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BIOMETRIC ANALYSES OF *NUMMULITES* ''*PTUKHIANI*'' Z. D. KACHARAVA, 1969 AND *NUMMULITES FABIANII* (PREVER IN FABIANI, 1905)

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ABSTRACT

Eight populations of microspheric and megalospheric individuals belonging to the species *Nummulites* ''*ptukhiani*'' (uppermost middle Eocene) and *N. fabianii* (upper Eocene) from northern Italy, Spain and Romania are described and discriminated biometrically. This distinction permits recognition of the middle/upper Eocene boundary in shallow carbonate platform facies. The name *N.* ''*ptukhiani*'' as used here applies only to the western European ancestors of *N. fabianii,* with *N. ptukhiani* from Armenia being a separate species.

In the megalospheric generation, test size, ornamentation, and external form show no direct correlation with geologic age and may have been paleoenvironmentally controlled. On the contrary, the examined B forms of *N.* ''*ptukhiani*'' are substantially smaller and more inflated than the *N. fabianii* B forms. Moreover, the ornamentation pattern of *N.* ''*ptukhiani*'' B (reticulated, granulated) is easily distinguishable from that of *N. fabianii* B (sinuous to meandering reticulate, non-granulated).

For the megalospheric individuals, internal features seem more independent of the paleoenvironment, but they may also have been environmentally controlled in some cases. Four parameters are used to distinguish the A forms: protoconch height, shape of the embryonic apparatus, mean chamber length, and coiling curves. None of these internal features has been found useful to distinguish between the B forms of the two species. Only the total number of whorls is different (two to seven more whorls in *N. fabianii* B than in *N.* ''*ptukhiani*'' B). The overall similarities between the two species and the gradual transition of the measured features confirm they are successive chronospecies that can, however, be separated by conventional limits, useful for biostratigraphy of the middle/upper Eocene carbonates of the Tethys.

INTRODUCTION

This work is part of the IGCP project 393 (neritic events at the middle/upper Eocene boundary). In the Tethys carbonate platforms, the larger foraminiferal biozonation (Shallow Benthic Zones of Serra-Kiel and others, in press) near the middle/upper Eocene boundary often relies on the correct identification of two species of the *Nummulites fabianii* lineage (Schaub, 1981): *Nummulites ptukhiani* Kacharava (= ''*N. praefabianii*'' auct.) in the upper part of the middle Eocene (''Biarritzian'' or Bartonian) and *N. fabianii* (Prever in Fabiani) in the upper Eocene (Priabonian). This identification presents some difficulties:

First, there is a nomenclatural problem with respect to *N. ptukhiani.* In my opinion, this name applies only to the Armenian specimens, whereas the western European ancestors of *N. fabianii* belong to a different species, herein referred to as *N.* ''*ptukhiani*'' (see the remarks on this species below).

Second, the name *N.* aff. *fabianii,* has been used both for a transitional form between *N.* ''*ptukhiani*'' and *N. fabianii* (Blondeau, 1972; Schaub, 1981) and as a synonym of *N.* ''*ptukhiani*'' itself (Castellarin and Cita, 1969a, b; Ungaro, 1969; Strougo, 1992). Castellarin and Cita (1969b) even introduced a *Nummulites* aff. *fabianii* Zone which Papazzoni and Sirotti (1995) subsequently renamed the *Nummulites variolarius*/*incrassatus* Zone to emphasize the questionable significance of the name *N.* aff. *fabianii.*

Third, many authors (e.g. Roveda, 1970) used to determine the species of the *N. fabianii* lineage relying mainly on the external test shape, diameter, thickness, and ornamentation. According to recent studies (e.g. Reiss and Hottinger, 1984; Hallock and Glenn, 1986; Racey, 1992; Pecheux, 1995) these features are largely influenced by environmental parameters, such as depth, substrate, light intensity, etc. Among the possible species-diagnostic characters, the more reliable (chamber/septa shape, spire coiling, marginal cord thickness, protoconch size; Racey, 1992) all require the observation of the equatorial section.

Barbin (1988) carried out biometric measurements on 64 specimens of *N. fabianii* from Buso della Rana (near Priabona), showing that there was no correlation between the protoconch diameter and the diameter to thickness ratio of the test. Previously in 1973 Herb and Hekel studied the *N. fabianii* group from the Possagno, Priabona and Mossano sections of the Veneto area, northern Italy, measuring test diameter, thickness, protoconch diameter, and whorl radius in the A forms. They noted that ''a distinction of the two forms is certainly difficult but seems generally possible if we are dealing with assemblages.'' However, they measured for instance the diameter of the protoconch only on 4 to 12 specimens per sample (exceptionally 40 specimens in one sample from Priabona). Therefore, a more comprehensive biometric study of various populations of *N.* ''*ptukhiani*'' and *N. fabianii* was undertaken to test the relative taxonomic importance of internal and external features in distinguishing between these two species for biostratigraphic purposes. A large number of specimens from each population was measured to obtain statistically reliable data.

SYSTEMATIC PALEONTOLOGY

Table 1 compares the key features used to define *N.* ''*ptukhiani*'' and *N. fabianii* from Roveda (1970), Blondeau (1972), Schaub (1981), and this work. A synonymy of the two species under study, along with some nomenclatural remarks, follows. The suprageneric classification follows Loeblich and Tappan (1987).

Suborder ROTALIINA Delage and Hérouard, 1896
Superfamily NUMMULITACEA de Blainville, 1827
Family NUMMULITIDAE de Blainville, 1827
Genus *Nummulites* Lamarck, 1801
Nummulites ''*ptukhiani*'' Z. D. Kacharava, 1969
Pl. 1, Figs. 16–24; Pl. 2, Figs. 16–21

?*Nummulites hormoensis* NUTTALL and BRIGHTON, 1931, p. 53, 54, pl. III, figs. 1–8.

TABLE 1A. Key features used by Roveda (1970), Blondeau (1972) and Schaub (1981) to define the species *N.* ''*ptukhiani*'', compared with the results of this work. Since Roveda (1970) did not describe *N. praefabianii*, his data on *N. hormoensis* are reported.

	Roveda, 1970		Blondeau, 1972		Schaub, 1981		This work	
	N. hormoensis		*N. praefabianii*		*N. ptukhiani*		*N.* ''*ptukhiani*''	
Feature	A form	B form	A form	B form	A form	B form	A form	B form
Test diameter	3.00 to 4.45 mm	5.10 to 8.00 mm (usually between 5.5 and 7.3 mm)	2 mm	4 mm	2.8 to 4 mm	4.5 to 6 mm	1.6 to 3.5 mm (mean 2.3–2.6)	2.1 to 5.1 mm (mean 3.5–3.8)
Test thickness	1.00 to 1.60 mm	1.20 to 2.10 mm (usually between 5.5 and 7.3 mm)	1 mm	1.8 mm	1 to 1.8 mm	1.8 to 2 mm	0.7 to 2.0 mm (mean 1.2–1.3)	1.0 to 2.6 mm (mean 1.7–2.0)
Surface	granules arranged in spiral to form a ''transverse lamina''; reticulation developed only near the periphery	granules arranged in spiral to form a ''transverse lamina''; reticulation not observed	rough reticulation, with big granules not merged in a secondary lamina	rough reticulation, with big granules not merged in a secondary lamina	granules partially merged to form a ''transverse lamina''; polar knob often present	granules partially merged to form a ''transverse lamina''	granules partially or totally merged to form a more or less regular reticulation; polar knob often present	granules always evident to form a quite regular reticulation
Protoconch diameter	0.132–0.185 mm	—	0.10–0.15 mm	—	0.15–0.22 mm	—	0.13–0.30 mm (mean 0.16–0.22)	—
P/D ratio	''protoconch followed by a small flattened semilunar deuteroconch''	—	isolepidine	—	not mentioned	—	1.0–1.1	—
Chamber length	chambers subquadrate in the first whorls, then becoming slightly longer than high	chambers subquadrate in the first whorls, then becoming slightly longer than high	height/length ratio from 1 to 0.5	height/length ratio from 1 to 0.5	chambers higher than long in the first whorls, then becoming isometric or slightly longer than high	chambers higher than long in the first whorls, then becoming isometric or slightly longer than high	0.25–0.28 mm on the 3rd whorl	0.27–0.30 mm on the 4th whorl
Spire opening	not mentioned	step slightly irregular	step constant on the whorls 1–2, increased 1.7 times on 3rd whorl, constant on the whorls 3–5, decreased on 6th whorl	step constant on the whorls 3–5, doubled on 6th whorl, then more or less constant	step regularly growing	regular, step regularly growing	regular; coiling diagram separate from that of *N. fabianii*	quite regular; coiling diagram completely overlapping that of *N. fabianii*
No. of whorls	not mentioned	8–9 on a diameter of 7–8 mm	5–6 on a radius of 1 mm	7–8 on a radius of 2–2.1 mm	not mentioned	9–10 on a radius of 2.6–33 mm	4–5 on a radius of 1.13–1.16 mm	7 on a radius of 2.07–2.08 mm

TABLE 1B. The same features as in Table 1A used to define *N. fabianii*.

	Roveda, 1970		Blondeau, 1972		Schaub, 1981		This work	
	N. fabianii		*N. fabianii*		*N. fabianii*		*N. fabianii*	
Feature	A form	B form	A form	B form	A form	B form	A form	B form
Test diameter	2 to 4 mm	8 to 9 mm	2.5 to 4.5 mm	6 to 10 mm	2 to 4.5 mm	8 to 12 mm	1.5 to 4.4 mm (mean 2.3–3.3)	4.3 to 14.0 mm (mean 5.5–10.0)
Test thickness	1.5 mm on average	2 to 3 mm	2 to 2.5 mm	2 to 3.5 mm	1 to 2 mm	2 to 3 mm	0.6 to 2.2 mm (mean 1.2–1.4)	1.4 to 4.0 mm (mean 1.6–3.3)
Surface	nearly equal to the B forms or reticulation composed by a spiral ''ridge'' crossed by the septal filaments	reticulation highly irregular and variable with small mesh	reticulation with rectangular mesh; granules merged to form a secondary lamina; big polar knob	reticulation with rectangular and polygonal mesh; granules merged to form a secondary lamina	reticulation formed by septal filaments and ''transverse lamina''; granules spirally arranged in the polar region	reticulation irregular, formed by septal filaments and ''transverse lamina''; youngs have a surface similar to that of the A forms	granules partially or totally merged to form a more or less regular reticulation; polar knob often present	sinuous to meandering reticulation; granules very small or absent, except on the polar region
Protoconch diameter	''of medium size''	—	0.20–0.25 mm	—	0.17–0.36 mm	—	0.17–0.45 mm (mean 0.22–0.32)	—
P/D ratio	~1	—	anisolepidine	—	not mentioned	—	1.2–1.5	—
Chamber length	chambers regular subquadrate in the first whorls, then becoming longer than high	chambers gradually becoming longer than high	height/length ratio equal to 1	height/length ratio less or equal to 1	not mentioned	chambers slightly longer than high, except in the central region	0.30–0.35 mm on the 3rd whorl	0.26–0.37 mm on the 4th whorl
Spire opening	regular; step (generally wide) growing gradually until the penultimate whorl	regular or subregular; step growing gradually	regular, step regularly growing	regular, step regularly growing	regular	regular	regular; coiling diagram separate from that of *N.* ''*ptukhiani*''	quite regular; coiling diagram completely overlapped from that of *N.* ''*ptukhiani*''
No. of whorls	6–7 on a diameter of 3.5 mm	10–13 on a diameter of 9 mm	5–6 on a radius of 1.3–1.6 mm	9–10 on a radius of 3.2–3.4 mm	4–6 on a radius of 1–2.2 mm	12–15 on a radius of 3.8–6.2 mm	5 on a radius of 1.28–1.77 mm	9–14 on a radius of 3.03–5.66 mm


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Non *Nummulites praefabianii* Varentsov and Menner—PTUKHYAN, 1964, p. 52, pl. I, figs. 5–8.

