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Nephrolepidina in the Oligo-Miocene section of the Gran Sasso (Central Apennines): environment-evolution relations

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KEY WORDS – *Larger Foraminifera*, *Lepidocyclinidae*, *Biometry*, *Evolution*, *Paleoecology*, *Oligocene*, *Miocene*, *Central Italy*.

ABSTRACT – A sequence of populations of *Nephrolepidina* in the calcarenitic Oligo-Miocene of the Gran Sasso has been subjected to biometric analysis of the embryonic and nepionic chambers. An evolutionary development was recognized which, in general, remains in accordance with the principles of embryonic and nepionic acceleration: a progressive increase in time both of the average value of the degree of embracement of the protoconch by the deuterococonch, and of the average number of adauxiliary chambers.

However, some deviations from the expected trends were also revealed, which therefore assume oscillating trends already recognized several times in orbitoidal larger *Foraminifera*. A correlation between deviations of the evolutionary characteristics and deviations in the average values of the diameters of the embryonic apparatus was also observed.

Resedimentation phenomena, which are also present, do not seem sufficient to explain, alone, the magnitude of these deviations. On the contrary, the data regarding the variations of the sedimentological and faunistic characteristics that intervene in the section would confirm the hypotheses of the intervention of some factors limiting the average dimensions of the embryonic apparatus: 1) reduction of the population density because of variation of the environmental conditions and/or because of competition between different taxa; 2) modalities concerning the adaptive strategies in relation to the environmental characteristics; 3) interaction of a possible paratrimorphous reproductive cycle.

Moreover, in conditions of reduced population density, as a bottleneck consequence there could be temporary affirmations of morphotypes with primitive characteristics, followed by resummptions of the overall evolutionary trends, in accordance with the «pulsating evolution» model recently proposed as an alternative to the «gradualist» and «punctualist» models.

RIASSUNTO – [*Nephrolepidina* nella sequenza oligo-miocenica del Gran Sasso (Appennino centrale): rapporti ambiente-tendenze evolutive] – Una sequenza di popolazioni di *Nephrolepidina* nell'Oligo-Miocene calcarenitico del Gran Sasso è stata sottoposta ad analisi biometrica delle camere embrionali e nepioniche. È stato riconosciuto uno sviluppo evolutivo che, nelle linee generali, si mantiene in accordo con i principi dell'accelerazione embrionica e nepionica: progressivo aumento nel tempo sia del valore medio del grado di abbracciamento della protoconca da parte della deuterococonca, sia del numero medio di camere ausiliarie.

Tuttavia, sono state anche evidenziate alcune deviazioni dai trend attesi, che assumono quindi andamenti oscillanti già riconosciuti più volte nei macroforaminiferi orbitoidali. È stata anche osservata una correlazione tra deviazioni dei caratteri evolutivi e deviazioni nei valori medi dei diametri dell'apparato embrionale.

Fenomeni di risedimentazione, pur presenti, non sembrano sufficienti a spiegare, da soli, l'entità di dette deviazioni. I dati relativi alle variazioni delle caratteristiche sedimentologiche e faunistiche che intervengono nella sequenza confermerebbero invece le ipotesi di intervento di alcuni fattori regolanti le dimensioni medie dell'apparato embrionale: 1) riduzione della densità di popolazione a causa di variazione delle condizioni ambientali e/o a causa di rapporti di competizione tra differenti taxa; 2) modalità inerenti le strategie adattative in relazione alle caratteristiche ambientali; 3) interazione di un possibile ciclo riproduttivo paratrimorfico.

Inoltre, in condizioni di ridotta densità di popolazione, si potrebbero avere, per effetto «bottleneck», affermazioni temporanee di morfotipi con caratteristiche primitive, seguite da riprese dei trend evolutivi generali, in accordo con il modello di «evoluzione pulsante» recentemente proposto quale alternativa ai modelli di evoluzione «gradualista» e «punctualista».

INTRODUCTION

The aim of the present paper is to make a further contribution to the biometric researches on *Nephrolepidina*, by investigating material sampled in the first part of the Oligo-Miocene section outcropping on the west side of the Gran Sasso. The previous studies of the evolutionary development of the embryonic and nepionic chambers of this genus have shown oscillating trends or stagnation phases

both at the level of the intermediate stages, represented by *N. morgani*, and at the level of the more advanced stages, represented by *N. tournoueri*. This led to the resolving power of the Mediterranean *Nephrolepidinae* being jeopardized in the biostratigraphic application of extreme detail, particularly in the identification of the Oligo-Miocene boundary and in the finest subdivision of the Aquitanian-Burdigalian interval.

In the last few years the knowledge of the

reproductive cycle and of the ecology of the living larger Foraminifera has greatly increased, and the intervention of the environmental factors in modifying some morphological characteristics of the shell has been recognized.

Consequently, attempts have been made to apply this knowledge to investigations aimed at improving the understanding of the evolutionary processes of the exclusively fossil larger Foraminifera. In this case *Nephrolepidina* has been neglected. Rather there has been a tendency to consider some biometric parameters, indicators of an evolutionary development of the embryonic and neponic chambers, as too much controlled by phenomena linked both to the reproductive cycle and to the variability of the environmental factors.

The biometric studies carried out previously on the Lepidocyclinidae in the Oligo-Miocene outcropping in the central Apennines (Pieroni, 1965; Matteucci & Schiavinotto, 1977; Schiavinotto, 1979) have for a long time had an evident limitation: the available material and the outcropping conditions prevented investigations from being carried out on a large number of populations distributed in the same section. In fact, only in the case of Monte La Rocca was it possible to establish a confirmation of the evolutionary processes in a sequence of hardly two populations coming from samples separated by a small thickness of sediments (Matteucci & Schiavinotto, 1977); in the other cases it was a question of populations coming from a single level.

It was therefore urgent to start collecting data on several populations that represented the various evolutionary stages of the *Nephrolepidinae* in the same sedimentary succession of the Central Apennines, in order to obtain surer indications on the application of the biometric methods in the taxonomic, phylogenetic and above all the biostratigraphic field, with particular regard to the problem of identifying the Oligo-Miocene boundary, which is especially difficult in the Tertiary sediments outcropping in the Abruzzi area. In fact, because of the numerous local variations in the Tertiary sediments at the edges of the L'Aquila basin, the sedimentary events are rather difficult to reconstruct: these events were the prelude (in the Palaeogene-Lower Miocene) to the general transgression that affected the Laziale-Abruzzese platform in the middle Miocene.

The Gran Sasso section, with its considerable vertical development (about 60 m) and its lithology, predominantly calcareous, was quite favourable for a taxonomic, phylogenetic and detailed biostratigraphic study. In fact, both environmental variations and lacunosity could now be considered

reduced to a minimum, as well as the resedimentation phenomena that involve the larger Foraminifera in the predominantly marly facies.

On the other hand, the study was subsequently difficult because it had to face the task of obtaining a large number of thin sections of hard rock, in series, that would make it possible to recover significant quantities of specimens well oriented according to the equatorial plane of the shell.

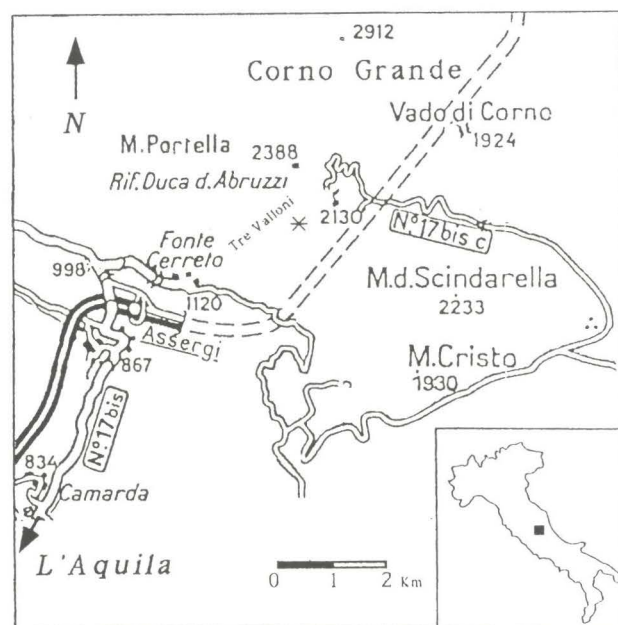
THE GRAN SASSO SECTION

LOCATION

The succession sampled is situated in an area called «Tre Valloni», on the western slopes of the Gran Sasso (Text-fig. 1).

The outcrop is reached by following the footpath that starts from the station of the cable railway at elevation 2100 m, until a deep gully is reached at the elevation of about 1885 m; going down along this gully to the elevation of about 1840 m, there is a confluence with another gully; going up again along the latter, after a few meters, the first layers of the sampled succession are encountered; they begin at elevation 1850 m and rest on probably Eocene conglomerates.

The layers have a NW-SE direction and an inclination of about 40° NE.



Text-fig. 1 - Location map of the investigated outcrop. (* = sampled succession).

GEOLOGICAL AND STRATIGRAPHIC SETTING

The development of the sedimentary complexes present in the Central Apennines originates from the geodynamic evolution of a Triassic carbonatic platform that developed along the passive edge of the Tethys (Parotto & Pratlurion, 1975; Carbone, 1984).

Within these sedimentary complexes we can distinguish: platform, edge, slope, basin and seamount complexes. Each of these is characterized by associations of recurrent lithotypes, which alternate and are repeated in various ways in relation to the evolution of the area they characterize (Accordi *et al.*, 1988). This development of heteropic successions, deposited predominantly on continental crust, is the result of substantial changes in the palaeogeography of the sedimentary environments. The factors that have contributed mostly to determining the different evolutionary stages of the primitive Triassic platform are: tectonics, the variation of the growth potential of the carbonatic platform and of the edges, and the sea-level changes on a global scale (Vail *et al.*, 1977; Vail & Hardenbol, 1979; Haq *et al.*, 1988).

In the Cenozoic, geodynamic conditions connected to the closing process of the Tethys, cause the emersion and break-up of the platform, causing at first local lacunose phenomena, and then the complete disarticulation of the whole carbonatic unit with shortenings of the structures and the formation of folds and overthrusts with E and NE vergence (Accordi, 1963, 1966; Parotto & Pratlurion, 1975). In the Gran Sasso area the Cenozoic formations are different in the Palaeocene and in the Eocene, with sedimentation of the Scaglia with planktonic Foraminifera in some areas, while in other areas red calcarenites develop that continue up to the Oligocene.

In the Miocene there is an increase of the tectonic subsidence in some connecting areas between emerged structural heights and basins. In these narrow, elongated depressions there accumulate, in the Lower Miocene, potent marly successions (Marne con Cerroghna). Subsequently open neritic platform conditions are set up, in which organogenous formations are deposited (Calcari a Briozoi e Litotamni) that are transgressive on a large part of the Cretaceous platforms. In front of the Gran Sasso there is a calcarenitic succession of the Lower Miocene, which reaches thicknesses of a hundred metres, in which Miogypsinae and Lepidocyclinae are present.

The palaeogeographic evolution of this area has been greatly conditioned by the compressive tec-

tonics which acted during the Alpine orogeny on the various sedimentary units that developed in the Meso-Cenozoic.

PREVIOUS STUDIES

The first studies on the geology and in particular on the palaeontology and stratigraphy of the area being examined date back to Parona (1897, 1899), Chelussi (1903, 1904), Cassetti (1904, 1906), Sacco (1906, 1907), Crema (1912, 1913), Principi (1935).

Renz (1936) carried out a careful study on some successions in the L'Aquila area and in particular on a succession near the one examined in this paper.

Baumann (1970) considered the succession of Mt. Torretta (Preturo - L'Aquila) and proposed a correlation between the Zones with planktonic Foraminifera and the Zones with Nannoplankton, but he excluded the Miocene forms from his study.

Sartoni (1974) described the fauna with planktonic Foraminifera in an Oligo-Miocene outcrop on the east side of Mt. La Rocca (Tornimparte - L'Aquila).

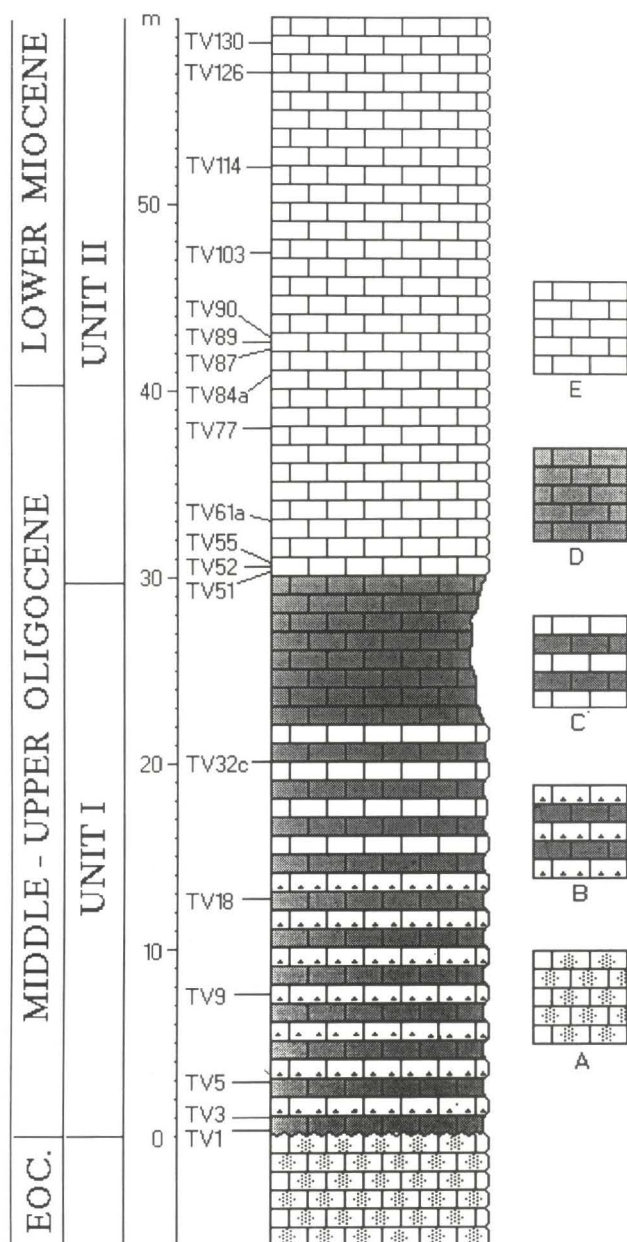
Matteucci & Schiavinotto (1977, 1980, 1985) and Schiavinotto (1979) were concerned with the above-mentioned locality, and examined the Oligocene of Mt. La Rocca and the Miocene of Mt. La Serra. These studies, essentially aimed at a better knowledge of the fauna with larger Foraminifera by means of the biometric method, also made possible a more detailed stratigraphy.

Schiavinotto & Verrubbi (1994) reported preliminary data on a part of the same material studied in the present paper.

DESCRIPTION OF THE SUCCESSION SAMPLED

The succession of the lithotypes and of the faunas found by us is in good agreement with the analysis done by Renz (1936) in the Oligo-Miocene succession existing in the vicinity of the one being examined in this paper. Renz distinguished: a lower part, containing only Lepidocyclinae and characterized by limestones, for the most part red in colour, intercalated by brick-red marly limestones; an upper part, represented by lightbrown-grey limestones, in which Miogypsinae are present in large numbers.

For a better description of the succession we therefore decided to divide it into two informal Units. Unit I, which has a total thickness of about 30 m, is composed of the layers between TV1 and TV51, while Unit II, which has a thickness of about 29 m, is formed of the layers between TV52 and TV130 (Text-fig. 2).



Text-fig. 2 - Lithostratigraphical column of the Tre Valloni sections. A = Eocene conglomerate; B = wackestone with lithic inclusions; C = wackestone; D = packstone; E = grainstone.

The sampling was done layer by layer; the thickest layers were sampled at their bottom and at their top.

Thin sections of rock were obtained in about 50% of the calcarenitic samples. The samples without marked lithologic and/or faunistic changes were omitted; however, the samples studied cover the entire succession. From each sample in which

the populations of *Nephrolepidina* were studied, about 10-15 thin sections of rock were obtained.

Much attention was paid to the orientation of the cutting of the rock, in order that the specimens might be disposed with their equatorial plane parallel to the plane of the thin section.

Very small «populations» (with $N = 4-5$) were obtained from some samples: such a number of specimens was considered statistically not significant and the relevant biometric data, even if in good accordance with the observed overall trend, were not inserted in the present study.

