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Embryo size variation in larger foraminiferal lineages: stratigraphy versus paleoecology in *Nephrolepidina praemarginata* (R. Douvillé, 1908) from the Majella Mt. (Central Appennines)

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ABSTRACT - The Mediterranean *Nephrolepidina* lineage has been thoroughly investigated in a number of studies. Here, we investigate biometrically two late Rupelian *Nephrolepidina* populations (E77', n=54; E76J, n=9) from the northern Majella Mt. (Central Italy), considering three parameters and three factors and their mean values.

The A_i factor (degree of enclosure of the deuteroconch on the protoconch) and the parameter C (number of adauxiliary chamberlets) suggest that both populations belong to *N. praemarginata* (R. Douvillé, 1908).

The mean sizes of protoconch and deuteroconch are distinctly larger than other known populations of *N. praemarginata*. This is interpreted to reflect environmental factors.

Increase in embryo size is a general feature among many larger foraminiferal lineages. In addition, studies on recent larger foraminifera indicate that embryo size varies along the depth gradient; however, this variation is poorly investigated.

In recent nummulitids, the diameter of the embryonic chambers may either increase up to the ecological optimum and then decrease, or increase linearly with depth.

Investigating embryo size may thus be rewarding either in a sequence of populations when sea-level change occurs or when anomalously large values of embryo size are attained in a population.

Utilizing evidence from models derived from recent species, although it is uncertain how far they can be extended to extinct radial foraminifers, and sequence stratigraphy, it is inferred that the two populations come from a depth not far from the ecological optimum of the species. Recognition of this ecological optimum in the fossil record is generally hampered by conspicuous transport and mixing along the depth gradient.

KEY WORDS: biometry, paleoecology, larger foraminifers, Nephrolepidina, Oligocene, Majella

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INTRODUCTION

Nephrolepidina praemarginata was originally described by R. Douvillé in 1908 on isolated specimens from the lower Oligocene marls of Dego (Liguria, Italy) and later biometrically investigated by De Mulder (1975), Matteucci and Schiavinotto (1977) and Schiavinotto (1978) from other Mediterranean localities. The biometric approach according to the rationale outlined in Drooger (1993) is linked to the conventional boundary fixed by De Mulder (1975), who subdivided the late Rupelian-Burdigalian phyletic lineage of Nephrolepidina in the Mediterranean area into three chronospecies: N. praemarginata, N. morgani (Lemoine and R. Douvillé, 1904), and N. tournoueri (Lemoine and R. Douvillé, 1904). This approach of subdividing a lineage into chronospecies for biostratigraphic purposes is illustrated by the diagram of Drooger and Rohling (1988) (here redrawn and modified in Fig. 8). The biometry of *N. morgani* and *N.* tournoueri has been investigated in detail by several authors (e.g., Serpagli and Sirotti, 1966; Schiavinotto, 1979; Schiavinotto and Verrubbi, 1994; Giannini et al., 2007). In contrast, less is known about N. praemarginata and especially about its ancestor(s).

Modern Oligo-Miocene larger foraminiferal biostratigraphy has been established by combining first and last occurrences of various taxa and chronospecies of radial foraminifers lineages (Drooger and Laagland, 1986). Revision and correlation of these data with independent biozonal schemes, sequence-stratigraphic data and magnetostratigraphy allowed Cahuzac and Poignant (1997) to establish biochronozones for this timespan in the frame of the Mediterranean Tethys *Shallow Benthic Zonation* (SBZ). Future developments of the Paleogene time scale (Luterbacher et al., 2004) are likely to determine significant changes to this zonation, especially as concerns the Rupelian-Chattian boundary.

Sequences of fossil populations of radial larger foraminifers represent classical examples of evolutionary processes such as nepionic acceleration (Tan Sin Hok, 1936), consisting in the reduction of the ancestral spiral, and embryonic acceleration (Drooger and Freudenthal, 1964), defined as the trend of the deuteroconch to increase its degree of embracement on the protoconch becoming globular (circular in equatorial section). Obviously, both embryonic chambers in *Nephrolepidina*, the protoconch and the deuteroconch, tend to increase in size according to embryonic acceleration, although studies on recent larger foraminifers show the variation of the diameter of the protoconch along the depth gradient (Fermont, 1977a, 1977b; Fermont et al., 1983; Reiss and Hottinger, 1984; Yordanova and Hohenegger, 2004).