Non *Nummulites ptuchiani* Z. D. KACHARAVA, 1969, p. 497, 498.

?*Nummulites hormoensis* Nuttall and Brighton.—ROVEDA, 1970, p. 299–303, pl. 24, figs. 7, 8, text-figs. 112–117.

Nummulites praefabianii Varentsov and Menner.—FERRER, 1971, p. 33, pl. 2, figs. 4, 5.

Nummulites praefabianii Varentsov and Menner.—BLONDEAU, 1972, p. 155 [partim], pl. XXVIII, figs. 8, 9, 16–20 (not 10–15); not pl. XXIX, fig. 1.

Nummulites fabianii praefabianii Varentsov and Menner.—HERB and HEKEL, 1973, p. 432, 433 [partim], text-figs. 24a, b (not d, e).

Non *Nummulites ptuchiani* Z. Kacharava.—BOMBITA, 1975, p. 76–79, pl. VI, figs. 27–30, pl. VII, figs. 12a, b, 13.

Nummulites ptukhiani Z. D. Kacharava.—SCHAUB, 1981, p. 125, 126 [partim], pl. 49, figs. 33–48, tab. 15h.

Non *Nummulites ptuchiani* Z. Katcharava.—BOMBITA, 1984, p. 42–47, pl. I, figs. 1–7.

Nummulites cf. *hormoensis* Nuttall and Brighton.—PAPAZZONI and SIROTTI, 1995, p. 64, pl. 1, figs. 11, 12.

Material. Megalospheric specimens from samples VIC 3 (middle Eocene of Vic, Cataluña, Spain), MOSS 11 (middle Eocene of Mossano, Veneto, northern Italy), and MC 2 (middle Eocene of Monte Cavro, Veneto, northern Italy), 81 to 85 individuals per sample. Five microspheric specimens from sample MC 2, and eleven from sample MOSS 11. No microspheric specimens were found in the sample VIC 3.

Remarks. According to Schaub (1981) the direct ancestor of *N. fabianii* (Prever in Fabiani) should be *N. ptukhiani* Kacharava (=*N.* ''*praefabianii*'' in western Europe). Unfortunately, Schaub did not illustrate any specimens of *N. ptukhiani* from Armenia. The author of the latter species, Kacharava (1969) did not designate a holotype, referring to Ptukhyan (1964) for the illustration. However, Ptukhyan's illustrations are of poor quality, and are therefore of limited use in understanding the internal features. Roveda (1970) did not describe *N. praefabianii*, because original material and high-quality photographs of this species were unavailable. The illustrations of Blondeau (1972) clearly show that *N.* ''*praefabianii*'' from Syria, Lebanon and Turkey (Pl. XXVIII, Figs. 8, 9, 16–20) differs from *N.* ''*praefabianii*'' from Armenia and possibly from southern France (Pl. XXVIII, Figs. 10–15). Bombita (1975, 1984) noted morphological differences between the middle Eocene *N.* ''*praefabianii*'' of western Europe and the uppermost-upper Eocene *N. praefabianii* Varentsov and Menner from Georgia. He also suggested that *N. ptukhiani* Kacharava from Armenia was the real ancestor of *N. fabianii.* However, some morphological differences between the Armenian *N. ptukhiani* and western European specimens were noted, and descriptions and illustrations of Armenian specimens including *N. ptukhiani* topotypes were provided. The Armenian *N. ptukhiani* (A form) has a nearly biconical test with a pronounced central knob, a very large protoconch (up to 0.60 mm in diameter) and a high spire beginning from the first whorl that remains fairly constant in subsequent stages. In contrast, western Europe and eastern Mediterranean specimens have a lenticular test, lack the prominent central knob, have a much smaller protoconch (0.15–0.30 mm in diameter) and a spire of regularly increasing height. Consequently, the name *N. ptukhiani* Kacharava should not be used to designate the specimens currently reported under this name from the western part of the Tethys.

The problem of what name should be applied to the ancestor of *N. fabianii* remains. Among the possible candidates, *N. praefabianii* Varentsov and Menner, 1933 (*fide* Ellis and Messina, 1940 *et seq.*) is not acceptable because of its poor illustration and different stratigraphic range (Kacharava, 1969). *Nummulites garganicus* Tellini, 1890, thoroughly redescribed by Matteucci (1971), is too primitive and may only be the ancestor of the western Tethys *N.* ''*ptukhiani*''. *Nummulites broachensis* Carter, 1857 (*fide* Ellis and Messina, 1940 *et seq.*) has a distinctly smaller protoconch, and its chambers are wider than high (Hodgkinson, 1989). *Nummulites hormoensis* Nuttall and Brighton, 1931 closely resembles *N.* ''*ptukhiani*'', but the original description of the A form is very concise and the illustrations are poor. However, Roveda (1970) examined topotypes at the Sedgwick Museum (Cambridge), provided some additional information and illustrations (see also Table 1A), and designated as lectotype the A form depicted by Nuttall and Brighton (1931, Pl. 3, fig. 6). From this information, *N. hormoensis* seems to have a protoconch size (130–185 μm in diameter) similar to that of *N.* ''*ptukhiani*''; the rate of spire opening and the chamber shape (isometric or slightly wider than high in the outer whorls) are also quite similar. *Nummulites hormoensis* A differs from *N.* ''*ptukhiani*'' mainly by its larger test diameter and flatter test profile. The B form is also larger than *N.* ''*ptukhiani*'', but the surface shows the same ornamentation pattern with well-developed granules only partially merged to form a reticulation.

Since a direct comparison of the specimens under study with the topotypes of *N. hormoensis* is not possible at present, because the name *N. ptukhiani* is currently widely employed, I chose to retain this species in open nomenclature. Following the guidelines of Bengtson (1988), the specimens under study are assigned to *N.* ''*ptukhiani*'', pointing out the substantial differences between them and the correctly named Armenian *N. ptukhiani.*

Nummulites fabianii (Prever in Fabiani, 1905)
Pl. 1, Figs. 1–15; Pl. 2, Figs. 1–15

Bruguierea fabianii PREVER, in FABIANI, 1905, p. 1805, 1811 (*fide* Ellis and Messina, 1940 *et seq.*).

Nummulites fabianii (Prever, in Fabiani).—ROVEDA, 1970, p. 285–287, text-figs. 71–73, 79, 80.

Nummulites subfabianii (Prever, in Fabiani).—ROVEDA, 1970, p. 287–291, pl. 25, figs. 3, 9, text-figs. 70, 74–78, 81–98.

Nummulites fabianii fabianii Prever.—HERB and HEKEL, 1973, p. 425–431, text-figs. 13–18, 24c, f, g.

Nummulites fabianii praefabianii Varentsov and Menner.—HERB and HEKEL, 1973, p. 432, 433 [partim], text-figs. 24d, e (not a, b).

Nummulites fabianii (Prever).—SCHAUB, 1981, p. 126–128, pl. 49, figs. 57–69, pl. 50, figs. 1–4, tab. 15i, text–fig. 88.

Nummulites fabianii (Prever).—PAPAZZONI and SIROTTI, 1995, pl. 2, figs. 8–10.

Nummulites fabianii Prever.—RACEY, 1995, p. 43. 44, pl. 4, figs. 8–13, text-fig. 37.

Material. Megalospheric and microspheric specimens from the samples PRB 1, 2 (upper Eocene of Priabona, Veneto, northern Italy), GRA (upper Eocene of Grancona, Veneto, northern Italy), SG 10 (upper Eocene of San Germano dei Berici, Veneto, northern Italy), and R 7b (upper Eocene of Cluj-Napoca, Transylvania, Romania), 81 to 85 A forms and 6 to 30 B forms per sample.

Remarks. Prever (in Fabiani, 1905, *fide* Ellis and Messina, 1940 *et seq.*) originally described *N. fabianii* from the vicinity of Grancona (Berici Mountains, northern Italy), but he did not designate a holotype. Roveda (1970) established a neotype from Grancona, illustrating its external features and three equatorial sections of additional specimens (text-figs. 83–85). Roveda (1959) described *Nummulites retiatus* as a new species of the *fabianii* group from the upper Priabonian of Maiella (Abruzzo, central Italy). However, he subsequently regarded it as a

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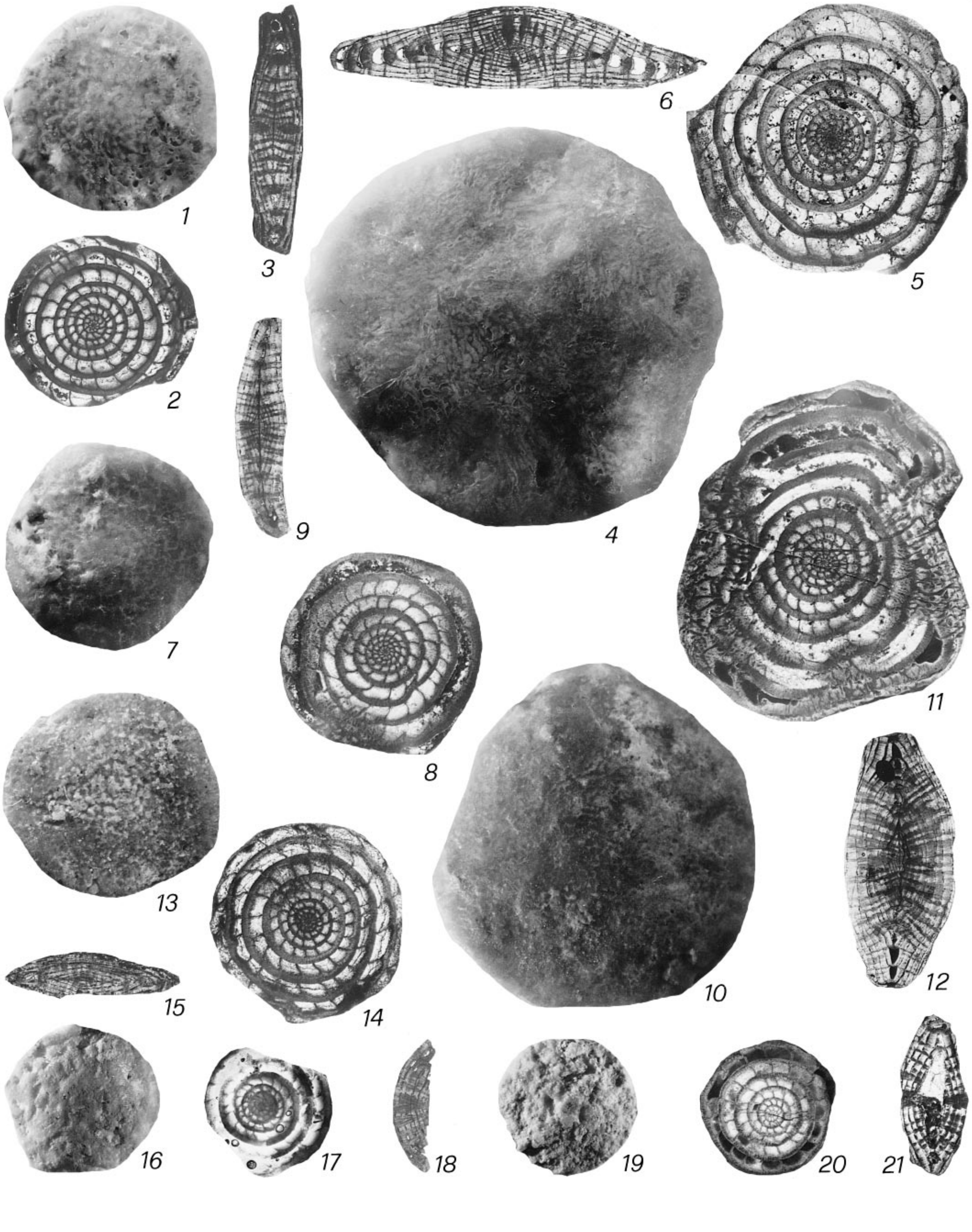
PLATE 1

