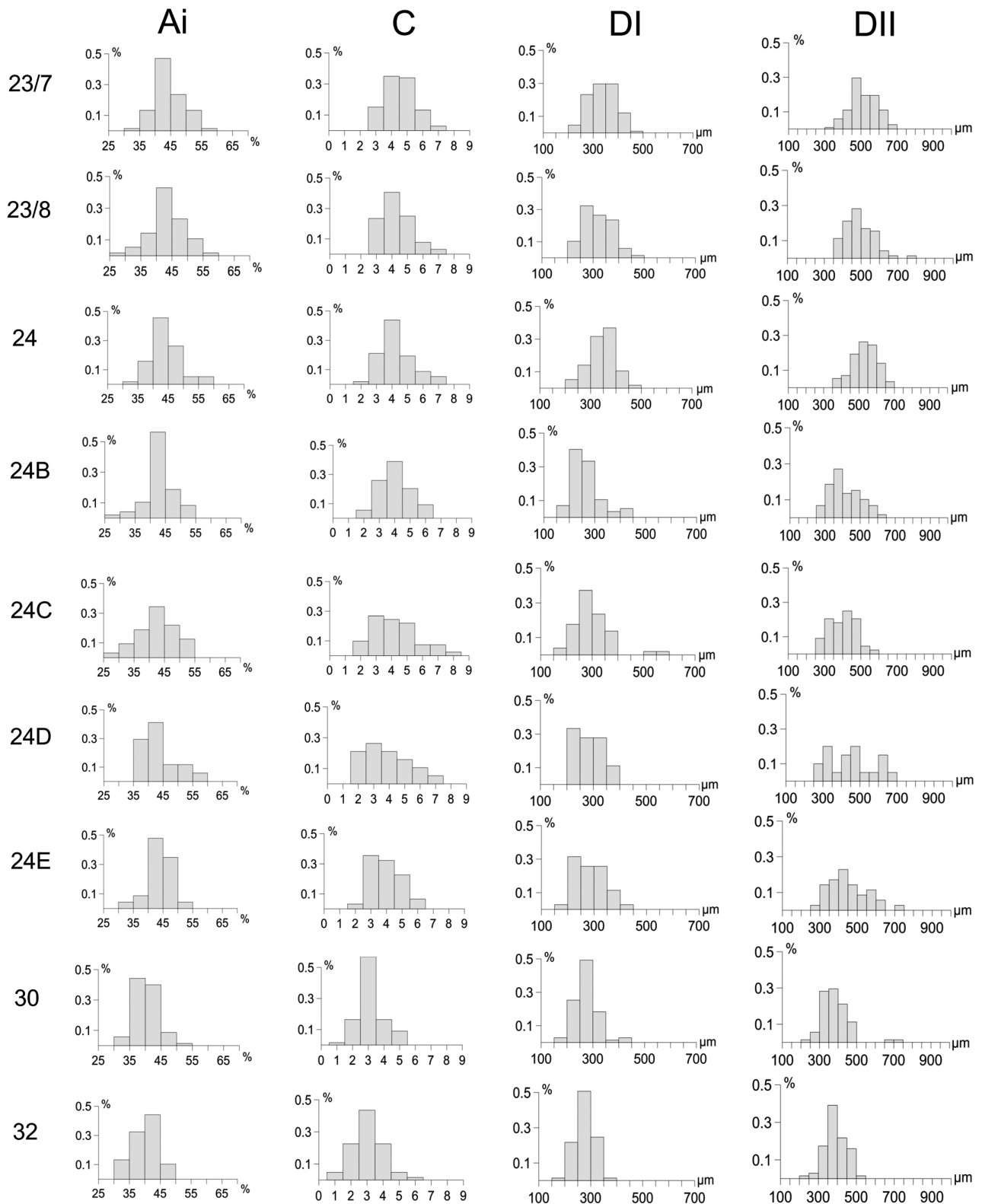


Fig. 4 - Histograms showing the frequency of the values of the factor Ai and parameters C, DI and DII obtained in the first half PMT *Nephrolepidina* populations sequence.

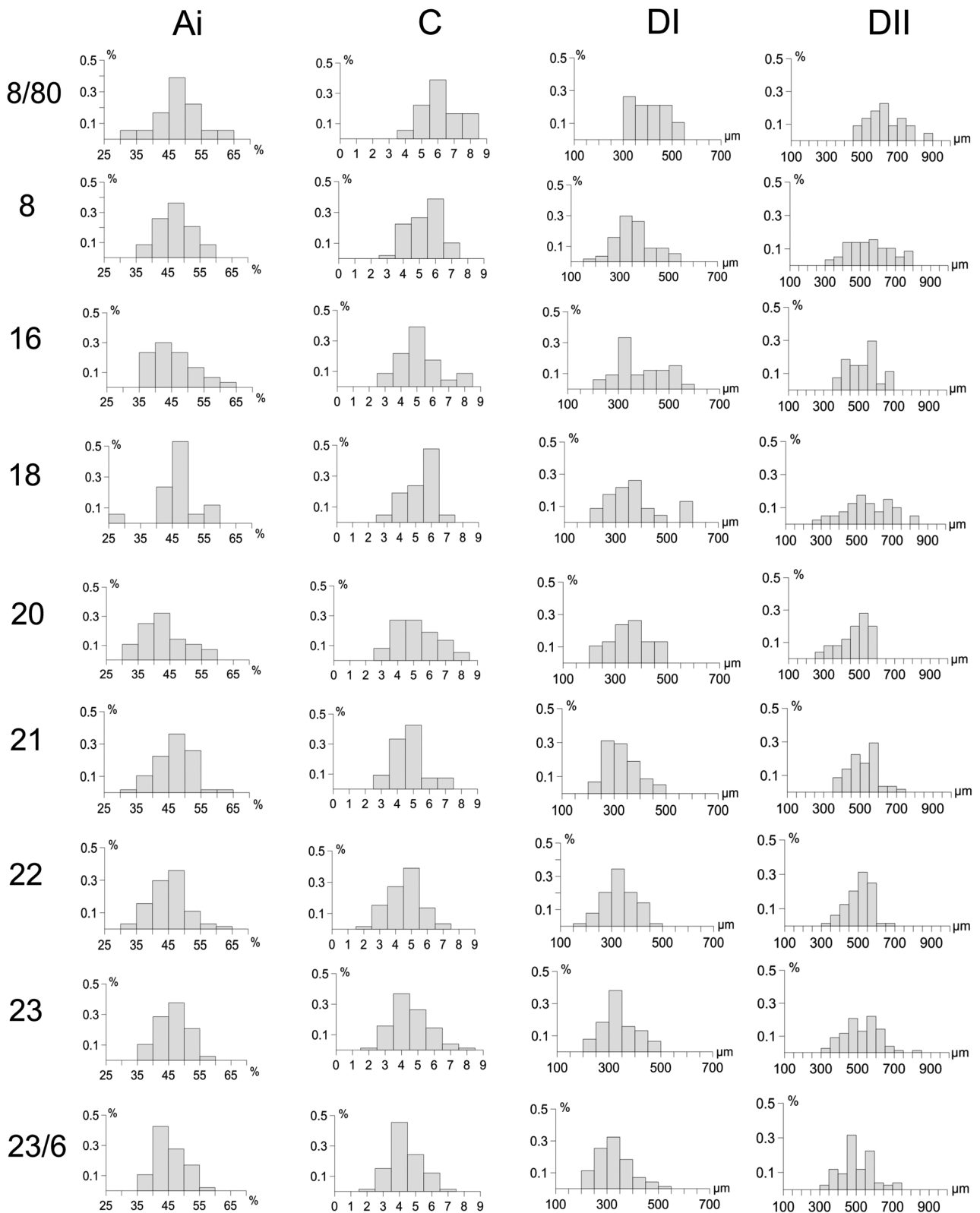


Fig. 5 - Histograms showing the frequency of the values of the factor Ai and parameters C, DI and DII obtained in the second half PMT *Nephrolepidina* populations sequence.

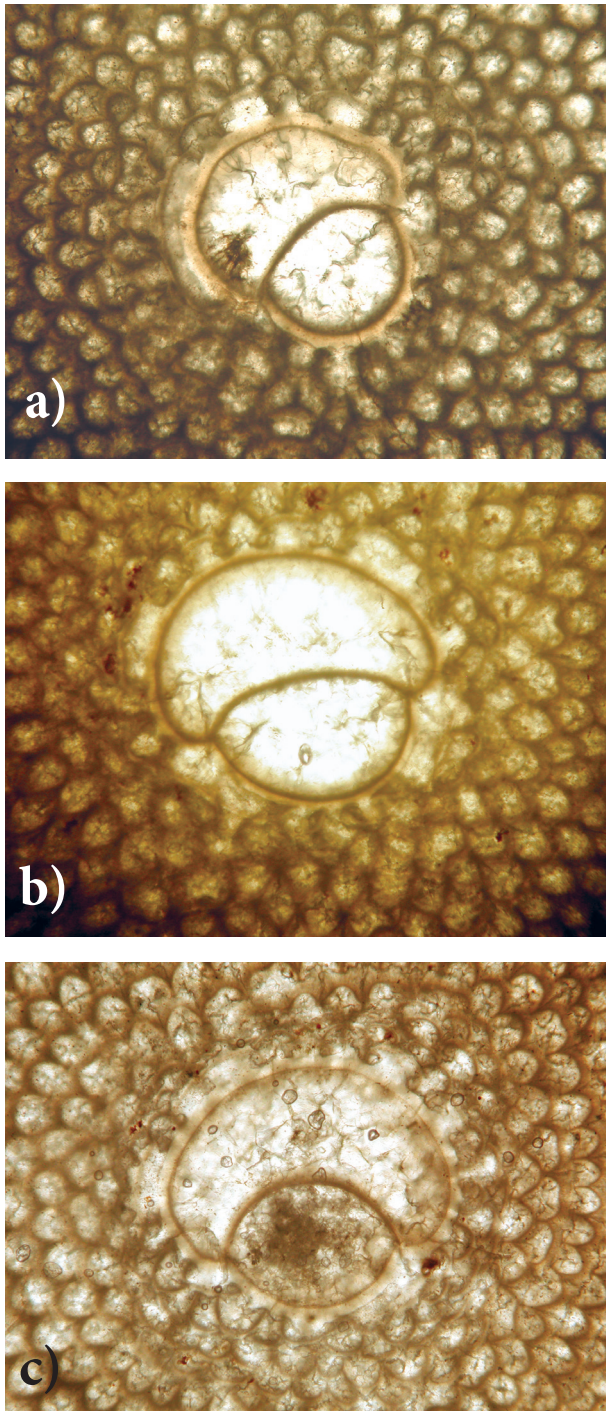


Fig. 6 - a) Specimen with A_i below 40%; Sample PMT32, no 30, 90x.; b) “Nephrolepidine-type” specimen (A_i between 40 and 45%); sample PMT24, no 15, 85x; c) “Trybliolepidine-type”, with A_i above 50%; sample PMT8, no 25, 50x.