The bathymetric distribution of larger foraminifers is strictly linked to light intensity, activity of the symbiont algae, productivity, and population density (Fermont et al., 1983; Reiss and Hottinger, 1984; Pécheux, 1995).

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In living *Heterostegina depressa* d'Orbigny, 1826 (Fermont et al., 1983) and *Operculina ammonoides* (Gronovius, 1781) (Pécheux, 1995), the protoconch diameter increases up to the ecological optimum, indicated by highest population density, where the ecological factors create the most favourable conditions for growth, then decreases basinward, roughly following a bell-shaped curve. The diameters of the protoconch in extant *Heterostegina* and *Operculina* populations reach maximum values at about 80 m according to Fermont, (1977a, 1977b) and Pécheux (1995); in contrast, however, Yordanova and Hohenegger (2004) recognize a linear trend of decrease in embryo size with depth from Sesoko and Minna Islands, Okinawa (Japan).

We extend the ecological significance and the depth distribution patterns of recent symbiont-bearing nummulitids to the extinct Mediterranean *Nephrolepidina* lineage assuming that the lateral chamberlets in orbitoidiforms can be interpreted as symbiont greenhouses and that symbiosis represents a depth signal characterizing the photic zone (Hottinger, 1997).

Test shape of larger foraminifers is controlled by both illumination and water motion influencing the deposition of secondary lamellae (Hallock, 1985), and so thick-walled specimens live in shallow water with high illumination and relatively high water turbulence, whereas specimens with thinner wall live at greater depth. In stressed zones, at the marginal distribution of a species, affected by limiting conditions such as water turbulence, high salinity, water turbidity, low temperature, insufficient food or light, oxygen depletion low pH, etc., the population increases its fitness by producing a larger number of offspring with smaller proloculi, according to the r-strategy model (Hallock, 1985; Beavington-Penney and Racey, 2004). In stable environments, close to the ecological optimum, sexual reproduction prevails and reproductive success results in the production of larger and more numerous offspring (Fermont et al., 1983).

In this work we carried out a biometric investigation of the megalospheric embryos of two *Neprolepidina* populations, with the aim to discuss both biostratigraphical and paleoecological constraints to the interpretation of embryo size.

GEOLOGICAL SETTING

The "African Promontory" (Argand, 1924), "Adria microplate" (Channel et al., 1979) or "Apulian plate" (Lort, 1971) played a key-role in the geodinamical history of the central Mediterranean area. In Cretaceous and Paleogene times, the Apulian domain was characterized by distally steepened ramps and unaffected by terrigenous influx. Paleobiogeographically this domain was closely linked with sectors of the eastern Mediterranean region ranging as far as Anatolia and the Arabian platform. According to Ricou et al. (1986) these relationships weakened gradually during the Lower Oligocene, until the break-up of the eastern Mediterranean connection (Adams et al., 1983).

Detailed sequence stratigraphy in the Majella distally steepened ramp proves the role played by sea-level fluctuations in controlling sedimentation (Vecsei et al., 1998), excluding for the examined time-span a significant local tectonical overprint. In the Apulian domain, the Majella carbonate platform represents the best outcropping example of a Paleogene succession of related depositional environments (inner and external platform, slope, proximal basin). Its biostratigraphic interest is strongly increased by

the occurrence of relatively thick larger foraminiferal carbonates, recording shallow-water deposition during all post-Danian stages (Pignatti, 1995). Although generally in the Majella Mt. the recognition of biostratigraphic intervals and paleoecological environments for most of the earlier Paleogene is complicated by extensive resedimentation, reworking and major sedimentary hiatuses, during the Late Eocene and the Oligocene these limiting factors strongly decrease in importance, because of the development of a less steep carbonate ramp. Prograding reef carbonates, breccias, calcareous sand resediments and turbidites dominate in the lower portion of the Oligocene deposits, whereas the upper 20-30 m of the slope sequences are represented (in the external platform) by turbiditic coarsening and thickening up successions reflecting an increase in sediment supply (Vecsei et al., 1998); in the coarser beds larger foraminifers, and in particular Nephrolepidina, are locally abundant.