1–15 *Nummulites fabianii* (Prever in Fabiani), A forms. **1** external, sample SG 10. **2** equatorial section, sample SG 10. **3** axial section, sample SG 10. **4** external, sample R 7b. **5** equatorial section, sample R 7b. **6** axial section, sample R 7b. **7** external, sample GRA. **8** equatorial section, sample GRA. **9** axial section, sample GRA. **10** external, sample PRB 2. **11** equatorial section, sample PRB 2. **12** axial section, sample PRB 2. **13** external, sample PRB 1. **14** equatorial section, sample PRB 1. **15** axial section, sample PRB 1. **16–24** *Nummulites* ''*ptukhiani*'' Z. D. Kacharava, A forms. **16** external, sample MC 2. **17** equatorial section, sample MC 2. **18** axial section, sample MC 2. **19** external, sample MOSS 11. **20** equatorial section, sample MOSS 11. **21** axial section, sample MOSS 11. **22** external, sample VIC 3. **23** equatorial section, sample VIC 3. **24** axial section, sample VIC 3. All × 12.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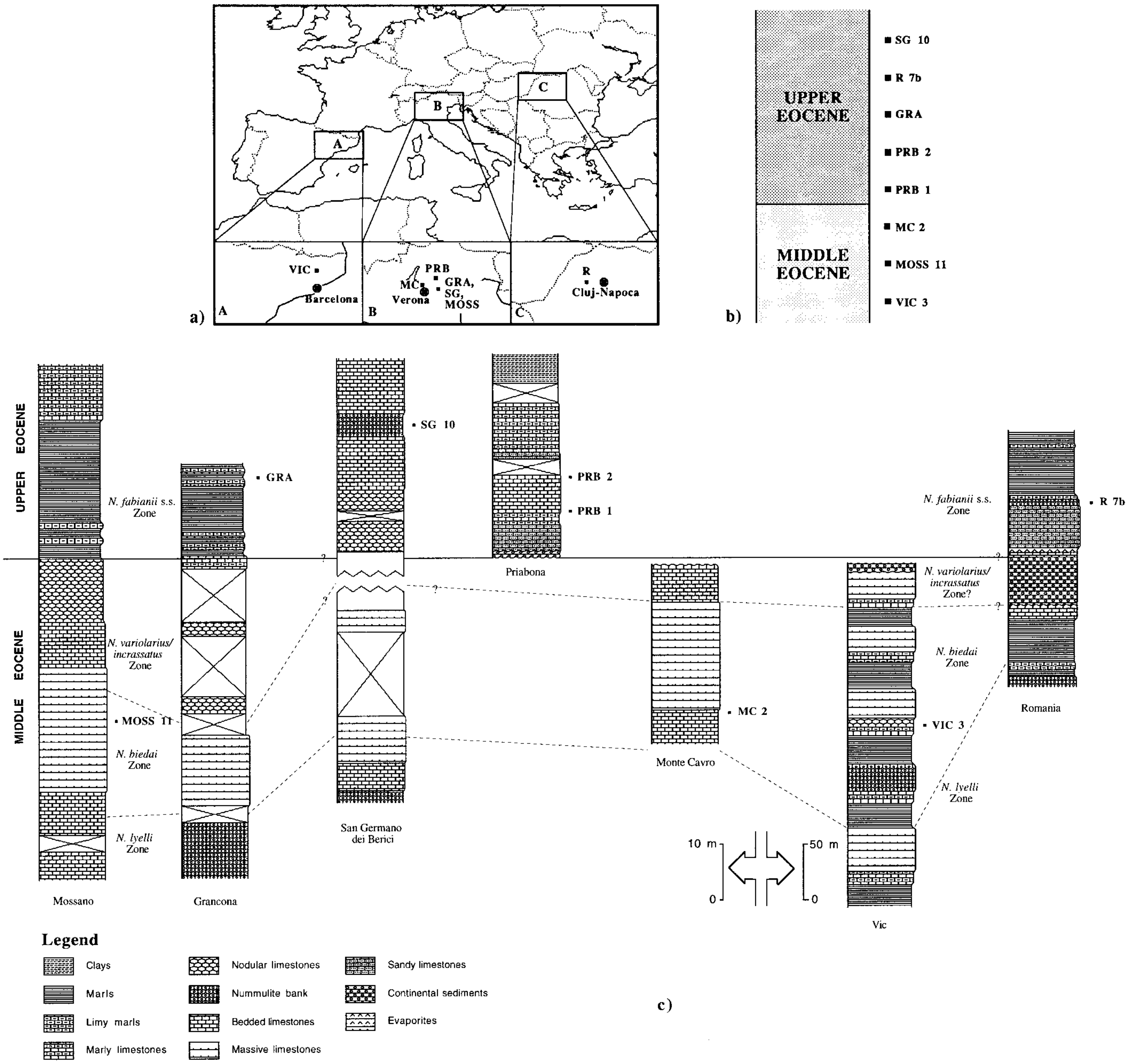

FIGURE 1. a. Location map of the samples. A) VIC = Vic (Cataluña, Spain). B) MC = Monte Cavro; PRB = Priabona; GRA = Grancona; SG = San Germano dei Berici; MOSS = Mossano (Veneto, northern Italy). C) R = Cluj-Napoca (Transylvania, Romania). b. Relative chronologic position of the populations under study. The stratigraphic spacing is arbitrary. c. stratigraphic location of the samples; the stratigraphic columns are (slightly modified) from Papazzoni and Sirotti (1995).

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PLATE 2

1–15 *Nummulites fabianii* (Prever in Fabiani), B forms. **1** external, sample SG 10. **2** equatorial section, sample SG 10. **3** axial section, sample SG 10. **4** external, sample R 7b. **5** equatorial section, sample R 7b. **6** axial section, sample R 7b. **7** external, sample GRA. **8** equatorial section, sample GRA. **9** axial section, sample GRA. **10** external, sample PRB 2. **11** equatorial section, sample PRB 2. **12** axial section, sample PRB 2. **13** external, sample PRB 1. **14** equatorial section, sample PRB 1. **15** axial section, sample PRB 1. **16–21** *Nummulites* ''*ptukhiani*'' Z. D. Kacharava, B forms. **16** external, sample MC 2. **17** equatorial section, sample MC 2. **18** axial section, sample MC 2. **19** external, sample MOSS 11. **20** equatorial section, sample MOSS 11. **21** axial section, sample MOSS 11. All × 6.

subspecies of *N. fabianii* (Roveda, 1970). Herb and Hekel (1973) described and discussed *N. fabianii fabianii* and *N. fabianii retiatus,* including biometric data. Currently, these subspecies are considered markers for the entire Priabonian and for the upper Priabonian, respectively. Problems in discriminating these subspecies are not discussed in detail here but distinction relies mainly on external features such as test shape and surface ornamentation. My observations confirm Herb and Hekel (1973) suggestion that test shape and ornamentation are highly variable and may have been paleoenvironmentally controlled (Trevisani and Papazzoni, 1996). Therefore, subspecific distinction is not made and all upper Eocene populations are grouped under the name *N. fabianii.*

MATERIALS AND METHODS

The populations studied come mainly from samples with well-known chronological position used to investigate the biostratigraphy near the middle/upper Eocene boundary (Fig. 1; for further details about locations see Papazzoni and Sirotti, 1995). From each sample 40 megalospheric specimens were selected to measure external features (test diameter/thickness), and 41 to 45 additional specimens were used to prepare equatorial sections in order to measure the internal features. The microspheric specimens of *N.* ''*ptukhiani*'' are usually difficult to find: in the sample VIC 3 no B forms were recognized; the samples MOSS 11 and MC 2 were collected again just to increase the number of microspheric specimens, but on the whole only 11 and 5 were found, respectively.

The number of specimens examined was intended to provide statistically significant mean values. However, an empirical test of the variation of statistical parameters was also conducted for different numbers of observations on the same feature from the same sample. The optimal number of specimens per sample was determined to be about 30; whereas with less than 10–15 specimens variations about the mean were always too high to give reliable results.

The traditional measurements of nummulites (in particular the radii of the whorls) do not seem useful as such to understand the growth process (see for instance Pecheux, 1995); nevertheless, to compare the data with those existing in the literature requires maintaining such measurements. Thus, for the megalospheric specimens, the outer protoconch and deuteroconch heights and the radius of each whorl were measured (Fig. 2a) and the number of septa per whorl were counted (in the first whorl this number comprises the deuteroconch wall), following Herb and Hekel (1973). In the microspheric specimens only the radius of each whorl (Fig. 2b) and the number of septa per whorl were measured, as Schaub (1981) did.

The mean chamber length (Cl) for each whorl was calculated by dividing the length of the arc of the spiral (approximated by a circumference whose radius is the mean between R_i and R_{i-1}; Fig. 2c) by the number of septa (S_i), with the following expression:

$$Cl_i = \pi(R_i + R_{i-1})/S_i$$

where R_i is the radius and S_i the number of septa of the i-th whorl. For the first whorl $R_0 = (P + D)/2$.