5.1.1.1.1.1. Neanic trends - Mean values of Factors FD5 and SI5 are compared with mean values of A_i and C (Fig. 16) and of DI and DII (Fig. 17). A neanic trend towards an increase of the values is evidenced. The oscillating pattern appears to be softened and, frequently, it is reverse.

The data indicate that the evolutionary process according to the progressive increase of the “stolonic

distalization” is a trend strong enough, at least up to the construction of the 6th annulus. At this stage of growth, the trend appear to be superimposed on attenuations that may be caused by the physical environment, and not by the adaptive strategy -reproduction cycle - embryo size relations. The greater distalization of the stolons, and therefore a more radial disposition of them, would be an advantageous characteristic probably permitting a greater efficacy in the quicker construction of the equatorial plane. Thus, “greater facility of movement for the cytoplasm in the construction of wider annuli = more elongated chambers” (Schiavinotto, 1995, p. 281) could be related with the new delineation of the spiral growth in *Nephrolepidina*, suggested by Benedetti (2014), i.e., that more elongated chamberlets are a consequence of their increasing packing.

6. NEANIC ACCELERATION

The scatter diagram $\bar{FD5} - \bar{SI5}$ in Figure 18 might be a significant representation of the trend that is defined as “neanic acceleration”.

It is also of particular interest that the mean values of FD5 and SI5 of many PMT populations are closer to the mean values regarding the T1 population, still differing from TLS76 and AC5.

These results evidence that the herein investigated intermediate *Nephrolepidina* can be differentiated from the more primitive and from the more advanced stages, at the level of the studied ontogenetic stage (5th pseudo-annulus), on the basis of the “degree of stolonic distalization” and of the “shape index”. This discrimination is much more marked than those obtained for populations of *N. tournoueri* and *N. praemarginata* (Schiavinotto, 1992, 1994). Therefore, the variations of the parameters/factors, as a whole, evidence the following tendencies in the changes of the morphology of neanic equatorial chamberlets in *Nephrolepidina*:

- increase of the degree of elongation;
- increase of the lateral length “c” of the common wall between contiguous chamberlets;
- consequent increase of the Degree of Stolonic Distalization;
- increase of the Shape Index, tending to more elongated chamberlets with smaller degree of curvature of the frontal wall.

So, the data obtained on the degree of stolonic distalization in *Nephrolepidina* from Mt. Torretta provide another quantitative definition of the ontogenetic development already described qualitatively by Grimsdale (1959), Eames et al. (1962), Sirotti (1982 a,b) and Adams (1987) for *Nephrolepidina*, and by van Gorsel (1975, 1978) for *Orbitoides* and *Lepidorbitoides*. In fact, the distal end of the common wall between contiguous chamberlets fits with the position of the radial (intercyclic) stolons; the more this wall is developed, the greater also is the distance of the annular (concylic) stolons from the proximal end of the common walls (Eames et al., 1962; Adams, 1987).

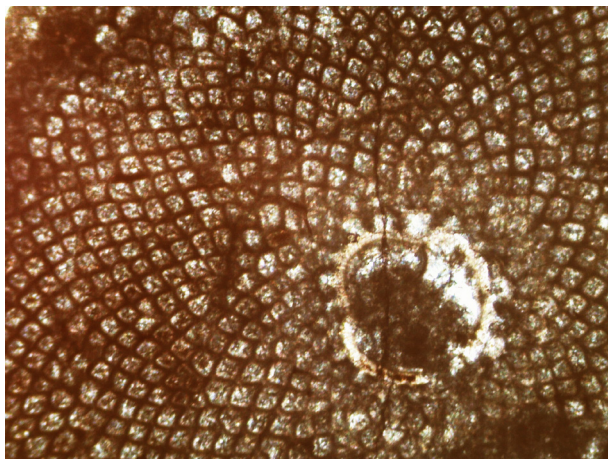


Fig. 7 - Specimen with a "degree of distalization" (FD5) around 50%; sample PMT8, no 12, 40x.

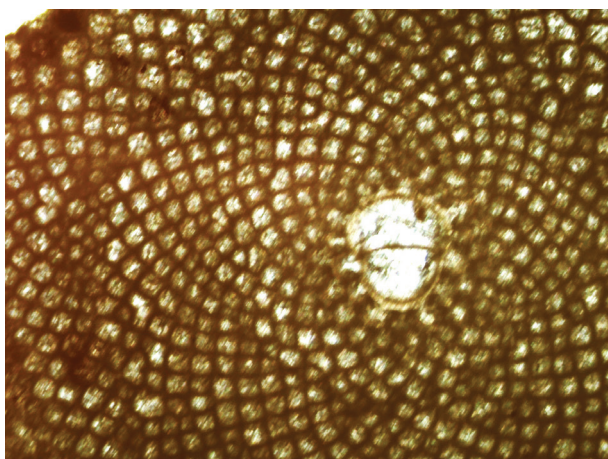


Fig. 8 - Specimen with rather primitive equatorial chambers (FD5 between 15 and 25%); sample PMT32, no 22, 35x).

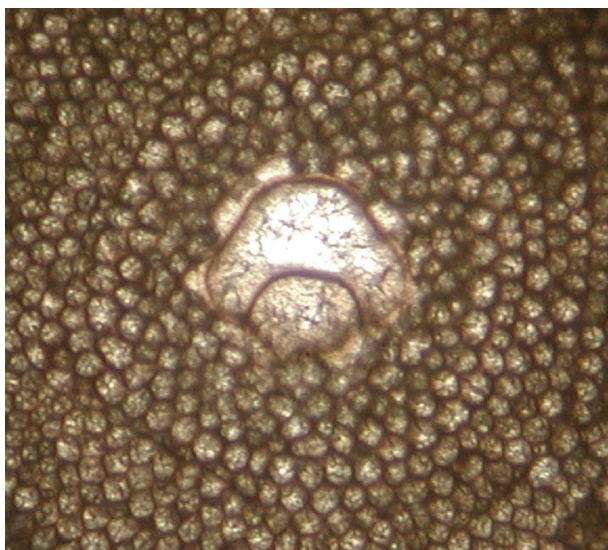


Fig. 9 - Specimen with FD5 around 60%; sample PMT23, no 55a, 40x.

The Factor SI5 confirms the progressive weakening of the initially pointed-arcuated characteristic of the front wall, which can be connected with a more distal position and a less radial trend of the intercytic radial stolons; consequently, the morphological differences between chamberlets of successive pseudo-annuli are emphasized.

6.1. Combined trends

The $\bar{A}i - \bar{F}D5$, $\bar{C} - \bar{F}D5$ and $\bar{F}D5 - \bar{S}I$ scatter diagrams (Figs. 19, 20, and 21) show that the PMT populations are arranged in agreement with the previously detected combined trends towards higher values; three groups of populations appear clearly discriminated.

Perhaps, further additional data may evidence more subtle discriminations.

7. TAXONOMY

The ranges of the mean values of Ai and C are at the basis of the taxonomy of *Nephrolepidina*, at a specific level. These features have been considered for a long time to be useful to describe the *Nephrolepidina* evolutionary trends from both the Mediterranean and the Indo-Pacific area (van der Vlerk, 1959 a,b, 1963, 1964, 1968; Drooger and Freudenthal, 1964; de Mulder, 1975; van Vessem, 1978). The definition of the lineages that are present in the different biogeographic provinces were correlated with the stratigraphic scale; these delineations were accompanied by various attempts to transpose specific taxa at a supraspecific level (Cole, 1960, 1963; Eames et al., 1962; Hanzawa, 1962, 1964; Sirotti, 1982 a,b; Adams, 1987; BouDagher-Fadel and Price, 2010).

According to the phylogenetic classification of the Lepidocyclinidae proposed by Sirotti (1982 a,b), the investigated specimens belong to the genus *Nephrolepidina*. As yet, the Mediterranean *Nephrolepidina* species have been defined on the basis of the average values of the factor Ai and the parameter C . According to de Mulder (1975) and van Heck and Drooger (1984), the boundaries between the species are:

Nephrolepidina praemarginata

$35 < \bar{A}i \leq 40$ and $1 < \bar{C} \leq 3$

Nephrolepidina morgani

$40 < \bar{A}i \leq 45$ and $3 < \bar{C} \leq 5.25$

Nephrolepidina tournoueri

$45 < \bar{A}i$ and $\bar{C} > 5.25$

Following the chronospecies criteria of de Mulder (1975), the mean values of Ai are adequate to refer the PMT populations to the entire sequence *N. praemarginata* (R. Douvillé, 1908) - *N. morgani* (Lemoine and R. Douvillé, 1908) - *N. tournoueri* (Lemoine and R. Douvillé, 1908).

In Table 8, PMT22 has an ambiguous, problematic specific reference, probably because the parameter C has not a normal distribution.

The final part of the sequence of populations results improved, with a more gradual, univocal assignment to a transition *morgani-tournoueri*, up to the definitive *tournoueri* in the upper populations PMT8 and PMT8/80.