The relevance of the Majella shallow-water carbonates is increased by the circumstance that it is the only outcropping portion in the northern Apulian domain in which Oligocene deposits occur. No Oligocene deposits are known with certainty from the Gargano promontory and Tremiti Islands. The closest relatives of the Majella Oligocene deposits are to be found in southeastern Apulia, in which Chattian slope and reefal carbonates are recorded (Luperto, 1962; Parente, 1994), but their study is limited by less favourable outcrop conditions.

The relevance of the Apulian area for studies in larger foraminifers is mirrored already in the earliest comprehensive attempt of systematization of nummulitids (d'Archiac and Haime, 1853). Most foraminiferal studies in the region focussed on Eocene taxa; the first monographic study of the Eocene nummulitid assemblages of the region and the recognition of an Apulian biogeographical realm is due to Tellini (1890), whose collections have been reordered (Pignatti and Ventura, 1994), but they do not contain any Oligocene taxa. Although the turbiditic resediments of the S. Spirito Valley (northern Majella), type locality of *Nummulites retiatus*, established by Roveda (1959), have been doubtfully referred to by the author to the lower Oligocene, these deposits are of late Priabonian age.

As yet, the Oligocene larger foraminifers of the Majella platform have been never studied biometrically, although the occurrence of Oligocene deposits on the slope of the Majella carbonate platform has been recorded by several authors (Bonarelli, 1951; Di Napoli et al., 1958; Crescenti, 1969; Crescenti et al., 1969; Catenacci, 1974; Accarie, 1988; Vecsei, 1991; Pignatti, 1995; Rusciadelli and Di Simone, 2007).

MATERIALS AND METHODS

The two investigated *Nephrolepidina* populations come from calcareous well-bedded resediments of the Santo Spirito Formation (Crescenti et al., 1969) from the southern flank of the S. Croce hill (N42°09'57"; E14°00'45"), facing the town of Caramanico Terme (Pescara) (Fig. 1). In the examined section the Oligocene deposits may be subdivided into two sequences, the first one represented by channelized breccias formed of reefal carbonate clasts and shallow-water grainstone (lower Rupelian); bioclastic carbonate sand tubiditic resediments rich in the larger foraminifers investigated in the present work alternating with hemipelagic deposits form the second sequence (upper Rupelian-Chattian) (Fig. 2). A truncation surface between



Fig. 1 - Sketch map of the investigated area. The location of the investigated section is indicated and corresponds to the upper part of the Santa Croce profile in Vecsei (1991).

these two sequences is not clearly visible in the S. Croce section, but elsewhere in the Majella and especially in its northern part it has been widely recognized (Vecsei, 1991).

In the sequence-stratigraphic interpretation of Vecsei (1991), the *Nephrolepidina*-bearing levels correspond to his Supersequence 5.7 and belong either to the transgressive or to the highstand systems tract.

This study is based on thin sections of megalospheric specimens obtained from two samples, E77' (54 specimens from 15 thin sections) and E76J (9 specimens from 3 thin sections). We did not attempt to investigate the ratio of A versus B forms, which in nummulites may provide a useful taphonomical signal (Aigner, 1985), because in the investigated thin sections, obtained parallel to bedding, many uncentered secrions of specimens cannot be assigned unambiguously to either generation.

Microfossil content and texture of the two samples are identical, represented by poorly-sorted packstonegrainstone rich in *Amphistegina* sp., *Planoperculina complanata* (Defrance, 1822), *Eulepidina formosoides* H. Douvillé, 1924, smaller rotaliids, echinoid fragments, and bryozoans. In addition, rare *Sphaerogypsina globulus* (Reuss, 1848), *Planorbulina* sp., textulariids, and planktonic foraminifers are present.

The thin sections investigated in this study are stored in the Department of Earth Sciences, "Sapienza" University, Rome.

THE BIOMETRIC STUDY

Morphometric characters of the embryonic-nepionic chamber arrangement were studied on megalospherical specimens obtained from rock thin sections parallel to the bedding plane. Since no isolated specimens were available for our investigation, we are unable to describe the external characters of the *Nephrolepidina* populations. The following morphometric parameters have been used (Fig. 3):

 A_i (*Grade of enclosure* of Van der Vlerk, 1959): measuring the degree of enclosure of the deuteroconch on the protoconch:

$$A_i = \frac{c.w.}{lc_l} \times 100$$



where *c.w.* is the length of the common wall between protoconch and deuteroconch measured from *p* to *q* and lc_l is the length of the inner circumference of the protoconch.