The study of the frequencies of the various taxa, as Wildenborg (1991) pointed out, presents some problems. In fact, some sedimentary processes, such as the gradation and sorting of the alloclasts, can considerably affect the significance of the results. The absolute frequency is the element that proves to be the one most affected by these processes. The problems that arise in the study of the absolute frequency are partly attenuated if we consider the relative frequency. In that case, the relation between the various taxa considered is sufficiently representative of the original biotic community. For a greater reliability of the data obtained, from each sample in which the relative frequency of the taxa considered was studied, thin sections were obtained at various heights and orientations of the sample itself; the relative frequencies were calculated on the basis of the total number of specimens of each taxon determined on all the thin sections made in the sample.

Samples and thin sections are stored in the Dipartimento di Scienze della Terra, Università «La Sapienza», Rome.

Lithological characteristics

Unit I: The lithotypes composing this Unit have very variable depositional textures. In the lower part and in the middle part an alternation of wackestone and packstone can be noted (Pl. 1, figs. 4, 7, 8); in the lower part there are often present lithic inclusions of small dimensions.

The upper part consists of wackestone. This part of the Unit, which has a thickness of about 8 m, cannot easily be observed because it is extensively covered by a grassy pad.

The sedimentary structures are also rather variable. The thicknesses of the layers fluctuate between 10 and 50 cm. However, some layers, especially among the clayey lithotypes, have thicknesses of the order of a few cm, while others, among the calcarenitic lithotypes, have thicknesses that in some cases exceed 2 m. In all the lithotypes

there is often present a fine lamination that frequently assumes a lenticular shape. In the calcarenitic layers there has often been found a direct, rarely an inverse gradation, and the alloclasts are slightly chaotic. The colour of the layers varies mainly from rosy to brick-red; only a few layers have a Havana-grey colour.

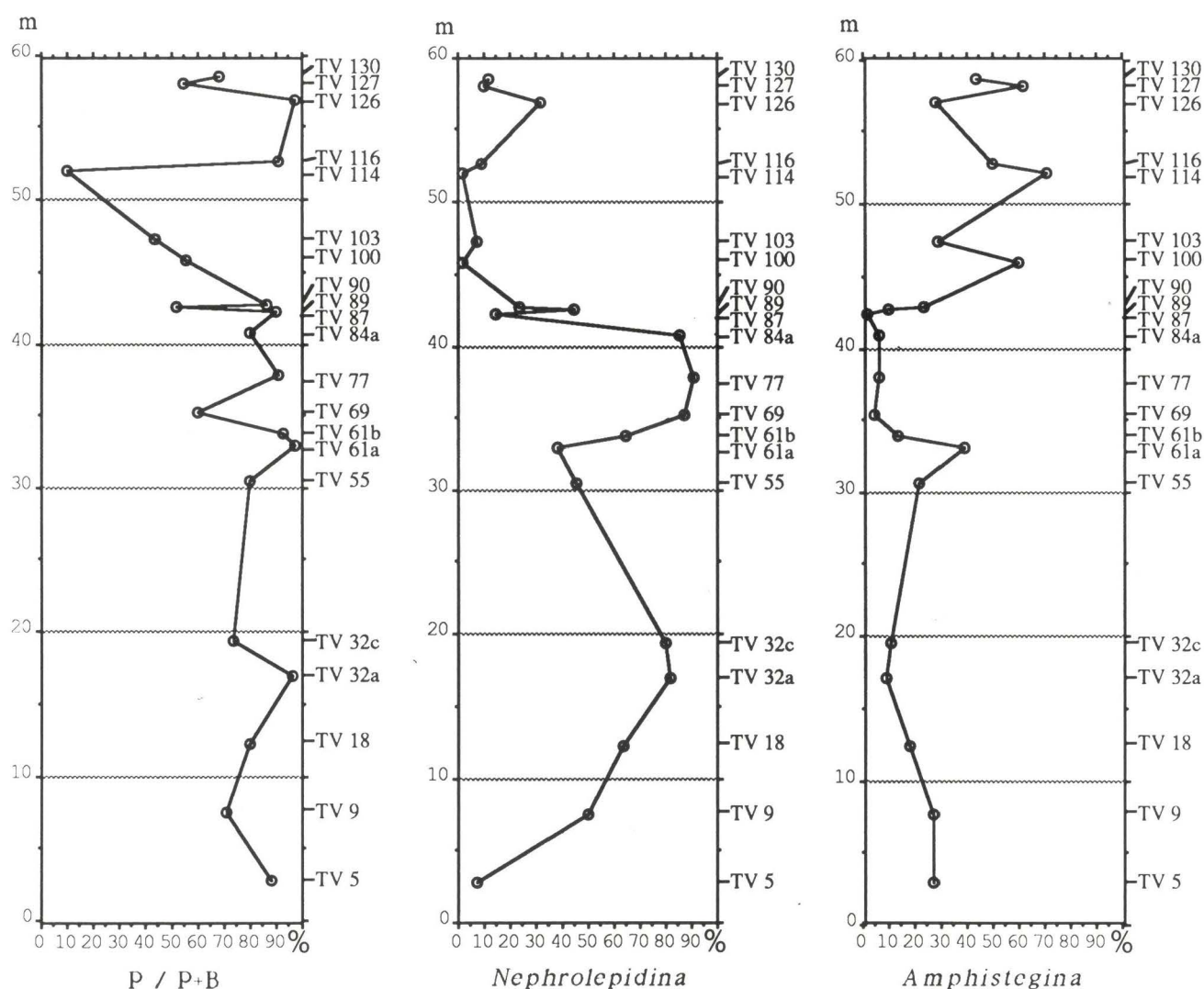
Unit II: This Unit has less variable depositional textures than the preceding one; in fact, it mainly consists of packstone with variable percentages of matrix (Pl. 2, figs. 3, 4), and in a few cases of grainstone with a high accumulation of alloclasts (Pl. 2, figs. 4, 7). In many layers a direct, rarely an inverse gradation can be seen, and the alloclasts are slightly chaotic. The wackestone are rare and their

thicknesses are of the order of a few cm. Glauconite is present in all the Unit.

The stratification is less evident than in the Unit underneath; the colour of the calcarenitic layers is light grey without significant variations, while their thickness varies between 5 and 60 cm in the lower part, and between 30 and 70 cm in the upper part. The colour of the rare interbedded marly levels, which are present above all in the lower part, is light green.

Faunistic content

The fossil associations are composed of organisms of neritic environment and of pelagic en-



Text-fig. 3 - P/(P+B) ratio and relative frequencies of *Nephrolepidina* and *Amphistegina* in thin-sections of the samples in the Tre Valloni section.

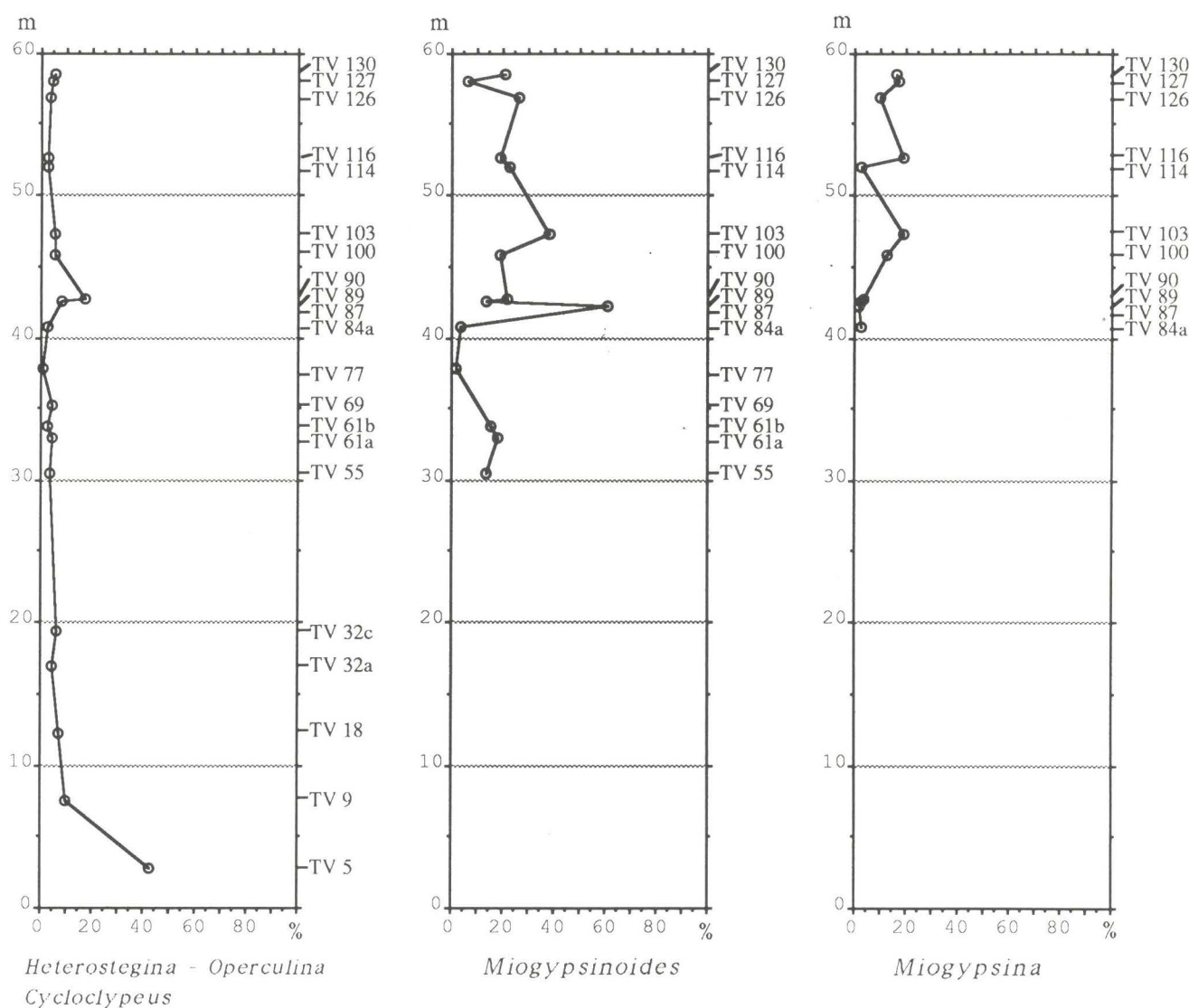
vironment. From the analysis of the relative frequencies of the benthonic Foraminifera and of the plankton/plankton+benthos ratio, we can obtain useful palaeoecological indications.

The P/P+B ratio (Text-fig. 3) fluctuates around medium-high values in the whole succession; however, significant drops are present. The gradual decrease seen between samples TV100 and TV114 also seems significant; in the latter there is the lowest value recorded.

The Nephrolepidinae appear, in very few occurrences, in sample TV3 (Pl. 1, fig. 7) but its relative frequency becomes evident in TV5 and tends to increase up to sample TV9 (Text-fig. 3); then their frequency fluctuates around rather high values

up to sample TV55, where a decrease starts that continues up to TV61a. In TV61b the frequency of the Nephrolepidinae returns to high values until it reaches TV84a (Text-fig. 3; Pl. 1, fig. 1). Between TV84a and TV90 there are extensive fluctuations of the relative frequency; in samples TV87 and TV90 significant drops can be seen. In the samples following TV90 the value of the frequency fluctuates around very low values (Pl. 2, figs. 1-7), except in TV126 in which a positive peak is recorded.

Amphistegina appears, with very rare specimens in sample TV3, but its relative frequency becomes significant in TV5 and is not very frequent until sample TV100, except for a positive peak in TV61a.



Text-fig. 4 - Relative frequencies of *Miogypsinoidea*, *Miogypsina* s.s., and Nummulitids (*Operculina*, *Heterostegina* and *Cycloclypeus*) in thin sections of the samples in the Tre Valloni section.

From TV100 its relative frequency reaches medium-high values with rather marked fluctuations (Text-fig. 3; Pl. 1, fig. 1; Pl. 2, figs. 1-8).

The frequency of *Eulepidina* (not shown) keeps medium-low values (10-15%) up to TV18, then it undergoes a decrease and shows values around 1% up to TV130 (Pl. 1, fig. 6; Pl. 3, fig. 4).

The nummulitids (*Heterostegina*, *Operculina*) have a frequency that fluctuates around medium-low values for the whole succession, while *Cycloclypeus* is present with rare specimens up to the sample TV55 (Text-fig. 4; Pl. 3, figs. 5-8).

In sample TV55 *Miogypsinoides* appears (Text-fig. 4; Pl. 1, fig. 4), and in TV84a *Miogypsina* appears (Text-fig. 4; Pl. 1, fig. 1). The relative frequency of the miogypsinids fluctuates around rather high values in Unit II. In this part specimens of *Gypsina* are also associated (Pl. 3, fig. 2).

In all the samples studied the organogenous remains of Bryozoa and coralline algae are found to be rare; the remains of echinoids are more frequent. In some samples, as for example TV90, planorbuliniform Foraminifera are quite frequent (Pl. 3, fig. 1).

Biostratigraphic setting

The first biostratigraphic considerations in the Gran Sasso section can be made on the basis of the vertical distributions of *Cycloclypeus* and of the Miogypsinidae, as reported by Drooger & Laagland (1986, p. 145, fig. 1) and Laagland (1990).

References based on the zonations with planktonic Foraminifera can only be indirect to date, because the material at our disposal has not provided reliable indications (specimens badly preserved in the washing residues). The sequence of our samples can therefore be referred to the biostratigraphic scheme of Laagland (1990, p. 22, fig. 4; p. 118, fig. 60) as indicated in Text-fig. 5. On the basis of the following observations, samples TV3 and TV5, although it has not been possible to make determinations biometrically, can be referred to the lower and middle part, respectively, of the *N. praemarginata* Zone. In fact, in TV3 there is the appearance of *Eulepidina* with embryonic apparatuses having a smaller diameter than what has been found to date in the Central Apennines area (Matteucci & Schiavinotto, 1977). In the absence of average values, they can be referred to *Eulepina* cf. *formosoides* (Douville'), already found in deposits referable to the *G. opima opima* Zone (N2) in association with *N. praemarginata* at very primitive evolutionary stage (Van Heck & Drooger, 1984, p. 302). In TV5 there is the appearance of *Nephrolepidina* cf. *praemarginata*,

with a few rather small specimens; the absence of *Cycloclypeus*, if it is not due to environmental factors, would justify the reference of this sample to the middle part of the *N. praemarginata* Zone.

From TV9 up to TV55 there is the presence of *Cycloclypeus*: the samples are easily referable to the *Cycloclypeus* Zone, with an indirect correlation to the middle-high part of the *G. opima opima* Zone and the lower-middle part of the *G. ciperoensis* Zone (P21/N2 - P22/N3).

The appearance of *Miogypsinoides* in the packstone of sample TV52 makes it possible to refer the base of Unit II to the *Miogypsinoides* Zone. The primitive character of the nepionic spirals in the megalospheric individuals makes it possible to assign them to *Miogypsina* (*Miogypsinoides*) cf. *complanata*, and to refer them to the respective subzone, already recognized in the area at Monte La Rocca, type-level of *Cycloclypeus mediterraneus* (sample T1 of Matteucci & Schiavinotto, 1977, 1985; and sample JT911 of Laagland, 1990); an indirect reference to the scale with planktonic Foraminifera would indicate the middle part of the *G. ciperoensis* Zone (P22/N3).

In TV55, the coincidence between the presence of the last *Cycloclypeus* and the appearance of *Miogypsinoides* makes it possible to attempt a further refinement: the nepionic characteristics of *Miogypsinoides*, although they have not yet been studied at population level, seem to permit a reliable reference to *Miogypsina* (*Miogypsinoides*) cf. *formosensis*, because specimens with a nepionic spiral consisting of more than 20 chambers are rare, while individuals with nepionic spirals with 15-16 chambers are more frequent. Consequently, the association between a rather primitive evolutionary stage of *M. formosensis* and the last representatives of *Cycloclypeus* would be in good agreement with the stratigraphic distributions recognized to date for the two taxa in the Mediterranean area; a reference of sample TV55 to the *Miogypsinoides* Zone, a *M. formosensis* subzone (low part) would therefore be reliable. The reference to the scale with planktonics, still indirect, would be possible for the high part of the *G. ciperoensis* Zone (P22/N3).

TV77 is to be referred to the *Miogypsinoides* Zone, a *M. formosensis* subzone that can be correlated with the lower part of the *Globorotalia kugleri* Zone (Upper Chattian).