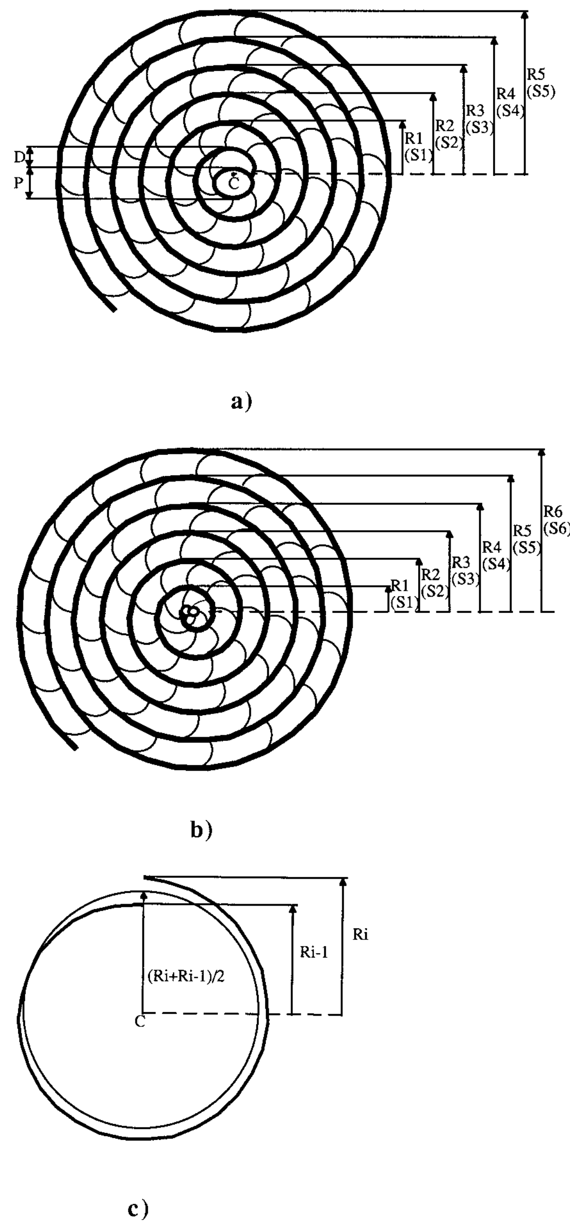

FIGURE 2. a. Sketch of an equatorial section of a megalospheric individual, showing the position of the recorded parameters. Each radius (R1, R2, etc.) was measured from C = (P + D)/2. P = outer protoconch height (wall included); D = outer deuteroconch height (wall included); Rn = radius of the n-th whorl; Sn = number of septa in the n-th whorl. b. Sketch of an equatorial section of a microspheric individual, showing the position of the recorded parameters. The radii (R1, R2, etc.) were measured from the center of the proloculus. Abbreviations as in a. c. Sketch of the i-th whorl showing the parameters used to calculate the mean chamber length (cl). For abbreviations, see text.

STRATIGRAPHIC ORDER OF THE SAMPLES

Populations were preliminarily ordered according to relative chronologic position (Fig. 1b). Samples VIC 3, MOSS 11, and MC 2 are all from the upper middle Eocene *Nummulites biedai* Zone (Papazzoni and Sirotti, 1995). The remaining samples belong to the *Nummulites fabianii* Zone (Fig. 1c). To determine the relative position of each sample belonging to the same biozone, the increasing size trend of the protoconch in the *Assilina alpina* lineage was utilized. For each sample, the inner protoconch diameter (p.d.) of some specimens of megalospheric *A. schwageri* (uppermost middle Eocene) and *A. alpina* (upper Eocene) were mea-

TABLE 2. Results of the measurements of the A forms. Statistical values calculated for each parameter measured in the eight megalospheric populations of *N.* ''*ptukhiani*''-*fabianii.* d = diameter of the test; t = thickness of the test; P = protoconch height; D = deuteroconch height; Rn = radius of the n-th whorl; Sn = number of septa in the n-th whorl; n = number of observations; min. = minimum value recorded; max. = maximum value recorded; med. = median; se = standard error; σ = standard deviation; cv = coefficient of variation.

d (mm)	n	min.	max.	med.	mean	se	σ	cv	R4 (μm)	n	min.	max.	med.	mean	se	σ	cv
SG 10	40	2.0	4.2	3.0	3.0	0.1	0.5	18.3	SG 10	38	1147	1591	1406	1411	15.5	95.5	6.8
R 7b	40	1.5	4.4	3.5	3.2	0.1	0.8	24.0	R 7b	31	1221	1832	1462	1457	24.5	136.4	9.4
GRA	40	2.3	4.4	3.4	3.3	0.1	0.6	18.1	GRA	30	1119	1582	1365	1356	22.9	125.3	9.2
PRB 2	40	1.9	3.5	2.5	2.6	0.1	0.4	15.6	PRB 2	17	1082	1332	1193	1193	16.8	69.4	5.8
PRB 1	40	1.8	2.6	2.3	2.3	0.0	0.2	10.7	PRB 1	33	768	1424	1018	1035	21.9	125.5	12.1
MC 2	40	1.6	3.3	2.4	2.4	0.1	0.4	18.5	MC 2	13	999	1314	1166	1156	25.5	91.9	8.0
MOSS 11	40	1.7	3.3	2.3	2.3	0.1	0.4	17.3	MOSS 11	24	944	1295	1184	1147	22.2	108.8	9.5
VIC 3	40	1.6	3.5	2.6	2.6	0.1	0.6	21.5	VIC 3	37	870	1350	1166	1128	21.2	129.2	11.5
t (mm)									R5 (μm)								
SG 10	40	0.8	2.1	1.3	1.3	0.0	0.3	19.5	SG 10	10	1443	1887	1689	1680	35.9	113.6	6.8
R 7b	40	0.6	1.7	1.2	1.2	0.0	0.3	23.7	R 7b	11	1508	2026	1804	1766	44.5	147.7	8.4
GRA	40	0.9	1.8	1.3	1.3	0.0	0.2	18.3	GRA	7	1397	2007	1684	1688	83.5	220.8	13.1
PRB 2	40	0.9	2.2	1.4	1.4	0.1	0.3	20.2	PRB 2	2	1286	1397	1342	1342	55.5	78.5	5.9
PRB 1	40	0.9	1.8	1.1	1.2	0.0	0.2	15.8	PRB 1	7	1184	1480	1240	1281	37.8	100.1	7.8
MC 2	40	0.8	1.7	1.3	1.3	0.0	0.2	17.2	MC 2	0	—	—	—	—	—	—	—
MOSS 11	40	0.8	2.0	1.2	1.2	0.1	0.3	23.8	MOSS 11	3	1276	1572	1406	1418	85.6	148.4	10.5
VIC 3	40	0.7	1.7	1.2	1.2	0.0	0.3	23.1	VIC 3	18	1156	1646	1517	1449	36.6	155.1	10.7
P (μm)									S1								
SG 10	41	166	333	259	257	5.8	37.3	14.5	SG 10	41	6.0	9.0	7.0	7.3	0.1	0.8	10.8
R 7b	44	259	444	314	320	6.6	43.8	13.7	R 7b	43	6.0	9.0	7.0	6.9	0.1	0.6	8.8
GRA	43	185	296	222	233	4.9	32.1	13.8	GRA	43	6.0	9.0	8.0	7.6	0.1	0.7	9.3
PRB 2	42	204	352	278	287	4.4	28.3	9.8	PRB 2	42	6.0	9.0	7.0	7.4	0.1	0.8	10.4
PRB 1	45	111	259	166	167	4.9	32.9	19.7	PRB 1	45	6.0	9.0	8.0	7.7	0.1	0.7	9.3
MC 2	41	166	296	222	216	4.5	28.5	13.2	MC 2	41	7.0	11.0	8.0	8.3	0.1	0.9	10.9
MOSS 11	41	148	240	185	192	3.8	24.2	12.6	MOSS 11	41	7.0	10.0	8.0	8.1	0.1	0.8	9.2
VIC 3	45	130	204	166	162	3.3	21.9	13.5	VIC 3	45	6.0	10.0	8.0	8.1	0.1	0.7	9.1
D (μm)									S2								
SG 10	41	166	259	222	211	4.2	26.8	12.7	SG 10	41	10.0	15.0	13.0	12.8	0.2	1.4	10.7
R 7b	44	148	296	222	211	4.9	32.3	15.3	R 7b	43	10.0	17.0	13.0	13.2	0.3	1.8	13.7
GRA	43	130	259	185	197	4.3	28.3	14.4	GRA	43	10.0	16.0	13.0	13.1	0.2	1.4	10.5
PRB 2	42	148	296	222	214	4.6	29.5	13.7	PRB 2	42	11.0	18.0	14.0	13.6	0.3	1.7	12.4
PRB 1	45	92	259	166	165	5.0	33.4	20.2	PRB 1	44	8.0	15.0	12.0	12.3	0.2	1.4	11.0
MC 2	41	130	278	185	190	4.3	27.5	14.5	MC 2	39	11.0	18.0	14.0	14.2	0.3	1.6	11.2
MOSS 11	41	111	278	185	188	5.1	32.7	17.4	MOSS 11	41	12.0	17.0	14.0	13.7	0.2	1.2	8.8
VIC 3	45	74	185	148	144	3.7	25.1	17.4	VIC 3	45	12.0	17.0	14.0	14.2	0.2	1.1	7.9
R1 (μm)									S3								
SG 10	41	370	555	490	480	7.6	48.4	10.1	SG 10	41	13.0	21.0	16.0	16.3	0.3	1.8	10.8
R 7b	44	407	629	495	506	7.7	51.1	10.1	R 7b	41	13.0	22.0	17.0	17.5	0.3	2.0	11.6
GRA	43	352	527	426	428	7.2	47.5	11.1	GRA	42	13.0	18.0	15.0	15.2	0.2	1.1	7.2
PRB 2	42	388	574	472	469	5.9	37.9	8.1	PRB 2	33	15.0	20.0	17.0	16.9	0.2	1.2	7.3
PRB 1	45	231	500	342	343	7.5	50.2	14.7	PRB 1	41	11.0	17.0	14.0	14.1	0.3	1.8	12.4
MC 2	41	324	638	388	397	8.6	55.1	13.9	MC 2	28	14.0	19.0	16.5	16.6	0.3	1.5	8.8
MOSS 11	41	278	500	379	378	6.7	42.8	11.3	MOSS 11	40	12.0	20.0	16.0	15.8	0.3	1.7	10.8
VIC 3	45	240	426	333	336	6.0	40.2	12.0	VIC 3	43	14.0	22.0	17.0	17.1	0.3	1.7	9.8
R2 (μm)									S4								
SG 10	41	574	888	740	742	10.6	67.5	9.1	SG 10	35	14.0	21.0	18.0	17.5	0.3	1.9	10.8
R 7b	44	638	934	754	769	12.1	80.5	10.5	R 7b	28	15.0	23.0	19.0	18.9	0.4	2.0	10.6
GRA	43	564	814	684	680	10.2	66.6	9.8	GRA	24	13.0	20.0	17.0	17.3	0.4	1.8	10.6
PRB 2	42	601	870	689	695	8.1	52.6	7.6	PRB 2	13	13.0	22.0	18.0	17.7	0.7	2.6	14.8
PRB 1	45	342	722	564	551	10.7	71.5	13.0	PRB 1	30	12.0	18.0	15.0	14.8	0.4	1.9	12.9
MC 2	39	444	740	620	614	9.4	58.8	9.6	MC 2	7	13.0	22.0	18.0	18.0	1.1	3.0	16.7
MOSS 11	41	444	777	601	606	9.5	61.1	10.1	MOSS 11	25	14.0	25.0	18.0	17.8	0.6	2.8	15.6
VIC 3	45	444	684	555	554	8.6	57.8	10.4	VIC 3	34	15.0	26.0	18.0	18.7	0.4	2.2	11.8
R3 (μm)									S5								
SG 10	41	832	1240	1073	1062	13.0	83.2	7.8	SG 10	12	16.0	26.0	20.5	20.6	1.1	3.7	17.8
R 7b	42	934	1388	1115	1109	17.4	112.6	10.2	R 7b	7	17.0	23.0	20.0	20.4	0.7	1.9	9.3
GRA	39	805	1184	1018	1006	15.6	97.6	9.7	GRA	4	17.0	21.0	20.5	19.8	1.0	1.9	9.6
PRB 2	42	823	1175	962	962	10.5	67.8	7.1	PRB 2	0	—	—	—	—	—	—	—
PRB 1	44	546	1092	796	792	14.5	96.0	12.1	PRB 1	6	16.0	20.0	16.5	17.2	0.7	1.6	9.3
MC 2	37	703	1036	888	883	12.0	72.7	8.2	MC 2	0	—	—	—	—	—	—	—
MOSS 11	41	684	1110	879	874	13.5	86.4	9.9	MOSS 11	2	20.0	21.0	20.5	20.5	0.5	0.7	3.5
VIC 3	45	648	1054	796	812	12.7	85.1	10.5	VIC 3	14	18.0	25.0	19.5	20.9	0.7	2.4	11.6