R (*Degree of curvature* of Van der Vlerk, 1968): i.e., the degree of curvature of the common wall between the protoconch and the deuteroconch:

$$R = \frac{hr}{br} \times 100$$

where br is the distance between the two extreme points (p and q) of common wall and hr is the distance between br and the common wall.

 d_{ll}/d_l (e.g. Chaproniere, 1980): ratio between the diameter of the deuteroconch and protoconch, excluding the thickness of the wall.

C (Drooger and Socin, 1959; Drooger and Freudenthal, 1964): number of adauxiliary chamberlets on the deuteroconch.

RESULTS OF THE BIOMETRIC STUDY

The results obtained from the statistical evaluation of the measures obtained from the two populations are summarized in Tabs. 1, 2 and graphically shown in Figs. 4-6.

The embryonal megalospherical apparatuses are of the *lsolepidina-Nephrolepidina*-type, with a rather moderate range of variation (Fig. 7; Tabs. 1, 2).

The grade of enclosure *A_i* exceeds 40% only in 4 specimens (1 in E76J, 3 in E77'): the role of the *Nephrolepidina*-type is therefore subordinate. The relatively homogeneous character of the population results from an examination of the histograms, with a distribution of the values close to normality for all parameters and factors in E77', whereas this is less supported in E76J because of the low number of specimens. These results are confirmed by the Kolmogorov-Smirnov statistical test of normality (Tabs. 1, 2).

Following the criteria of De Mulder (1975), populations E76J and E77' are attributed to *N. praemarginata* (R. Douvillé, 1908), marking chronobiozone SBZ22A (Cahuzac and Poignant, 1997). The normal distribution of the values of A_i and *C* confirms that each population is monospecific; this is



Fig. 2 - Schematical lithological log of the Oligocene portion of the Santa Croce section (Caramanico, northern Majella, Central Italy).



Fig. 3 - Equatorial section of the embryonal apparatus of megalospheric *Nephrolepidina*; I= protoconch; II= deuteroconch; P.A.C.= principal auxiliary chambers; A.A.C.= adauxiliary chamberlets.



Fig. 4 - Distribution of the values in population E76J; the sample passes the Kolmogorov-Smirnov normality test (Tab. 1), but the data sample is very small (n=9). Ai=degree of embracement of the protoconch by the deuteroconch; C=number of adauxiliary chamberlets on the deuteroconch; dl=diameter of the protoconch; dll=diameter of the deuteroconch; dll=diameter of the nucleoconchs; R=degree of curvature.



Fig. 5 - Distribution of the values in population E77' (n=54); the sample passes the Kolmogorov-Smirnov normality test (Tab. 2) except for parameter C, possibly due to the small number of histogram bins (four bins only); Ai=degree of embracement of the protoconch by the deuteroconch; C=number of adauxiliary chamberlets on the deuteroconch; dl=diameter of the protoconch; dl=diameter of the deuteroconch; R=degree of curvature.

further confirmed by the normal distribution of all other parameters.

The two populations, plotted in the *A_i-C* scatter diagram of Fig. 8, based on Drooger and Rohling (1988) and including also additional populations, fit well in the *N. praemarginata* field and are one of the most primitive *Nephrolepidina* populations found in Italy.

The factors *R* and d_{II}/d_I have been generally considered as correlated with A_i (e.g. van der Vlerk et al., 1973), being a measure of an increase in deuteroconch size as compared to the protoconch in time and of the increase in the curvature of the common wall between the two embryonic chambers. In our samples d_{II}/d_I has a *CV* close to that of A_i , whereas *R* has a wider variability. This is probably due to the frequence of the isolepidine morphotype within the nephrolepidine-type populations. The parameter *hr*, which is positively correlated with *R*, ranges from 4 to 107 µm proving the wide variability in these collected data. d_{II}/d_I may be, therefore, a good candidate to substitute the factor A_i in the evolutionary study of lepidocyclinids because of its easier computation.

All these data indicate that the two populations are biometrically very similar, as expected by their stratigraphic closeness.