Sample TV84a makes it possible to establish another valid biostratigraphic reference on the basis of the appearance of representatives of *Miogypsina* s.s.; they have nepionic chambers disposed according to a single spiral, with more frequent morphotypes with 11-12 chambers; it is possible to attribute them

Age m.y.	Series Stages	ZONATION				SAMPLES
		Plankt. foraminifera	calcareous nannoplank.	Larger foraminifera		
25	MIOC. AQUIT.	N4	<i>G. kugleri</i>	NN1	<i>gunteri</i>	TV130
	CHATTEAN	P22	<i>G. ciperoensis</i>	NP25	<i>Miogypsinoides formosensis</i>	TV84a
		N3			<i>complanatus</i>	TV77
						TV55
	OLIGOCENE	P21	<i>G. optima optima</i>	NP24	<i>Cycloclypeus mediterraneus</i>	TV32c
		N2			<i>droegeri</i>	TV9
	RUPELIAN	P19	<i>G. ampli-apertura</i>	NP23	<i>praemarginata</i>	TV5
		N20				TV3
35	EOC. PRL.	P18	<i>C. chipolensis</i>	NP22	<i>fichteli</i>	
				NP21		
		P17	<i>G. cerro-azulensis</i>	NP19/20		

Text-fig. 5 - Biostratigraphic scheme (after Laagland, 1990) whit estimated stratigraphic position of some significant samples from the Tre Valloni section.

to *Miogypsina* cf. *gunteri*. According to Laagland's scheme (1990), sample TV84a would indicate the base of the Aquitanian (*G. kugleri* Zone). In the next samples no significant changes are observed in the frequency of the morphotypes of the unispiralled miogypsinids; there do not appear either morphotypes with two nepionic spirals, or representatives of *Mioplepidocyclina*. Consequently, all these samples can be referred to the *M. gunteri* Zone.

Depositional environment

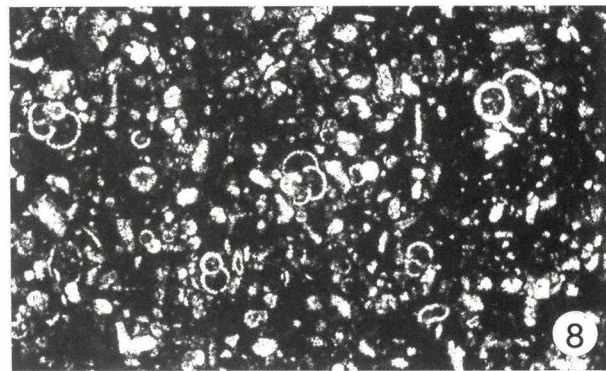
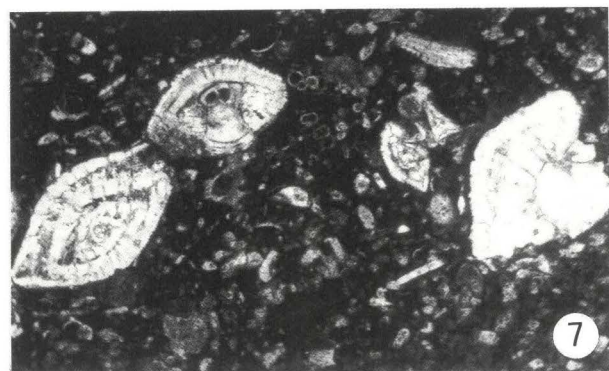
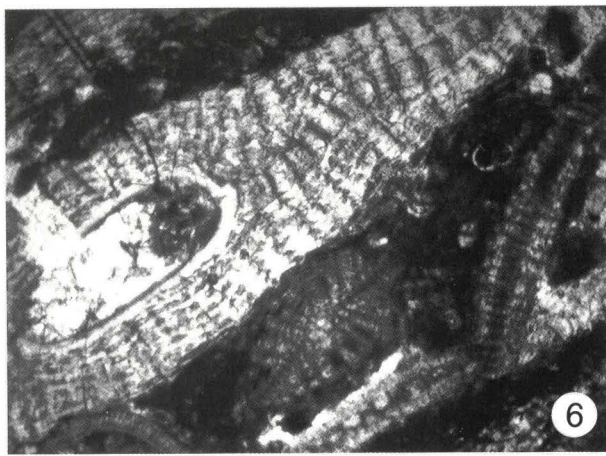
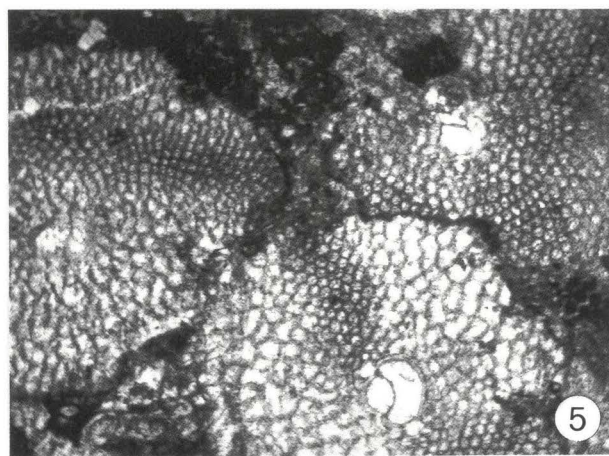
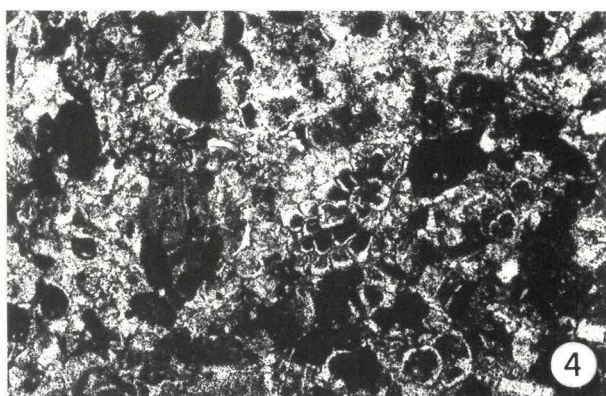
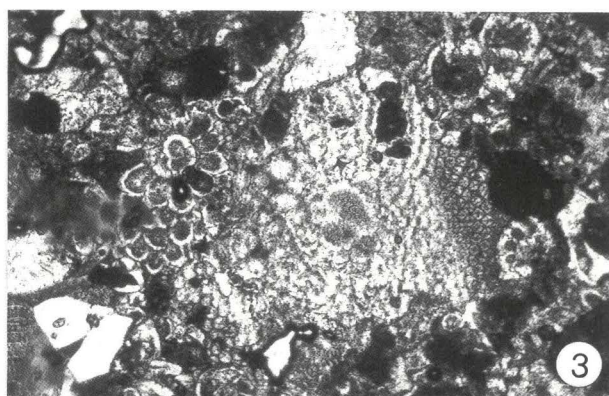
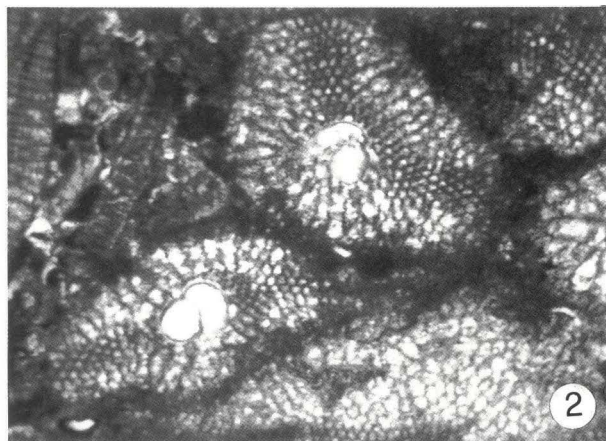
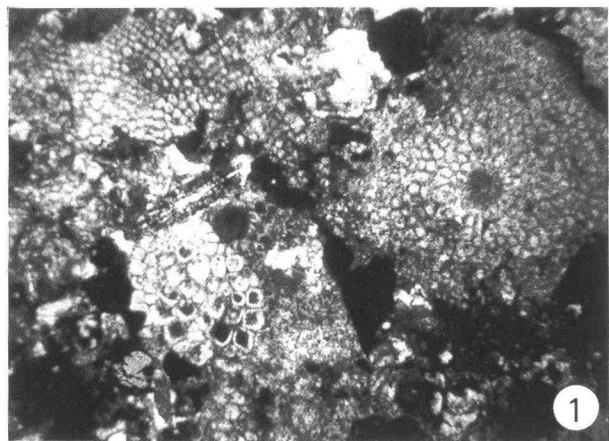
The lithological, textural and faunistic characteristics found by us indicate that the sedimentation of the succession happened along a depositional slope. Tectonic instability and eustatic variations on a global scale would have caused changes in the sedimentary conditions, causing an evolution of the facies.

Unit I shows characteristic that can be associated with the deepest parts of the depositional slope. In this part of the succession the wackestones contain traces attributable to the «ichnofacies with *Zoophicos*», which is indicative of muddy sea-bottoms in the transition between the littoral zone and the bathyal one (Seilacher, 1967; Pemberton *et al.*, 1990). In this environment, we find the best conditions for the development of a mixed sedimentation of autochthonous material and allothigenous material transported along the slope. The detrital-organogenous calcarenites appear to be linked to depositional mechanisms of turbiditic flow type. The characteristics of the fossil association indicate that the calcarenites come from the upper part of the slope, where they have been deposited in an in-

EXPLANATION OF PLATE 1

Figs. 1-8 - Microfacies from some levels in the Tre Valloni section (Middle Oligocene - Lower Miocene; Gran Sasso, Central Apennines); from above downwards:

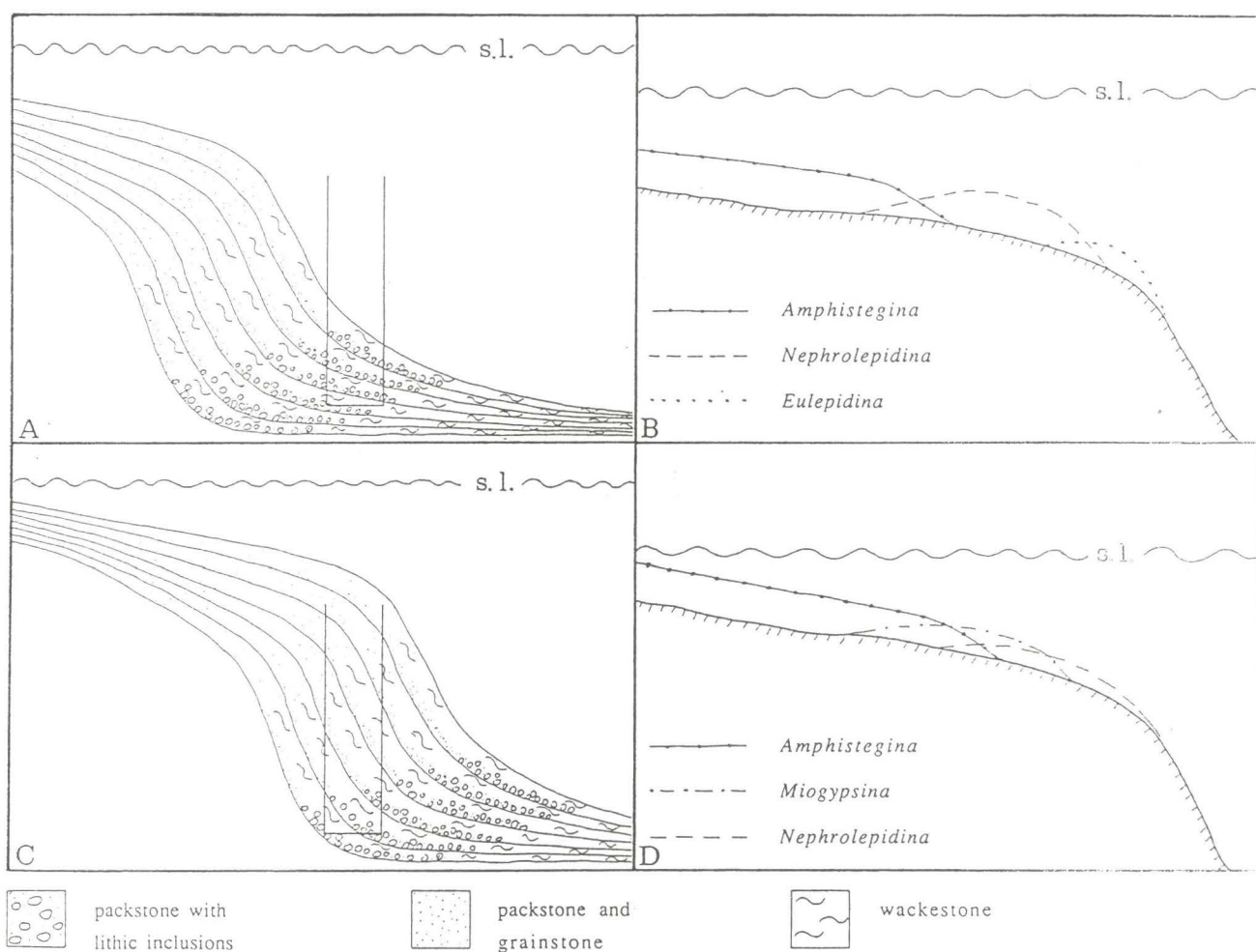
- 1) Packstone with *Nephrolepidina tournoueri* (frequent) and miogypsinids (rare). Middle part of Unit II, *Miogypsina gunteri* Zone. Sample TV84a; x 20.
- 2) Packstone with very frequent *Nephrolepidina* ex. interc. *morgani-tournoueri*. Lower-middle part of Unit II, *Miogypsinoides formosensis* subzone. Sample TV77; x 20;
- 3) *Nephrolepidina morgani* (frequent) and *Miogypsinoides* (rare) in a packstone of the lower part of Unit II. *Miogypsinoides formosensis* subzone. Sample TV61a; x 20;
- 4) Packstone with *Miogypsina* (*Miogypsinoides*) cf. *formosensis*. Lower part of Unit II. Sample TV55; x 20;
- 5) Packstone with very frequent *Nephrolepidina morgani*. Unit I, *Cycloclypeus mediterraneus* subzone. Sample TV32c; x 20;
- 6) Packstone with *Eulepidina* sp. and *Nephrolepidina praemarginata*. Unit I, *Cycloclypeus droegeri* subzone. Sample TV9; x 20;
- 7) Packstone with amphisteginids and rotaliids. Lower part of Unit I. Sample TV3; x 20;
- 8) Wackestone with planktonic Foraminifera. Lower part of Unit I. Sample TV1; x 40.



franeritic environment with open circulation. The low frequency of Bryozoa, coralline Algae and corals indicates that the sea-bottoms from which the materials constituting the calcarenites came were mobile and devoid of bioconstructed structures (Text-fig. 6A, C).

In Unit II a change of facies can be seen. The lithology, the depositional textures and the fossiliferous content indicate an evolution of the environment towards less distal conditions that can be associated with the upper part of the depositional slope. The calcarenites reflect characteristics linked to proximal turbidites. Their faunistic content indicates that the environment from which they come

is infraneritic with open circulation, closer to the boundary with the epineritic environment compared with Unit I. In fact, in the calcarenites of Unit I there are specimens of *Eulepidina* and *Cycloclypeus*, which usually indicate the deepest part of the neritic environment. In Unit II, on the contrary, we find specimens of Gypsinae and planorbuliniforms that are indicators of weak bathymetry. Moreover, the frequency of *Eulepidina* becomes very low, while there is an increase in the presence of *Amphistegina* that can be connected with an increase of the light intensity. The relative frequencies of the organogenous component suggest that the bottoms from which the calcarenites were mobilized were



Text-fig. 6 - Schematic representation of the sedimentary - faunistic variations originating the Tre Valloni succession: A) Unit I - mixed sedimentation of autochthonous and allothigenous material transported along a depositional slope. The detrital-organogeneous calcarenites appear to be linked to depositional mechanism of turbiditic flow type; B) frequency (density) curves of main larger Foraminifera in the productive sea-bottom for Unit I; these curves were obtained considering both our data and what indicated in Buxton & Pedley (1989), (the relative height of the curves with respect to the sea-bottom represents the relative frequency of the taxa); C) Unit II - the environment changes towards less distal condition that can be associated with the upper part of the depositional slope (proximal turbidites); D) frequency (density) curves of main larger Foraminifera in the productive sea-bottom for Unit II; these curves were obtained considering both our data and what indicated in Buxton & Pedley (1989), (the relative height of the curves with respect to the sea-bottom represents the relative frequency of the taxa).

not very stabilized, and with a low hydrodynamism (Text-fig. 6B, D).

The Gran Sasso section has some elements comparable with the «Complesso di Termo Forà» studied by Ferrero (1987) in her paper on the Miogypsinids of the Oligo-Miocene deposits of the Collina di Torino. In the Complesso di Termo Forà we find variously marly-silty pelites, sedimented in a bathyal environment, alternating with coarse detrital levels coming from the coastal platform, which contain Miogypsinidae and Miolepidocyclinae.