TABLE 3. Results of the measurements of the B forms. Statistical values calculated for each parameter measured in the seven microspheric populations of *N.* "*ptukhiani*"-*fabianii*. Abbreviations as in Table 2.

d (mm)	n	min.	max.	med.	mean	se	σ	cv	R7 (μm)	n	min.	max.	med.	mean	se	σ	cv
SG 10	21	5.5	10.3	7.7	7.8	0.3	1.4	17.6	SG 10	14	2091	3145	2664	2646	90.3	337.7	12.8
R 7b	30	5.8	14.0	10.0	10.0	0.4	2.1	20.7	R 7b	20	1554	2331	1943	1957	46.8	209.4	10.7
GRA	18	5.5	8.4	7.1	7.0	0.2	1.0	14.1	GRA	9	1998	2775	2257	2321	77.6	232.7	10.0
PRB 2	6	5.4	11.1	9.0	8.8	0.9	2.2	24.7	PRB 2	4	1739	2479	2202	2155	182.1	364.3	16.9
PRB 1	20	4.3	7.5	5.4	5.5	0.2	0.8	15.5	PRB 1	11	1961	2479	2183	2183	44.1	146.1	6.7
MC 2	5	2.1	4.9	3.5	3.5	0.6	1.2	35.6	MC 2	2	1832	2331	2082	2082	249.5	352.8	17.0
MOSS 11	11	2.3	5.1	3.7	3.8	0.3	0.9	25.0	MOSS 11	3	1887	2220	2109	2072	97.9	169.6	8.2
t (mm)									R8 (μm)								
SG 10	21	1.4	2.7	2.1	2.1	0.1	0.4	18.6	SG 10	10	2664	3626	3256	3197	106.7	337.5	10.6
R 7b	30	1.5	3.1	2.3	2.2	0.1	0.4	17.8	R 7b	20	2054	3071	2590	2585	59.9	267.9	10.4
GRA	18	1.7	3.0	2.0	2.1	0.1	0.3	16.2	GRA	7	2664	3774	2923	3005	138.4	366.2	12.2
PRB 2	6	2.0	4.0	3.5	3.3	0.3	0.7	22.7	PRB 2	4	2257	3219	2701	2720	257.5	514.9	18.9
PRB 1	20	1.4	2.2	1.5	1.6	0.1	0.2	14.4	PRB 1	2	2553	2849	2701	2701	148.0	209.3	7.7
MC 2	4	1.6	2.4	2.0	2.0	0.2	0.3	16.3	MC 2	0	—	—	—	—	—	—	—
MOSS 11	9	1.0	2.6	1.6	1.7	0.2	0.5	31.4	MOSS 11	0	—	—	—	—	—	—	—
R1 (μm)									R9 (μm)								
SG 10	15	111	259	185	184	10.3	39.8	21.7	SG 10	5	3330	4292	3811	3789	170.6	381.5	10.1
R 7b	20	111	222	158	170	8.8	39.2	23.0	R 7b	17	2627	3700	3293	3241	79.8	328.9	10.1
GRA	9	111	185	148	148	8.7	26.2	17.7	GRA	5	3256	3848	3293	3492	130.6	292.0	8.4
PRB 2	2	185	185	185	185	—	—	—	PRB 2	2	2627	2849	2738	2738	111.0	157.0	5.7
PRB 1	17	93	222	148	149	8.5	34.8	23.4	PRB 1	1	3034	3034	3034	3034	—	—	—
MC 2	5	130	185	167	159	9.4	21.0	13.2	MC 2	0	—	—	—	—	—	—	—
MOSS 11	9	111	222	185	169	10.9	32.6	19.4	MOSS 11	0	—	—	—	—	—	—	—
R2 (μm)									R10 (μm)								
SG 10	15	296	518	370	395	16.8	65.1	16.5	SG 10	2	4366	4440	4403	4403	37.0	52.3	1.2
R 7b	20	241	407	306	315	11.2	50.2	16.0	R 7b	13	3145	4292	3885	3795	111.4	401.6	10.6
GRA	10	259	370	306	309	11.1	34.9	11.3	GRA	0	—	—	—	—	—	—	—
PRB 2	3	296	370	333	333	21.4	37.0	11.1	PRB 2	1	3404	3404	3404	3404	—	—	—
PRB 1	17	222	444	296	298	14.3	58.8	19.7	PRB 1	0	—	—	—	—	—	—	—
MC 2	5	259	370	333	318	18.9	42.2	13.3	MC 2	0	—	—	—	—	—	—	—
MOSS 11	10	259	407	333	333	17.4	55.2	16.6	MOSS 11	0	—	—	—	—	—	—	—
R3 (μm)									R11 (μm)								
SG 10	15	518	944	629	662	29.5	114.4	17.3	SG 10	0	—	—	—	—	—	—	—
R 7b	20	389	629	481	489	15.0	67.2	13.7	R 7b	10	3700	4995	4625	4477	146.1	462.1	10.3
GRA	10	481	611	509	522	15.3	48.5	9.3	GRA	0	—	—	—	—	—	—	—
PRB 2	4	407	592	546	523	44.3	88.5	16.9	PRB 2	1	4033	4033	4033	4033	—	—	—
PRB 1	17	352	777	444	490	25.4	104.8	21.4	PRB 1	0	—	—	—	—	—	—	—
MC 2	5	463	629	518	540	28.3	63.2	11.7	MC 2	0	—	—	—	—	—	—	—
MOSS 11	10	444	666	537	540	20.6	65.1	12.0	MOSS 11	0	—	—	—	—	—	—	—
R4 (μm)									R12 (μm)								
SG 10	15	851	1406	999	1019	38.0	147.2	14.5	SG 10	0	—	—	—	—	—	—	—
R 7b	19	592	851	703	720	16.1	70.0	9.7	R 7b	5	4255	5698	4440	4743	263.6	589.3	12.4
GRA	10	703	925	796	799	22.9	72.3	9.1	GRA	0	—	—	—	—	—	—	—
PRB 2	4	592	925	814	786	69.8	139.7	17.8	PRB 2	0	—	—	—	—	—	—	—
PRB 1	17	574	1221	740	766	36.5	150.6	19.7	PRB 1	0	—	—	—	—	—	—	—
MC 2	5	703	944	777	803	39.6	88.5	11.0	MC 2	0	—	—	—	—	—	—	—
MOSS 11	10	666	925	805	814	23.6	74.6	9.2	MOSS 11	0	—	—	—	—	—	—	—
R5 (μm)									R13 (μm)								
SG 10	15	1221	1961	1480	1489	53.0	205.3	13.8	SG 10	0	—	—	—	—	—	—	—
R 7b	20	851	1258	1036	1043	22.4	100.1	9.6	R 7b	2	4514	4884	4699	4699	185.0	261.6	5.6
GRA	10	1036	1314	1184	1192	27.9	88.2	7.4	GRA	0	—	—	—	—	—	—	—
PRB 2	4	851	1369	1277	1193	122.1	244.3	20.5	PRB 2	0	—	—	—	—	—	—	—
PRB 1	17	907	1943	1110	1156	59.9	246.9	21.4	PRB 1	0	—	—	—	—	—	—	—
MC 2	4	999	1258	1147	1138	53.1	106.3	9.3	MC 2	0	—	—	—	—	—	—	—
MOSS 11	10	925	1388	1147	1173	40.5	128.1	10.9	MOSS 11	0	—	—	—	—	—	—	—
R6 (μm)									R14								
SG 10	15	1499	2775	2072	2065	77.6	300.4	14.5	SG 10	0	—	—	—	—	—	—	—
R 7b	20	1129	1776	1445	1460	36.8	164.7	11.3	R 7b	1	5661	5661	5661	5661	—	—	—
GRA	10	1406	2035	1739	1737	60.4	191.1	11.0	GRA	0	—	—	—	—	—	—	—
PRB 2	4	1314	1887	1702	1651	134.9	269.7	16.3	PRB 2	0	—	—	—	—	—	—	—
PRB 1	17	1295	2849	1591	1656	86.6	356.9	21.6	PRB 1	0	—	—	—	—	—	—	—
MC 2	2	1369	1739	1554	1554	185.0	261.6	16.8	MC 2	0	—	—	—	—	—	—	—
MOSS 11	7	1277	1924	1554	1625	92.9	245.9	15.1	MOSS 11	0	—	—	—	—	—	—	—

TABLE 3. Continued.