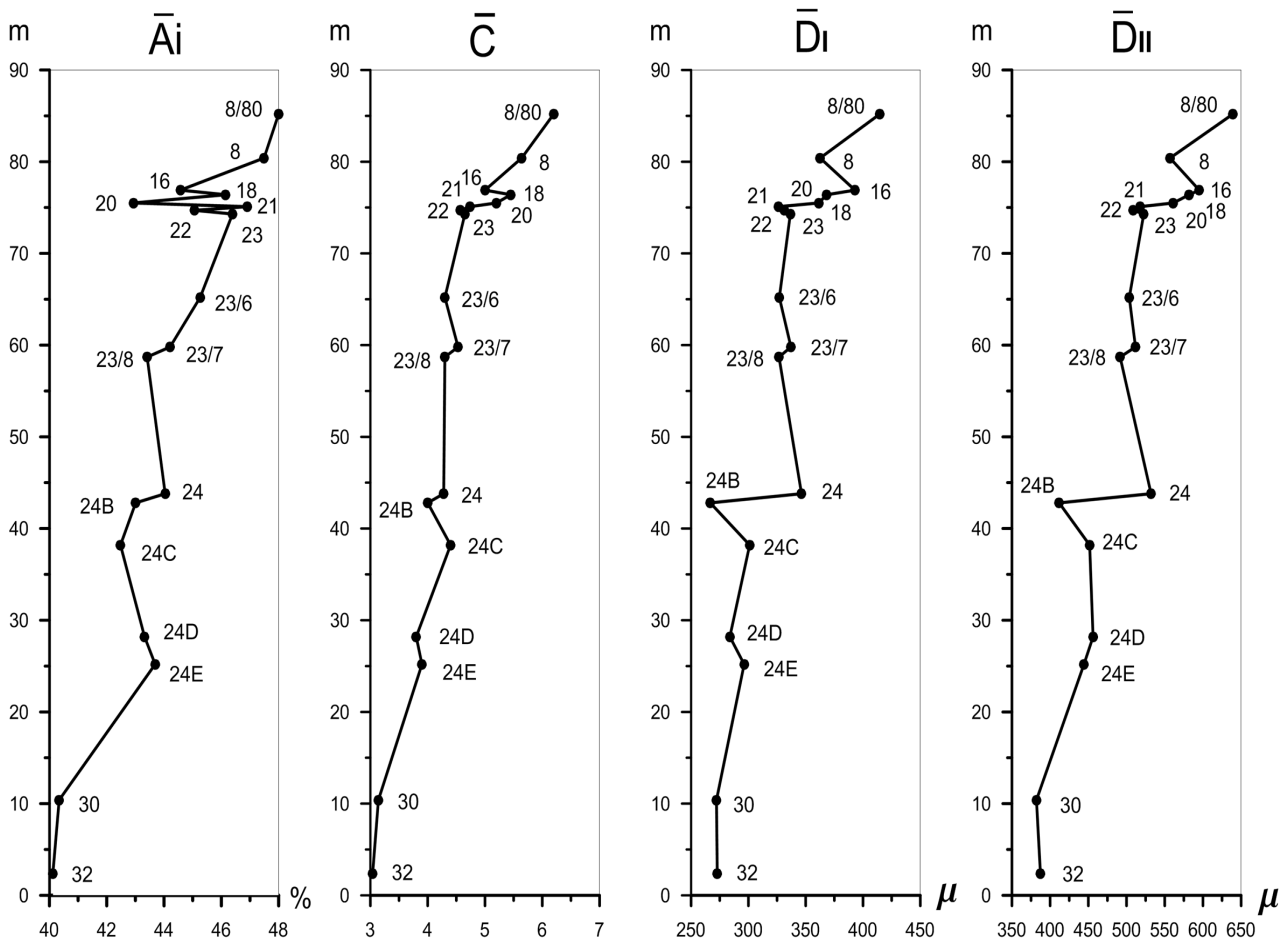


Fig. 10 - Variation of the mean values of embryonic-nepionic factors and parameters measured in the *Nephrolepidina* populations from Mt. Torretta section.

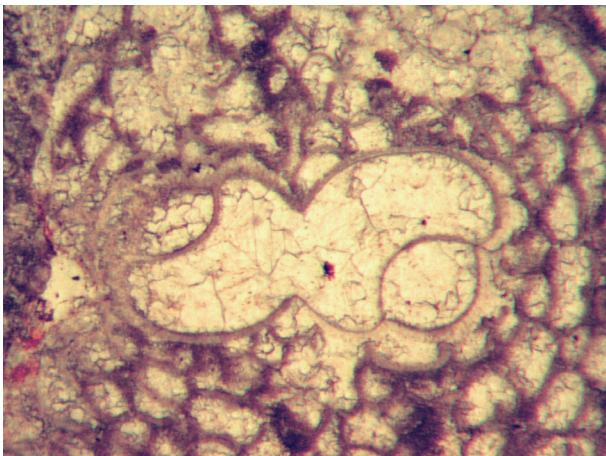


Fig. 11 - Twin embryos, Sample PMT23/6, 50x.

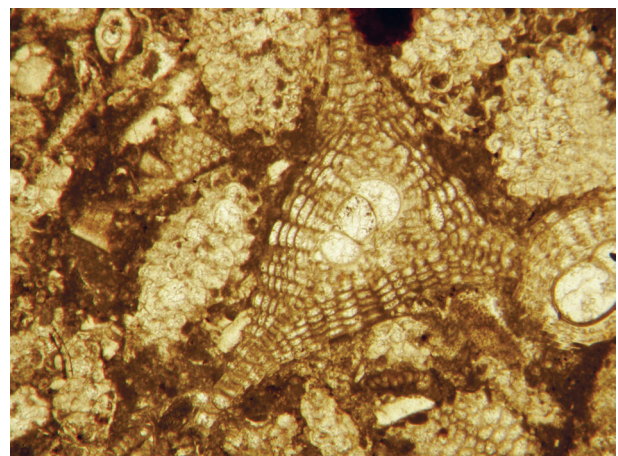


Fig. 12 - Twin embryos, Sample PMT18, 20x.

The investigated populations, plotted in the $\bar{A}_i - \bar{C}$ scatter diagram of Figure 13, give more evidence to the results in Table 8.

However, the evolutionary stages of the Mt. Torretta populations are quite high both for \bar{A}_i and \bar{C} , enough to result without significant differences when compared with some populations from Turkey, as KIR, HAC2-4,

HAC6-8, referred to *N. ex.interc. morgani-tournoueri* and *N. tournoueri-morgani* (Özcan et al., 2009a). Populations in Özcan et al. (2010), referred to the new species *N. musensis*, are significantly more primitive only for \bar{C} .

N. praemarginata populations from the Majella Mt. (Santo Spirito Formation) studied by Benedetti et al. (2010) and from Sicily (Benedetti and Pignatti, 2013),

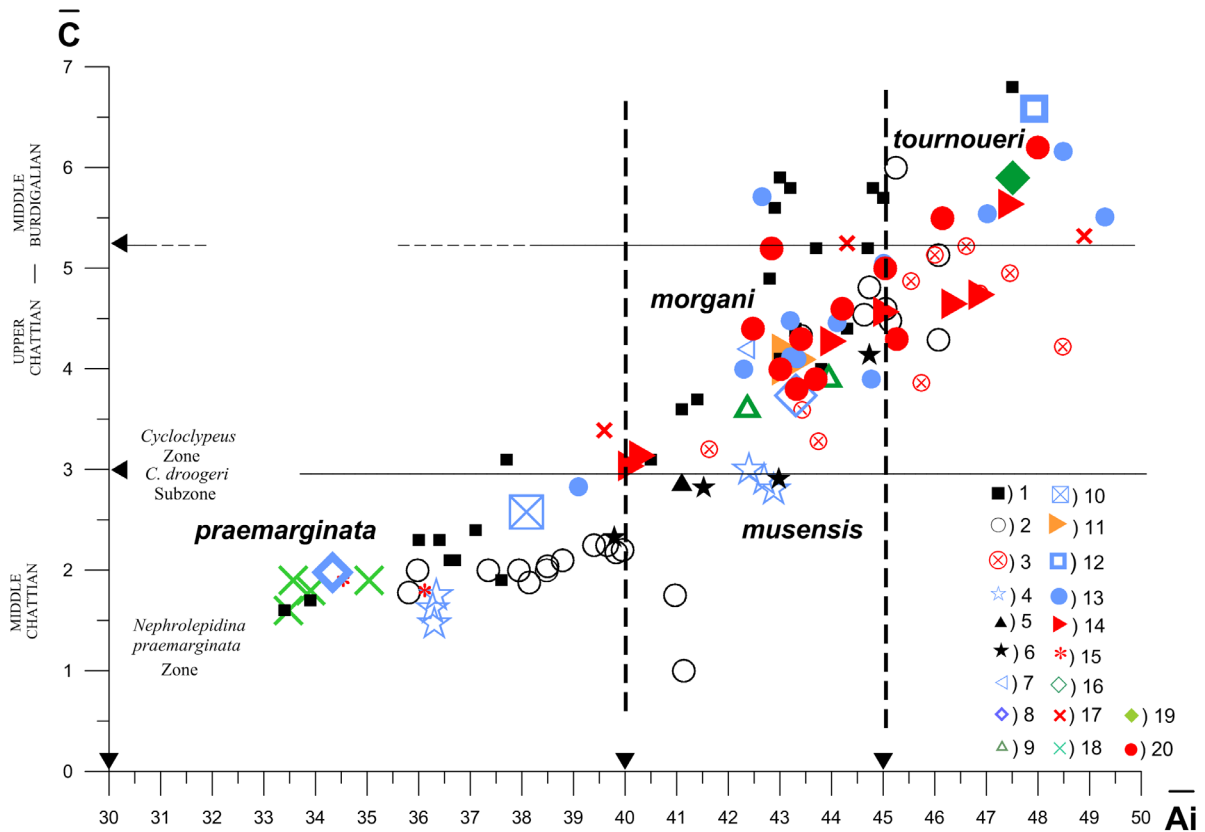


Fig. 13 - $\bar{A}_i - \bar{C}$ scatter diagram for a significant part of the available data on the Mediterranean *Nephrolepidina* populations: 1) Greece, de Mulder, 1975; 2) western Taurids, Özcan et al., 2009a; 3) Sivas basin-central Turkey, Özcan et al., 2009b; 4) eastern Turkey, Özcan et al., 2010; 5) Piedmont, Meulenkamp and Amato, 1972; 6) northern Italy, Matsumaru, 1971; 7) northern Italy, Serpagli and Sirotti, 1966; 8) northern Italy CVM76, Schiavinotto, 1978; 9) northern Italy LND, Schiavinotto, 2010; 10) Monte La Rocca TRMn, Matteucci and Schiavinotto, 1977; 11) Majella DE208, Schiavinotto, 2015; ; 12) Monte La Serra TLS76, Schiavinotto, 1979; 13) Gran Sasso TV, Schiavinotto and Verrubbi, 1994, 2000; 14) Monte Torretta PMT, Giovagnoli and Schiavinotto, 1995; 15) Majella, Benedetti et al, 2010; 16) Monte La Rocca T1, Matteucci and Schiavinotto, 1977; 17) Sicily, Wildenborg, 1991; 18) Sicily, Benedetti and Pignatti, 2013; 19) Sardinia AC5, Giovagnoli and Schiavinotto, 1990; 20) Monte Torretta PMT, Giannini et al., 2007, corrected (this paper).