Also in Wildenborg's paper (1991) concerning the evolutionary aspects of the Miogypsinids in the Oligo-Miocene carbonates near Mineo (Sicily), it is possible to find some environmental analogies with the Gran Sasso section. The Author divides the Mineo sections into six Units; in particular, the packstones and grainstones in Unit V are referred to a sedimentation in an open sublittoral environment. Moreover, the high relative frequency of the planktonic Foraminifera suggests to the Author that the area in which Unit V was deposited was far away from the coast.

THE NEPHROLEPIDINAE OF THE GRAN SASSO

BIOMETRIC METHODS

The following measurements, schematized in Text-fig. 7, were taken on the embryonic and nepionic chambers of specimens sectioned according to the equatorial plane of the shell:

Factor Ai = «degree of embracement» of the protoconch by the deutoconch (Van Der Vlerk, 1959a, b; 1963):

$$Ai = c.w./ic \cdot 100$$

where

c.w. = length of the common wall between protoconch and deutoconch, taken on the internal side of the protoconch.

ic = length of the whole inside wall of the protoconch.

Parameter C = Number of the adauxiliary chambers:

$$C = \Sigma AACII$$

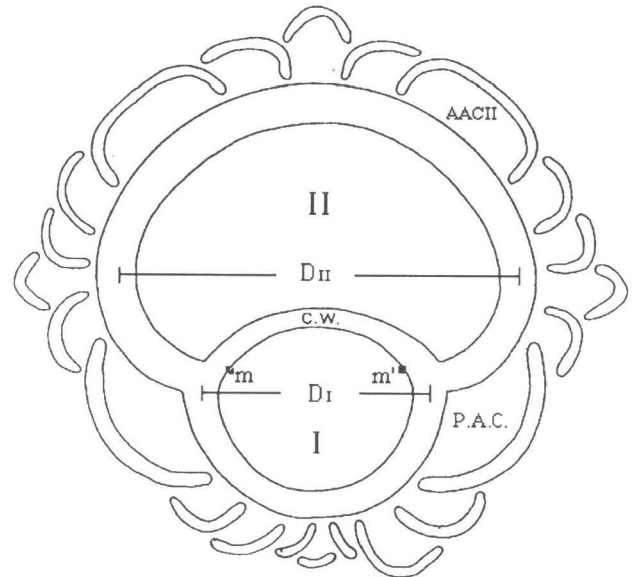
DI = diameter of the protoconch; half thickness of the wall is included.

DII = diameter of the deutoconch; half thickness of the wall is included.

The measurements for *Ai* were taken with a curvimeter on photographic enlargements (x 500) of the nucleococonches.

Evolutionary and biostratigraphic significance

The evolutionary development of *Nephrolepidina* is characterized by a progressive increase in



Text-fig. 7 - Schematic drawing showing the methods of counting and measuring the internal features in horizontally sectioned embryonic-nepionic stage of megalospheric *Nephrolepidina*. Meaning of the symbols: I = protoconch, II = deutoconch, PAC = principal auxiliary chamber, AACII = adauxiliary chamber.

time of the average value, in the succeeding populations, of the degree of embracement of the protoconch by the deutoconch («Embryonic Acceleration» by Drooger & Freudenthal, 1964) and of the average number of adauxiliary chambers («Nepionic Acceleration» by Tan Sin Hok, 1936a, b; 1937a, b). The average values of *Ai* and *C* enable a specific attribution of the various populations to be made, according to the limits set for defining a succession of evolutionary stages connected with the chronostratigraphic scale (De Mulder, 1975). However, there was also identified a stagnant phase at the level of the intermediate stages of the evolutionary development, which are not considered useful for detailed biostratigraphic studies, in particular for the identification of the Oligo-Miocene boundary (Drooger *et al.*, 1976; Drooger & Laagland, 1986). Here measurements have not been taken of other factors and parameters that, to date, had been extensively used in the literature, such as the «degree of embracement» measured on the external side of the wall of the protoconch (Factor *Ao* of Drooger & Freudenthal, 1964), the «degree of curvature» of the common wall between protoconch and deutoconch (Van Der Vlerk, 1964), the «degree of evolution» and the «embryonic index» (Factors *DE* and *Ie* of Ambroise & Beretti, 1974). These variables have always proved useful in

confirming the evolutionary processes, but without bringing substantial improvements in the taxonomic and biostratigraphic fields.

DATA

The results of counts and measurements are summarized in Tabs. 1-4, in which: N = number of specimens measured; R = range; M = mean value; S = standard deviation; SM = standard error of the mean; v = coefficient of variability; SK and SK, st = indices of skewness.

The values useful for two statistical tests on the normality of the distributions are also reported: χ^2 = experimental value for the Chi-Square test, with the relevant number of degrees of freedom (d.f.) and K-S = experimental value for the Kolmogorov - Smirnov test (Massey, 1951).

The resort to this double analysis was necessary because, for some populations, the Chi-Square test could not be done since the number of observations was small and so a sufficient number of degrees of freedom was not reached.

The significance of the Chi-Square experimental values was analysed by means of the comparison with the tabular values in Snedecor & Cochran (1980, p. 470) and Camussi *et al.* (1986, p. 462, Pl. 3). The significance of K-S was analysed by means of the comparison with the tabular values in Siegel (1967, p. 209, Pl. E).

Distributions

The distributions of the data are expressed in the histograms of Text-fig. 8.

Factor Ai – It is shown that all the populations are represented predominantly by specimens of nephrolepidine type, with a degree of embracement from 40 to 50%; most of the frequency maxima come in the 40 - 45% class.

The specimens of isolepidine type, with Ai = 25 - 30%, are present (with only one specimen) in the TV61a population; this is probably due to the wider sampling (N = 55) that could be done in this case.

The presence of the isolepidine morphotype is very fluctuating with Ai = 30 - 35% (Pl. 4, figs. 5, 6), already very subordinate in TV9 and then sporadically.

The nephrolepidine morphotype with Ai = 45 - 50% (Pl. 4, figs. 2, 4) enters already in TV9 with only one specimen, but it increases its frequency rapidly in the subsequent populations, until it represents the absolute maximum in populations TV69 and TV77; subsequently, there is a drop in the frequency until it reaches a peak again in population TV130.

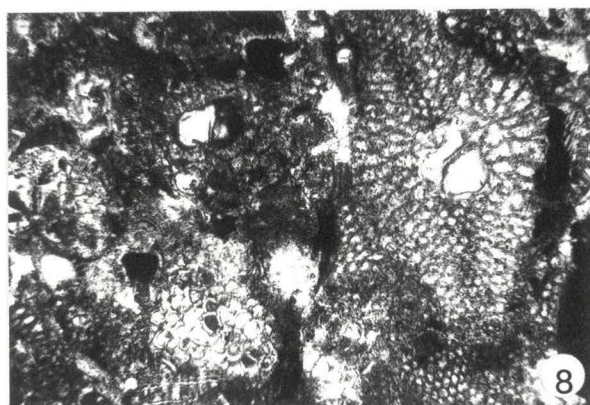
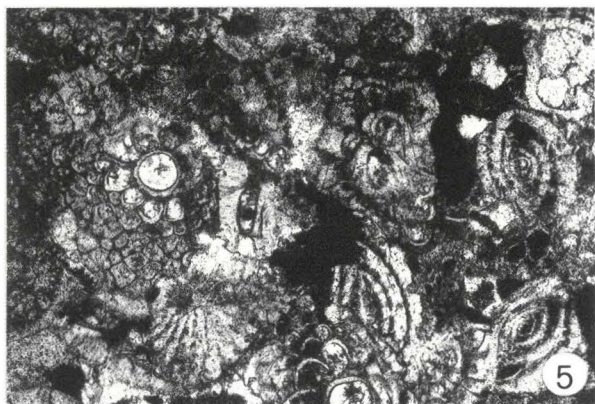
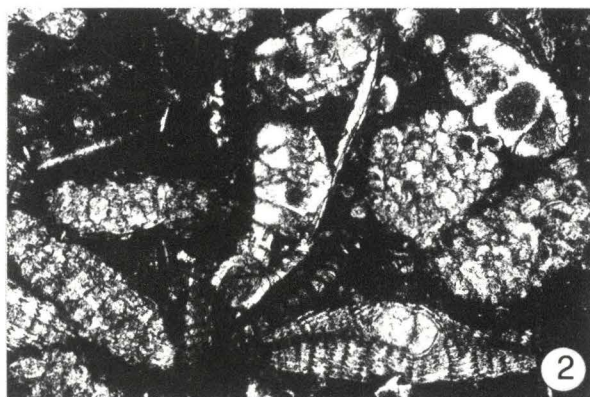
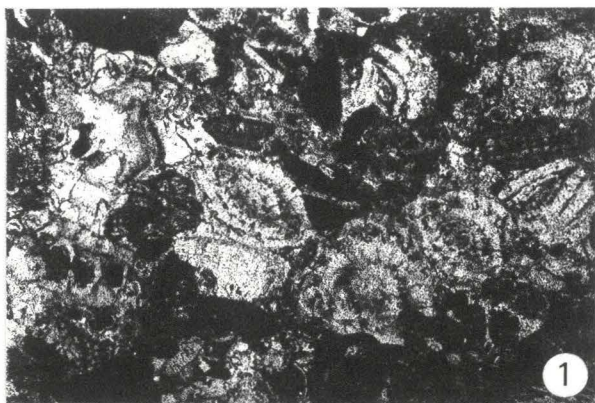
The appearance of very advanced nephrolepidine morphotypes, with Ai beyond 50%, occurs in population TV55, as already shown by the value of the variability index increasing up to population TV61a (Tab. 1) (Pl. 4, fig. 3).

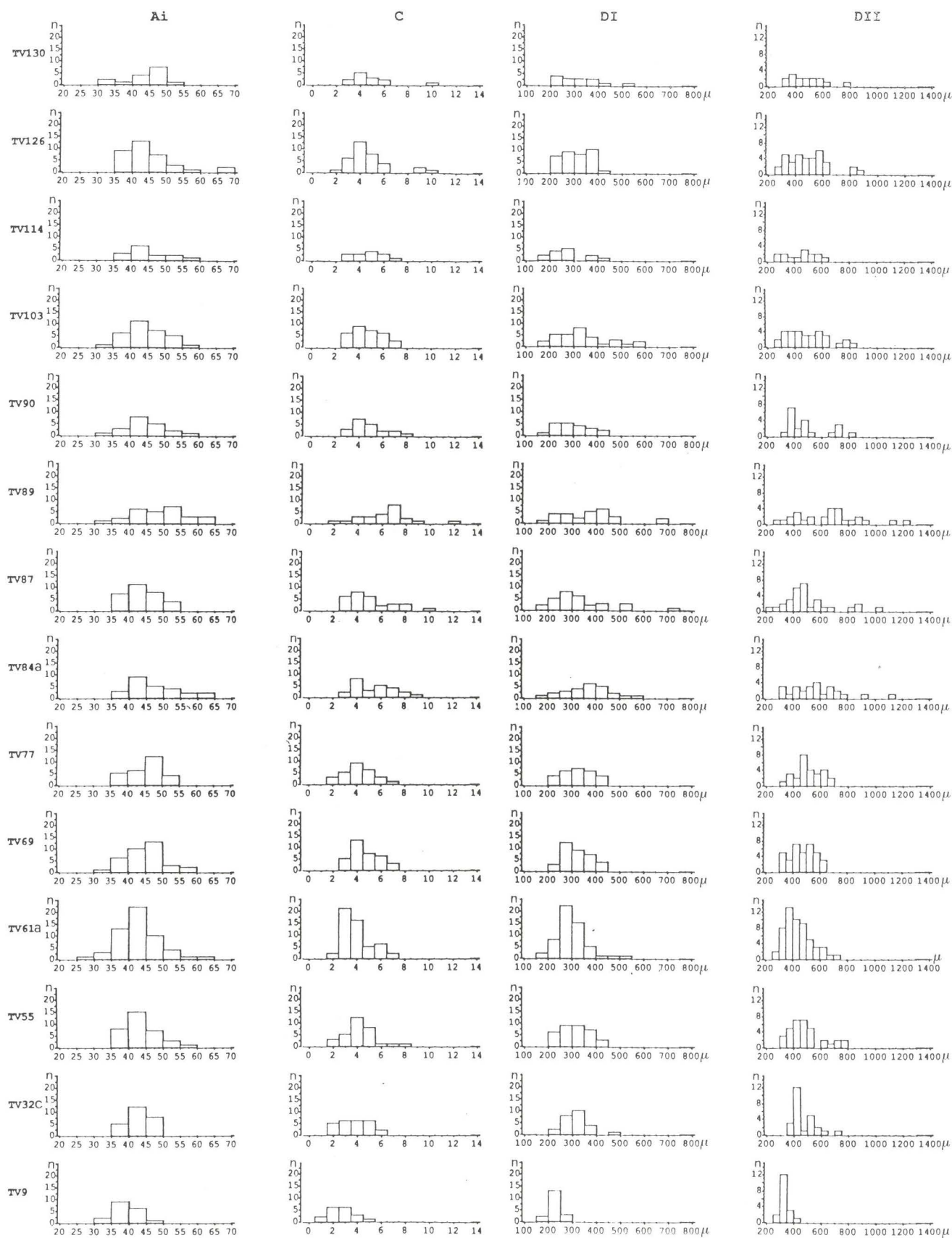
The subsequent fluctuations of index v are linked to an extreme irregularity in the frequencies of the various classes up to the interval represented by the trybliolepidine morphotypes with Ai between 60 and 65%, which are recorded in populations TV84a (Pl. 4, fig. 1) and TV89; in concomitance there are two peaks of the variability index. The maximum value of the variability index coincided with the appearance of specimens with Ai between 65 and 70% in population TV126, the exceptional nature of which is shown even more clearly by the fact that the class is not represented between 60 and 65%.

EXPLANATION OF PLATE 2

Figs. 1-8 - Microfacies from some levels in the Tre Valloni section (Middle Oligocene - Lower Miocene; Gran Sasso, Central Apennines); from above downwards. All x 20.

- 1) Packstone with *Amphistegina* (frequent), miogypsinids (subordinate) and *Nephrolepidina morgani* (rare). Upper part of Unit II, *Miogypsina gunteri* Zone. Sample TV130;
- 2) Packstone with well represented *Miogypsina s.s.* and *Miogypsinoides* sp., but subordinate to *Nephrolepidina* ex. interc. *morgani-tournoueri*. Upper part of Unit II, *Miogypsina gunteri* Zone. Sample TV126;
- 3) Packstone with good relative frequency of *Amphistegina* sp. in the upper part of Unit II, *Miogypsina gunteri* Zone. Sample TV126;
- 4) Grainstone with frequent *Amphistegina* sp. and phosphate granules. Upper Part of Unit II, *Miogypsina gunteri* Zone. Sample TV114;
- 5) Packstone with amphisteginids (frequent) and miogypsinids (subordinate); *Nephrolepidina* is rare. Upper part of Unit II, *Miogypsina gunteri* Zone. Sample TV114;
- 6) Packstone with high concentration of *Amphistegina* sp.. Upper part of Unit II, *Miogypsina gunteri* Zone. Sample TV114;
- 7) Grainstone with *Miogypsina s.s.*, *Miogypsinoides* sp., *Amphistegina* sp.. Upper part of Unit II, *Miogypsina gunteri* Zone. Sample TV114;
- 8) Packstone with *Nephrolepidina tournoueri* and *Miogypsina s.s.* Middle part of Unit II, *Miogypsina gunteri* Zone. Sample TV89.



Text-fig. 8 - Histograms of Ai, C, DI and DII for *Nephrolepidina* in the samples of the Tre Valloni section.

POPULATIONS	N	R	M	S	SM	v	Sk	Sk,st.	χ^2 (d.f.)	K-S
TV130	15	33.30-52.51	43.60	5.28	1.36	12.11	-0.58	-0.92	-	0.170
TV126	35	35.07-66.60	44.70	7.31	1.23	16.35	1.45	3.52		0.171
TV114	14	35.65-59.35	44.36	6.84	1.82	15.41	0.76	1.17	-	0.189
TV103	31	34.00-58.60	44.59	6.07	1.09	13.61	0.40	0.92	0.599 (1)	0.111
TV90	20	34.06-55.62	44.45	5.53	1.23	12.44	0.30	0.54	-	0.130
TV89	27	32.53-61.22	49.14	7.73	1.48	15.73	-0.33	-0.71	0.646 (1)	0.122
TV87	30	35.25-54.30	44.07	5.22	0.95	11.84	0.32	0.72	0.565 (1)	0.140
TV84a	25	36.34-61.90	47.38	7.03	1.40	14.83	0.40	0.82	0.980 (1)	0.120
TV77	27	38.70-52.76	45.30	4.30	0.82	09.49	-0.19	-0.40	3.746 (1)	0.134
TV69	35	32.41-56.85	44.21	5.44	0.91	12.30	0.28	0.69	0.966 (1)	0.150
TV61a	55	29.23-63.00	42.48	6.16	0.83	14.50	0.81	2.48	2.617 (2)	0.102
TV55	34	36.04-55.48	42.90	4.63	0.79	10.79	0.74	1.77	1.100 (1)	0.125
TV32c	25	36.50-49.77	43.55	3.63	0.72	08.33	-0.12	-0.25	0.497 (1)	0.099
TV9	18	31.87-45.38	38.76	3.34	0.78	08.61	-0.28	-0.49	-	0.174

Tab. 1 - Statistical results for the Factor Ai measured in the *Nephrolepidina* populations from the Tre Valloni section (N = number of measured specimens; R = range; S = standard deviation; SM = standard error of the mean; v = coefficient of variability; SK and SK, st = indexes of skewness; χ^2 = experimental value for the Chi Square test; d.f. = degrees of freedom; K-S = experimental value for the Kolmogorov-Smirnov test; bold type = significant values at P = 95%).