S1 (μm)									S7								
SG 10	5	5.0	7.0	5.0	5.6	0.4	0.9	16.0	SG 10	10	17.0	26.0	19.5	20.0	0.9	2.9	14.3
R 7b	2	6.0	7.0	6.5	6.5	0.5	0.7	10.9	R 7b	16	17.0	25.0	20.0	20.1	0.5	2.1	10.4
GRA	0	—	—	—	—	—	—	—	GRA	4	17.0	20.0	19.0	18.8	0.6	1.3	6.7
PRB 2	0	—	—	—	—	—	—	—	PRB 2	1	23.0	23.0	23.0	23.0	—	—	—
PRB 1	0	—	—	—	—	—	—	—	PRB 1	9	12.0	21.0	17.0	17.0	0.9	2.7	15.8
MC 2	0	—	—	—	—	—	—	—	MC 2	0	—	—	—	—	—	—	—
MOSS 11	1	7.0	7.0	7.0	7.0	—	—	—	MOSS 11	0	—	—	—	—	—	—	—
S2									S8								
SG 10	13	9.0	11.0	10.0	9.9	0.2	0.8	7.7	SG 10	6	19.0	25.0	21.5	22.0	0.9	2.2	10.0
R 7b	3	10.0	12.0	11.0	11.0	0.6	1.0	9.1	R 7b	12	20.0	25.0	21.0	21.5	0.5	1.6	7.3
GRA	5	9.0	11.0	10.0	9.8	0.4	0.8	8.5	GRA	2	21.0	23.0	22.0	22.0	1.0	1.4	6.4
PRB 2	2	10.0	11,0	10.5	10.5	0.5	0.7	6.7	PRB 2	0	—	—	—	—	—	—	—
PRB 1	10	10.0	13.0	11.0	10.9	0.3	1.0	9.1	PRB 1	1	20.0	20.0	20.0	20.0	—	—	—
MC 2	2	9.0	9.0	9.0	9.0	0.0	0.0	0.0	MC 2	0	—	—	—	—	—	—	—
MOSS 11	5	9.0	11.0	11.0	10.4	0.4	0.9	8.6	MOSS 11	0	—	—	—	—	—	—	—
S3									S9								
SG 10	14	11.0	14.0	12.0	12.1	0.2	0.8	6.9	SG 10	1	18.0	18.0	18.0	18.0	—	—	—
R 7b	9	11.0	17.0	14.0	13.7	0.7	2.1	15.1	R 7b	11	17.0	30.0	24.0	23.5	1.0	3.4	14.7
GRA	8	11.0	14.0	12.0	12.3	0.4	1.0	8.5	GRA	1	22.0	22.0	22.0	22.0	—	—	—
PRB 2	2	13.0	13.0	13.0	13.0	0.0	0.0	0.0	PRB 2	0	—	—	—	—	—	—	—
PRB 1	16	10.0	15.0	12.0	12.0	0.4	1.4	11.8	PRB 1	1	19.0	19.0	19.0	19.0	—	—	—
MC 2	5	12.0	15.0	13.0	13.2	0.6	1.3	9.9	MC 2	0	—	—	—	—	—	—	—
MOSS 11	6	12.0	14.0	12.0	12.5	0.3	0.8	6.7	MOSS 11	0	—	—	—	—	—	—	—
S4									S10								
SG 10	15	12.0	17.0	14.0	14.5	0.4	1.5	10.4	SG 10	0	—	—	—	—	—	—	—
R 7b	13	12.0	17.0	15.0	14.8	0.4	1.3	9.1	R 7b	5	18.0	25.0	22.0	21.4	1.3	2.9	13.5
GRA	10	12.0	17.0	13.5	13.8	0.5	1.7	12.2	GRA	0	—	—	—	—	—	—	—
PRB 2	2	14.0	16.0	15.0	15.0	1.0	1.4	9.4	PRB 2	0	—	—	—	—	—	—	—
PRB 1	16	10.0	18.0	13.0	13.6	0.5	1.8	13.5	PRB 1	0	—	—	—	—	—	—	—
MC 2	5	14.0	19.0	15.0	15.8	0.9	1.9	12.2	MC 2	0	—	—	—	—	—	—	—
MOSS 11	8	12.0	15.0	14.5	14.1	0.4	1.1	8.0	MOSS 11	0	—	—	—	—	—	—	—
S5									S11								
SG 10	14	14.0	21.0	17.0	17.1	0.5	2.1	12.0	SG 10	0	—	—	—	—	—	—	—
R 7b	15	14.0	21.0	17.0	16.6	0.5	2.0	11.8	R 7b	3	20.0	30.0	29.0	26.3	3.2	5.5	20.9
GRA	9	11.0	18.0	15.0	15.2	1.0	2.9	18.8	GRA	0	—	—	—	—	—	—	—
PRB 2	3	16.0	18.0	16.0	16.7	0.7	1.2	6.9	PRB 2	0	—	—	—	—	—	—	—
PRB 1	16	11.0	17.0	15.0	15.0	0.4	1.7	11.4	PRB 1	0	—	—	—	—	—	—	—
MC 2	2	16.0	18.0	17.0	17.0	1.0	1.4	8.3	MC 2	0	—	—	—	—	—	—	—
MOSS 11	7	14.0	17.0	16.0	15.7	0.4	1.1	7.1	MOSS 11	0	—	—	—	—	—	—	—
S6																	
SG 10	12	14.0	24.0	18.0	18.6	0.8	2.6	14.0									
R 7b	17	15.0	22.0	18.0	18.3	0.5	2.2	12.0									
GRA	8	12.0	21.0	17.5	17.4	1.3	3.7	21.1									
PRB 2	2	17.0	19.0	18.0	18.0	1.0	1.4	7.9									
PRB 1	12	14.0	23.0	17.0	17.0	0.7	2.4	14.2									
MC 2	1	17.0	17.0	17.0	17.0	—	—	—									
MOSS 11	3	15.0	17.0	15.0	15.7	0.7	1.2	7.4									

sured. According to these data the order is (younger to older):

8) SG 10 (mean p.d.= 168 μm; 10 specimens measured);
7) R 7b (mean p.d.= 164 μm; 8 specimens measured);
6) GRA (mean p.d.= 162 μm; 9 specimens measured);
5) PRB 2 (mean p.d.= 143 μm; 6 specimens measured);
4) PRB 1 (no *Assilina* found), which underlies PRB 2;
3) MC 2 (mean p.d.= 121 μm; 11 specimens measured);
2) MOSS 11 (mean p.d.= 119 μm; 8 specimens measured);
1) VIC 3 (mean p.d.= 102 μm; 7 specimens measured).

The samples MOSS 11 and MC 2 in the *N. biedai* Zone and the samples GRA, R7b, and SG 10 in the *N. fabianii* Zone have very similar mean p.d., so they could belong to about the same stratigraphic levels.

DISCUSSION OF RESULTS

The biometric measurements were statistically elaborated to determine mean values useful to compare the different populations (Tables 2 and 3). The surface ornamentation shows different patterns in the microspheric and megalospheric specimens of the two species. In the A forms Bous-

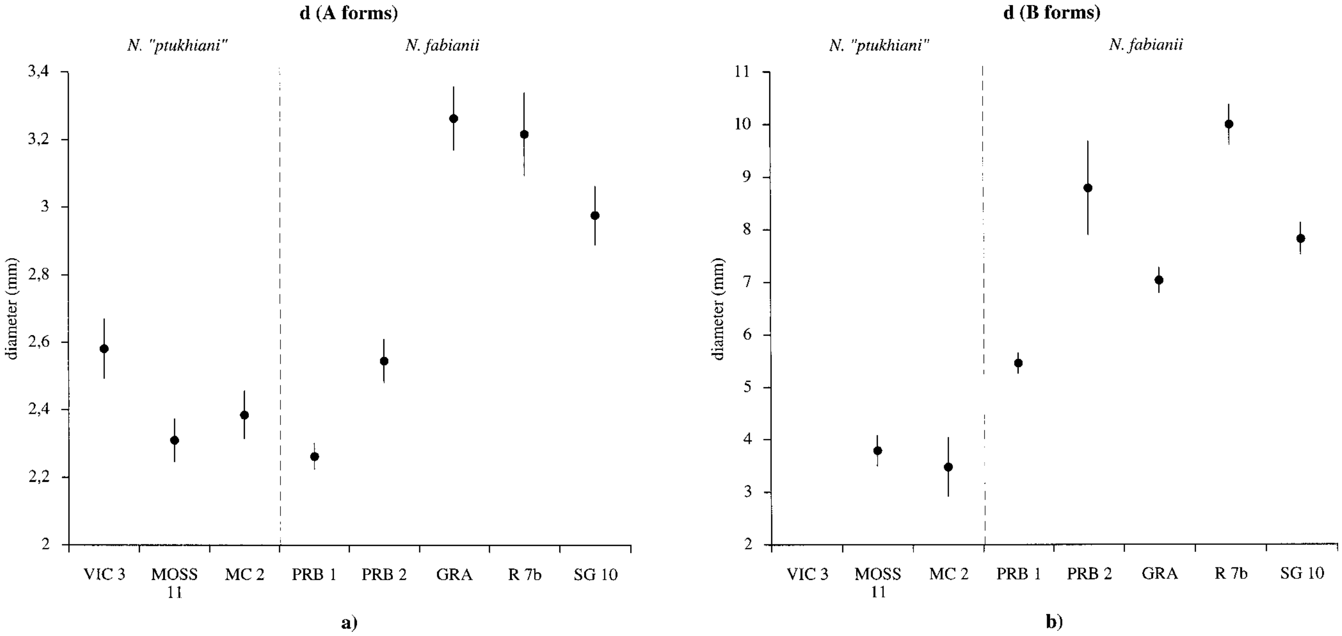

FIGURE 3. Mean diameter (d) of the test (±se) of: a. megalospheric; b. microspheric forms of *N.* ''*ptukhiani*'' and *N. fabianii.*

sac (1906) previously described the formation of the so-called ''transverse lamina'' from the connection of spirally arranged granules. The former descriptions of *N.* ''*ptukhiani*'' A (Table 1A) pointed out the lack of a complete reticulation in this species. From my observations, this feature is not constant; some *N.* ''*ptukhiani*'' have a complete reticulation (e.g. Pl. 1, fig. 22), whereas some *N. fabianii* lack it (e.g., Pl. 1, fig. 7). The B forms of *N.* ''*ptukhiani*'' show quite large granules (Pl. 2, figs. 16, 19) partially or totally merged to form a reticulation very similar to that of the corresponding A forms. In *N. fabianii* B the reticulation instead is sinuous to meandering with small granules more evident near the poles of the test (Pl. 2, figs. 1, 4, 7, 10, 13). The overall diameter of the test (d) does not distinguish the A forms of *N.* ''*ptukhiani*'' and *N. fabianii* (Fig. 3a). The B forms, however, have clearly different diameters (Fig. 3b; see also Table 1), that is 3.5–3.8 in *N.* ''*ptukhiani*'' versus 5.5–10.0 mm in *N. fabianii.* The shape of the test, approximated by the diameter/thickness ratio (d/t), also shows no obvious correlation with the age (Fig. 4a) in the megalospheric individuals. The microspheric forms of *N.* ''*ptukhiani*'' have more inflated tests (mean d/t 1.9–2.3) than *N. fabianii* (mean d/t 2.7–4.5; Fig. 4b). According to several authors (e.g., Reiss and Hottinger, 1984; Hallock and

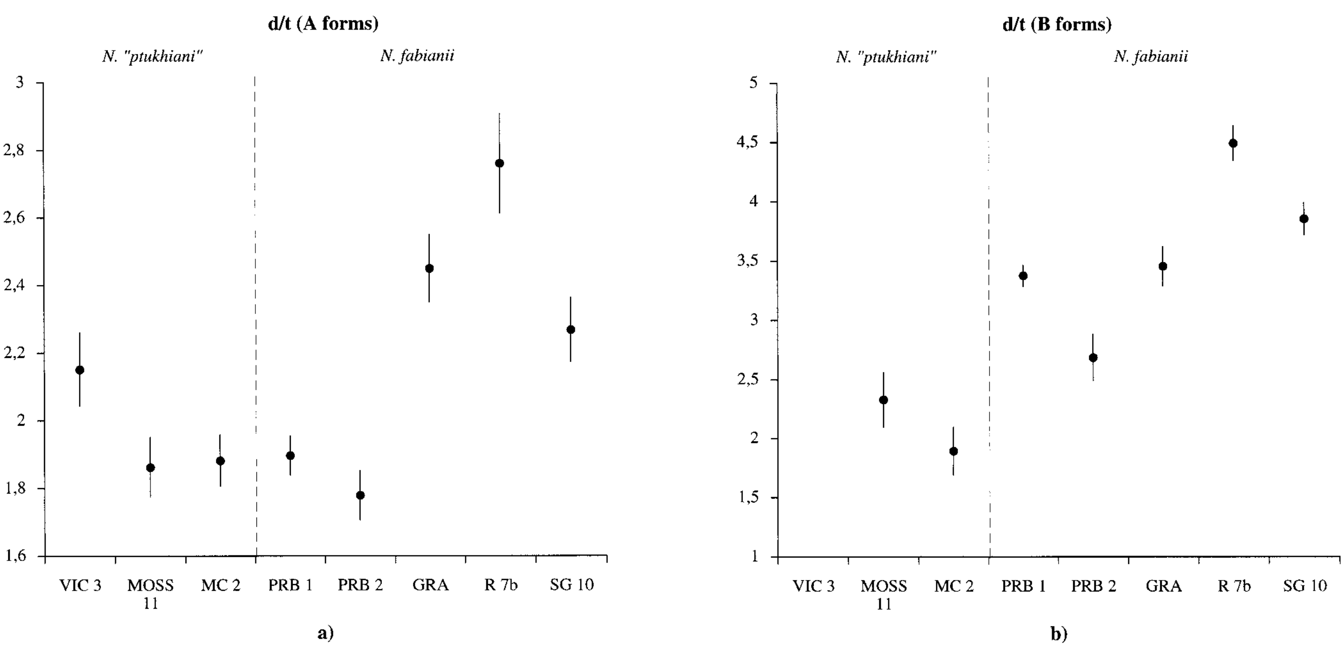

FIGURE 4. Mean diameter/thickness (d/t) ratio (±se) of: a. megalospheric; b. microspheric forms of *N.* ''*ptukhiani*'' and *N. fabianii.*