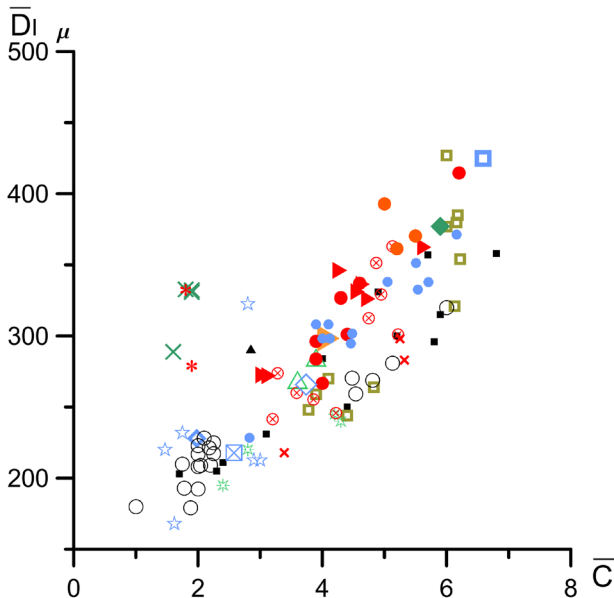


Fig. 14 - $\bar{C} - \bar{D}_I$ scatter diagram with PMT population that are plotted into the field of mean values obtained from the previous literature. \square) Droogier and Freudenthal, 1964; \star) Piedmont, Vervloet, 1966; other symbols as in Figure 13.

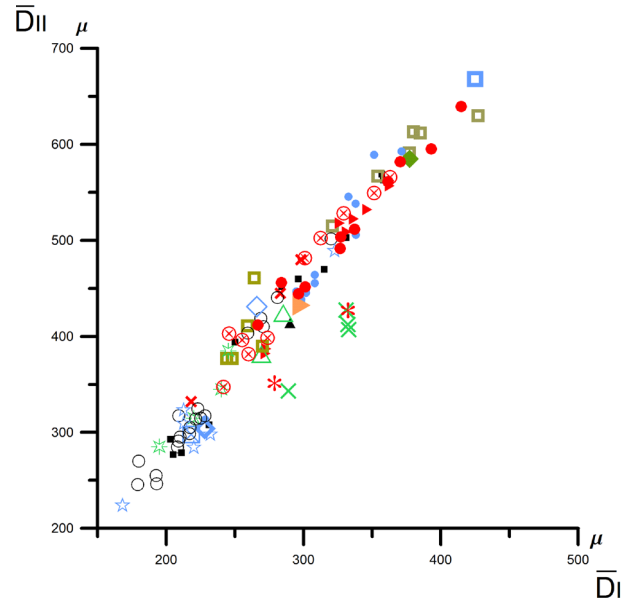


Fig. 15 - $\bar{D}_I - \bar{D}_{II}$ scatter diagram. PMT populations are plotted with mean values from the literature. Symbols as in Figure 13 and 14.

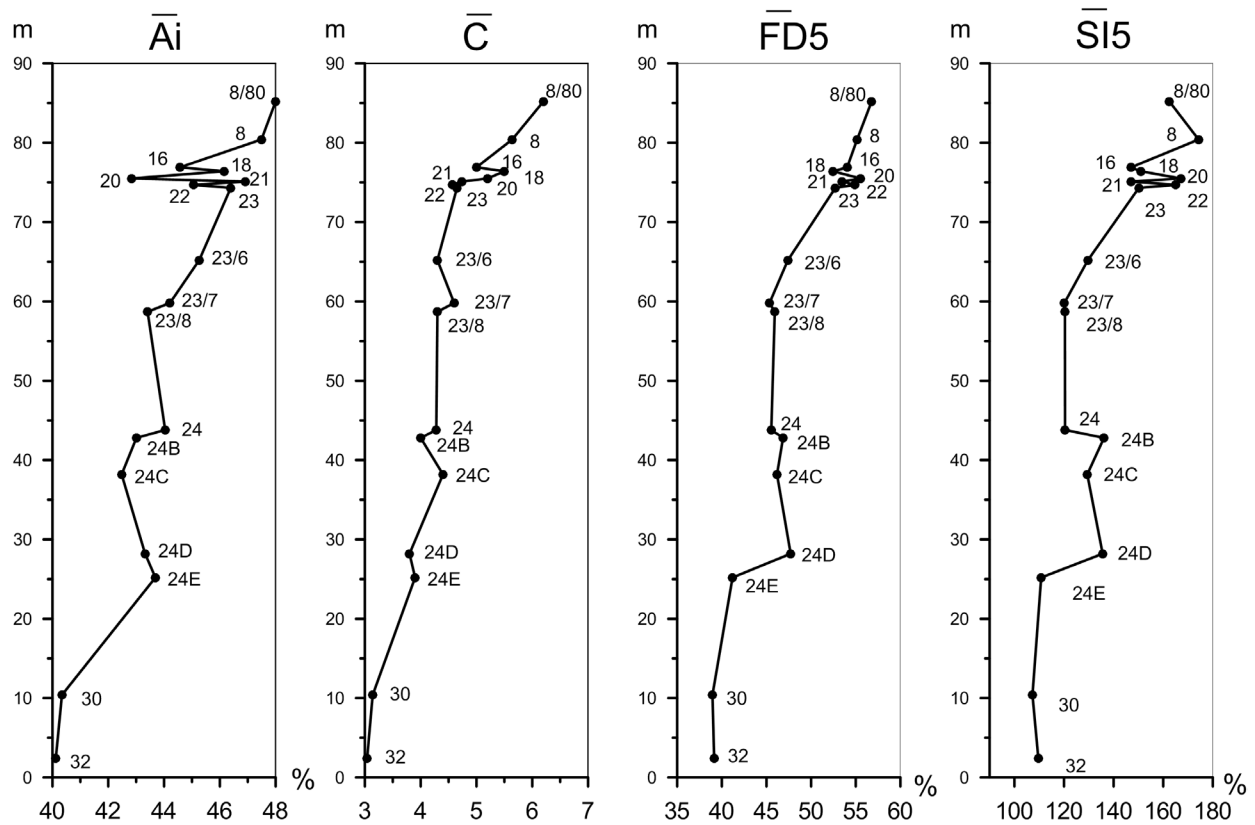


Fig. 16 - Comparison between the variation of the mean values of embryonic-nepionic factor \bar{A}_i , parameter \bar{C} and the neanic factors $\bar{FD5}$ and $\bar{SI5}$, measured in the *Nephrolepidina* populations from Mt. Torretta section.

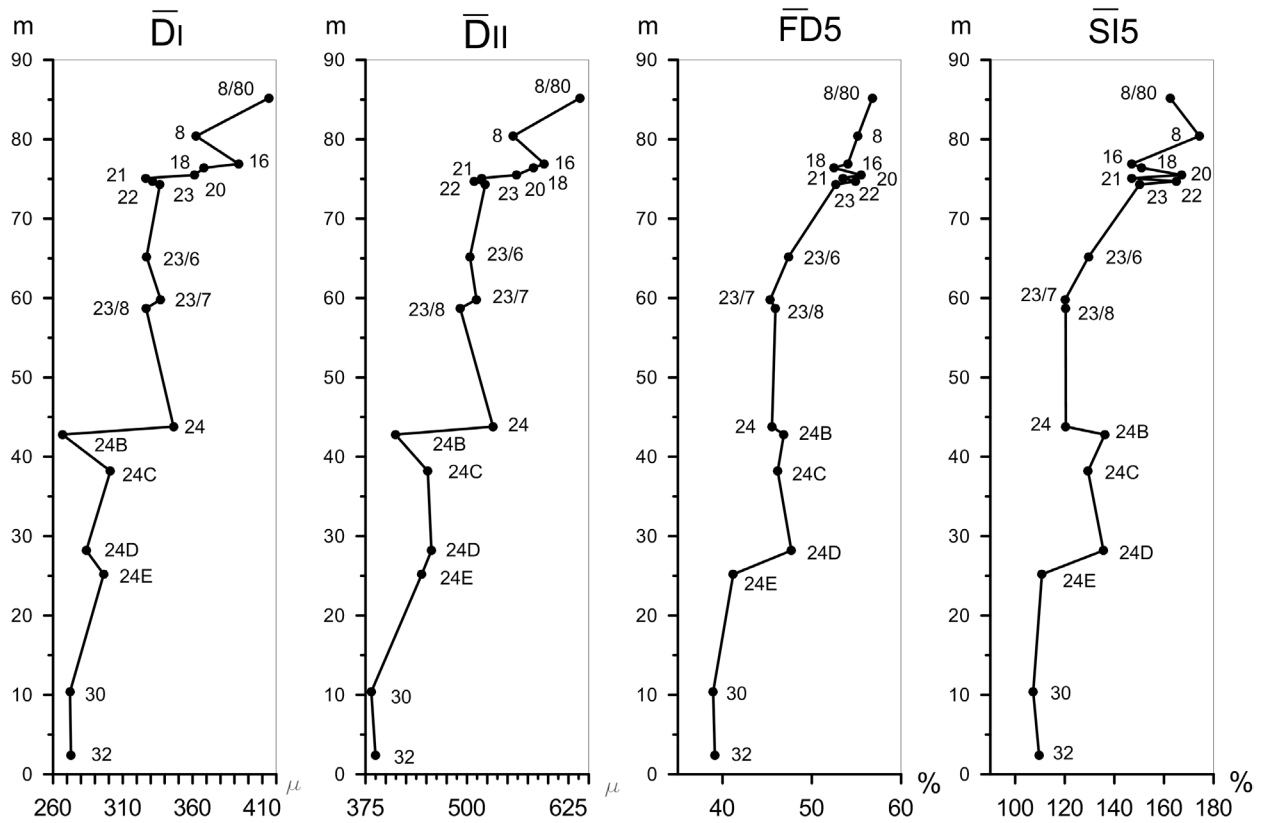


Fig. 17 - Comparison between the variation of the mean values of embryonic dimensions \bar{DI} , \bar{DII} and the neanic factors $\bar{FD5}$ and $\bar{SI5}$, measured in the *Nephrolepidina* populations from Mt. Torretta section.