The histograms are unimodal, except for the bimodality recorded in population TV89.

The data regarding the skewness index point out skewness on the left (negative) in the two stratigraphically lowest populations (TV9 and TV32c), then in TV77, TV89 and finally in TV130.

In most of the populations, the index points out skewness on the right.

However, these indices seem to be very dependent on the magnitude of the values identified on the left or on the right of the modal class, determining the position of the mean value with respect to the mode that does not coincide with the effective representation of the frequencies at the two sides of the mode. If we observe the frequencies relating to the two sides of the mode, we therefore obtain other indications:

a) a numerical preponderance of specimens on the left of the mode is found in TV69 and it confirms the skewness on the left of TV77, TV89 and TV130;

b) in the majority of populations with a higher number of specimens on the right of the mode are also included the two stratigraphically lowest populations TV9 and TV32c;

c) the frequencies at the sides of the mode in TV61a are substantially symmetrical;

d) in the bimodal distribution of TV89, the principal frequency maximum is shifted into the field of the highest values.

Only in population TV61a is there a specimen that falls outside the upper limit of the interval $M \pm 3S$.

When it is applicable, the «Chi-Square» test does not record significant deviations from the normal distribution. The same can be said for the results given by the Kolmogorov-Smirnov test.

Parameter C – For the number of adauxiliary chambers, the ranges are represented mainly by the morphotypes characterized by 3 to 6 chambers on the deuteroconch (Pl. 4, figs. 1, 4, 5).

Morphotype 3 represents the frequency maximum only in populations TV9 and TV61a; morphotype 4 represents the frequency maximum in most of the populations.

The most primitive morphotypes are present irregularly: only two specimens with 1 adauxiliary chamber were recognized in population TV9, and then they definitely disappeared; morphotype 2 (Pl. 4, fig. 6) is present in population TV9 with a fairly high frequency, but it gradually decreases until it disappears in population TV69, and then it reappears sporadically in some subsequent populations.

Morphotype 7 (Pl. 4, fig. 3) makes its first appearance in TV55 and gradually reaches the frequency maximum in population TV89; in the succeeding populations it decreases sharply until it disappears in the two stratigraphically highest populations.

The morphotypes with a number of chambers higher than 7 appear in such a way as to increase their presence especially in the middle-lower part of Unit II, but they always form fragmentary tail-ends on the right of the distributions. Their presence appears to be well connected to high peaks in the values of the variability index (Tab. 2).

POPULATIONS	N	R	M	S	SM	v	Sk	Sk,st.	χ^2 (d.f.)	K-S
TV130	13	3 - 10	4.84	1.81	0.50	37.39	2.03	2.99	-	0.235
TV126	35	2 - 10	4.68	1.74	0.29	37.17	1.57	3.79	10.921 (3)	0.228
TV114	14	3 - 7	4.71	1.26	0.33	26.75	0.09	0.14	-	0.160
TV103	31	3 - 7	4.70	1.27	0.22	27.02	0.27	0.62	0.791 (1)	0.195
TV90	20	3 - 8	4.80	1.39	0.31	28.95	0.77	1.42	-	0.216
TV89	24	2 - 12	6.20	2.08	0.42	33.54	0.45	0.90	-	0.185
TV87	29	3 - 10	5.06	1.86	0.34	36.75	0.91	2.01	3.070 (2)	0.204
TV84a	25	3 - 9	5.44	1.66	0.33	30.51	0.41	0.83	-	0.207
TV77	27	2 - 7	4.15	1.29	0.24	31.08	0.16	0.35	-	0.175
TV69	34	3 - 7	4.67	1.19	0.20	25.48	0.45	1.07	2.661 (1)	0.243
TV61a	52	2 - 7	3.96	1.22	0.16	30.80	0.88	2.60	13.918 (2)	0.237
TV55	31	2 - 8	4.19	1.32	0.23	31.50	0.71	1.63	2.019 (1)	0.203
TV32c	25	2 - 6	3.76	1.26	0.25	33.51	0.09	0.18	-	0.165
TV9	18	1 - 5	2.72	1.07	0.25	39.46	0.30	0.52	-	0.193

Tab. 2 - Statistical results for the parameter C counted in the *Nephrolepidina* populations from the Tre Valloni section (Symbols as in Tab. 1).

The histograms are for the most part unimodal; in the two populations at the beginning of the succession (TV9 and TV32c) there is no distinct principal maximum; the distributions of TV61a, TV84a and TV87 are bimodal.

The values of the skewness indices are all evidence for skewness on the right; if we consider the total number of representatives in each side of the modal class (in the unimodal distributions), the skewness is confirmed in many cases with the exception of TV9, TV32c, TV89 and TV114.

In the bimodal distributions, the secondary frequency maximum is always on the right of the principal maximum.

It can also be deduced that the skewness index is affected also for C by the very high individual values (even when they are only a few) on the right of the mode, while the latter has a position definitely on the left of the range of many populations (in particular in TV61a).

No specimen falls out of the ranges $M \pm 3S$.

The Chi-Square test points out a distribution that departs from the normal trend for populations TV61a and TV126; the K-S test indicates unfitting with the normal distribution for TV69 and confirms it in TV61a.

DI - The ranges of the diameter of the protoconch show very differentiated extents along the sequence of populations, with fluctuations due to successive new appearances of protoconches with increasing diameter, up to maxima of 685 - 740 μ in populations TV87 and TV89; this generally happens in accordance with a progressive increase of the values of the variability index (Tab. 3).

Starting from population TV90, there is the appearance of very large embryos, with a fluctuating tendency of the variability index to decrease.

By using class intervals with an amplitude of 50 μ , it can be seen that the classes that represent a large part of the ranges go from 200 μ to 450 μ (Text-fig. 8).

Small protoconches (between 150 μ - 200 μ) are present starting from the basal populations, with subsequent intermittent presences up to TV114, after which they definitely disappear.

Specimens with diameters over 300 μ appear starting from TV32c (Pl. 4, fig. 5); already from this population diameters over 400 μ almost always represent tail-ends with classes of weak frequency in the right part of the distributions. The 400 - 450 μ class represents the principal frequency maximum only in TV89.

The histograms show a unimodal trend predominantly in the populations of Unit I; bimodal distributions are found in populations of the middle-high part of Unit II (TV84a, TV87, TV89, TV103, TV126).

In the unimodal distributions, the values of the skewness index (Tab. 3) prove to be indicators of great skewness on the right in TV32c, TV61a, TV114 and TV130. A higher number of specimens on the right of the modal class confirms this indication in TV61a and TV130, while it is also recorded in TV69 and TV90.

As regards the position of the modal class, it furnishes a contrasting indication compared with the preceding ones, as it is on the left of the range in TV61a, TV69, TV90 and TV130; in the latter it also

POPULATIONS	N	R	M	S	SM	v	Sk	Sk,st.	χ^2 (d.f.)	K-S
TV130	15	227 - 511	317.26	80.74	20.84	25.44	0.95	1.51	-	0.131
TV126	35	202 - 420	312.08	60.63	10.24	19.42	-0.22	-0.55	1.628 (1)	0.168
TV114	14	182 - 426	273.85	72.92	19.49	26.62	0.87	1.33	-	0.171
TV103	31	193 - 583	337.64	107.05	19.22	31.70	0.73	1.66	1.324 (1)	0.134
TV90	20	187 - 432	299.10	73.94	16.53	24.72	0.27	0.50	-	0.135
TV89	27	187 - 685	374.29	121.39	23.36	32.43	0.95	2.01	1.400 (1)	0.107
TV87	30	176 - 740	332.96	122.24	22.31	36.71	1.53	3.42	2.684 (1)	0.173
TV84a	25	182 - 592	361.88	100.81	20.16	27.85	0.21	0.43	0.426 (1)	0.069
TV77	27	232 - 440	324.20	62.50	12.03	19.27	0.14	0.31	0.631 (1)	0.114
TV69	35	227 - 437	318.88	58.00	09.80	18.18	0.24	0.58	0.504 (1)	0.088
TV61a	55	176 - 500	294.18	65.51	08.83	22.26	0.99	2.99	1.092 (1)	0.151
TV55	34	204 - 443	314.05	61.28	10.51	19.51	0.29	0.69	1.130 (1)	0.072
TV32c	25	224 - 450	313.92	50.60	10.11	16.11	0.69	1.41	0.406 (1)	0.105
TV9	18	186 - 274	228.50	24.30	05.70	10.66	0.17	0.30	-	0.112

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

POPULATIONS	N	R	M	S	SM	v	Sk	Sk,st.	χ^2 (d.f.)	K-S
TV130	15	301 - 796	478.06	130.35	33.65	27.26	0.94	1.48	-	0.121
TV126	35	252 - 851	491.65	144.15	24.36	29.31	0.82	1.99	0.531 (1)	0.089
TV114	14	267 - 602	447.42	114.12	30.50	25.50	-0.32	-0.41	-	0.160
TV103	31	256 - 833	490.35	152.29	27.35	31.05	0.59	1.36	0.767 (1)	0.095
TV90	20	318 - 805	489.50	153.05	34.22	31.26	0.96	1.76	-	0.232
TV89	27	250 - 1235	651.48	238.65	45.92	36.63	0.54	1.14	4.079 (1)	0.124
TV87	30	244 - 1037	509.26	187.10	34.16	36.73	1.34	3.00	4.502 (2)	0.219
TV84a	25	307 - 1148	573.52	197.40	39.48	34.41	0.09	2.23	2.407 (1)	0.120
TV77	27	342 - 682	510.90	94.50	18.20	18.49	0.12	0.25	2.031 (1)	0.113
TV69	35	312 - 639	473.31	89.93	15.20	19.00	-0.07	-0.16	1.230 (2)	0.090
TV61a	55	273 - 740	438.34	102.07	13.76	23.28	0.89	2.70	3.004 (3)	0.138
TV55	34	301 - 787	482.47	126.11	21.62	26.13	0.96	2.30	3.525 (1)	0.186
TV32c	25	382 - 702	474.48	79.80	15.90	16.82	1.12	2.30	5.216 (1)	0.239
TV9	18	270 - 420	330.67	36.30	08.57	11.00	0.90	1.55	-	0.205

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

corresponds to the class at the extreme limit of the distribution.

In the bimodal distributions there are different positions of the secondary maximum compared with the principal one: on the left in TV84a, TV89 and TV126, while it is on the right in TV87 and TV103.

Only one specimen falls out of the range $M \pm 3S$ in populations TV61a and TV87.

The values of Chi-Square and K-S agree in indicating a significant fitting with the normal distribution for all the populations.

DII – The diameter of the deutoconch shows great fluctuations in the characteristics of the distributions.

The ranges are mostly represented by the classes between 300 and 500 μ (Text-fig. 8) in the first part of the succession. Deutoconches with a diameter lower than 300 μ appear intermittently along the whole succession; deutoconches with a diameter higher than 700 μ are already present in the low part of the succession (TV32c), with a maximum value of 787 μ recorded in TV55.

Subsequently, there is a substantial withdrawal

POPULATIONS	Ai - C	Ai - DI	Ai - DII	C - DI	C - DII	DI - DII
TV130	0.812	0.465	0.624	0.887	0.942	0.939
TV126	0.751	0.448	0.689	0.627	0.872	0.822
TV114	0.762	0.165	0.566	0.590	0.817	0.808
TV103	0.576	0.310	0.501	0.540	0.691	0.916
TV90	0.723	0.377	0.481	0.628	0.731	0.804
TV89	0.836	0.503	0.646	0.739	0.841	0.902
TV87	0.592	0.292	0.373	0.790	0.883	0.958
TV84a	0.782	0.611	0.653	0.725	0.807	0.852
TV77	0.469	0.347	0.760	0.272	0.465	0.786
TV69	0.762	0.493	0.675	0.516	0.769	0.868
TV61a	0.667	0.154	0.488	0.310	0.643	0.747
TV55	0.716	0.373	0.630	0.702	0.824	0.885
TV32c	0.557	0.182	0.363	0.270	0.454	0.869
TV9	0.267	-0.049	0.446	-0.338	0.083	0.676

Tab. 5 - Correlation coefficient r obtained in the relations Ai - C, Ai - DI, Ai - DII, C - DI, C - DII and DI - DII of each *Nephrolepidina* population from the Tre Valloni section. Italic and bold type = below the significant minimum value.

up to populations TV84a, TV87 and TV89, where deutoconches appear with a diameter even over 1000 μ , although with very low frequencies.

In the final stretch of the succession there is a return to maximum values around 800 μ . The fluctuations are reflected in the trend of the values of the variability index.

The histograms are unimodal in few populations; in most of the cases there are bimodal distributions, and then plurimodal in the middle-high part of the succession.

In the unimodal distributions, the skewness index shows deviations to the right; however, the mode is always distinctly on the left of the range.

In the bi-plurimodal distributions there is a great variability in the position of the principal maximum, as well as in the positions of the secondary maxima. In this case, population TV89 can be a point of reference: in it the principal maximum can be considered in a central position in the range, and it is comprised between two secondary maxima.

Below TV89, the bimodalities have a secondary maximum on the right (TV32c, TV87). Above, the

secondary maximum is on the left of the principal maximum (TV114). As regards the plurimodalities, below TV89 the principal maximum is sometimes not very distinct, as in TV69; however, it seems to be generally between two secondary peaks. Above TV89, there are two secondary peaks on the left of the modal class only in TV126, while in the other two cases (TV90 and TV103) they are located on the right.