The most interesting feature of the two populations concerns embryo size, which attains the largest values among populations as yet described from the Mediterranean Rupelian for *N. praemarginata*.

Fig. 6 shows the mean values of the diameter of protoconch and deuteroconch of the two populations and the few other *N. praemarginata* populations for which these data are available (Matteucci and Schiavinotto, 1978; Schiavinotto, 1978; van Heck and Drooger, 1984). Our data indicate a marked difference in the embryo size in the Majella populations with others possessing similar values of *C* (Fig. 6).

The problem of protoconch size and its variation in larger foraminifers is a long standing issue. Notably, protoconch and deuteroconch size and their increase in time within lineages have been mainly used as a biostratigraphic tool and interpreted according to Cope's rule (De Mulder, 1975). In contrast, little use has been made of protoconch size in fossil larger foraminifers for interpreting ecological gradients or clines, although there are models based on extant taxa which could be tested against fossil populations. In other words, emphasis on the use of biometrical features for biostratigraphic purposes has obscured the meaning of embryonal size for detecting paleoecological gradients. This is surprising, because ecological variation in size of e.g. protoconch diameter is large and potentially threatening its biostratigraphic use.

As lepidocyclinids are extinct and there are no close modern analogues, it is necessary to use for comparison other recent symbiont-bearing Rotaliina. Hottinger (1997) suggested that orbitoidiforms (and thus *Nephrolepidina*) may have had symbionts living in the lateral chamberlets as in the present-day *Baculogypsinoides*, for which unfortunately no depth-related biometrical data are available and the depth range is probably shallower (Renema, 2003). Thus, we have to make use of those Rotaliina for which depth gradients have been investigated in greater detail, i.e. nummulitids.

Evidence gained in the Gulf of Aqaba on recent nummulitids by Fermont (1977a, b; Fermont et al., 1983) and Pécheux (1995) shows that along the depth gradient the protoconch diameter attains maximum values in correspondence to the ecological optimum; lesser values



Fig. 6 - The embryonal apparatus of *N. praemarginata* from the upper Rupelian of the Majella Mt. is distinctly larger than in other coeval populations.

characterize the marginal populations at the extremes of the full depth range (Fig. 9).

The most parsimonious explanation for the large protoconch and deuteroconch diameters reported here is to interpret the two populations as belonging to the ecological optimum, although the interpretation of the sediments in which they were found clearly implies some degree of allochthony. This poses a further question, i.e., why has the ecological optimum escaped recognition as yet in the fossil record of larger foraminifers? In the sequence-stratigraphic interpretation of Vecsei (1991), the *Nephrolepidina*-bearing levels investigated here correspond to his Supersequence 5.7 and belong either to the transgressive or to the highstand systems tract: we interpret these levels as reflecting highstand shedding.

In larger foraminiferal assemblages, both recent and fossil, downslope transport and mixing of specimens from different populations along the depth gradient, is apparently widespread, thus minimizing the recognition and the effect of specimens from the ecological optimum zone.



Fig. 7 - Drawings of selected equatorial sections of *N. praemarginata* from Santa Croce section (Majella Mt.). Labels correspond to sample and specimen number. Scale bar=0.5 mm.

CONCLUSIONS

The biometrical analysis of the embryonic apparatus of 63 *Nephrolepidina* specimens from two samples collected near Caramanico Terme (Pescara) allows us to refer them to the species *N. praemarginata*, a key marker of the SBZ22A chronobiozone (Cahuzac and Poignant, 1997).

The key issue of the present work is to record and investigate the meaning of the distinctly larger diameter of the protoconch in comparison to other coeval populations of this species. At least in one population for which a large number specimens has been investigated (sample E77'), the biometrical data evidence a normal distribution and it is reasonable to infer that we are dealing with an allochthonous population without significant intermixing with populations from different depths.