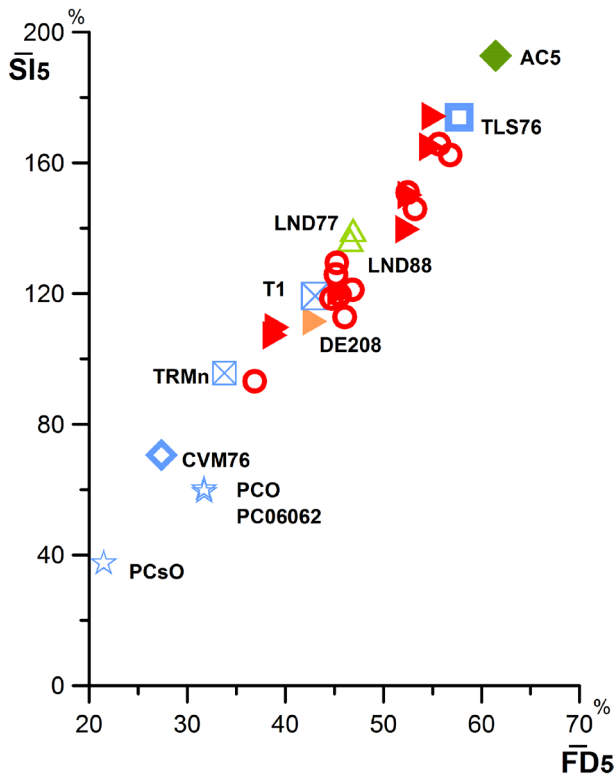


Fig. 18 - $\bar{FD}5$ - $\bar{SI}5$ scatter diagram for the *Nephrolepidina* populations studied to date. Mean values after Schiavinotto (1992, 1993, 1994, 2010, 2015; Benedetti and Pignatti, 2013). (○) same PMT populations in Giannini et al. (2007), other symbols as in Fig.13.

are at a very low evolutionary stage and very significant differences result from comparisons with PMT32-PMT30 populations.

8. BIOSTRATIGRAPHIC REMARKS

The PMT32-PMT30 populations may be referred to the early Chattian, whereas the low stage *N. praemarginata* was yet referred to the late Rupelian (SBZ22A of Cahuzac and Poignant, 1997), (Benedetti et al., 2010).

The intermediate populations, up to PMT23/7 are referred to the nominal species *N. morgani*.

The occurrence of fragments, transversal sections, and a microspheric specimen of *Cycloclypeus* (Fig. 22) in the sample PMT24B restricts its age at least to the early Chattian (SBZ22B of Cahuzac and Poignant, 1997). In addition, the population PMT24 shows biometrical affinities with the population T1 from Mt. La Rocca (Matteucci and Schiavinotto, 1977, 1985), type level of the species *Cycloclypeus mediterraneus* marking the SBZ23. A possible correlation with the *Miogypsinoides complanatus* Subzone, according to the biostratigraphic scheme of Laagland (1990), with reference to Berggren et al. (1995) and Berggren and Pearson (2005).

The PMT24 population fit with *N. morgani* from Lonedo (Schiavinotto, 2010) and from Decontra (Schiavinotto, 2015, sample DE208).

The following populations, assigned to *N. tournoueri*, are referable to the upper part of the SBZ24 (upper Aquitanian) because of the occurrence of *Miogypsina tani* (PMT8) and Miolepidocyclinids (PMT8/80), according to Delicati and Schiavinotto (1987).

The upper part of the section may be referred to the lower part of SB25 (lower Burdigalian) by the presence of *M. globulina*, but no populations of *Nephrolepidina* were reliable for biometric studies, because of the rarity or absence of specimens, and very random orientation of the tests in the thin sections of hard-rocks.

Nephrolepidina populations at the same evolutionary degree have been described in association with *M. globulina* and *M. intermedia*, and referred to the late Aquitanian-Burdigalian (Drooger and Socin, 1959; Drooger and Freudenthal, 1964; de Mulder, 1975; Schiavinotto, 1979; Drooger and Laagland, 1986; Giovagnoli and Schiavinotto, 1990).

Although the PMT23 population shows mean value of \bar{A}_i perfectly comparable with that of TLS76, the index \bar{C} is significantly lower. Consequently, the nepionic acceleration seems to happen at a lower rate than does the embryonic acceleration.

The same comparisons are evidenced with the more advanced populations from Turkey: the *N. morgani* assemblages, quite ex.interc. with *N. tournoueri* are referred to the SBZ25 of Cahuzac and Poignant (1997), mainly based on the *Miogypsinids* indicating a Burdigalian age. In the \bar{A}_i - \bar{C} scatter diagram of Figure 13, PMT21 and PMT23 drop from the field of *N.*

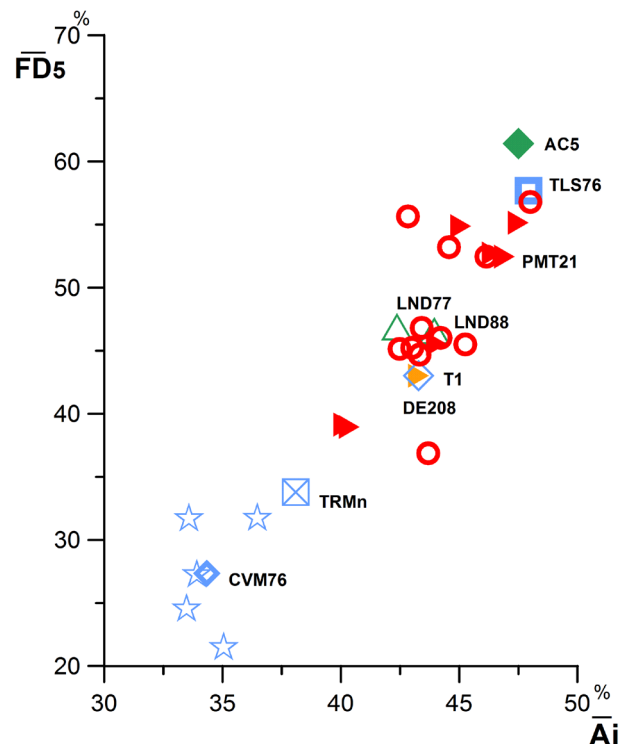


Fig. 19 - \bar{A}_i - $\bar{FD}5$ scatter diagram for the *Nephrolepidina* populations studied to date. Mean values after Schiavinotto (1992, 1993, 1994, 2010, 2015; Benedetti and Pignatti, 2013). Symbols as in Fig. 18.

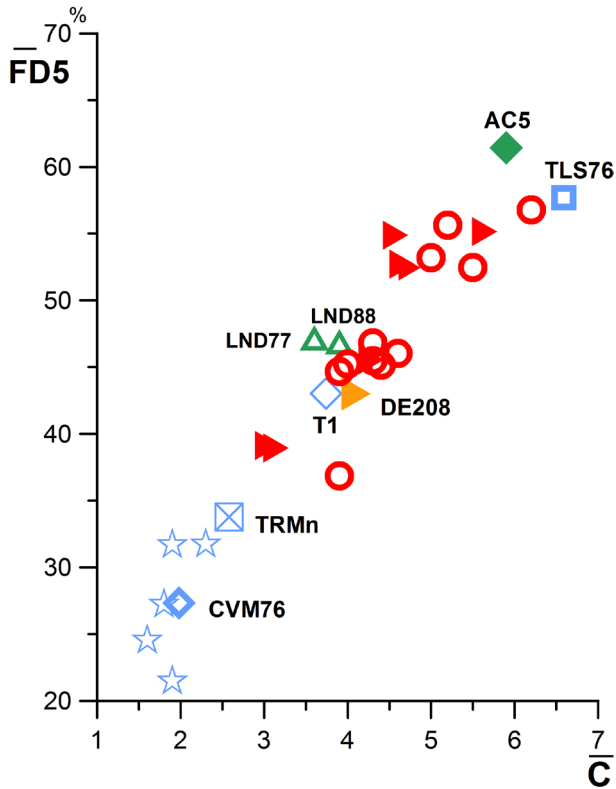


Fig. 20 - \bar{C} - $\bar{FD5}$ scatter diagram for the *Nephrolepidina* populations studied to date. Mean values after Schiavinotto (1992, 1993, 1994, 2010, 2010; Benedetti and Pignatti, 2013). Symbols as in Fig. 18.

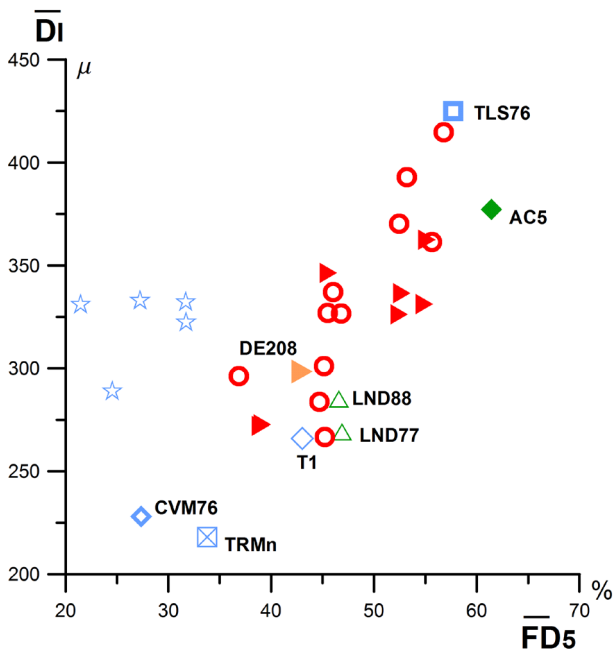


Fig. 21 - $\bar{FD5}$ - \bar{DI} scatter diagram for the *Nephrolepidina* populations studied to date. Mean values after Schiavinotto (1992, 1993, 1994, 2010, 2010; Benedetti and Pignatti, 2013). Symbols as in Fig. 18.

turnoueri to the underlying uncertain field, because of their too much low \bar{C} value. Moreover, PMT18 fits in the *turnoueri* field, because of the low number of studied specimens, with consequent high Sm both for \bar{A}_i and \bar{C} .