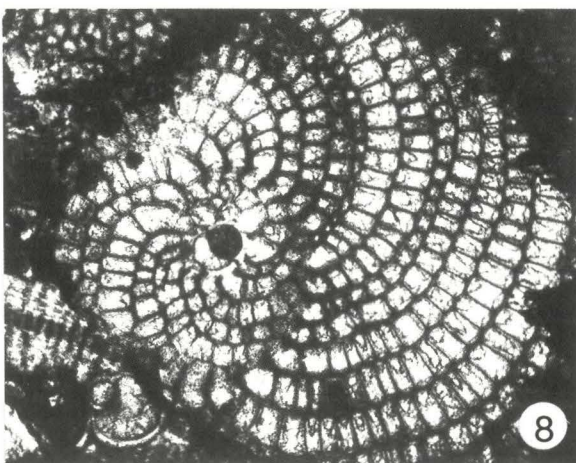
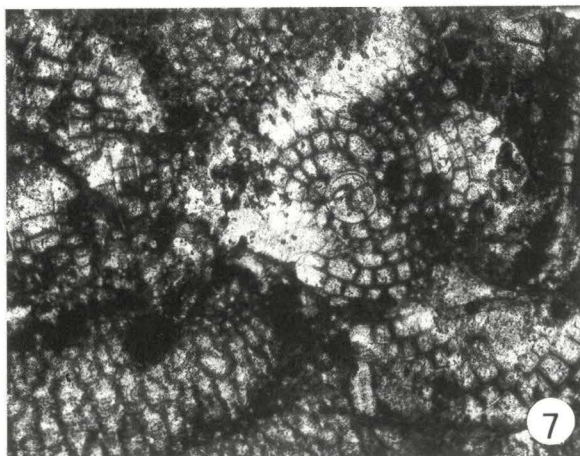
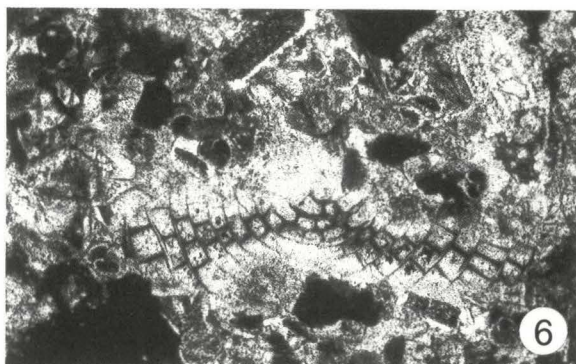
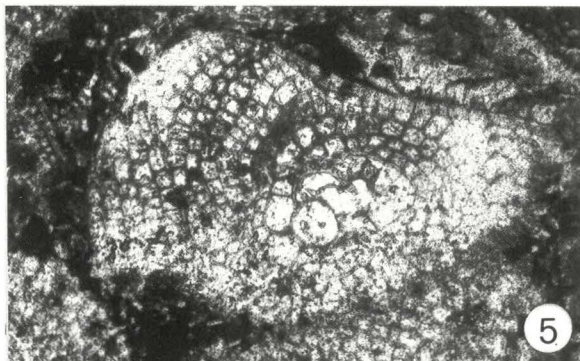
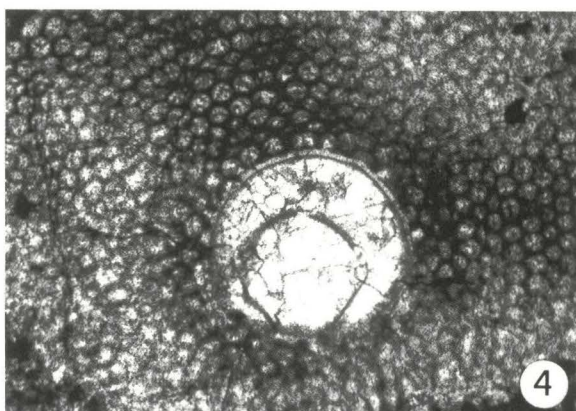
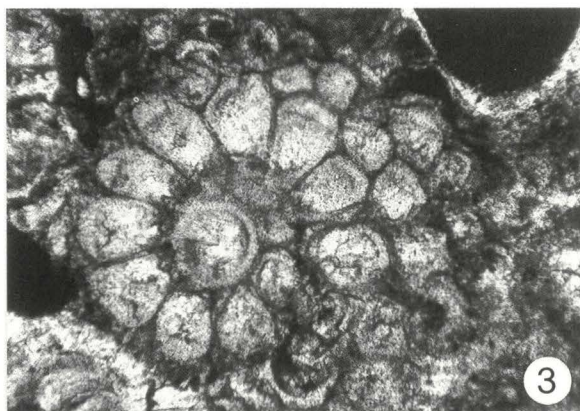
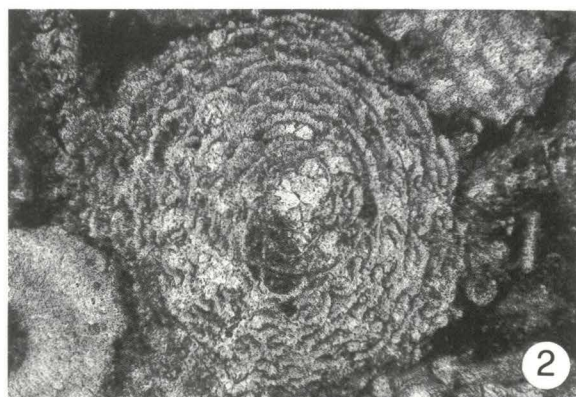
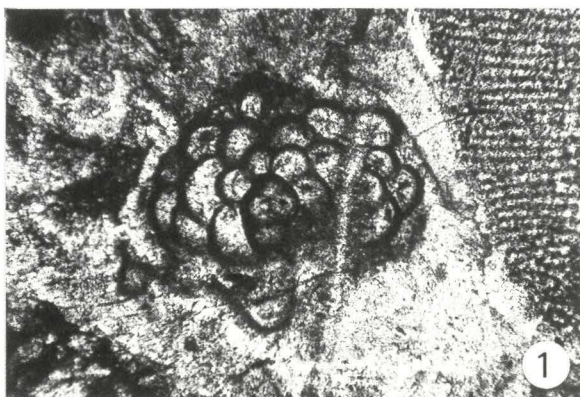
In general, in spite of the long tails at the upper end of the distributions, a larger number of specimens can be noted in the left part of the distributions. In all the populations no specimen falls out of the ranges $M \pm 3S$. The statistical check of the normality indicates significant deviations for TV32c and TV89, only on the basis of the Chi-Square test (Tab. 4).

The overall statistic normality of the distributions (K-S test in Tabs. 1 - 4) indicates that the populations are homogeneous. Even if very few reworked specimens may be present in all the analysed populations, their incidence on the quantitative results is not significant.

EXPLANATION OF PLATE 3

Figs. 1-8 - Some faunistic components accompanying *Nephrolepidina* in the Tre Valloni section (Middle Oligocene - Lower Miocene; Gran Sasso - Central Apennines).

- 1) Planorbulinids in Sample TV90; x 55;
- 2) *Gypsina* sp. in Sample TV32c; x 55;
- 3) *Miogypsina* (*Miogypsinoidea*) cf. *bantamensis* (Tan Sin Hok) in Sample TV114; x 65;
- 4) *Eulepidina dilatata* (Michelotti) in Sample TV9; x 20;
- 5) *Cycloclypeus* cf. *mediterraneus* (Matteucci & Schiavinotto) in Sample TV32c; x 25;
- 6) *Cycloclypeus* sp. in Sample TV55; x 25; 7) *Cycloclypeus* cf. *droogeri* (Matteucci & Schiavinotto) in Sample TV9; x 25;
- 8) *Heterostegina* sp. in Sample TV55; x 25.



Correlations

Tab. 5 summarizes the values of the correlation coefficient r obtained in the relations Ai-C, Ai-DI, Ai-DII, C-DI, C-DII, and DI-DII of each population.

The significance of these values was checked by comparing them with the significant minimum values (Camussi *et al.*, 1986, p. 481, Pl. 10).

Ai-C: the correlation is not significant only in TV9; however, in view of a strong fluctuation, the values in TV32c, TV77, TV87, and TV103 can be considered rather low. The highest correlation is recorded in TV89.

Ai-DI: there are few significant values in TV55, TV69, TV84a, TV89, and TV126.

Ai-DII: there are in great part significant correlations, although with very fluctuating values;

the two characteristics are insufficiently correlated only in TV32c.

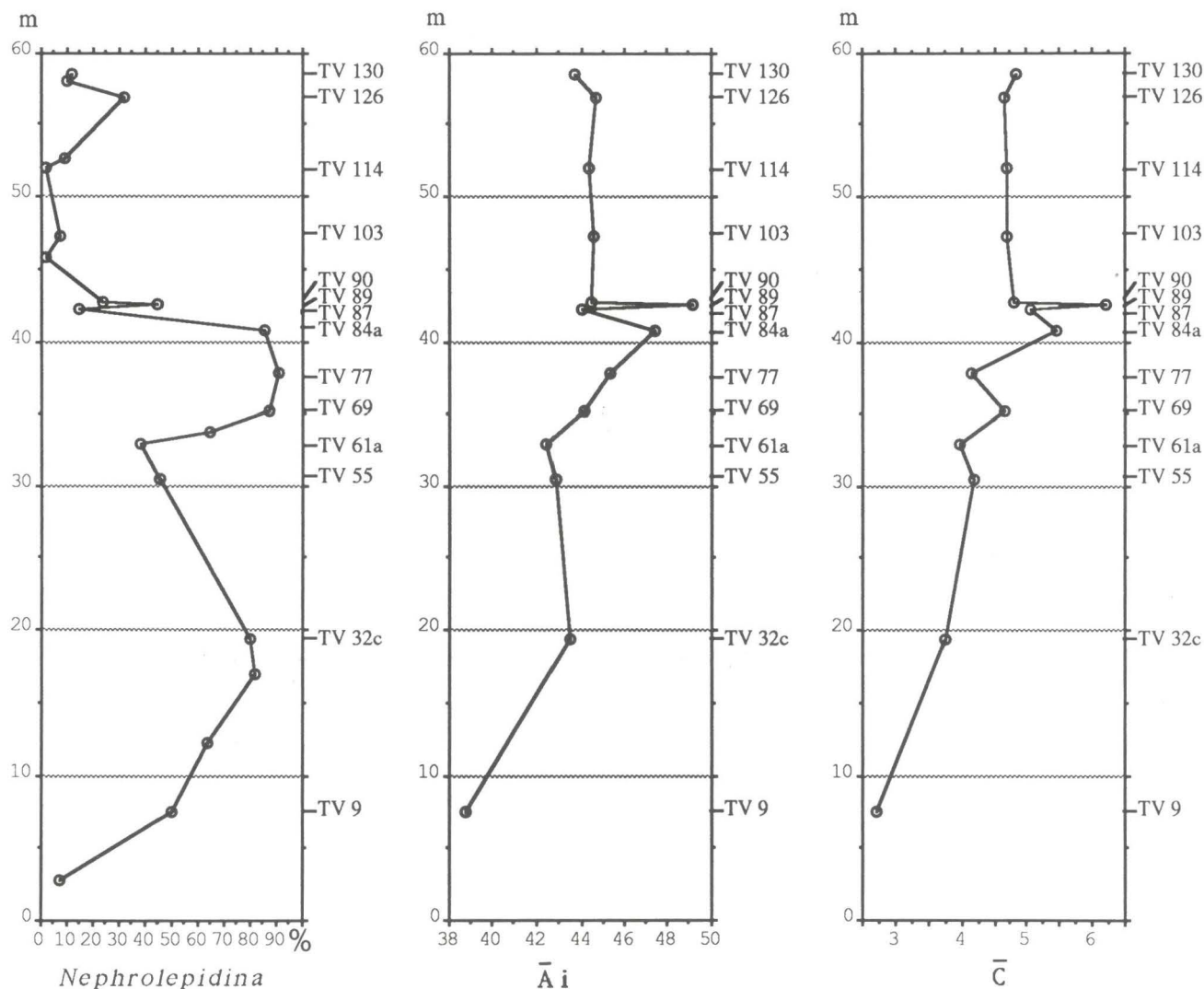
C-DI: there are not significant correlations in TV9, TV32c and TV77; in most of the cases the correlation appears good, although with fluctuation.

C-DII: the correlation, appears for the most part high; the two characteristics appear not to be correlated only in TV9.

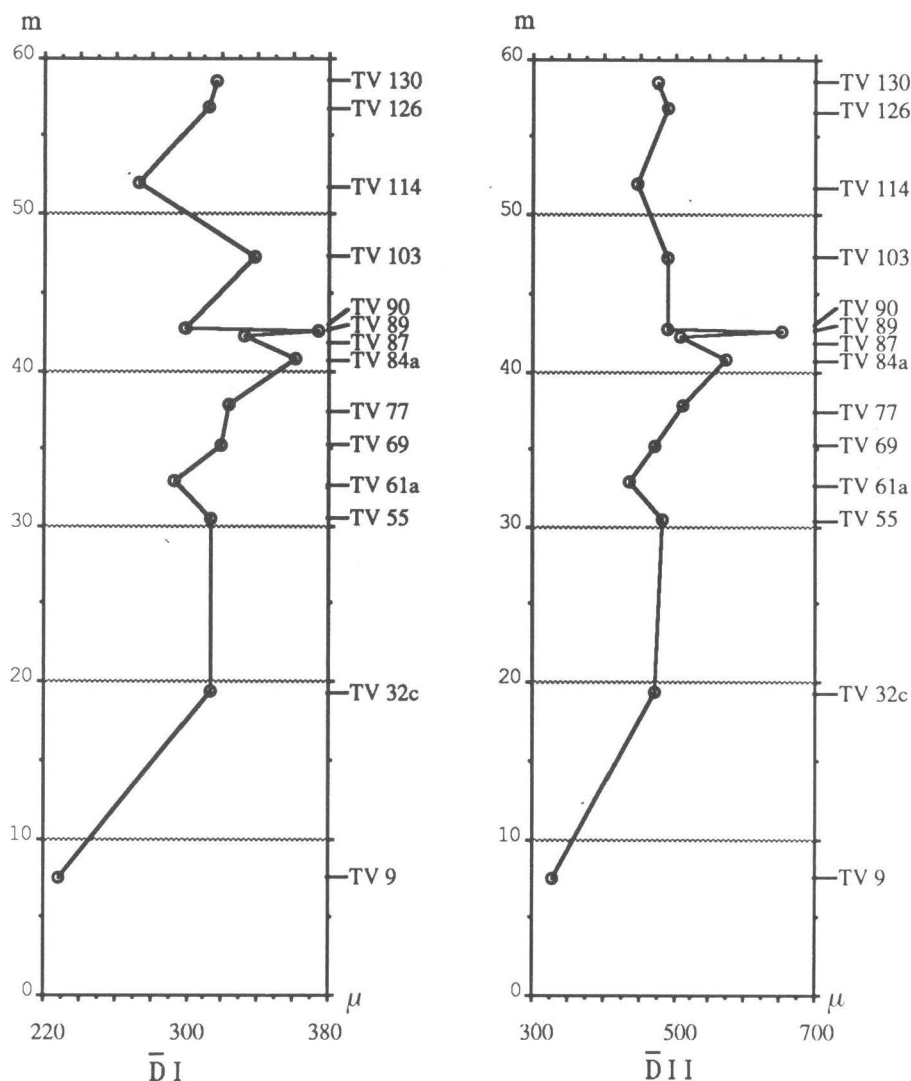
DI-DII: the correlations are all significant, with very high values of r .

TRENDS

The graphs of Text-fig. 9 and Text-fig. 10 show the variation of the average values of embryonic-nepionic factors and parameters along the sequence of the populations studied.



Text-fig. 9 - Trends in $\bar{A}i$ and $\bar{C}$ and relative frequency of *Nephrolepidina* in the Tre Valloni section.



Text-fig. 10 - Trends in $\bar{D}I$ and $\bar{D}II$ of *Nephrolepidina* in the Tre Valloni section.

These trends are compared, in the same graphs, with the trend of the variation of the relative frequencies of *Nephrolepidina* in the various associations, as already expressed in Text-fig. 3. This is because a possible effect of the frequency variations of *Nephrolepidina* represents a common presupposition in the various attempts to interpret the deviations from an «expected» evolutionary trend, if this relative frequency is considered an estimate, although with approximation levels that are sometimes high, of the population density that *Nephrolepidina* reached in the original biocoenoses.

Although recognizing, therefore, that the investigation method can have many limits and that it needs to be improved, we consider it important to refer to the paper done by Wildenberg (1991, p. 107, fig. 44), which showed how marked evolutionary changes coincide with decreases of the relative

frequencies in the associations with *Miogypsinids*.

Besides, if improvements in the method can be achieved, this will be all the more possible, the more the available case reports are increased.

Factor A_i

The trend follows an «expected» increase up to the maximum average value connected with population TV89, in accordance with the principle of «Embryonic acceleration» (Van Der Vlerk, 1959 a, b, 1963; Drooger & Freudenthal, 1964).

In general, this increase can be referred to a situation of general high relative frequency in *Nephrolepidina*.

In detail we have: 1) a slight decrease of $\bar{A}_i$ from TV32c to TV61a, which goes in parallel with a decrease of the relative frequency; 2) a continuous

progression of $\overline{Ai}$ from TV69 to TV84a, in perfect coherence with a maximum relative frequency phase; 3) the maximum value of $\overline{Ai}$, reached in TV89, is situated between two phases of great withdrawal of the variable, coinciding with great decreases of the relative frequency (TV87 and TV90).

Starting from TV90, there is a sequence of practically constant values, all below 45%; this constancy, or evolutionary stasis, coincides with a prolonged phase of low relative frequency of *Nephrolepidina*.

Parameter C

The number of adauxiliary chambers also confirms a trend towards the increase of the average values up to population TV89, in accordance with the principle of «Nepionic acceleration» of Tan Sin Hok (1936a, b; 1937a, b). The trend is interrupted by a drop in TV77 (as already noted for $\overline{Ai}$), in TV87 and in TV90. In this case, only the example of TV77 reveals an «anomalous» character, since it occurs in correspondence with the maximum relative frequency reached by *Nephrolepidina* in the whole sequence of associations.

The constantly low values of $\overline{C}$ after the drop at the level of TV90 are clearly consistent with the phase of prolonged low frequency of *Nephrolepidina* in the associations.

Embryo size

The embryonic chambers show a strong tendency to the increase of the average size values, going from the base of the succession up to population TV89, where the maximum values are reached.

The trend is analogous for the two diameters, but shows much more accentuated deviations in $\overline{DII}$.

The average value of the diameters shows a very marked increase from TV9 to TV32c, and then has a phase of stasis followed by a drop at the level of TV61a; subsequently there is a progression until the maximum values are reached in TV89. Once again,

these maximum values are comprised between two drops in TV87 and TV90. Starting from the latter population, the average diameters undergo a dramatic and definitive return to values comparable with those of the populations in the initial part of the succession. An attempt to resume the trend is recorded in TV103 for $\overline{DI}$ and in TV126 for both the diameters, but between them there is a further sharp drop in TV114.