According to studies on recent larger foraminifers, protoconch size depends from a number of environmental factors such as illumination, productivity, salinity and temperature (e.g., Hottinger, 1997; Fermont et al., 1983; Beavington-Penney and Racey, 2004) and attains its maximum value at the ecological optimum (Fermont, 1977a, b; Fermont et al., 1983; Pécheux, 1995) as shown in Fig. 9. Basically, as the factors above vary according to depth, protoconch and deuteroconch size are depth dependent (ecological constraint). The most parsimonious interpretation in our view is that the two populations come from a depth close to the ecological optimum. Recognition in the fossil record of this ecological optimum depth is particularly critical because several of the biometrical parameters employed for biostratigraphic purposes (stratigraphical constraint) are

	Ν	min	Max	Mean	Median	SD	SE	CV	Skew	Kurtosis	K-S
d	9	241.59	481.80	332.36	313.94	74.83	24.94	0.23	0.90	0.77	0.19
d _{II}	9	343.64	590.59	427.24	418.19	75.28	25.09	0.18	1.28	2.01	0.20
С	8	1	3	1.80	1.50	0.89	0.31	0.51	0.62	-1.48	0.30
A	9	30.55	42.84	36.12	37.08	3.82	1.27	0.11	0.02	0.10	0.20
R	9	3.14	22.15	11.93	13.48	5.64	1.88	0.47	0.14	0.40	0.17
d _{II} /d _I	9	1.06	1.46	1.30	1.29	0.14	0.05	0.11	-0.45	-0.59	0.15

Tab. 1 - Biometrical data for population E76J. N: number of observations; *min*: minimum value recorded; *Max*: maximum value recorded; *Mean*: sample mean; *Median*: sample median; SD: standard deviation; *SE*: standard error; *CV*: coefficient of variation; *Skew*: coefficient of skewness; *Kurtosis*: coefficient of kurtosis; K-S: Kolmogorov-Smirnov test for normal distribution (bold values are significant at the 95% confidence interval).

	Ν	min	Max	Mean	Median	SD	SE	CV	Skew	Kurtosis	K-S
d	54	191.23	492.40	278.78	271.09	60.24	8.20	0.22	1.16	2.12	0.10
d _{II}	54	226.72	681.03	351.34	334.62	81.85	11.14	0.23	1.41	3.68	0.12
С	46	1	4	1.90	2.00	0.77	0.11	0.40	0.72	0.66	0.29
A	54	27.64	43.76	34.54	34.35	3.50	0.48	0.10	0.33	0.20	0.10
R	54	2.13	23.05	11.48	11.40	5.81	0.79	0.51	0.20	-0.90	0.09
d _{II} /d _I	54	0.94	1.69	1.27	1.23	0.15	0.02	0.12	0.51	0.40	0.12

Tab. 2 - Biometrical data for population E77'. Abbreviations as in Tab. 1.



Fig. 8 - A_i versus C scatter diagram in the Mediterranean lineage of *Nephrolepidina* (modified after Drooger and Rohling, 1988); the two populations from the Majella Mt. fit in the central part of the values recorded for *N. praemarginata*.



Fig. 9 - Interpretation of embryo size in larger foraminifers is affected by two independent constraints, one reflecting ecology along the depth gradient (maximum diameter at ecological optimum depth) (Fermont, 1977; Pécheux, 1995), the other stratigraphy (increase of size in time) (Drooger, 1993). Fluctuating (A), gradual (B) or stepwise-punctuated (C) patterns are well-known theoretical models of phenotypic and genetic divergence associated with increase in size through time.

correlated with the size of the embryonic apparatus. Ironically, transport along the depth gradient and timeaveraging which introduce strong biases in the paleoecological interpretation of fossil assemblages seem to be extremely common in larger foraminiferal deposits and are an invaluable ally for the use of statistical populations of tests in biometrically-driven biostratigraphy. ACKNOWLEDGEMENTS - We are grateful to Carles Ferràndez-Cañadell (Faculty of Geology, University of Barcelona) and Guillem Mateu Vicens (MARUM, University of Bremen) for insightful comments on an earlier draft of the manuscript.

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Pl. 1 - Selected equatorial or subequatorial centered sections of measured specimens of *N. praemarginata* from the upper Rupelian of Santa Croce section near Caramanico (Majella Mt.). 1. E77_09; 2. E77_23; 3. E77_19; 4. E77_36; 5. E77_42. Scale bar=0.5 mm.

Pl. 2 - Selected equatorial or subequatorial centered sections of measured specimens of *N. praemarginata* from the upper Rupelian of Santa Croce section near Caramanico (Majella Mt.). 1. E77_50; 2. E77_48; 3. E76J_03; 4. E77_53; 5. E76J_04. Scale bar=0.5 mm.