According to Özcan et al. (2009a, 2010), *N. morgani* has a long stratigraphic range from the late Chattian to the early Burdigalian (SBZ 23 to the early part of SBZ 25) whereas *N. turnoueri* spans from the latest Aquitanian to the whole Burdigalian (late SBZ 24 and SBZ 25).

9. PERSISTENT TAXONOMIC AND BIO-STRATIGRAPHIC DIFFICULTIES

There is more evidence that the classification of de Mulder (1975) does not allow an optimal correlation with the plankton biostratigraphic scale because of the excessive range of *N. morgani*, unsuitable to define the Oligo-Miocene boundary, and to provide an unquestionable discrimination from *N. turnoueri*.

This criticism is amply documented in Schiavinotto (1996b) and briefly revisited here, as follows:

a) a phase of stasis at the level of the intermediate stages of the evolutionary process was shown; these stages are identified as *Nephrolepidina morgani* (Lemoine and R. Douvillé); consequently, this species is considered as not very useful for detailed biostratigraphic studies, in particular for the identification of the Oligo-Miocene boundary (Drooger et al., 1976; Drooger and Laagland, 1986).

b) Drooger et al. (1976, p. 322) state: “Among the orbital larger Foraminifera some four evolutionary lineages are thought to cross any Paleogene-Neogene boundary. Three of these have to be discarded immediately, *Eulepidina* and *Planolinderina* because their evolution is indistinct or of dubious value, nephrolepidinid *Lepidocyclina* because development is too slow. European deposits of reputed late Oligocene and early Miocene age all seem to contain the same species, *L. morgani*. Only the Miogypsinidae are thought to evolve more rapidly”.

c) Drooger and Laagland (1986, p. 138) added: “Following de Mulder’s classification (1975) of European *Nephrolepidina* (...) it is fairly certain that *L. morgani* crossed the Oligocene/Miocene boundary, being replaced during the Burdigalian or somewhat earlier, in the Aquitanian, by *L. turnoueri*, the next, more highly evolved species in the lineage” (...) “The slow numerical progress in this lineage and especially the double morphometric definition of the species limits have led to the recognition of a wide array of morphologically intermediate assemblages (...) For actual stratigraphic correlations these negative aspects entail that we must reckon with along indefinite time range corresponding to the transition from *L. praemarginata* to *L. morgani*”.

Also, Özcan et al. (2009b, p. 574), when discussing the difficulties in discriminating *N. morgani* from *N. turnoueri*, evidence “a clear contradiction to de Mulder’s suggestion of adopting the morphometric limits of both parameters to differentiate the two taxa”

Point “c” is a long-time taxonomic problem, affecting also the biostratigraphic field. Moreover, it is a problem that cannot be solved using uniquely a species-discrimination with the methodology based on typological criteria.

Criticism about numbers of species perceived as

Populations	$\bar{A}_i \pm S_m$	$\bar{C} \pm S_m$	\bar{A}_i and \bar{C}
PMT8/80	<i>ournoueri</i>	<i>ournoueri</i>	<i>ournoueri</i>
PMT8	<i>ournoueri</i>	<i>ournoueri</i>	<i>ournoueri</i>
PMT16	ex. interc. <i>morgani-ournoueri</i>	ex. interc. <i>morganiournoueri</i>	ex. interc. <i>morgani-ournoueri</i>
PMT18	ex.interc. <i>ournoueri-morgani</i>	ex.interc. <i>ournoueri-morgani</i>	ex.interc. <i>ournoueri-morgani</i>
PMT20	<i>morgani</i>	ex. interc. <i>morganiournoueri</i>	ex. interc. <i>morganiournoueri</i>
PMT21	<i>ournoueri</i>	<i>morgani</i>	ex.interc. <i>ournoueri-morgani</i>
PMT22	ex.interc. <i>ournoueri-morgani</i>	<i>morgani</i>	ex.interc. <i>ournoueri-morgani</i>
PMT23	<i>ournoueri</i>	<i>morgani</i>	ex.interc. <i>ournoueri-morgani</i>
PMT23/6	ex.interc. <i>ournoueri-morgani</i>	<i>morgani</i>	ex.interc. <i>ournoueri-morgani</i>
PMT23/7	<i>morgani</i>	<i>morgani</i>	<i>morgani</i>
PMT23/8	<i>morgani</i>	<i>morgani</i>	<i>morgani</i>
PMT24	<i>morgani</i>	<i>morgani</i>	<i>morgani</i>
PMT24B	<i>morgani</i>	<i>morgani</i>	<i>morgani</i>
PMT24C	<i>morgani</i>	<i>morgani</i>	<i>morgani</i>
PMT24D	<i>morgani</i>	<i>morgani</i>	<i>morgani</i>
PMT24E	<i>morgani</i>	<i>morgani</i>	<i>morgani</i>
PMT30	ex.interc. <i>morgani-praemarginata</i>	<i>morgani</i>	ex.interc. <i>morgani-praemarginata</i>
PMT32	ex.interc. <i>morgani-praemarginata</i>	ex.interc. <i>morgani-praemarginata</i>	ex.interc. <i>morgani-praemarginata</i>

Tab. 8 - Different specific determinations of *Nephrolepidina*, as result on the basis of each single variable (\bar{A}_i mean and \bar{C} mean), and according to the combination of the mean vales of \bar{A}_i and \bar{C} .

excessive has historical origins, as evidenced by a pioneer of Italian micropaleontology (Silvestri, 1914, p. 28-29), who reviewing a work by Douvillé (1912), wrote as follows:

“Nel corso del lavoro è contenuto un saggio critico su varie *Lepidocyclina* (*L. dilatata*, *L. Carteri*, *L. Gallieni*, *L. insulaenatalis*, *L. Gigantea*, *L. Ngembali*, *L. Provalei*, *L. formosa*, *L. Richtofeni*, *L. inermis*, *L. Verbeeki*, *L. Tournoueri var. angulosa* e *var. inflata*, *L. sumatrensis*), ed a proposito di esse afferma l'A che « les caractères les plus précis pour la distinction des espèces sont donnés par la forme et la disposition des piliers latéraux »; in ciò non

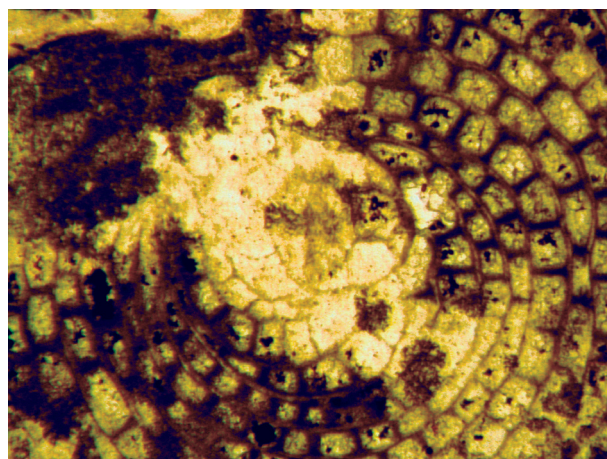


Fig. 22 - *Cycloclypeus* sp. , equatorial section in Sample PMT24 B, 100x.

possiamo trovarci d' accordo con lui, perchè riteniamo che tali pilastri sieno quanto mai variabili, e che quindi vi venga a far difetto quella tale precisione di caratteri, la quale egli utilizzerebbe per distinguere nelle *Lepidocyclina* le specie. Riteniamo poi che tutte le numerose e sedicenti specie di *Lepidocyclina*, si possano ridurre, quando a tutti i caratteri diagnostici diasi il giusto valore, a pochissime, e ciò con vantaggio reale per la geologia, e nessun danno per la paleontologia, che di specie mal istituite ne conta ormai fin troppe”.

Thus, according to Silvestri (1914): a) the pillars are a very variable character and consequently, there is a lack of precision using them to discriminate species in *lepidocyclinids*; b) the large number of *Lepidocyclina* species can be reduced to a few, “giving the right value to every diagnostic character, with true benefit for geology and no damage for paleontology, the latter possessing yet far too many poorly established species”.

These words were written more than a century ago, but the present situation is not changed, with the biometric studies that are followed by a minority, at least for the larger foraminifera, despite the present-day upgraded knowledge.

Frequently, both for *Miogyxina* and *Nephrolepidina* the morphotype-based approach ignores the results obtained with a population approach, or vice versa.

Moreover, many studies suffer from the need to obtain quick results from randomly oriented specimens in hard-rock samples, rarely with visible nepionic chambers; in this case, the non time-consuming approach based on morphotypes is generally used.

9.1. Biometry as a tool for the typological methodology

The use of morphometry as a tool, simply to define morphotypes as taxa and use them for biostratigraphic purposes, may be considered to lead to ambiguous or doubtful results, although justified by the need to overcome the difficulties that are encountered mainly working with specimens in thin sections of hard-rocks.

The main literature based on the biometrical

methodology was summarized by Drooger (1993). In contrast, the rationale of typological workers has been stated by BouDagher-Fadel and Banner (1997, p. 3), as follows:

“Species of the genus have been used to zone and date the Neogene, whilst many generic and subgeneric names have been proposed to accommodate the morphological changes which have been observed to occur with time. However, many of these genus-group names are considered to be unusable due to a lack of designated type species, misunderstanding of the nature of the type species available, or even subsequent designation of type species which were not in morphological conformity with the intentions of the author of the original genus-group name”.