Also for the embryonic diameters it can be verified that the increase phases correspond to phases of high relative frequency of *Nephrolepidina*, while the drops of $\overline{DI}$ and $\overline{DII}$ in TV61a and TV87, which go to disturb the increase phase up to the maximum values, correspond to a decrease (more marked in TV87) of this relative frequency.

The next phase characterized by low values of $\overline{DI}$ and $\overline{DII}$ coincides with the definitive reduction of *Nephrolepidina* to a distinctly subordinate role in the associations. A fairly effective attempt at resumption is recorded in TV126, where there is again a correspondence with an admittedly small increase of the average values of the diameters.

These results confirm, with a more detail, the preliminary indications reported in Schiavinotto & Verrubbi (1994).

THE DEVIATIONS FROM THE TREND

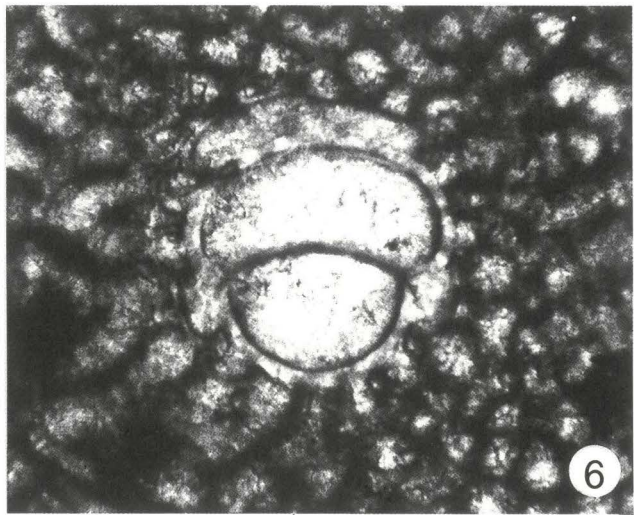
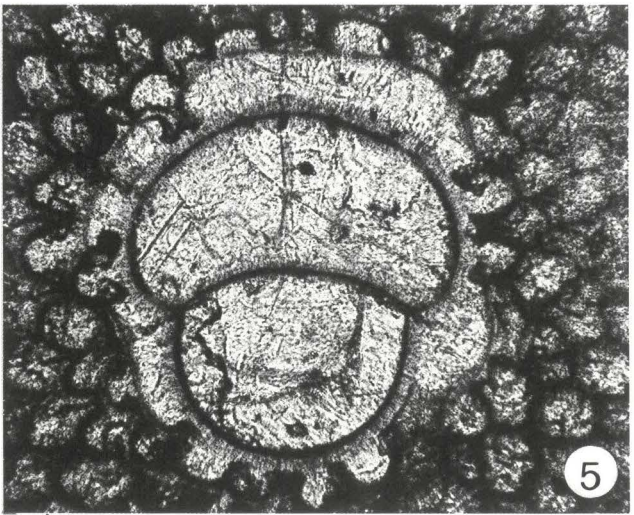
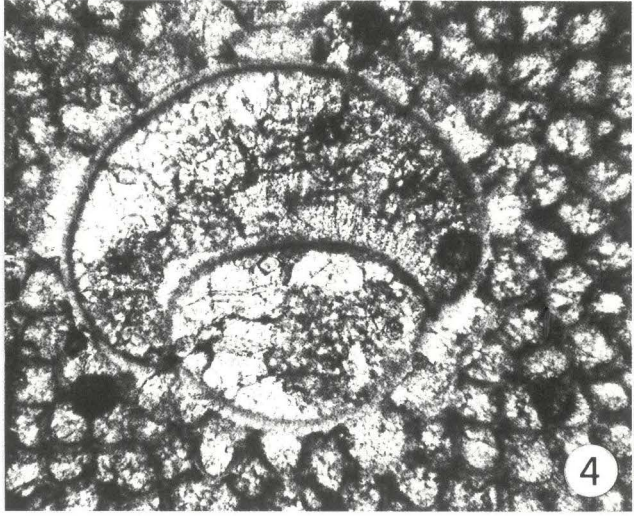
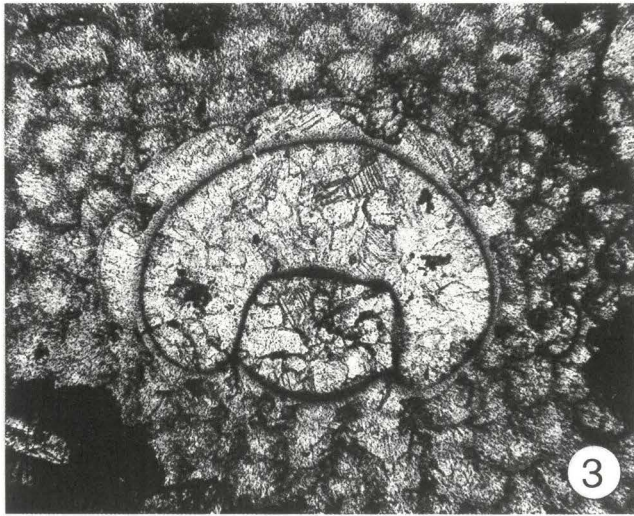
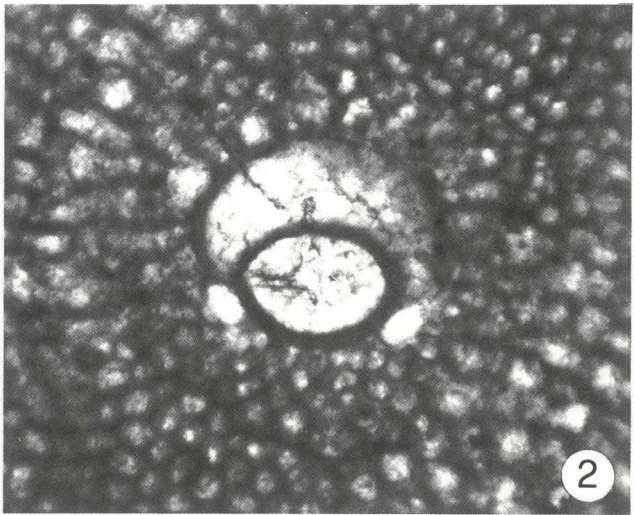
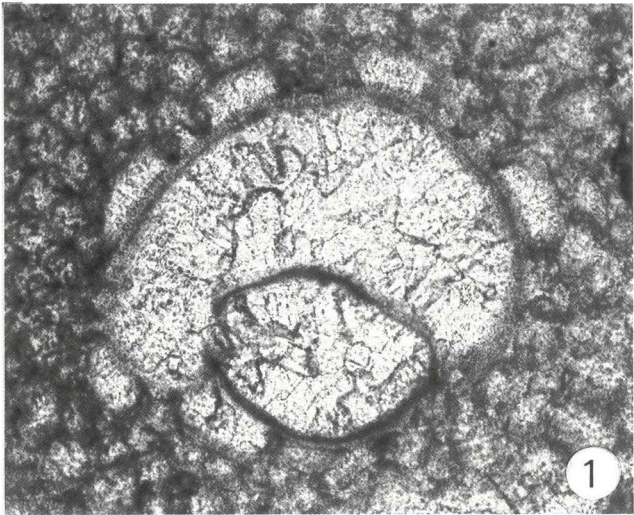
Pulsating evolution

A first consideration on the fluctuations of the trends could be referred to the evolutionary model proposed by Drooger (1984) and defined «Pulsating evolution» as an alternative to the «gradualist» model and of «Punctuated equilibria» of Eldredge & Gould, 1972, 1978; Gould & Eldredge, 1977. The «Pulsating evolution» develops according to a fluctuating trend due to a process that is triggered off in very small populations, in which the distributions of the morphometric characteristics assume a «bottleneck» trend («Bottleneck» of Stanley, 1978, 1979, pp. 26-28, pp. 173, 174; redefined by Drooger, 1984); there would be periods of homeostasis followed by

EXPLANATION OF PLATE 4

Figs. 1-6 - Variability of the embryonic chambers of *Nephrolepidina* from the Tre Valloni section:

- 1) *N. tournoueri* (Lemoine & R. Douvillè); Specimen TV 84a-3; x 80;
- 2) *N. ex. interc. morgani-tournoueri* (Lemoine & R. Douvillè); Specimen TV 77-7n.5; x 60;
- 3) *N. morgani* (Lemoine & R. Douvillè); Specimen TV 61a-10n.2; x 64;
- 4) *N. morgani* (Lemoine & R. Douvillè); Specimen TV 32c-2n.1; x 108;
- 5) *N. morgani* (Lemoine & R. Douvillè); Specimen TV 32c-6n.2; x 108;
- 6) *N. praemarginata* (R. Douvillè); Specimen TV 9-1n.2; x 108.



morphogenetic changes not necessarily linked to small allopatric populations, but rather to great reductions in the number of individuals forming a population, caused by unfavourable environmental factors. In these «small populations» in sympatric conditions, there would consequently be morphogenetic changes sometimes in an opposite direction to the general evolutionary trend, which should in any case take the upper hand again subsequently (Drooger, 1984).

The coincidences between negative fluctuations of the trends of $\bar{A}_i$ and $\bar{C}$ and the episodes of low relative frequency of *Nephrolepidina* (Text-fig. 9) seem to strengthen a process of pulsating evolution in the Nephrolepidinae of the Gran Sasso; in this case the variations of the population density can be in tune with the evolution undergone by the environment, as schematized in Text-fig. 6.

Adaptive strategies

A further consideration on the deviations from the expected trends concerns the dynamics of the populations in the palaeoecological context in which the Tre Valloni section was deposited. The data at our disposal agree in pointing out appreciable changes of the environment in passing from Unit I to Unit II; these changes are both of physical nature, triggered off by a variation of the bathymetry, probably connected with the eustatic variations on a global scale, and of faunistic nature, with the disappearance of taxa such as Miogypsinids and with the increase of taxa already present, such as Amphisteginids.

The environmental stability is compromised in a physical and biological sense, involving the creation of new competition relations and a reduction of the areas available in the sea-bottom (Text-fig. 6).

The first evident response that *Nephrolepidina* opposes to these variations is the contraction of its relative frequency in the associations: a sign that the variations must have been rather unfavourable for this taxon.

This response as regards the environment may have happened in harmony with some adaptive strategies.

The environmental stability makes possible the development of a selective K environment (K is the carrying capacity of the environment), in which the species that destine most of their resources for the increase of competitiveness are favoured, i.e. the survival of individuals is entrusted above all to an increase of specialization. In physically unstable environments, characterized by extensive, unforeseeable and frequent fluctuations, on the

contrary, the species are favoured that destine most of their available resources to reproduction and that therefore possess a high value of r (intrinsic growth rate) (Mac Arthur & Wilson, 1967; Pianka, 1970). In reality these extreme conditions can hardly be found; many present populations have variable or intermediate patterns. Solbrig (1971) maintains that r and K strategists can even be found within the same species. However, in an environment that favours the r selection it does not mean that the K strategists are excluded. The two modalities are not excluded in turn and, although one could in different moments dominate over the other, they coexist in the same population.

In tropical regions, in which, relatively, there are not seasonal alternations, the K selection tends to predominate, while the r selection tends to predominate in temperate environments with a distinct seasonality; in the latter case the growth of the populations follows an exponential trend with catastrophic declines.

If a stable environment has slightly different characteristics in relation to the bathymetry, the morphology of the sea-bottom, etc., the K selected species adapt themselves to this spatial heterogeneity by producing highly specialized individuals able to make the best use of the available resources. In this framework, the K selected species can be characterized by a high degree of variability. Moreover, in stability conditions, the species have greater possibilities of implementing their evolutionary trends.

If extensive, rapid changes are produced in a stable environment, the best adapted species, i.e. the K selected species, are the ones that suffer most. The more the species have lived in stability conditions, and have therefore been able to produce individuals with a greater degree of specialization, the more a change will have negative repercussions on the K selected species.

Within a species, the individuals that have fewer probabilities of overcoming a fluctuation of the physical characteristics of the environment could be those which have better adaptive characteristics, and therefore a greater degree of specialization. This could mean that, when a stable environment undergoes a variation, the decrease of individuals in a K selected species in this environment could be mostly at the expense of the most specialized individuals, which could therefore express more advanced biometric characteristics in an evolutionary sense. In this case the average evolutionary degree of the species could suffer a decrease.

In the Tre Valloni section, the lithological textures of Unit I indicate an open infraneritic environ-

ment, in which very significant fluctuations have not occurred. In such an environment, the rather low environmental unforeseeability has favoured much more a type K adaptive strategy; hence the specialization and implementation of the evolutionary trends characteristic of larger Foraminifera.

In layer TV90 we see a change of the environment probably connected with a eustatic lowering. The frequency of *Nephrolepidina* undergoes a considerable decrease and so does its average evolutionary degree. In the succeeding layers the lithological characteristics indicate a less deep environment compared with Unit I, undoubtedly more subject to physical disturbances (seasonal cycles, storms, etc.). In such an environment *Nephrolepidina* could have carried out a different adaptive strategy and, in any case, the role of the K strategy could have had less weight. The smaller environmental stability did not allow the level of specialization and of competitive capacity that there was in Unit I to be reached; this could explain why the value of the biometric parameters, which indicate the evolutionary level reached in the carrying out of the various trends, fluctuates below the value reached in the populations preceding TV90.

The lower relative frequency of *Nephrolepidina* compared with Unit I could be due to a reduction of the areas in which the Nephrolepidinae were living.

Embryo size

If we consider only the size of the embryonic chambers, we can note that in the phylogeny of all the groups of larger Foraminifera there is a general, but irregular, trend towards the increase of these (Drooger, 1983). Many cases summarized by Drooger (1983) suggest that many precautions should be adopted: it is a question of cases of deviations of the trend that can be caused by the influence of many factors that are widely debated in the literature. In addition to what has been considered in the previous paragraphs, in the particular case of the embryo size we can also refer to the following factors:

1) *Paratrimorphic reproductive cycle*, recognized in many living larger Foraminifera (Röttger, 1974; Röttger & Schmaljohann, 1976; Fermont, 1977a; Hottinger, 1984; Reiss & Hottinger, 1984; Bieckart *et al.*, 1985; Röttger *et al.*, 1986, 1990). Some indications of a possible paratrimorphic reproductive cycle in exclusively fossil groups have been obtained in *Orbitoides* (Cassan & Sigal, 1961; Meriç, 1964, 1966a, b, 1970, 1971, 1975; Neumann & Poisson, 1970; Eggink & Baumfalk, 1983).

Specimens with systems of bilocular embryonic chambers grouped in a number varying from 2 to 7, or with multilocular embryos, have also been recognized in Discocyclinids of the Eocene (Vaughan, 1945; Cole, 1942, 1960a, b; Meriç, 1972) and in Lepidocyclinids (Cole 1960a, b, 1961a, b, 1962, 1963a, b; Eames *et al.*, 1962; Serpagli & Sirotti, 1966a, b; Matsumaru, 1971). The interpretations of these cases as examples of schizogony in megalospheric specimens are still greatly debated and, in any case, not exhaustive.

The data of the literature seem to confirm, in general, that the gamont megalospheres (generation A2) can have a larger size than that of the schizont megalospheres (generation A1) (Laagland, 1990, p. 102; Zohary *et al.*, 1980).

2) *Bathymetry-embryo size relations* studied both in living taxa, and in fossil material (Krijnen, 1972; Drooger & Raju, 1973; Drooger & Roelofsen, 1982; Fermont, 1982; Fermont *et al.*, 1983; Reiss & Hottinger, 1984; Laagland, 1988, 1990).

The bathymetry is in turn connected with the intensity of the light, the activity and quantity of the symbiont algae, density of the populations, and productivity (Kloos & Mac Gillavry, 1978, 1985; Zohary *et al.*, 1980; Hottinger, 1983; Kloos, 1984; Reiss & Hottinger, 1984). A relation between the dimensions of the embryonic apparatus of *Nephrolepidina* and the depth of the sea-bottom, in relations to the activity of the symbiont algae, is debatable, since *Planorbulinella*, the only living taxon provided with a perforated calcareous shell with orbitoidal type architecture, but without lateral chambers, does not have these symbionts (Reiss & Hottinger, 1984), which generates the suspicion that this could also have occurred in the exclusively fossil orbitoidids.

However, the data on the trend of the embryonic dimensions recognized in Discocyclinids of the Eocene of Elat (Fermont, 1982) show variations of the average values that can be connected with the depth. For some species an increase of dimensions in favour of maintaining the activity of the symbiont algae in the presence of a decrease of the light intensity is not ruled out.