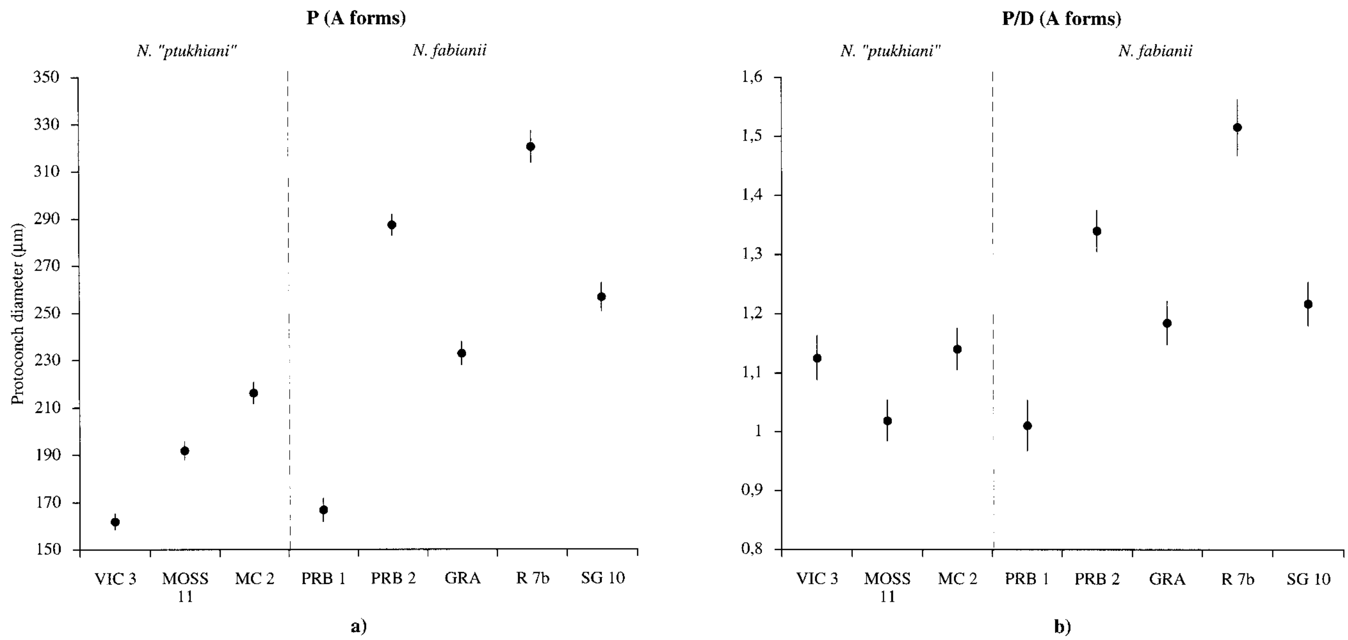

FIGURE 5. a. Mean protoconch height (P) (±se); b. mean protoconch height/deuteroconch height (P/D) ratio (±se) of *N. ''ptukhiani''* and *N. fabianii.*

Glenn, 1986) test shape in larger foraminifera is mainly influenced by light intensity (enabling algal symbiosis) and water energy, both of which vary with water depth. Specimens with thicker tests live in high-energy, high-light environments, whereas thinner tests usually occur in low-energy, low-light environments. Pecheux (1995) showed that in recent *Operculina ammonoides* the t/d ratio depends mainly on the type of substrate (hard/soft) and depth. I observe that flatter tests of both generations all come from marly sediments (samples VIC 3, GRA, SG 10, R 7b; Fig. 4a, b), whereas more inflated tests were collected either from pure limestones (MOSS 11, MC 2) or from marly limestones with abundant coarse quartz grains (PRB 1, 2). This relationship suggests an environmental control on test shape, which is consequently not conclusive for biostratigraphic purposes.

In the A forms the protoconch heights (P) show a clear trend towards increasing size through time (Fig. 5a), with the remarkable exception of the PRB 1 population. These observations corroborate those of Herb and Hekel (1973): at the base of the type-Priabonian, specimens of *N. fabianii* have a small protoconch, very similar to that found in the uppermost middle Eocene *N. ''ptukhiani''*. The trend of the protoconch size to increase through time fits the well-known ''law of nepionic acceleration''; consequently it is regarded as an evolutionary character, even if the possible environmental influence suggests caution.

The deuteroconch heights (D) are, with few exceptions, quite constant in all the populations examined (Table 2). However, the P/D ratio (Fig. 5b) is on average close to unity (isolepidine embryo) for all the *N. ''ptukhiani''* populations and for the PRB 1 *N. fabianii* population; whereas the embryo shifts towards anisolepidine (P/D ratio of ~1.2 or more) in the typical *N. fabianii* populations.

The fields occupied by the mean coiling curves (±2 units of standard error) of the A forms of *N. ''ptukhiani''* (samples VIC 3, MOSS 11 and MC 2) and *N. fabianii* (samples GRA, PRB 2, SG 10 and R 7b) are separated (Fig. 6a). Only the PRB 1 population has an anomalous pattern, with a mean coiling curve clearly outside the *N. fabianii* field, but consistent with the *N. ''ptukhiani''* field. The microspheric populations cannot be recognized by means of the coiling curve (Fig. 6b). Only the overall number of whorls permits a distinction: *N. ''ptukhiani''* B has on average 7 whorls (Table 1A), whereas *N. fabianii* B has 9–14 whorls (Table 1B). The different number of whorls explains the different diameters recorded. The coiling curves are currently employed to distinguish among species of the same lineage (e.g., Schaub, 1981), but usually they were applied to the B forms. Racey (1995) reports the coiling curves of both generations. My results do not confirm the usefulness of these curves to distinguish microspheric *N. ''ptukhiani''* and *N. fabianii.* Instead, they appear to be more useful to distinguish between the megalospheric generations.

For the megalospheric populations it proved useful to examine the mean chamber length for each whorl (Cl). The chambers (Fig. 7a) are on average shorter in *N. ''ptukhiani''* (190 to 390 µm) than in *N. fabianii* (210 to 500 µm). If we look at the Cl in one selected whorl (for instance the third; see also Table 1) we can easily distinguish *N. ''ptukhiani''* (250–290 µm) from *N. fabianii* (300 to 350 µm). Note that Cl in PRB 1 population is on average larger than *N. ''ptukhiani''* Cl (300 µm in the third whorl). Thus, it seems the most stable character for distinguishing A forms. Unexpectedly, the B forms do not show significant variations in Cl between *N. ''ptukhiani''* and *N. fabianii* (Fig. 7b).

Finally, it is noteworthy that, contrary to the A forms, the microspheric specimens of the PRB 1 population shows no significant differences with the other *N. fabianii* populations. The megalospheric PRB 1 population represents a se-

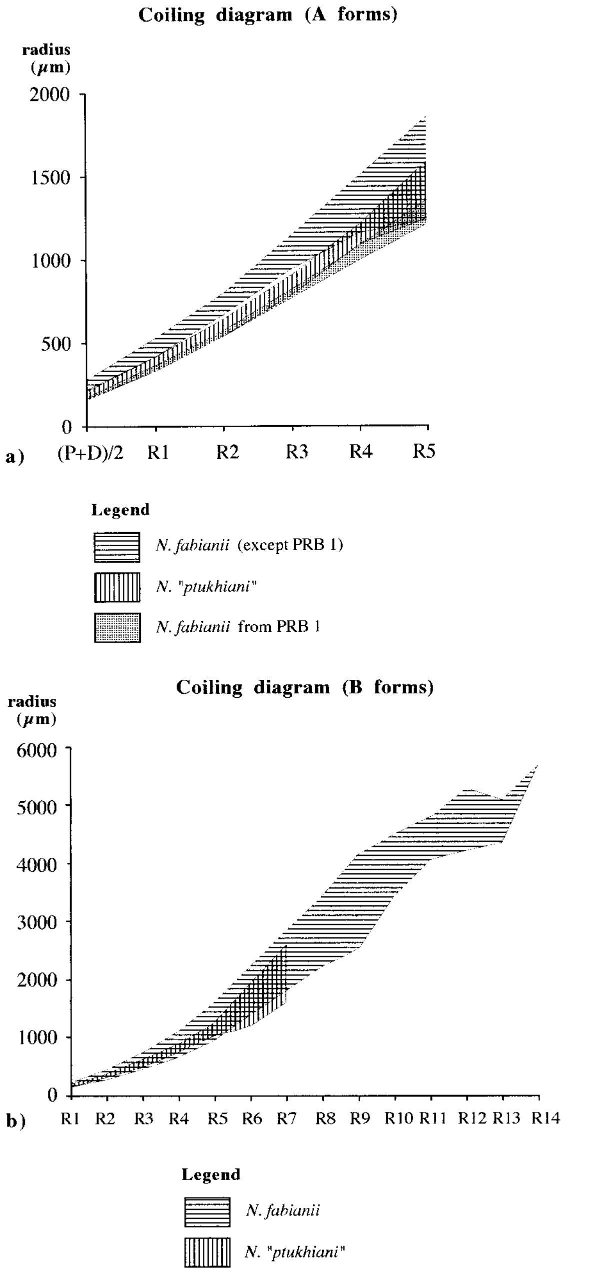

FIGURE 6. a. Coiling diagram fields for the A forms of *N.* ''*ptukhiani*'' (vertical hachure), *N. fabianii* except PRB 1 (horizontal hachure), and *N. fabianii* from PRB 1 (stippled); b. coiling diagram fields for the B forms of *N.* ''*ptukhiani*'' (vertical hachure) and *N. fabianii* (horizontal hachure). See text for further explanations.