And (p. 4):

“In order to make the genus-group nomenclature simple, reliable and useful, we endeavour in this paper to clarify the names and show how they can be used with stratigraphic value. Many of these taxa have been used by different authors in different ways, with different stratigraphic values attached to each. We intend to show how appropriate names can be rigorously and taxonomically correctly applied to the species-groups of the Tethyan Oligo-Miocene”.

In addition, designating a megalospheric neotype for *N. marginata* (p. 7):

“This is done in the interest of nomenclatural stability”. Michelotti (1841) published only an exterior view of his species “*marginata*”.

Finally:

“We do not, of course, distinguish differently ornamented types as separate species” may be endorsed by the biometry-inclined researchers.

Despite this acceptable start, the subsequent conspicuous scientific output by the first Author above was, and still is, inclined to stress the typological approach, with designations of many (perhaps too many?) species.

BouDagher-Fadel (2008, p. 461) considered the biometrically defined six species for the Indo-Pacific *Nephrolepidina* (van Vessem, 1978) as “probably an over simplification, as many more morphotypes can be distinguished, some of which may deserve species rank”.

Nevertheless, at p. 400 in the same valuable monograph, the biometric methodology, used for the Miogypsinidae, is described as an “useful tool”.

In some instances, biometric indexes are used improperly to define new species based on few, or on a single specimen, poorly preserved or in poorly oriented sections. Ferrandini et al. (2010), despite the biometric characters introduced by Drooger (1963) listed as the followed methodology, established two new species of Miogypsinidae based on very few poorly oriented specimens in thin sections of hard rocks. *Miogypsinodella pillaria* Ferrandini M. and J., BouDagher-Fadel, Oudet, André 2010, is based on a microspheric holotype in axial section, without data on megalospheric embryonic chambers, number of nepionic chambers and so on. Moreover, all the bispiralled taxa are identified without

using the V factor (i.e., the degree of symmetry of the two nepionic spirals). These results are methodologically questionable. So, new species are added to the plethora of useless, forgotten similar taxa of which that the previous literature is replete. This reflects a basic misunderstanding of the original purposes of van der Vlerk (1959 a,b, 1963) and Drooger (1952, 1963).

The problem of naming new species based only on material from thin sections of hard rocks is rather complex. Indeed, Boudagher-Fadel and Lord (2000) start from a reasonable premise:

“As the specimens studied here are from random thin sections of reefal limestones, biometric measurements on isolated, solid specimens of *Lepidocyclina* sensu lato are rarely possible. We attempt to combine the broad results gained by equatorial sections of the megalospheric nepiont (as published by Chaproniere, 1984; van Vessem 1978) with those obtained by vertical sections of the whole test (as followed by Cole, 1957, 1963)”.

But after this preliminary, very reasonable statement, *L. (N.) nephrolepidinoides* Boudagher-Fadel and Lord 2000) is established on a holotype and a paratype that are both in axial section, just following only Cole; observations about the embryo-nepionic-equatorial chambers are few and irrelevant, from a biometrical perspective.

9.1.1. “Time-consuming” as a nightmare.

Conversely, additional confusion can be obtained also by the biometric approach.

Boukhary et al. (2008), although apparently endorsing biometric procedures in orbitoidal foraminifera, erroneously erected the new species *N. sinaica*. This “species”, in fact, could be an useful new entry for the Mediterranean lineage, but it is not. At p. 183 they state: “the total circumference of the protoconch calculated for 4 (better more) specimens”. In fact, the results are obtained with $N = 5$. Perhaps, the available material was scarce, because “only” 60 paratypes are mentioned. Anyway, the target “to save time” was obtained. This frequent behaviour seems to be a consequence of fear of time-consuming procedures, not of haste to publish.

Anyway, the suggested discriminating characters of *N. sinaica* are the DI and DII larger than in *N. morgani*, without considering that in the previous literature these dimensions, ascertained in *N. morgani* from other Chattian samples, are larger than in *N. sinaica* (e.g. in de Mulder, 1975; Matteucci and Schiavinotto, 1977; Drooger and Freudenthal, 1964; Schiavinotto, 2010, 2015).

Another issue is whether the dimensions of the embryonic chambers represent a specific character. A recent study suggests that these dimensions, related to the environment, are highly variable (Benedetti, 2015).

9.1.2. A welcome “over complication”

Quoting again the so called “over simplification” (BouDagher-Fadel, 2008), this may become easily an over complication, when it is used with a typological point of view, because the current taxonomic situation for the

Mediterranean *Nephrolepidina* lineage appears as follows: 1) a sequence of only three species (chronospecies) (*praemarginata*, *morgani*, *ournoueri*), following the biometric, population-based methodology (de Mulder, 1975);

2) a sequence of five species (*praemarginata*, *praetournoueri*, *morgani*, *ournoueri*, *aquitaniae*), following the morphotypic approach (BouDagher-Fadel and Price, 2010).

Actually, five species (stages) may be only apparently an “over complication” and, in contrast, represent the right solution to define biometrically a very variable taxon as the Mediterranean *Nephrolepidina* lineage, but this suggestion requires extreme caution.

There is no need to discuss here the meticulous analysis done by Boudagher-Fadel and Banner (1997) to find similarities and differences that have suggested to choose a megalospheric neotype for *N. marginata* and to re-consider *N. praetournoueri* and *N. aquitaniae*. Here, what appears interesting and relevant is the outline of the development of the Mediterranean lineage as given by BouDagher-Fadel and Price (2010, Fig. 14) who state (p. 99):

“... they form a well-documented lineage, with five evolutionary stages: *L. (L.) praemarginata*, *L. (N.) praetournoueri*, *L. (N.) morgani* and *L. (N.) marginata*, *L. (N.) aquitaniae*. The oldest form of this lineage, *L. (N.) praetournoueri*, appears to have evolved directly from *L. (L.) praemarginata*”.

The interpretation of *N. aquitaniae* as the final evolutionary stage in the Mediterranean lineage appears to be very interesting. However, some difficulties are hampering a stringent and objective application of this taxon. In fact, it has a rather low level of embryonepionic acceleration, and could thus be considered as representative of a backward evolutionary deviation. Additionally, this species has been referred to the Serravallian of the Aquitanian Basin, a quite unusual age for Mediterranean lepidocyclinids which needs to be confirmed.

Then, it would be more consistent to consider the morphotypes with square-shaped protoconch instead of *N. aquitaniae*, just according to what is stated immediately before the above mentioned quote: “The European representatives of *L. (Nephrolepidina)* never reached the advanced phylogenetic evolutionary stages seen in the Indo-Pacific, where the protoconch became quadrate and completely enclosed by the deutoconch ...”.

A protoconch “completely enclosed by the deutoconch” would imply A_i values of ca. 90-95%, thus maybe *Eulepidina*, but considering the suggestion of *Tryblyolepidina* = *Eulepidina* (BouDagher-Fadel and Banner, 1997), this may be understandable.

It should be noted that these forms (Fig. 23 a,b), with a protoconch tending to be subquadrate-subrectangular, have been found in Italy since a long time ago, and have been figured, e.g. by Matteucci and Schiavinotto (1977, Pl. 2, Fig. 4), Schiavinotto (1979, Pl. 4, Figs. 4-6; 2010, Pl. 3, Fig. 6; 2015, Pl. 1, Figs. 5, 6), Giovagnoli and Schiavinotto

(1990, Pl. 2, Fig. 6; 1995, Pl. 3, Fig. 3), Schiavinotto and Verrubbi (1994, Pl. 4, Fig. 3), and Giannini et al. (2007, Pl. 3, Fig. 5; Pl. 4, Fig. 4). In the material from Gran Sasso (Schiavinotto and Verrubbi, 1994), these forms occur from the middle part of the section (Chattian) (Schiavinotto, work in progress).

What about the above? Following the typological perspective, to extract these specimens from the originary populations and to establish one (or perhaps more) species, seems to be possible. Moreover, this new species could be hypothesized as an ancestor of the advanced phylogenetic evolutionary stages seen in the Indo-Pacific. Anyway, at the moment, the writer prefers to remain a “lumper”.

Probably, the above quoted words that Silvestri wrote in 1914 may be indicative that to find mutual concessions by both the different methodologies can be a sort of “Sisyphean task”. After all, *N. aquitaniae* was established by Silvestri (1912) himself.

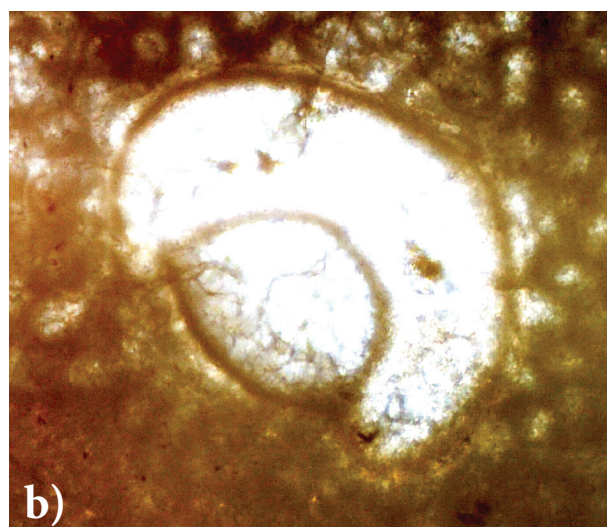
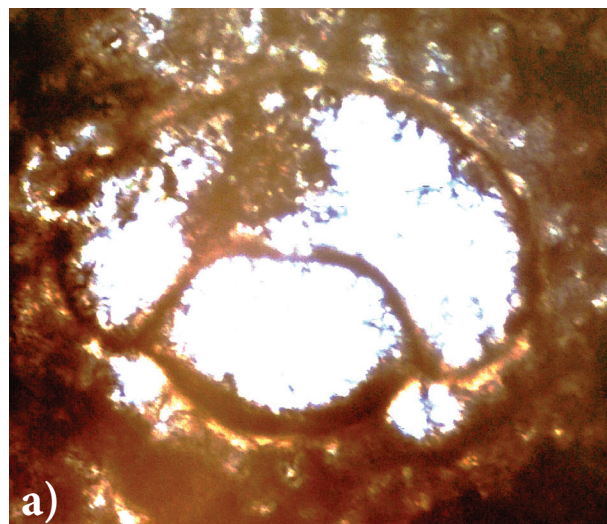


Fig. 23 - Subquadrate protoconch in *Nephrolepidina* from Mt. Torretta section; a) Specimen PMT8, n. 9, 100x; b) Specimen PMT22, n. 40, 80x.