Such variations in relation to depth and light intensity have already been hypothesized for orbitoidal Foraminifera such as Miogypsinidae, the latitude being added as a further regulatory factor of the light intensity (Drooger & Raju, 1973).

Consequently, it seems right to extend to *Nephrolepidina* the hypothesis of a symbiosis with the algae.

3) *Productivity*. Laagland (1990, p. 109), starting from observations of Fermont *et al.* (1983) on *Oper-*

culina, makes a series of observations useful for a correlation between the various environmental factors and a variation of productivity, translated in terms of population density. This involves the relative frequency of the megalospheres A1 and A2, since the success of the sexual reproduction is generally connected with a high population density; in fact, the probability of two gametes meeting would thus be increased and the time interval between the release of the gametes and their meeting-fusion would be reduced (Laagland, 1990, p. 111).

Laagland (op. cit., p. 112) also remarks that Rötger (1974) and Hallock (1985) point out that the larger the schizont megalospheres are, the larger the number of individuals produced by each one of them. Moreover, Laagland (1988) has suggested that the number of individuals produced by the schizont megalospheres in *Operculina* increases at the expense of the size of the embryo, when the environmental conditions are close to the upper and lower limits of their bathymetric range.

This could be interpreted as an attempt to compensate for the lower number of specimens produced by low density populations, which are characteristic of the submarginal zones of the distribution area. With a relatively higher population density, on the contrary, there would be a larger adaptive value of the megalospheres to sexual reproduction (Laagland, 1990, pp. 112-116).

The productivity increase by the schizont megalospheres in conditions of low population density caused by a less favourable environment, can be considered a deviation of the K selection towards a phase of r selection (Laagland, op. cit., p. 130).

However, there are indications that this could not be generally valid. In fact, Kloos & Mac Gillavry (1978, 1985) and Kloos (1984) furnish data on the reproduction of living A1 megalospherical individuals of *Sorites orbiculus*: each individual produces megalospherical embryos with similar dimensions to those of its own embryonic apparatus; the embryonic dimensions of the individual parents are significantly correlated with the average values of the embryonic dimensions of the individuals belonging to the respective «broods»; on the contrary, the number of individuals of each «brood» is not found to be correlated either with the dimensions of the parent embryonic apparatus, or with the average dimensions of the embryonic apparatuses of the same «brood». There would thus be shown on the one hand a genetic diversity within a clone, and on the other the absence of a differential fertility.

The disagreement between the various data may be based on the fact that they are obtained from in-

dependent taxa: nummulitids and amphisteginae with a perforated lamellar shell on the one hand, and soritids with an imperforate shell on the other; the former with an extensive bathymetric range, if compared with the habitat of the soritids. The hypothesis may be reliable that, on the basis of the structure of its shell, *Nephrolepidina* has carried out reproductive processes comparable with those of nummulitids and soritids.

These presuppositions, together with the indications on the environmental and faunistic evolution recognized along the Gran Sasso section, enable us to outline some indications on the variations of the embryonic dimensions in our *Nephrolepidina* populations.

Unfortunately, the study of the samples in thin sections of rock has not enabled us to make a sufficiently indicative analysis of the frequency of the microspherical specimens. We cannot then make qualitative and quantitative evaluations on the possible variations in the frequency of the two generations, sexual and asexual, in relation to the depth and to the other environmental characteristics. However, the distributions with two or more frequency maxima recorded for the DI and the DII of numerous populations (Text-fig. 8), which could nevertheless be due to the number of specimens not being high, induce us not to exclude the presence of two types of megalospheres that may also differ in the mode of reproduction. However, the adaptations to the normal distribution, confirmed on a statistical basis, would bear witness to the cospecificity of the two types of megalospheres.

A first consideration, which can be obtained from our data, concerns the increase of the dimensions in relation to the depth. Our data seem to be consistent with what is described in the literature. In fact, it can be seen that a general increase of the embryonic dimensions, until the maximum average values are reached, has happened in Unit I and in the middle-lower part of Unit II, represented by the deposition of materials coming from a productive area situated at a greater depth than the productive area of the following part of the succession.

The decrease of the average values of DI and DII in the upper part of Unit II, on the basis of the sedimentological and faunistic data, is to be put in relation to a decrease of the bathymetry in the productive area.

The increase of size in relation to the bathymetry could be referred to the adaptive strategy that *Nephrolepidina* may have adopted in relation to the environmental characteristics. At greater depths the environment can be considered more stable in its physical parameters, and in par-

ticular less dependent on the seasonality. As already mentioned, this would have favoured an adaptive strategy of selective type K, in which specialization plays a fundamental role. Moreover, assuming the presence of symbiont algae, we can consider the light a resource of vital importance. The tendency to specialization could have caused an increase of the embryonic dimensions, in order to obtain a greater activity of the symbiont algae, in conditions of less luminosity.

In the upper part of Unit II, the decrease of bathymetry made the environment less stable and prevented high levels of specialization from being reached. Moreover, the luminosity was greater and the activity of the symbiont algae was a less serious problem. This could have caused a decrease of the average dimensions of the embryonic chambers, since smaller nucleoconches would have been enough for the activity of the symbiont algae, in conditions of increased light intensity.

The decrease in frequency of the Nephrolepidinae in the upper part of Unit II could indicate that environmental conditions had become less favourable: in relation to this, we can make a further consideration, to be taken with the due precautions. Hottinger (1977b) supposed that only in favourable conditions was there a sexual reproduction in *Operculina* and *Heterostegina*, while there was an asexual reproduction in the marginal zones of the distribution area. In our case, therefore, the less favourable environment could have caused an increase of the frequency of the A1 schizont megalospheres. In that case, as suggested by Laagland (1990), the number of individuals produced would increase at the expense of the dimensions of the embryo. This consideration could be indicated as a further concomitant cause of the reduction of the average dimensions of the embryonic chambers that occurs in the Nephrolepidinae of the upper part of Unit II.

TAXONOMIC INDICATIONS

The biometric classification at present applied for *Nephrolepidina* of the Mediterranean area is that of De Mulder (1975), with slight supplementations by Van Heck & Drooger (1984). It is based on the average values of $\bar{A}_i$ and $\bar{C}$, the following limits being proposed between the species:

N. praemarginata (R. Douvillé)
 $35 < \bar{A}_i < 40$ and $\bar{C} < 3$

N. morgani (Lemoine & R. Douvillé)
 $40 \leq \bar{A}_i \leq 45$ and $3 \leq \bar{C} \leq 5.25$

N. tournoueri (Lemoine & R. Douvillé)
 $45 < \bar{A}_i$ and $\bar{C} > 5.25$.

By applying this classification to the populations in the Gran Sasso section, the determinations shown in Tab. 6 are obtained.

It is immediately clear that the classification based on the two combined characteristics leads to satisfactory results in the populations of Unit I and of the middle-lower part of Unit II, marking well the passage from *N. praemarginata* to *N. morgani*, followed by various evolutionary stages well referable to *N. morgani* and from a gradual transition phase up to the definitive affirmation of the maximum evolutionary stage, referable to *N. tournoueri* (population TV89).

Up to this level, the fluctuations in the evolutionary trend do not lead to repercussions on the classification. On the contrary, the big deviation towards lower average values that the trends have in the sequence of populations following TV89 is reflected in specific determinations, all indicators of a *morgani*-*tournoueri* transition phase. The fluctuations tending to the resumption of the trends do not succeed in recovering sufficient values for a full reference to *N. tournoueri*, at least in its first evolutionary stages.

The fluctuating levels of the significance in the $\bar{A}_i$ - $\bar{C}$ correlations in the various populations (Tab. 5) coincide with the different responses that the two characteristics oppose to the environmental factors.

This leads to more evident repercussions for the classification based on the individual parameters. In fact, for $\bar{A}_i$ there is a classification that shows a very fluctuating passage between *morgani* and *tournoueri*: already TV84a is referable to *tournoueri*, and returns to an ex. interc. in TV87.

For $\bar{C}$, on the contrary, we obtain the indication of a longer succession referable constantly to *N. morgani*, with a more gradual transition up to *N. tournoueri* in TV89. The separate classifications are in perfect agreement in the stratigraphically lowest populations, up to TV61a, and in TV89.

After TV89, the drop of the average values has greater repercussions on the classification based on $\bar{C}$, with distinct references to *N. morgani* up to TV126.

In the last population TV130, the two characteristics furnish indications in sharp contradiction: this time it is only $\bar{A}_i$ that returns completely in the range of *N. morgani*.

The different behaviours of the two variables in the classification are already a reflection of the fluctuating values of the significance of the correlation coefficients in Tab. 5.

However, the correlation between $\bar{A}_i$ - $\bar{C}$, with $r = 0.90$, is highly significant and is at the basis of the greater consistency that is obtained in the classification based on both the characteristics.

POPULATIONS	$\bar{A}i \pm S_M$	$\bar{C} \pm S_M$	$\bar{A}i$ and $\bar{C}$
TV130	<i>morgani</i>	ex. interc. <i>morgani-tournoueri</i>	ex. interc. <i>morgani-tournoueri</i>
TV126	ex. interc. <i>morgani-tournoueri</i>	<i>morgani</i>	ex. interc. <i>morgani-tournoueri</i>
TV114	ex. interc. <i>morgani-tournoueri</i>	<i>morgani</i>	ex. interc. <i>morgani-tournoueri</i>
TV103	ex. interc. <i>morgani-tournoueri</i>	<i>morgani</i>	ex. interc. <i>morgani-tournoueri</i>
TV90	ex. interc. <i>morgani-tournoueri</i>	<i>morgani</i>	ex. interc. <i>morgani-tournoueri</i>
TV89	<i>tournoueri</i>	<i>tournoueri</i>	<i>tournoueri</i>
TV87	ex. interc. <i>morgani-tournoueri</i>	ex. interc. <i>morgani-tournoueri</i>	ex. interc. <i>morgani-tournoueri</i>
TV84a	<i>tournoueri</i>	ex. interc. <i>morgani-tournoueri</i>	ex. interc. <i>morgani-tournoueri</i>
TV77	ex. interc. <i>morgani-tournoueri</i>	<i>morgani</i>	ex. interc. <i>morgani-tournoueri</i>
TV69	ex. interc. <i>morgani-tournoueri</i>	<i>morgani</i>	ex. interc. <i>morgani-tournoueri</i>
TV61a	<i>morgani</i>	<i>morgani</i>	<i>morgani</i>
TV55	<i>morgani</i>	<i>morgani</i>	<i>morgani</i>
TV32c	<i>morgani</i>	<i>morgani</i>	<i>morgani</i>
TV9	<i>praemarginata</i>	<i>praemarginata</i>	<i>praemarginata</i>

Tab. 6 - Different specific determinations of *Nephrolepidina*, as result on the basis of each single variable ($\bar{A}i$ or $\bar{C}$), and according to the combination of $\bar{A}i$ and $\bar{C}$ values.

Nevertheless, the results as a whole cannot be considered satisfactory: if one were to examine a single population among those coming after TV89 and for any reason one did not have the possibility of recovering other data, the specific determination would not even let one suspect that in the lower levels an evolutionary degree high enough for *N. tournoueri* could have been reached, which is one of the most advanced found in the whole Mediterranean area (Drooger & Laagland, 1986, fig. 1).

A taxonomic indication of the populations coming after TV89 of such little significance cannot fail to have repercussions on the reliability of the biostratigraphic indications.

BIOSTRATIGRAPHIC INDICATIONS

As it is possible to make use of the vertical distributions of *Cyclocypeus* and *Miogypsina* s.l. in the Gran Sasso section, as a biostratigraphic calibration for the populations of *Nephrolepidina*, particularly interesting indications are obtained.

The identification of *N. praemarginata* in TV9 is very consistent with the previous stratigraphic references: the evolutionary level of the species is high and enables a statistical comparison without significant difference (Student's t-test) to be made with the biometric characteristics of *N. praemarginata* in the sample TRMn of Monte la Rocca, the type-level of *Cyclocypeus droogeri* (Matteucci &

Schiavinotto, 1977, 1985). Here *Cyclocypeus* has an average value of the number of nepionic chambers higher than that of other populations in the Mediterranean area (Laagland, 1990); a reference of TV9 rather close to the middle part of the *Cyclocypeus droogeri* subzone (middle-high part of the *G. opima* Zone) therefore seems reliable.

The populations referable to *N. morgani* are equally in good agreement with the references to the *Cyclocypeus* Zone, up to the *Miogypsinoidea* Zone, a low part of the *M. formosensis* subzone: from TV32c up to TV61a there are no significant differences in the statistical comparison with the population of *N. morgani* in the sample T1 of Monte La Rocca, from the type-level of *Cyclocypeus mediterraneus* (Matteucci & Schiavinotto, 1977, 1985) referable to the *M. complanatus* subzone (sample JT7911 of Laagland, 1990). Statistically significant differences with the same population begin to appear in TV69, at the level of the nepionic chambers, and in TV77, at the level of the «degree of embracement», but the values of $\bar{A}i$ and $\bar{C}$ are compatible with reference to the *M. formosensis* subzone.

Then, *Nephrolepidina* has a considerably accelerated evolutionary process compared with what has been found to date in the Mediterranean area: the maximum evolutionary degree characteristic of *N. tournoueri* reached in populations TV84a and TV89 is found again at the first evolutionary stages

of *Miogypsina* cf. *gunteri* and of *M. (Miogypsinoides)* cf. *bantamensis*; the same evolutionary degree had been recognized previously only in populations associated with *M. globulina* and *M. intermedia* and referred to the Upper Aquitanian-Burdigalian (Drooger & Socin, 1959; Drooger & Freudenthal, 1964; De Mulder, 1975; Schiavinotto, 1979; Drooger & Laagland, 1986; Giovagnoli & Schiavinotto, 1990). It is possible to recognize not significant statistical differences between these populations and TV84a and TV89.

According to some data, however, the nepionic acceleration seems to happen at a lower rate than does the embryonic acceleration; for example, in TV84a $\bar{C}$ is significantly lower in comparison with the population TLS76 of Monte La Serra (Schiavinotto, 1979), while the values of $\bar{A}_i$ are perfectly comparable.

Finally, in the Gran Sasso there is an anticipation of the most advanced phase of the evolutionary development of *Nephrolepidina*, which is referable here to the lower part of the Aquitanian, as proved by the presence of *Miogypsina* cf. *gunteri*. Unfortunately, the populations following TV89 do not provide reliable stratigraphic indications: the average values of A_i and $\bar{C}$ would all support a reference to the Upper Oligocene. It has been seen that our data would indicate the environmental factors as a cause of the going back of the embryonic and nepionic morphometric values, much more than could have been the effect of the reworking processes.

CONCLUSIONS

The Nephrolepidinae in the Gran Sasso section show deviations in the evolutionary trends according to the principles of «Embryonic acceleration» and of «Nepionic acceleration». If significant interventions of reworking phenomena are excluded, these deviations can be well connected with: 1) casual changes of the genetic pool in conditions of low population density; 2) adaptive strategies in relation to the environmental characteristics; 3) variations of the morphometric characteristics in response to a paratrimorphic reproductive cycle.

It seems possible to hypothesize that the deviations are caused by an interaction of the above mentioned factors.

The deviations, whatever their cause may be, or the concomitant causes, in any case appear to be distinctly incisive on the biostratigraphic indications: to the evolutionary stagnation at the level of *N. morgani*, already recognized in the Mediterranean area for a time interval inclusive of

the Chattian-Aquitania boundary (Drooger *et al.*, 1976; Drooger & Laagland, 1986), there would be added an acceleration phase in the transition from *N. morgani* to *N. tournoueri*, at least in the Central Apennines. In this area, an easier identification of the Oligo-Miocene boundary, on the basis of the appearance of *N. tournoueri* in the Lower Aquitanian, is compromised by the succeeding evolutionary withdrawal, which makes a precise dating impossible of the sediments deposited in the Middle-Upper Aquitanian interval, but which are well characterized by the evolutionary development which in the Miogypsinidae leads from *M. gunteri* to *M. globulina* (Schiavinotto, 1979; Delicati & Schiavinotto, 1988).

It is proved that the evolution of *Nephrolepidina* in the Central Apennines at any rate led to a return of the characteristic biometric values of *N. tournoueri* in association with *M. globulina* (see Schiavinotto, 1979), after the stratigraphically lower association *N. tournoueri* - *M. cf. gunteri* in the Gran Sasso section; this would seem to give an iterative character to the evolutionary process of the Nephrolepidinae in the Central Apennines.

If this limitation of the biostratigraphic value of *Nephrolepidina* should be confirmed, a further development would become still more urgent of the researches concerning the evolutionary process based on the «Neanic acceleration» (Schiavinotto, 1992, 1993, 1994), which have provided promising preliminary indications.

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