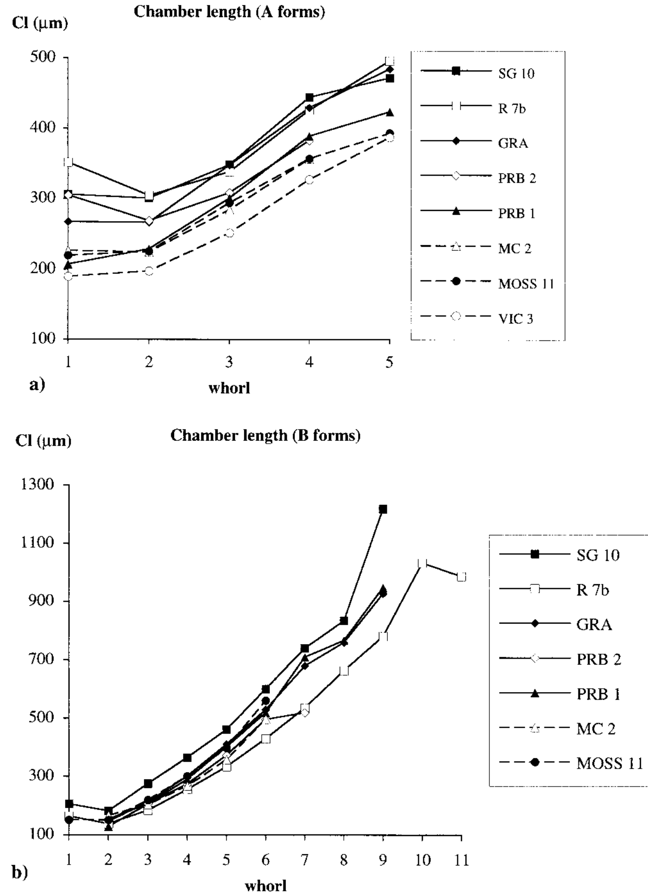

FIGURE 7. Mean chamber lengths (Cl) calculated for each whorl. a. megalospheric; b. microspheric forms of *N.* ''*ptukhiani*'' and *N. fabianii.*

rious exception in the material examined, and deserves additional consideration. Based on its measured characters, the megalospheric PRB 1 population is not *N. fabianii*, but rather *N.* ''*ptukhiani*''. Nevertheless, the overall appearance is that of a dwarfed *N. fabianii.* This effect is produced mainly by the elongated chambers (Fig. 7a), which clearly differ from the nearly isometric chambers of typical *N.* ''*ptukhiani*''. The abnormal size of specimens in PRB 1 population could be explained by its location in a very shallow environment with high quartzose sand input, probably close to the boundary of the *N. fabianii* ecological range. The inflated shape of the tests is in accord with a high-light environment (presence of abundant light-reflecting quartz grains). Thus, one must be careful when interpreting biometric data, because particular environmental conditions may even affect the internal features of the test.

CONCLUSIONS

The accurate identification of the species of the *N. fabianii* lineage represents a starting point in refining the biostratigraphy of the middle/upper Eocene. Therefore, the recognition of evolutionarily controlled (and consequently time-dependent) features in these species is of primary importance. A brief summary of the evolutionarily significant features follows:

A) megalospheric populations:

A1) protoconch height (P), 160–220 μm in *N.* ''*ptukhiani*'' vs. 220–320 μm in *N. fabianii* (Fig. 5a);

A2) embryonal arrangement, usually isolepidine in *N.* ''*ptukhiani*'' ($P/D < 1.2$) vs. anisolepidine in *N. fabianii* ($P/D \geq 1.2$; Fig. 5B);

A3) mean coiling curves, distinctly separated at least for the first three to four whorls, with tighter coiling in *N.* ''*ptukhiani*'' than in *N. fabianii* (Fig. 6a);

A4) mean chamber length for each whorl (Cl), shorter in

N. ''*ptukhiani*'' (190 to 390 μm; 250–290 μm in the third whorl) than in *N. fabianii* (210 to 500 μm; 300–350 μm in the third whorl; Fig. 7a), seemingly the most stable character even under unfavorable environmental conditions.

B) microspheric populations:

B1) the ornamentation of the surface has clearly distinct patterns in the two species: *N.* ''*ptukhiani*'' has a quite regular reticulation, but granules are always well-developed (Table 1A), whereas *N. fabianii* shows a sinuous to meandering reticulation with very small granules (Table 1B);
B2) overall diameter (d) of the test (Fig. 3b); larger in *N. fabianii* (5.5–10 mm) than in *N.* ''*ptukhiani*'' (3.5–3.8 mm);
B3) diameter/thickness ratio (d/t); *N.* ''*ptukhiani*'' is usually more inflated (d/t ranging from 1.9 to 2.3) than *N. fabianii* (d/t ranging from 2.7 to 4.5; Fig. 4b);
B4) overall number of whorls; *N.* ''*ptukhiani*'' has on average 7 whorls whereas *N. fabianii* has 9 to 14 whorls (Table 1).

The features observed show generally gradual transition from one to the other (chrono) species. So, the distinctions reported above are artificially marked for biostratigraphic use. It is worth mention that the position of the middle/upper Eocene boundary is still a matter of discussion (Papazzoni and Sirotti, 1995). However, having a biostratigraphic starting point for the recognition of biozones shall contribute to the resolution of this problem.

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REFERENCES

BARBIN, V., 1988, Reflexions sur *Nummulites fabianii* et *Nummulites fabianii retiatus,* leur signification stratigraphique et leur origine phyletique: Revue de Paléobiologie, v. spéc. 2, no. 2, p. 609–614.
BENGTSON, P., 1988, Open nomenclature: Palaeontology, v. 31, no. 1, p. 223–227.
BLONDEAU, A., 1972, Les Nummulites: Librairie Vuibert, Paris, 254 p.
BOMBITA, G., 1975, Remarques sur le groupe de *Nummulites fabianii:* Revista Española de Micropaleontología, v. 7, no. 1, p. 63–90.
———, 1984, Remarques complémentaires sur le groupe de *Nummulites fabianii:* Dari de Seama Institutul de Geologie si Geofizica, v. 68, no. 3, p. 39–66.
BOUSSAC, J., 1906, Développement et Morphologie de quelques Foraminifères de Priabona: Bulletin de la Société Géologique de France, ser. 4, v. 6, p. 88–97.
CARTER, H. J., 1857, Summary of the geology of India, between the Ganges, the Indus, and Cape Comorin, *in* Carter, H. J.: Geological papers on Western India, p. 628–667.
CASTELLARIN, A., and CITA, M. B., 1969a, La coupe priabonienne de Nago (Prov. Trento) et la limite Éocène-Oligocène: Mémoires du Bureau de Recherches Géologiques et Minières, v. 69, p. 93–117.
———, and ———, 1969b, Étude de quelques coupes priaboniennes dans le Monte Baldo (Prov. Verona et Trento, Italie) et discussion des limites de l'étage: Mémoires du Bureau de Recherches Géologiques et Minières, v. 69, p. 119–143.
ELLIS, B. F., and MESSINA, A. R., 1940 *et seq.*, Catalogue of Foraminifera: American Museum of Natural History Special Publication, New York.
FABIANI, R., 1905, Studio geo-paleontologico dei Colli Berici: Atti del Regio Istituto Veneto di Scienze, Lettere ed Arti, v. 64, p. 1797–1839.
FERRER, J., 1971, El Paleoceno y Eoceno del borde sur-oriental de la depresión del Ebro (Cataluña): Schweizerische Paläontologische Abhandlungen, v. 90, p. 1–70.
HALLOCK, P., and GLENN, E. C., 1986, Larger Foraminifera: a tool for paleoenvironmental analysis of Cenozoic carbonate depositional facies: Palaios, v. 1, no. 1, p. 55–64.
HERB, R., and HEKEL, H., 1973, Biostratigraphy, variability and facies relations of some upper Eocene Nummulites from Northern Italy: Eclogae Geologicae Helvetiae, v. 66, no. 2, p. 419–445.
HODGKINSON, R. L., 1989, *Nummulites broachensis* Carter, 1857 (Foraminiferida). New illustrations and information on a little known nummulite: Journal of the Palaeontological Society of India, v. 34, p. 83–90.
KACHARAVA, Z. D., 1969, O filogeneticheskom ryade gruppy *Nummulites fabianii:* Bulletin of the Academy of Sciences of the Georgian SSR, v. 55, no. 2, p. 497–500.
LOEBLICH, A. R., JR., and TAPPAN, H., 1987, Foraminiferal Genera and Their Classification: Van Nostrand Reinhold, New York, 2 vols., 970 p.
MATTEUCCI, R., 1971, Revisione di alcuni nummuliti significativi dell'Eocene del Gargano (Puglia): Geologica Romana, v. 9 (1970), p. 205–237.
NUTTALL, W. L. F., and BRIGHTON, A. G., 1931, Larger Foraminifera from the Tertiary of Somaliland: Geological Magazine, v. 68, no. 2, p. 49–65.
PAPAZZONI, C. A., and SIROTTI, A., 1995, Nummulite biostratigraphy at the middle/upper Eocene boundary in the northern Mediterranean area: Rivista Italiana di Paleontologia e Stratigrafia, v. 101, no. 1, p. 63–80.
PECHEUX, M. J.-F., 1995, Ecomorphology of a recent large foraminifer, *Operculina ammonoides:* Geobios, v. 28, no. 5, p. 529–566.
PTUKHYAN, A. E., 1964, O filogenii gruppy *Nummulites partshi:* Voprosy Geologii Kavkaza, Erevan, p. 49–55.
RACEY, A., 1992, The relative taxonomic value of morphological characters in the genus *Nummulites* (Foraminiferida): Journal of Micropalaeontology, v. 11, no. 2, p. 197–209.
RACEY, A., 1995, Lithostratigraphy and larger foraminiferal (nummulitid) biostratigraphy of the Tertiary of northern Oman: Micropalaeontology, v. 41, supplement, p. 1–123.
REISS, Z., and HOTTINGER, L., 1984, The Gulf of Aqaba. Ecological Micropaleontology: Springer-Verlag, Berlin, 354 p.
ROVEDA, V., 1959, *Nummulites retiatus* nouvelle espèce de nummulite réticulée des Abruzzes (Italie): Revue de Micropaléontologie, v. 1, no. 4, p. 201–207.
———, 1970, Revision of the Nummulites (Foraminiferida) of the *N. fabianii-fichteli* group: Rivista Italiana di Paleontologia, v. 76, no. 2, p. 235–324.
SCHAUB, H., 1981, Nummulites et Assilines de la Téthys Paléogène. Taxinomie, phylogénèse et biostratigraphie: Schweizerische Paläontologische Abhandlungen, v. 104–106, p. 1–236.
SERRA-KIEL, J., HOTTINGER, L., CAUS, E., DROBNE, K., FERRANDEZ, C., JAUHRI, A. K., LESS, G., PAVLOVEC, R., PIGNATTI, J., SAMSO, J. M., SCHAUB, H., SIREL, E., STROUGO, A., TAMBAREAU, Y., TOSQUELLA, J. & ZAKREVSKAYA, E., (in press), Larger foraminiferal Biostratigraphy of the Tethyan Paleocene and Eocene: Bulletin de la Société Géologique de France.

STROUGO, A., 1992, The middle Eocene/upper Eocene transition in Egypt reconsidered: Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, v. 186, no. 1–2, p. 71–89.

TELLINI, A., 1890, Le Nummulitidi della Majella delle Isole Tremiti e del Promontorio Garganico: Bollettino della Società Geologica Italiana, v. 9, no. 2, p. 359–422.

TREVISANI, E., and PAPAZZONI, C.A., 1996, Paleoenvironmental control on the morphology of *Nummulites fabianii* (Prever) in the late Priabonian parasequences of the Mortisa sandstone (Venetian Alps, Northern Italy). Rivista Italiana di Paleontologia e Stratigrafia, v. 102, no. 3, p. 363–366.

UNGARO, S., 1969, Étude micropaléontologique et stratigraphique de l'Éocène supérieur (Priabonien) de Mossano (Colli Berici): Mémoires du Bureau de Recherches Géologiques et Minières, v. 69, p. 267–280.

VARENTSOV, M. I., and MENNER, V. V., 1933, On the age of some horizons of the Paleogene of the Gorysk region of Georgia (in Russian): Neftianyi geologo-razvedochnyi Institut, Informatsionnyi Sbornik (Information Bulletin of the Oil Geological Institute), Moscow, no. 2–3, p. 102–105.

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