10. SEEKING AN INTEGRATED TAXONOMY/ BIOSTRATIGRAPHY

However, it must be admitted that this situation for *Nephrolepidina* is due to the partially not efficient taxonomy by de Mulder (1975).

Schiavinotto (1996c) suggested modified specific boundaries that should be able to scale down the deviations of $\bar{A}i$ and \bar{C} , including them all within the most advanced evolutionary stage of *Nephrolepidina*, and thus obtaining less confusion not only at the taxonomic, but also at the biostratigraphic level. This modification appeared at first to be consistent, but it is now obsolete, and needs further significant changes, because the data about the total range of the oscillations caused by the environment, and also by possible resedimentation/reworking processes, are not exhaustive as yet.

However, according to the presented data, it seems useful to focus the attention on the neanic features, in order to be able to identify a new basis for a possible implementation of the biostratigraphic resolution power of *Nephrolepidina*.

To use the neanic acceleration inserted in the framework of the “golden selection” (Benedetti, 2014), as an integration of de Mulder’s taxonomy of *Nephrolepidina*, seems to be possible. The wide gap of values between the group of populations scattered around T1, and the high group formed by TLS76, AC5, and six PMT populations might be an indication of the potentialities that are offered by the neanic factors for their application to an integration of the embryo-nepionic classification. In fact, further discriminations within the ranges of *N. morgani* and *N. tournoueri* might be possible.

Both the shape of the chambers and the type and position of the stolons are considered a feature of taxonomic value, at the specific level (Eames et al., 1962, p. 298; Adams, 1987). Consequently, the data obtained here confirm that in the *Nephrolepidina* populations, classified on the basis of the mean values of embryo-nepionic features, a further distinction can be made on the basis of the mean values of neanic features, as hypothesized in Schiavinotto (1993a, p. 304, Tab. 4).

The insertion of the neanic variables in the taxonomic thematic appears to be very promising.

Considering the $\bar{A}i$ - $\bar{F}D5$ scatter diagram in Figure 24, the populations might be separated in three main groups. So, the new provisional ranges proposed here are the following:

- N. praemarginata* $\bar{A}i \leq 40\%$ and $\bar{F}D5 \leq 35$
- N. morgani* $40 < \bar{A}i \leq 45$ and $35 < \bar{F}D5 \leq 50$
- N. tournoueri* $45 < \bar{A}i$ and $\bar{F}D5 > 50$

By means of all the collected data, it seems useful to focus the attention again on the neanic features, in order to identify a new basis for a possible implementation of *Nephrolepidina* in the biostratigraphic field.

Considering again the $\bar{A}i$ - $\bar{F}D5$ scatter diagram, redrawn in Figure 25, three main fields might be evidenced, placing a first very tentative boundary at $\bar{A}i = 45$ and $\bar{F}D5 = 50$

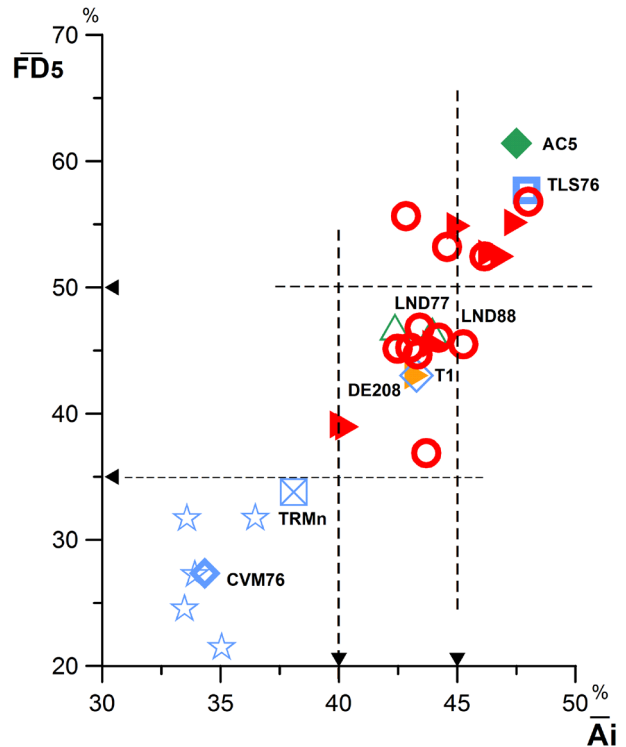


Fig. 24 - $\bar{A}i$ - $\bar{F}D5$ scatter diagram with the hypothesized taxonomic boundaries marked by arrows.

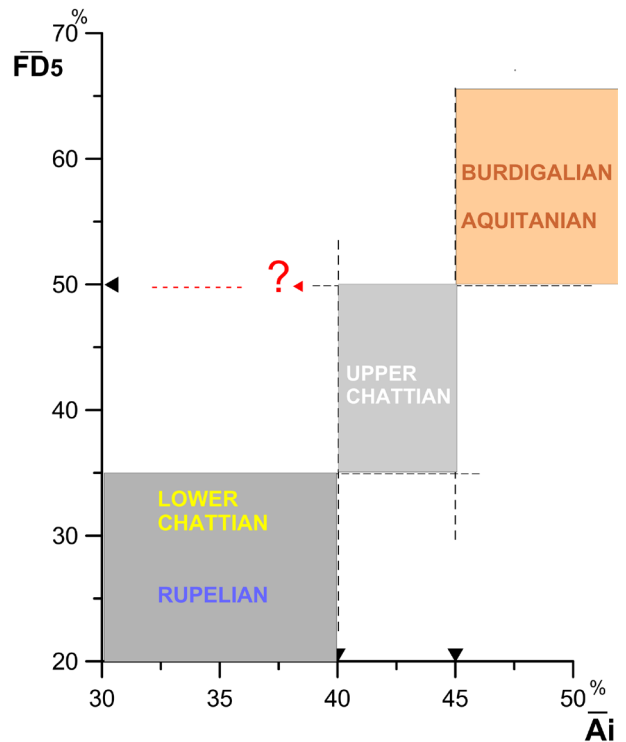


Fig. 25 - $\bar{A}i$ - $\bar{F}D5$ scatter diagram with tentative correlation between neanic boundaries and age.

(still rough Oligo-Miocene boundary?).

$\bar{A}i \leq 40\%$ and $\bar{F}D5 \leq 35$	the provisional field indicative of Rupelian-lower Chattian (<i>N. praemarginata</i>)
$40 < \bar{A}i \leq 45$ and $35 < \bar{F}D5 \leq 50$	the provisional field related to upper Chattian (<i>N. morgani</i>)
$45 < \bar{A}i$ and $\bar{F}D5 > 50$	the provisional field that could be indicative of the Aquitanian - Burdigalian (highly developed <i>N. morgani</i> to <i>N. tournoueri</i>).

This may be the indication of a new, still rough path towards a tentative reassessment of the *Nephrolepidina* Mediterranean lineage, that must be checked by means of new data on calcareous nannofossils, planktonic foraminifera and/or geochemical techniques.

11. CONCLUSIONS

Although the previous substantial results in Giannini et al. (2007), for *Nephrolepidina* from the Mt. Torretta section, where reliable, the corrections made in this work confirmed even more the deviations in the evolutionary trends according to the principles of “Embryonic acceleration” and of “Nepionic acceleration”.

There is more evidence that the classification according to de Mulder (1975) do not allows an optimal correlation with the plankton biostratigraphic scale because the excessive range of *N. morgani*, too much frequently unable to define the Oligo-Miocene boundary, and to provide an unquestionable discrimination from *N. tournoueri*.

This is a long-time taxonomic problem, affecting also the biostratigraphic field.

This criticism was amply documented by Schiavinotto (1996c), and was revisited here.

There are evidences that the biometric population-based and the typological approaches in the taxonomy of *Nephrolepidina* and other orbital larger foraminifera must find mutual concessions-integrations. Using exclusively the typological methodology, some morphotypes, both from the studied section and other published materials, could be indentified as Indo-Pacific species, bringing more uncertainty and useless complication.

In contrast, the mean values of Factor FD5 appear useful for taxonomic purposes: the data obtained here confirm that in the *Nephrolepidina* populations, classified on the basis of the mean values of embryo-nepionic features, a further distinction can be made on the basis of the mean values of neanic features, mainly at the level of the intermediate species *N. morgani*.

An integration of de Mulder's taxonomy of *Nephrolepidina* with neanic acceleration seems thus feasible, within the framework of the “golden selection” (Benedetti, 2014).

In that way, the present specific/biostratigraphic

definition of the Mediterranean *Nephrolepidina* lineage could be improved by supplementing the embryonic and nepionic data with the neanic morphometric data, in order to detect especially the Oligocene/Miocene boundary. However, the spiral growth of the equatorial chambers, recently evidenced by Benedetti (2014), suggests the need of further developments in the biometrical approach. Consequently, because the mean values of Factors FD5 and SI5 appear to be useful for taxonomic purposes, two first specific/biostratigraphic boundaries are suggested, as a working hypothesis.

In conclusion, Trümpy's (1971) famous statement that “a bad fossil is more valuable than a good working hypothesis” should be replaced here with the following: “Any working hypothesis becomes more valuable with good fossils”.

ACKNOWLEDGEMENTS - Anna Farinacci (“La Prof.”) is thankfully remembered for introducing me to micropaleontology and as a mentor during a sort of lucky golden age of geo-paleontological researches in the Institute of Geology, Rome.

Warm thanks to Ruggero Matteucci for his friendly continuous support, suggestions and generous encouragement; the reviewers Andrea Benedetti and Johannes Pignatti shared very useful discussions and improved significantly the manuscript; Virgilio Frezza and Riccardo Manni kindly provided worthwhile articles; Laura Teresa Di Pietro and Maurizio Salvati carefully helped for drawings and difficult editing.

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